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20

Quantitative analysis and simulation of Mediterranean coastal ecosystems: The Gulf of Naples, a case study

Report of a workshop on ecosystem modelling Ischia, Naples, Italy 28 March to 10 April 1981 Organized by the United Nations, Educational, Scientific and Cultural Organization (Unesco) and the Stazione Zoologica, Naples

Editorial committee: G. Carrada,
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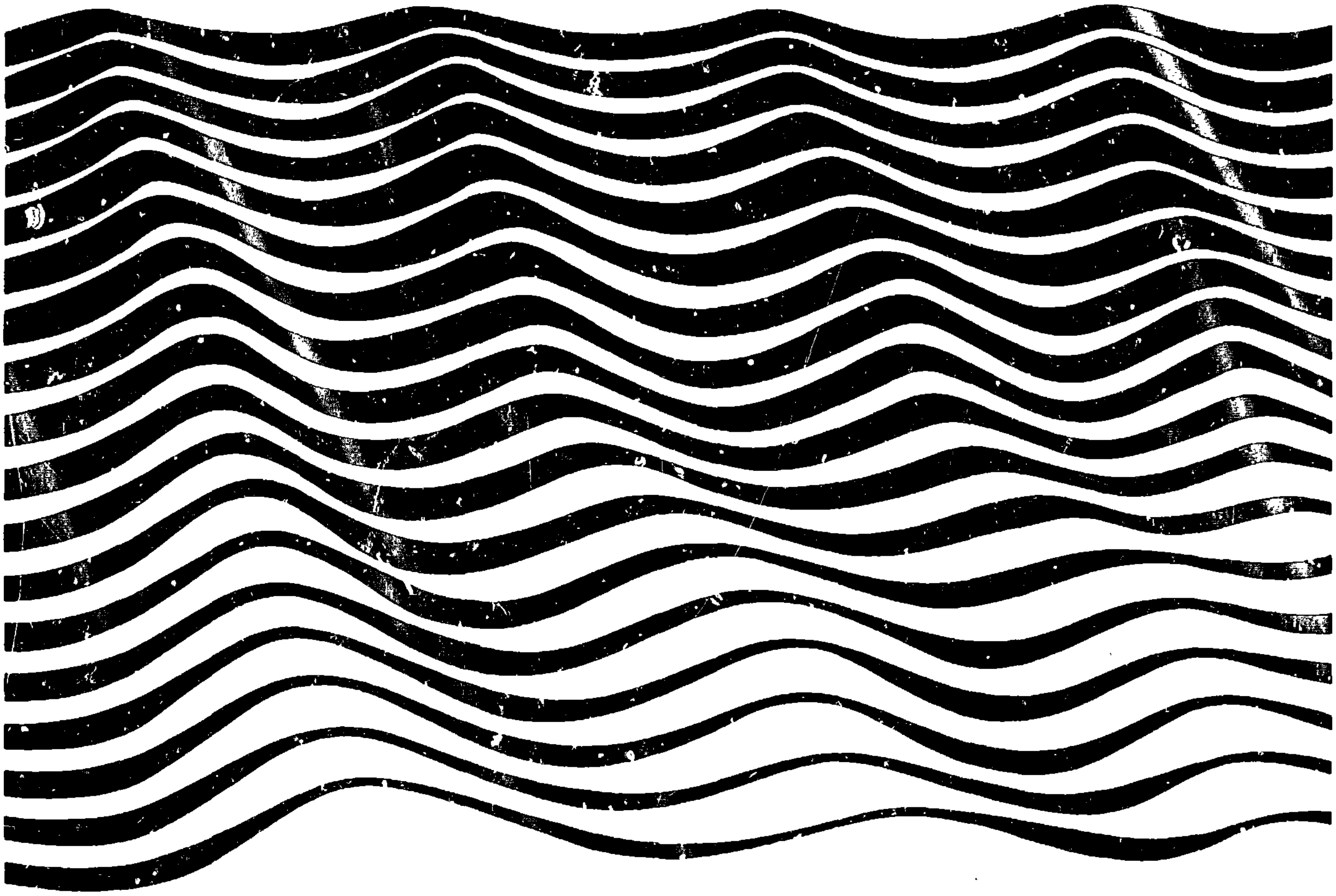

Unesco, 1983

UNESCO REPORTS IN MARINE SCIENCE

No.		Year
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11	Programa de plancton para el Pacífico Oriental Informe final del Seminario-Taller realizado en el Instituto del Mar del Perú, El Callao, Perú, 8-11 de septiembre de 1980 Spanish only	1981
12	Geología u geoquímica del margen continental del Atlántico sudoccidental, Montevideo, Uruguay, 2-4 de diciembre de 1980 Spanish only	1981
13	Seminario Latinoamericano sobre enseñanza de la Oceanografía Informe final del Seminario organizado por la Unesco en São Paulo, Brasil, 17-20 de noviembre de 1978 Spanish only	1981
14	Marine science and technology in Africa: present state and future development Synthesis of Unesco/ECA survey missions to African coastal states, 1980 Available in English and French	1981
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19	Mareas rojas en el Plancton del Pacífico Oriental Informe del Segundo Taller del Programa de Plancton del Pacífico Oriental Instituto del Mar, Callao, Perú 19-20 de noviembre de 1981 Spanish only	1982

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PREFACE

Unesco Reports in Marine Science are issued by the Unesco Division of Marine Sciences. The series includes papers designed to serve specific program needs and to report on project development. Collaborative activities of the Division and the Intergovernmental Oceanographic Commission, particularly in the field of training and education, are also represented in the series.

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ABSTRACT

A workshop on the modelling of Mediterranean coastal ecosystems was held in the Ischia Benthic Ecological Laboratory of the Naples Zoological Station from 28 March to 10 April, 1981. This was the third in a series of Unesco sponsored marine modelling workshops. The primary activity was the engagement of all participants in the various steps of model construction for the case study, the Gulf of Naples. This included an examination of the data base, design of a conceptual model, decomposition into submodels, formulation of relevant processes, definition of initial and boundary conditions, and programming and simulation. Secondary activities included a series of introductory lectures to establish a common modelling language among the participants, the presentation of other Mediterranean ecosystems, general discussions involving the practical application of modelling to particular situations, and a workshop critique.

CONTENTS

INTRODUCTION

Present knowledge on theory and observations of the hydrodynamics, the biogeochemical cycles, and the ecology within some of the Mediterranean basins is sparse and fragmentary. The output resolution of any marine ecosystem model is correspondingly restricted by its dimensional scales and by the detail in its accompanying data base. For these reasons and for practical reasons, a large scale (or regional) Mediterranean ecosystem model does not seem feasible at this time. However, smaller, mesoscale models of well defined coastal systems are less dependent on regional or international data bases and therefore within the capability of the many Mediterranean laboratories. Mesoscale models should be encouraged as a mechanism for improving multidisciplinary research, as a forum of comparison between individual laboratories, as a tool for assisting research management, and as an essential step towards the construction of larger regional models, as for example the Aegean Sea or even the Eastern Mediterranean.

BACKGROUND

Earlier activities of Unesco in marine ecosystem modelling in the Mediterranean included two workshops: Alexandria, 1974, and Dubrovnik, 1976, which are reported in the Unesco reports in marine sciences, Nos. 1 and 2. As a follow-up to these activities, and as a response to a proposal put forward to Unesco by the Stazione Zoologica di Napoli, two consultation meetings (Antalya,[1] November 1978, and Napoli,[2] March 1979) were held to generate opinion on how best to proceed, particularly in the light of two separate informal proposals: that for a workshop on Marine Ecosystem Analysis, Levantine Sea, and that for a training course on marine ecosystem concepts. After careful consideration, the Napoli consultation meeting recommended a workshop. The workshop program, dates, timetable, and other details were conceived and coordinated by the steering committee.[3]

The Dubrovnik workshop specified the following conditions as essential requirements in the selection of a marine area for a modelling study:

a. well defined physical boundaries,

b. existing data base,

c. existence of initial stage of modelling (conceptual),

d. existence of a minimum number of experts in modelling and in the various problems of interest for the particular model.

With these needs in mind, and in the interest of promoting marine modelling efforts, it seemed beneficial to select a coastal subregion which met these conditions sufficiently well and which could serve well as an instructive example for a group of Mediterranean scientists concerned with marine ecosystem modelling. On this basis, the various Mediterranean coastal subregions were reviewed, and the Gulf of Naples was selected to be used as a case study. An essential purpose of this workshop was to expose marine scientists to the concepts and methodologies used in model construction. To this end, the majority of the participants were selected from the Eastern Mediterranean countries in order to accelerate the level of understanding of ecosystem dynamics throughout the Mediterranean.

This workshop has been considered as one in a sequence of activities designed to promote modelling as a research and management tool among Mediterranean marine scientists. The two workshops of Alexandria and Dubrovnik served mainly as a forum for a familiarization with modelling. This workshop represents a shift toward more specific implementation of modelling technology, while at the same time, preserving its educational nature.

ORGANIZATION

The third workshop on marine ecosystem modelling in the Mediterranean was held in the Ischia Benthic Ecology Laboratory of the Naples Zoological Station from March 28 to April 10, 1981.

The participants (Appendix) at the Ischia workshop were welcomed by Prof. G. Carrada on behalf of the host institution and by Dr. S. Morcos on behalf of Unesco.[4] Dr. S. Morcos invited Prof. G. Carrada to act as Chairman, and Prof. L. Jeftić and Dr. T. Hopkins to serve as rapporteurs.

The planned objectives of the workshop were:

a. to provide an integrated exposure to the concepts of marine ecosystems and to the methodology of their modelling;

b. to construct a conceptual model of a mesoscale Mediterranean coastal ecosystem, specific to the Gulf of Naples;

c. to quantify submodels selected from the conceptual model, for example:

- a nearshore, soft bottom benthic community,
- the nutrient-phytoplankton-zooplankton dynamics of the coastal waters, and
- the physical mechanisms controlling the flux of coastal effluents offshore.

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[1] Participants: G. Carrada, A. Cruzado, Y. Halim, Lj. Jeftić, S. Morcos, P. Nival.

[2] Participants: G. Carrada, A. Cruzado, Y. Halim, T. Hopkins, Lj. Jeftić, S. Morcos, P. Nival.

[3] Steering Committee: G. Carrada, T. Hopkins, Lj. Jeftić, S. Morcos.

[4] Full text of the opening statement by S. Morcos is given in the Appendix.

d. to discuss some of the existing data bases from ongoing research programs in other coastal areas in light of the Gulf of Naples model and to identify in these areas the research requirements necessary to facilitate further model development.

All of these objectives were well satisfied during the Workshop, with the exception of (c), which was altered by consensus during the progress of the Workshop to include as much quantitative modelling as time and expertise would allow. It was felt that the expectations of this objective were exceeded.

The first two days of the workshop were devoted to introductory presentations which covered the general concepts of marine ecosystems, modelling of marine ecosystems, and short reviews of the Mediterranean ecosystem as a whole and the Gulf of Naples ecosystem in particular. It was not the objective of the workshop to give a comprehensive overview of these subjects nor to produce a report which will serve as a textbook. Therefore, it was left to the lecturers to choose, under the title given, either a broad approach or a particular problem which would reflect, in their opinion, a contemporary approach to the concepts and modelling of marine ecosystems. The first part of this report gives the introductory presentations.

The work on the numerical model of the Gulf of Naples started on the third day and continued through the thirteenth day of the workshop. After the initial work in plenary, which was devoted to the construction of the general conceptual model of the Gulf, defining objectives of the numerical model, system of interest, subsystem and state variables, the work proceeded in two working groups responsible for the construction of the hydrodynamical model and biological model. The second part of this report is organized to reflect, as appropriate, the modelling procedure, dilemmas, achievements, shortcomings, scientific rationale, processes, equations, computer programs, and outputs, all as a result of the work on the numerical model of the Gulf of Naples.

The last day of the workshop, was devoted to the presentation of available data base for several other Mediterranean small and mesoscale ecosystems and for the discussion on suggested research program improvements, and evaluation and recommendations of the workshop.

To the best of our knowledge the assemblage of participants was unique by virtue of its diversity of composition, consisting as it did of many scientists of different specialities (34 scientists from 12 nations) including experts on modelling in order to produce, as a collective effort, a numerical model of a mesoscale marine ecosystem.

The workshop was extremely successful in fulfilling stated objectives. It also proved to be a great educational exercise, not only in modelling but also in team work, which is such an important tool in multidisciplinary research.

The purpose of the workshop was to accomplish the working objectives discussed above. We would like to emphasize that this purpose was not to author a treatise on marine modelling applicable to the Mediterranean; therefore, this report should not be considered or judged as such. The following contents are meant only to convey to the reader the material covered and the activities accomplished during the workshop; and the reader is kindly asked to make allowances for any perceived omissions or inconsistencies. Nevertheless, we sincerely hope that this report will be to some degree as useful and inspirational to those aspiring to marine modelling as was the workshop itself to its participants.

ACKNOWLEDGMENTS

The workshop was funded by Unesco (Division of Marine Sciences) and by a grant from the Italian Ministry of Education. The Zoological Station provided additional administrative support. The Zoological Station, under the support of CNR, developed the Gulf of Naples Ecological Program, which provided the scientific core for the modelling sessions of the workshop. The Brookhaven National Laboratory under the NSF Grant INT77-27730 contributed to the establishment of the physical data base, developed the machine language file for GONEP, and assisted in the editing. The participants of the workshop gratefully acknowledge Dr. D. Fazio who sympathetically intervened on the behalf of the Zoological Station with the necessary financial support, to the administrative staff of the Zoological Station, in particular, Mr. G. DeVivo whose attention eliminated all practical problems, and Dr. E. Fresi and his Ischia Laboratory staff for serving so well as hosts.

This volume was edited by an editorial committee composed of T.S. Hopkins (Chief Editor), G.C. Carrada, Lj. Jeftić, and S.A. Morcos. The considerable time and effort spent by Dr. Hopkins in editing and co-ordinating the production of this volume is especially acknowledged.

INTRODUCTORY PRESENTATIONS

The first portion of the workshop was devoted to a review of the concepts of marine ecosystems, of their modelling, of the Mediterranean in general, and of the Gulf of Naples in particular. This review consisted of the following series of invited lectures which also served to provide the participants with a common language and a basis for interaction. These lectures were intended to emphasize the holistic, multidisciplinary approach that is inherent to ecosystem modelling. They are presented here with the intent to reflect the content and emphasis considered important by the lecturers and not to provide a complete or balanced coverage of the material.

GENERAL CONCEPTS OF MARINE ECOSYSTEMS

Physical Processes

Introduction

A marine ecosystem often represents some environmental domain with components described in terms of the quantities of mass or energy. The relevant physical processes are those that cause a 'redistribution' of mass or energy among the components of the system in a non-chemical and non-biological way. The redistribution can be the result of energy or mass forced through the boundaries of the domain or by internal exchanges between components.

Effectively all such redistributions are tied to the amount of kinetic energy of the environmental media (water). Under static conditions (KE=0) distributions are governed only by molecular diffusion and/or nonphysical processes. The rate of redistribution we define as a flux, i.e., the time rate by which a component changes through an area. In a Eulerian sense, the flux (gm/cm^2/sec) is the product of the flow (cm/sec) times the parameter (M) concentration (gm M/gm water) times the density (gm water/cm^3). For any given volume, it is the changes in flux occurring through the volume that are important. The spatial gradient of the flux is sometimes called the flux divergence. If the gradient is zero, rearrangements may occur but will be unresolvable.

Physical Redistribution of Mass

Mass in a unit volume of water is accounted for, in the Eulerian frame, by the following relationship:

$$\underbrace{\frac{\partial M}{\partial t}}_{\text{Local Change}} = -\underbrace{\nabla \cdot (vM)}_{\text{Flux Divergence}} + \underbrace{S}_{\text{Source}} \qquad (1)$$

where in this case M is simply a concentration of mass per unit water volume, $\nabla \cdot$ the divergence operator, v the velocity field, and S some internal conversion of mass. The source term is often called the non-conservative term in the sense that it includes all non-physical effects such as biological or chemical conversion of mass from one form to another. The flux divergence term includes the conservative physical processes that affect the distribution but not the form of the mass. The local change is merely the difference between the other two and is, in fact, what is observed in nature.

The flux divergence term can be expanded into components as follows:

$$\nabla \cdot (v\,M) = \frac{\partial (uM)}{\partial x} + \frac{\partial (vM)}{\partial y} + \frac{\partial (wM)}{\partial z} \qquad (2)$$

where each of these components represents the difference in flux between each two sides of a unit volume.

To pursue the discussion let us examine one of these components and decompose it further

$$\frac{\partial}{\partial x}(uM) = \frac{\partial}{\partial x}\overline{u'M'} + u\frac{\partial \overline{M}}{\partial x} + \overline{M}\frac{\partial \overline{u}}{\partial x}\,. \qquad (3)$$

In equation 3, $\overline{u}$ and $\overline{M}$ refer to the low frequency portions of those variables and u' and M' to their high frequency portions. The second and third terms in equation 3 are commonly referred to as the diffusive and advective terms. In the context of a frequency separation, advection is a low frequency process and diffusion a high frequency process. This has a dimensional significance because the terms have units of concentration per time. Advection applies to changes over relatively longer periods of time, diffusion over shorter times. The distinction is arbitrary. In general, moving to higher frequencies involves the less deterministic more stochastic behavior associated with diffusion. The diffusive flux is conventionally taken as proportional to the mean gradient of M because u' and M' are not easily measurable. This allows the diffusive term in equation 3 to be written as

$$\frac{\partial}{\partial x}\overline{u'M'} = \frac{\partial}{\partial x}\left(K\,\frac{\partial M}{\partial x}\right) \qquad (4)$$

where K is a diffusion coefficient normally taken as a constant. Diffusion may or may not be important in a given situation, dependent on the amount of high frequency water movements that correlate with small-scale variations in M. The representation of equation 4 is expedient, but not reliably substantiated by observations.

The last term in equation 3 is important only in cases where M is not completely coupled with water movements. In this case, the M will not 'feel' the complete divergence of the flow, which is inevitably zero. To clarify we pose this simple example: consider warm surface water laden with dinoflagellates blown against a coast. The water downwells at the coast, with an accumulation of dinoflagellates but not heat. Why? Because, the dinoflagellates are motile enough to uncouple themselves from the weak downward movement of the water. This can be explained mathematically by

$$T\left[\frac{\partial u}{\partial x}+\frac{\partial w}{\partial z}\right]=0 \quad \text{since} \quad \frac{\partial u}{\partial x}=-\frac{\partial w}{\partial z} \qquad (5)$$

$$D\left[\frac{\partial u}{\partial x}+\frac{\partial (w-w_s)}{\partial z}\right]=D\frac{\partial u}{\partial x} \quad \text{if } w=w_s \qquad (6)$$

where w_s is the upward swimming speed of the dinoflagellates, D.

The advective flux (second term of equation 3) represents changes due to physical translation of gradients. For example, if there is a discharge of substance into a river, there will be a gradient of the substance which when carried past a point downstream by the river flow will result in an observed or local change.

The term $u\,\partial M/\partial x$ can be large by virtue of either a strong flow (u) or strong gradients ($\partial M/\partial x$). This is depicted in Fig. 1. The extreme case of high flow with small gradient is represented by a jet in homogeneous water, or of little flow with large gradient is represented by a sharp interface in a stagnant flow field. The null case is that of stagnant homogeneous conditions, and moving away from the origin in the middle of the quadrant is an increasing probability of redistribution.

The magnitude of u is affected directly by the physical dynamics forcing the flow. Under some circumstance, should M be heat or salinity, the distribution of M indirectly affects the flow field. In this case u is also a function of $\partial M/\partial x$. The magnitude of M obviously can be affected by biological or chemical processes, but also may be affected indirectly by the flow field through this advective flux term.

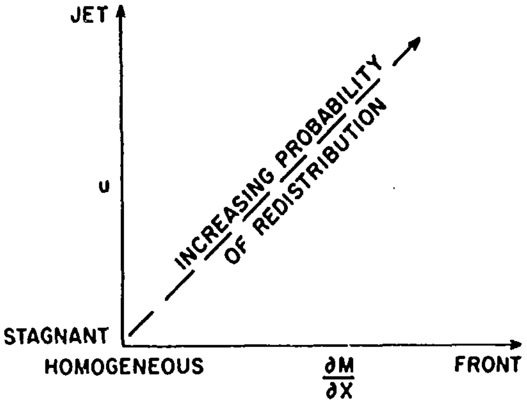

Fig. 1. The relative contribution of the two components of the advective term to redistribution of mass.

The Flow Field

Having made these distinctions, we will review briefly the processes involved in moving the water in coastal situations. It is useful to divide the movement into two classes, those in dynamic balance and those not in balance.

Balanced flows are flows represented by a frictionless balance of forces, such as geostrophic flow, inertial motion, internal wave motion, or tidal flow. These contribute to what is generally referred to as the mean flow and contribute to the redistribution of mass as low-frequency advective fluxes. They are quasi-deterministic, that is to say their dynamics are well behaved.

It is the unbalanced or frictional flows that are the most difficult or the least deterministic. They are perhaps as important as, or more important than, the mean flows, in terms of the redistribution of mass, since they are proportionally strongest near boundaries or because they have flow components normal to the mean flow. These are often referred to as ageostrophic flows, stressed flows, or transient flows. Because friction is important, these flows contain relatively more high frequency movements and therefore are more diffusive than the balanced mean flows. Their importance is enhanced in coastal situations due to the proximity of boundaries.

The different types of flows are discussed in terms of which forces prevail. The conventional set of forces is given in the following horizontal equations of motion

$$\frac{\partial u}{\partial t}-fv=\frac{g}{\rho}\frac{\partial e}{\partial x}-\frac{g}{\rho}\int^{z}\frac{\partial \rho}{\partial x}\,dz+$$

$$\frac{\partial}{\partial z}A_v\frac{\partial u}{\partial z}+\frac{\partial}{\partial x}A_h\frac{\partial u}{\partial x}+\frac{\partial}{\partial y}A_h\frac{\partial u}{\partial y} \qquad (7)$$

$$\frac{\partial v}{\partial t}+fu=\frac{g}{\rho}\frac{\partial e}{\partial x}-\frac{g}{\rho}\int^{z}\frac{\partial \rho}{\partial x}\,dz+$$

acceleration — Coriolis — barotropic pressure gradient — baroclinic pressure gradient

$$\frac{\partial}{\partial z}A_v\frac{\partial v}{\partial z}+\frac{\partial}{\partial x}A_h\frac{\partial v}{\partial x}+\frac{\partial}{\partial y}A_h\frac{\partial v}{\partial y} \qquad (8)$$

vertical friction — horizontal friction

where the terms are identified in equation (8). The object in modelling or in any quantitative analysis is to single out the dominant terms to represent a balance. There are two other equations that are needed, the vertical equation of motion which is simplified to its hydrostatic form

$$\rho g = \frac{\partial P}{\partial z} , \qquad (9)$$

and continuity

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0 . \qquad (10)$$

It is necessary to have some criterion for determining the dominant processes which are operative in a given situation. The physical oceanographer often uses dimensional scaling to accomplish this selective chore, in fact, Dimensional Analysis and Similarity Solutions represent a powerful tool for formulating and solving problems. The two main problems in applying the physical equations are (a) that the characteristic length and time scales are often a function of position or time and (b) that the nonlinearities even if small are not always neglectable.

Circulations

The terms in the above equations are discussed in detail in various texts (e.g. NEUMANN and PIERSON, 1966 or FOFFONOF, 1962). We will outline a few in the context of the Mediterranean.

Large scale thermohaline. In the Mediterranean system the sea level is depressed because of a net loss of water through evaporation. This causes water from the Atlantic to enter, in response to a barotropic pressure gradient. However, continued evaporation generates dense water which accumulates in the Mediterranean basin until forced out over the sill by a baroclinic (internal) pressure gradient. The flow over the sill is thus inward at the surface and outward at the bottom. The flow in is greatly in excess of what it would have been had its magnitude been dictated merely by the internal water deficit; in fact, this amount represents only a small difference between the two large flows.

The Mediterranean in fact has a three-layered flow structure due to a large important water intermediate mass produced in the Levantine Basin. Further discussion can be found in the section on the Mediterranean or in the references, e.g. HOPKINS (1978).

The large-scale flows affect the distribution of properties over long periods of time. Essentially this circulation represents a long and complicated pathway from the Atlantic and returning to the Atlantic. It is essential to know how each coastal system fits into this circulation.

Large scale geostrophic. Within each of the Mediterranean Basins large-scale geostrophic circulations exist. These are balances of the Coriolis force with the sea level slopes (barotropic) and with the inclinations of the internal field of mass. The above mentioned thermohaline circulations are two dimensional in the sense of occurring in the vertical and along the basin axis between the sill and the place of dense water formation. The inclusion of Coriolis force adds the lateral dimension and geostrophy to these conditions, that is, the along axis pressure gradients created by water mass formation and atmospheric buoyancy extraction are balanced by Coriolis force and result in cross-basin and well defined boundary flows. The flow scale is determined essentially by the basin dimension and the intensity of the pressure gradients.

At this scale variations in the wind over the basin cause disturbances in the mean sea level due to spatial inequalities in the wind transport. The resulting geostrophic circulations are cyclonic about a sea level low and anticyclonic about a sea level high. Summer wind patterns in the Mediterranean tend to be less extensive, causing the length scale of these circulations to diminish.

The pressure field due to the sea level gradient tends to be adjusted for by the internal field of mass. The associated barotropic and baroclinic velocities are in opposition such that at the depth of pressure equalization there is no motion. This adjustment takes place slowly depending on the internal density differences. Consequently there never is complete adjustment, i.e., to the high frequency fluctuations of the sea level which are manifest as barotropic velocity fluctuations all the way to the bottom. Another important point about these two flows is that the barotropic flow is dissipated only at the bottom and lateral boundaries, whereas the baroclinic flow is dissipated internally at those points in the water column where large shears exist, as for example, within the pycnocline.

It is this large-scale geostrophic circulation that controls the open boundary condition for coastal systems, and therefore is required information for coastal circulation models.

Coastal circulations. The basic difficulty with coastal circulations is that virtually the entire suite of forces listed in the equations is or can be important. It is useful to think of the coastal region as being characterized by three dynamical regimes: external or ocean, internal or mid-shelf, and boundary or nearshore. These are shown schematically in Fig. 2.

The importance of the external regime is that it controls the open boundary condition (assuming that the coastal region has some exposure to the open Mediterranean). This boundary is arbitrary but most logically must be determined on the basis of responsiveness. Generally this means bathymetric control, that is, deep water columns are less responsive to local forcing then are shallow ones. Consequently, we choose the open boundary to coincide with the shelf break. In some cases such as the Gulf of Naples, the lateral bathymetry acts to uncouple the coastal regime from the open sea.

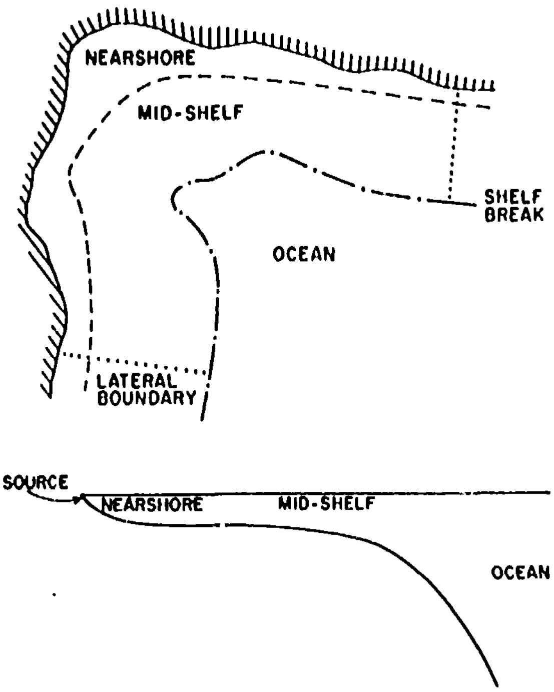

Fig. 2. An example of a coastal region defined for the purpose of modelling and the dynamical regimes mentioned in the text. The upper panel is a plan view, and the lower a cross section.

The internal regime consists of the deeper portion of the shelf, or regime, in which geostrophy dominates. Here some simplifications can be made to facilitate modelling, such as:

a. considering the wind field as homogeneous

b. representing the bottom friction as proportional to the geostrophic flow

c. using a diagnostic or multi-layer approach to represent the baroclinic field

d. coupling with the boundary region may be excluded (if not requisite) and a pseudo-coastal barrier imposed, or

e. neglecting the alongshore variability which renders the circulation two-dimensional (more appropriate for those cases with straight coasts and weak coupling at open boundary).

The two major difficulties involved to some degree with any or all of these simplifications are:

a. an inadequate functional dependence of the sea level on the wind stress, and

b. poor accuracy in the ageostrophic or cross-stream flow component.

Both of these relate very much to the need to model the boundary, or nearshore regime.

In the boundary regime, friction strongly influences the dynamics, that is to say for example, that the ageostrophic portion of the flow becomes significant. The water columns, being shallow, are more responsive, resulting in high accelerations. Lateral friction becomes significant, and baroclinic effects are reduced due to nearshore mixing.

It is in the boundary region that the effect of wind-induced transports cause the sea level to distort. The distortion begins at the shore and extends offshore according to the magnitude and duration of the forcing. If it extends outside the boundary region, it also forces mid-shelf flow. The amount of potential energy put into the sea level distortion is less for shoaling nearshore bathymetry than for the vertical wall approximation because of the greater bottom area per water column available for dissipation.

Of great importance is the magnitude of the offshore flow component in the boundary region, for it is this term that determines the advective flux offshore of substances released at the coast. The dispersive behavior of the boundary region can very significantly alter the concentration and location of a point source effluent into the coastal interior flow.

Chemical Processes

Chemical Constituents of Sea Water

If particulate matter and organisms are excluded, sea water may be considered as an aqueous solution of solid and gaseous substances. The chemical composition of sea water is not easily determined, especially with the precision required, because of the large disproportion existing between the various chemical species and to the interferences encountered in many of the analytical procedures. It is beyond the scope of this lecture to include a detailed description of the various elements present in the sea water and of their biological and geochemical cycles. However, a brief account of the geochemistry of some of the more important elements might help to understand their cycling in connection with their ecological role.

The principle of 'constancy of the relative chemical composition' of sea water, commonly accepted and constituting the basis for the chlorinity:salinity:density relationship, should not concern us excessively since there are a great number of elements, especially the most important ones from the biological standpoint, that strongly deviate from such a behavior. In fact, all the exchanges of matter between the ocean and the atmosphere, the land, the sediments, and the organisms would alter their relative concentrations were it not by the large residence time of the elements in the oceans. Water, being itself one of the most mobile constituents, has a residence time of about 4000 years in the world's ocean.

A number of nearly identical tables are available for the chemical composition of sea water (SVERDUP et al., 1942; HORNE, 1969). It is customary to classify the elements into three groups, according to their relative concentrations.

Major elements. These are those elements basically determining the physicochemical characteristics of sea water as a medium, in particular, its density, electrical, thermal, and colligative properties. There are, besides hydrogen and oxygen, the halogens (especially chlorine with 55% by weight of all the dissolved materials) which served for many years as the basis for the determination of chlorinity, salinity and density. These are followed by the alkaline and alkaline-terreous metals (sodium, potassium, magnesium, calcium and strontium). Unlike sodium, potassium ion and the divalent ions enter the chemical composition of the organisms, and thus their concentrations may show important variations. In particular, the Ca/Mg ratio is much lower in the sea than in continental waters not only because of the precipitation of $CaCO_3$ in estuarine areas, but because of the differential uptake by shell-forming organisms. Ca also seems to play an important role in the $CO_2:HCO_3^-:CO_3$ equilibrium.

Carbon is another major element crucial for marine life. It is also very important as a regulator of the seawater pH, although very careful studies of the carbon system equilibrium constants suggest that other elements, such as boron and silicon and the organisms themselves might play a pH regulating role as important as, if not more important than, the carbon system itself.

Sulphur, mainly in the form of sulphate ion, plays an important role in areas where oxygen consumption is large, particularly when it is caused by heterotrophic bacteria. When oxygen concentrations are low, sulphate ion substitutes oxygen as an electron acceptor and is transformed into sulphite ion. Anoxic regions where sulphite ion is normally present are found generally in estuarine sediments, in deep waters of stagnant water bodies or under highly productive open-ocean regions.

Minor elements. These are those elements that may appear in relatively high concentrations, and yet they have only a small effect on the physicochemical characteristics of the sea water. Three groups may be identified: dissolved gases (oxygen, nitrogen and argon), nutrients (nitrogen, phosphorus and silicon) and metals constituting the crustal materials (aluminum, iron, manganese, etc.).

Atmospheric gases are normally in equilibrium with gases dissolved in sea water, and thus they are at saturating concentrations in the surface layers. While nitrogen and argon concentrations experience practically no variation by internal processes and can therefore be considered conservative properties, oxygen is strongly affected by biochemical and biological processes taking place in the water and sediments. However, there are some regulating factors in the distribution of the dissolved oxygen. In the surface layers, in contact with the atmosphere, the oxygen concentration is normally close to saturation although photosynthetic organisms normally present in these layers may cause supersaturation. Below the euphotic zone where respiration rates are greater than photosynthetic rates, oxygen concentrations decrease with increasing depth, reaching a minimum value that, in areas of large biological productivity, may attain zero, appearing as the phenomena derived from anoxia especially sulphide production. Diffusion and advection processes compensate for the downward decrease in oxygen concentrations. Since the water masses of the ocean are formed at the surface, they are initially saturated with oxygen and their evolution as subsurface water masses is characterized by lower oxygen concentrations. However, the deep water oxygen losses are slow, except in enclosed basins with stagnant circulations, and the relatively younger deep ocean waters show high oxygen concentrations. Both oxygen and the second group of minor elements, the nutrients, are the subject of discussions elsewhere in this report.

The third group of minor elements, basically formed by metals present in crustal materials, with low solubility in oxygenated sea water, are seldom involved in ecological processes, although some of them are known to be essential for many biochemical processes.

Trace elements. Most if not all of the elements present in nature may be found at the trace level in sea water. This group of elements is mainly formed by the heavy metals which form highly insoluble compounds. Although, in some cases, through their tendency to form complexes with Cl^- and F^- ions, they may appear in relatively high concentrations. Many of the components of this group of elements would be unnoticed in the environment were it not for the potential hazards to organisms and to human health. This is especially true of the radioactive isotopes, partly the result of natural radioactivity, partly introduced by human activities.

Elements Relevant to the Ecosystem and their Controlling Processes.

An ecosystem may be regarded as a system in which there is a cyclic interchange of material between the biotic and abiotic components. Marine ecosystems in particular are normally considered as having four main biotic components: producers, consumers, decomposers and detritus. Detritus, although not being an active component, is often included since it plays a major role in the trophic chain. Producers are organisms that, using sunlight as energy and inorganic carbon and nutrients as building materials, photosynthesize organic matter which is then partly grazed by consumers and partly converted, through decay, into detritus. Consumers, partly grazing on the producers and partly preying within their own compartment, also contribute to the detrital component, either upon death or by way of their fecal production. Decomposers are mainly saprobic bacteria that take energy out and matter from detritus. Along this cycle, carbon and nutrients are taken up by producers during photosynthesis and released by all three active components in respiration, while oxygen is released to the environment in photosynthesis and consumed in respiration.

The organic matter photosynthesized goes primarily into increasing the overall ecosystem biomass. However, not all the synthesized matter remains within the phytoplanktonic organisms to be grazed down by consumers. A fraction of the organic matter is immediately oxidized in respiratory processes; another fraction may be directly excreted practically unchanged, and yet another part may go directly into the detrital component to be degraded by bacteria without going through the grazing consumers. Only the remaining organic matter can be used by phytoplanktonic organisms to increase the size of the cells or to build new ones. Biomass production is therefore only one of the uses given by the ecosystem to photosynthesis, the remaining ones recycle without passing through the higher trophic level components.

REDFIELD et al. (1963) established the principle that the different elements involved in the production of organic matter (C:O:N:P:Si) in the ocean are taken up and regenerated by organisms in more or less definite proportions that roughly correspond to their actual concentrations in sea water. Because regeneration of the elements constituting the organic matter takes place mostly in the strata below the surface layer where oxygen is isolated from atmospheric exchange, better agreement is found between the regeneration of inorganic nutrients and the consumption of oxygen than is found in the reverse process of its production. The proportion of the elements involved in the mineralization of phytoplankton, on the basis of the final oxidation products, was found to be 276:16:1 for O:N:P (RICHARDS, 1965). However, the proportions given for the world ocean do not always hold for the Mediterranean Sea, and the principle completely fails for waters influenced by river discharges.

Nitrogen cycle. The principal forms of N occurring in marine water, if dissolved gaseous N_2 is excluded, are nitrate, nitrite, ammonia and organic N. The concentrations of the various forms of N in the water depend not only on the physical rates of supply but also on biological processes such as the uptake by phytoplanktonic algae and the mineralization by bacterial micro-organisms both in the water and in the sediments underlying it. In sediments, as in soils, the N is primarily in an organic form arising either from particulate material formed in the waters above or brought in by terrestrial runoff. Fig. 3 shows, in a very schematic way, the biotic and abiotic paths along which N can circulate in the marine ecosystem. The most important pathways are those determined by plant and bacterial microorganisms, but some animals may contribute in a non-negligible way to the mobilization of nitrogen (DUGDALE and GOERING, 1967). Because of the many complex and competing biological reactions occurring in a given ecosystem, it is extremely difficult to determine the relative importance of each individual microbial process. However, those that are likely to be most important in determining the availability of N are ammonification, nitrification, denitrification, and nitrogen fixation.

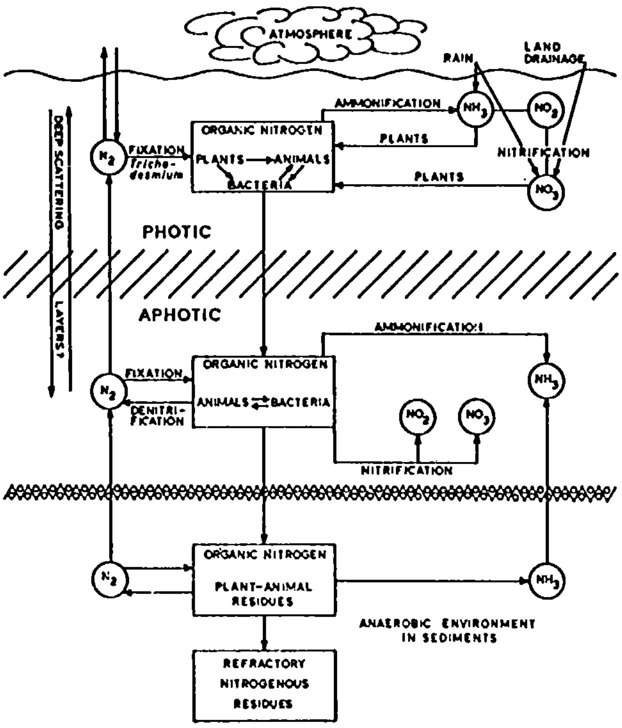

Fig. 3. A generalized scheme showing the sources of nitrogen and its organic circulation in the ocean. From COLLIER (1970), with permission of Wiley-Interscience.

Ammonification. Comparatively little information is available on either the micro-organisms or the environmental characteristics controlling the formation of ammonia from organic matter in the marine systems. Early studies show that ammonia can be produced by the decomposition of sinking detritus within the waters below the thermocline as well as from the sediments. Recent work has shown that the process is favored by anaerobic conditions. On the other hand, ammonia-N can also be produced by excretion (WHITLEDGE, 1972).

Nitrification. This process, resulting in the conversion of ammonia to nitrate, is carried on by obligate aerobic bacteria of the genera Nitrosomonas (ammonia to nitrite) and Nitrobacter (nitrite to nitrate) and has been extensively studied in terrestrial systems and in sewage purification processes. In sea water, the trophic level may determine whether the process is functional or not and its molecular oxygen requirement results in an overall increase in BOD (Biological Oxygen Demand) of waste-laden waters. The reverse process (nitrate to nitrite) has been described in Mediterranean waters (BLASCO, 1972) as being carried out by phytoplanktonic algae submitted to low light intensity and substantially high nitrate concentrations, conditions normally found in summer at the base of the photic zone.

Denitrification. In this process, nitrate and nitrite are biologically reduced to gaseous nitrogen oxides (N_2O and NO) and to molecular N_2. Nitrogen oxides are not known to be present in the environment and only gaseous N_2 is commonly observed in sewage sludges and highly eutrophic systems. A consequence of denitrification is the loss of N by highly eutrophic ecosystems, which may considerably reduce the overall amounts of N present in the system.

Nitrogen fixation. This is the reverse process to the latter in the sense that molecular N_2 is converted to organic N. The process appears to be light-dependent and therefore coupled to photosynthesis, although certain blue-green algae can also fix nitrogen in the dark. A considerable volume of data is available to show that nitrogen fixation occurs, usually in tropical waters (GOERING et al., 1966). Its occurrence in the Mediterranean Sea has been suggested although evidence has not been reported so far.

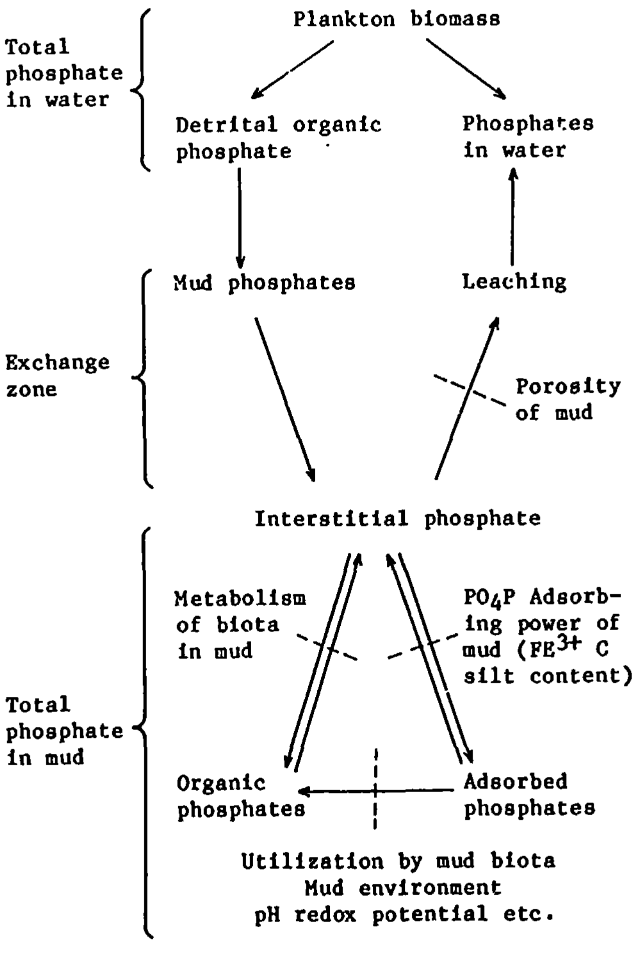

Fig. 4. The various forms in which phosphorus can be found in the marine ecosystem.

Phosphorus cycle. Unlike nitrogen, which is present in several inorganic forms, inorganic phosphorus occurs in sea water only as phosphate. However, like nitrogen, organic phosphorus is also a significant part of the phosphorus pool in the marine environment. Fig. 4 schematically reviews the various forms in which phosphorus can be found in the marine environment. Phosphorus bound to organic matter is released very rapidly. However, even less work has been published on specific bacteria active in the regeneration of phosphate than in the case of ammonia. One would assume that there are many micro-organisms which will bring about the solubilization of phosphate from organic phosphorus compounds present in detrital material.

In marine sediments, phosphorus is considered to exist as interstitial phosphate. It can be leached to the water above as adsorbed phosphate which can then be released by chemical processes as insoluble phosphate bound by such ions as Ca^{+2} and Fe^{+3}, and as phosphorus bound to organic matter. A large fraction (up to 20%) of the phosphate dissolved in freshwater entering the sea is lost to the sediments through the formation of insoluble phosphates deposited as silt on the bottom (PERKINS, 1974). Insoluble ferric phosphate is strongly bound to the sediments, but under reducing circumstances it becomes ferrous phosphate and may leach out to the aquatic phase. Thus, an oxygen deficiency created by bacterial action in the sediment may be expected to facilitate the release of phosphate by the substratum especially when shallow sediments are stirred by strong winds.

Silicon cycle. Unlike nitrogen and phosphorus, silicon is not widespread in the biological component of the ecosystem. Only diatoms, silicoflagellates, radiolarians and sponges require the presence of this element in order to build essential parts of their bodies. The monomeric form of orthosilicic acid is thought to be the normal state of dissolved silica in natural waters. Polymeric silica, crystallizing out as quartz, is stable in supersaturated solutions with respect to amorphous silica, but normal concentrations found in sea water are well below saturation levels. Orthosilicic acid dissociates in solution, but at the pH of sea water undissociated orthosilicic acid is the stable form. Electrolytes in sea water do not affect truly dissolved silica but coagulate colloidal silica which may be depolymerized in a few days, provided total silica concentration is below about 100 ppm.

Particulate silica may be crystalline or amorphous. Crystalline silica may take the form of quartz, chert or aluminosilicates such as kaolinite, montmorillonite, illite and glauconite. Orthosilicic acid is rapidly released by clays to silica-deficient water (MACKENZIE et al., 1967). This release is governed by formation of some ill-defined aluminosilicate of increased Al/Si ratio that ends up as kaolinite. Some authors have claimed sea-water silica concentrations to be controlled by alteration of clay minerals or by dissolution of finely divided quartz in sediment interstitial waters since solubility of quartz considerably increases when the particle size is below 10 µm and quartz is unknown in the fraction below the 0.1 µm. This is however very unlikely since interstitial waters can hardly be considered silica-deficient and amorphous silica and opal, mostly biogenous, are the most soluble species with a saturation concentration of about 120 ppm at 25°C for both, though opal has a much lower dissolution rate than amorphous silica.

The average residence time for silica in the ocean is approximately 4000 years (Fig. 5). The sources of particulate silica are river discharges, wind transport and glacial transport, and the main sink is sediment burial. As far as dissolved silica is concerned, biological uptake (8×10^{15} g/yr) by far over balances the input through river outflow (4×10^{14} g/yr) and re-solution of sediments (3×10^{12} g/yr) (HARRIS, 1966). Since the rate of formation of biogenous silica is about 20 times larger than river discharges and 3000 times larger than leaching from non-biogenic sediments, one may conclude that cycling of biogenous silica controls the concentrations of this nutrient in the sea water. Silica uptake takes place mainly at the euphotic zone by diatoms. The re-solution of silica is presumed to be a strictly inorganic hydrolytic process (GRILL and RICHARDS, 1964). As soon as diatoms are ingested by grazers, the silica is returned practically unchanged in the form of fecal pellets that become part of the detrital component rapidly settling to the bottom where decay produces regeneration of dissolved silica. A large part of the detrital silica may be re-solved in the water column during the sinking of the detritus, or at the water-sediment interface by further biological decomposition. It does not accumulate in the sediments unless the sedimentation rate is so high that it over balances the re-solution. Biogenous silica materials are converted through diagenesis into opal and even crystallized out as quartz or chert below highly productive areas.

Carbon and Oxygen Cycles. During the photosynthetic process an amount of oxygen equivalent to the carbon fixed is released to the water and eventually to the atmosphere. Inorganic carbon (as CO_2, HCO_3^-, or $CO_3^=$) is normally in excess in sea water even in the extreme case of large algal blooms. Besides, it has almost unlimited reserves in the atmosphere. Therefore we should not concern ourselves with the details of its pathways in the marine ecosystem. Oxygen, not being in itself a growth factor, plays a major role in the process of biological or chemical oxidation of the dead or living organic matter dissolved or dispersed in sea water since only in the presence of this element can organic matter be converted by respiration and aerobic bacterial action into CO_2 and simple inorganic salts. Oxidation of organic matter can, however, proceed beyond the availability of oxygen under anaerobic conditions by using NO_3^-, NO_2^-, or even $SO_4^=$ as oxygen donors although this occurs only in extreme eutrophic conditions and, so far, only the bottom of the Black Sea and some other smaller and localized areas in the world ocean are known to be affected by anoxia.

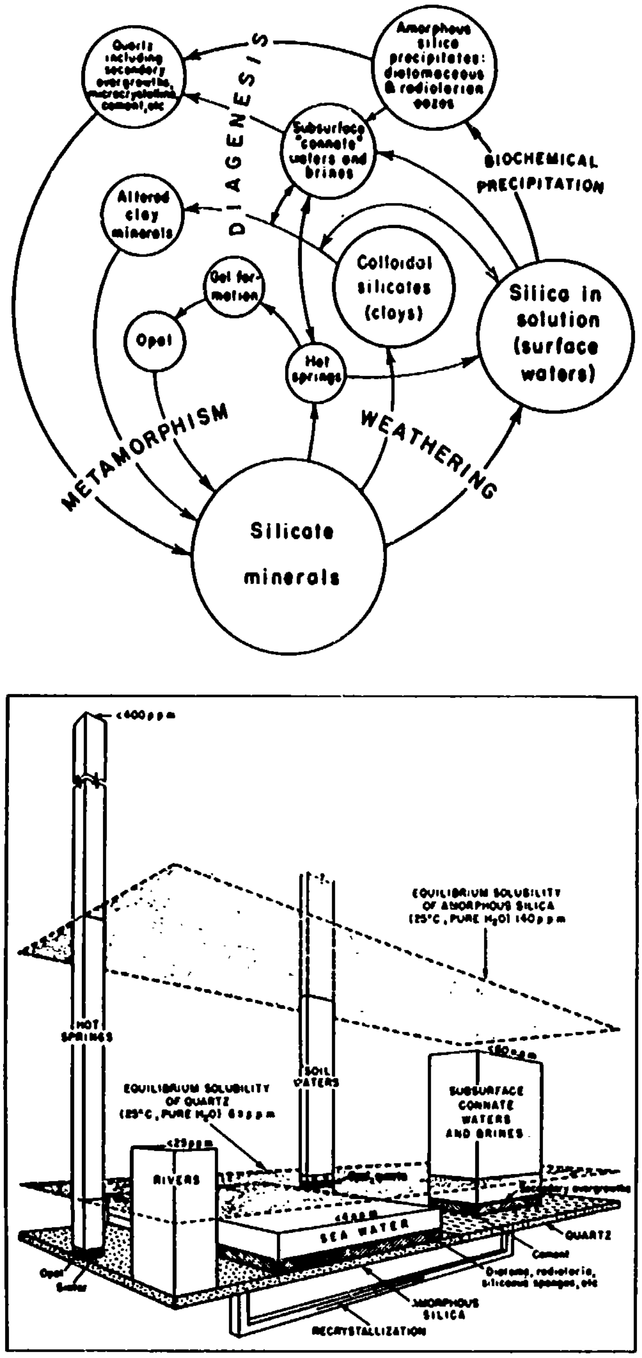

Fig. 5. a. The silica cycle. b. Silica abundance in natural waters. Volume of 'buildings' roughly proportional to absolute amounts of silica in solution. Height of 'buildings' roughly proportional to concentrations of silica in solution. From SIEVER (1957), with permission of American Mineralogist.

Oxygen, and to some extent, carbon dioxide dissolved in sea water, are mainly controlled by the combined action of several biological and physical processes:

a. direct exchange between the sea water and the air above it,

b. turbulent mixing with adjacent water layers,

c. photosynthesis carried out by plants, mainly phytoplankton, and

d. respiration and other biological and chemical processes.

(Note: a discussion of these processes is also included in the lectures on autotrophic processes.)

Process (a) acts both ways across the sea surface. Oxygen enters the sea when consumption in respiratory processes lowers its concentration below saturation, and is lost to the atmosphere when production by photosynthetic organisms causes supersaturation. Oil films or detergents dispersed in the surface layer may decrease the rate of exchange of oxygen and CO_2 through the surface of the water by as much as 20%, but it may be doubled by strong wave action (PERKINS, 1974). Optimal situations for process (c) are found only in those waters that have a good balance between the rate of supply of nutrients and the intensity of the incoming solar radiation within the adequate spectral range. Owing to the reduced nutrient supply in the upper portions of strongly stratified waters, process (c) occurs more efficiently between the thermocline and the compensation depth. This depth is usually established at or near the 100 m in strongly stratified waters of the Mediterranean due to their generally high transparency, producing a maximum oxygen layer between 50 and 75 m depth, typical of the oligotrophic regions of the ocean. On the other hand, vertical turbulence may strongly depress photosynthetic production by keeping the organisms for too long a time below the compensation depth.

During the stratified season, process (b) is enhanced by currents, and it is the principal process which actually supplies oxygen to the waters lying below the compensation depth. Process (d) acts everywhere in the sea and is the one responsible for the general decrease in dissolved oxygen concentrations with depth in the world ocean as well as for some specific features found in certain regions such as the oxygen minimum layers or the anoxic basins. This process is highly dependent on the temperature of the water and on the amounts of organic matter, dead as well as living, produced in the euphotic zone or discharged into the sea from nearby land-based sources.

Limiting Factors for Photosynthesis and Biomass Production

In order for a plant cell to be able to photosynthesize, CO_2, nutrients and light are required. A number of factors may affect the rate at which photosynthetic organisms are allowed to carry out this function. For a given area, the overall biomass production is always limited by nutrient availability though light intensity and nutrient concentrations always compete in limiting the actual photosynthetic rate. Light is provided in the marine environment directly from the sun, through scattering in the atmosphere and by re-radiation from clouds. Light intensity is reduced downwards in the sea through absorption and scattering by water molecules and dissolved and dispersed materials (JERLOV, 1968) including plants themselves. The distribution of nutrients in the seas has long been studied, and there is a great deal of literature on the subject. In general, concentrations are minimal at the surface and increase with depth until the 700 to 1000 meters depth is reached (Fig. 6). In this section, however, we shall be concerned mainly with the processes controlling the distribution of light and nutrients in the upper 200 m of the sea (Fig. 7) and their relative contribution to the photosynthetic rate.

If the kinetics of biomass production are analyzed, two phenomena should be distinguished: production of new material and regeneration. DUGDALE and GOERING (1967) have proposed to make this distinction on the basis of different nitrogen compounds. Production based on nitrate would be the new production while production based on ammonia would be the regenerated

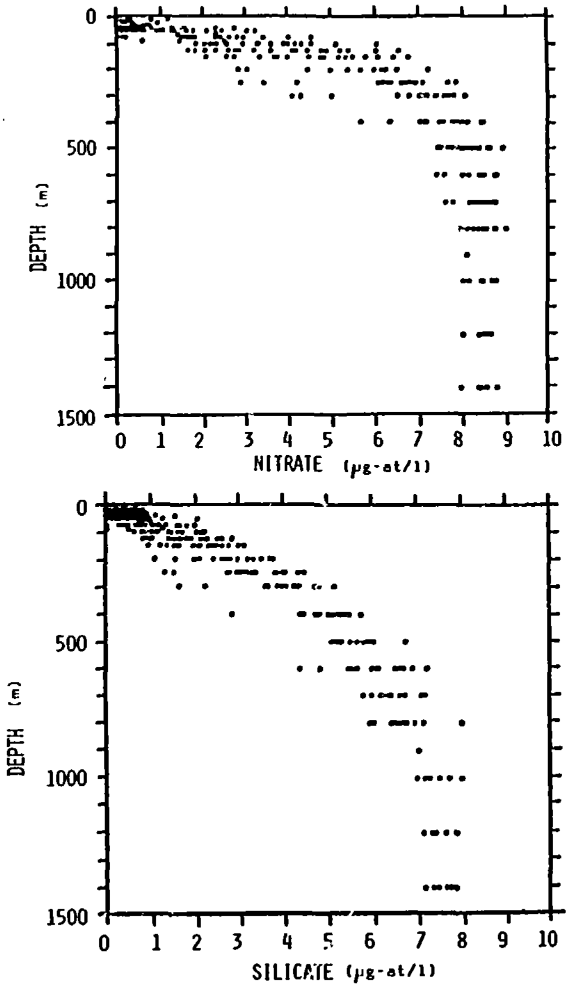

Fig. 6. Nutrient profiles in the Catalan Sea, a) Nitrate, and b) Silicate. From CRUZADO (1981).

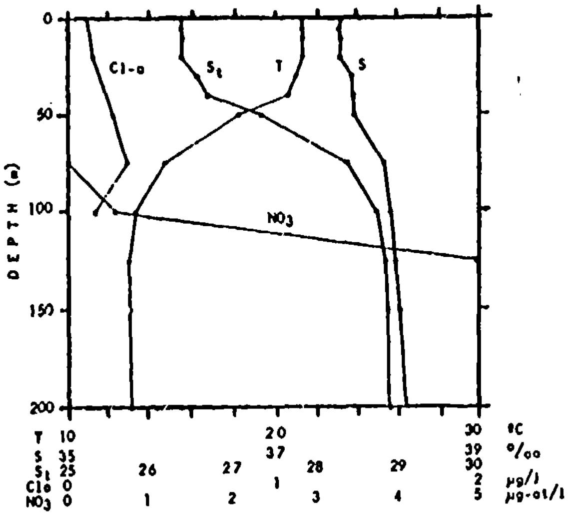

Fig. 7. Nitrate distribution in the upper 200m in relation to other variables in the Catalan Sea. From CRUZADO (1981).

production. Though this is a useful approach, the heart of the matter is the length of the pathway followed by N in the ecosystem. New production would be based on N having completed a long cycle through producers, consumers, detritus and decomposers, and being brought up to the surface layer by diffusion or advection. Regenerated production would be based on recently freed N in a short cycle including both producers and consumers, and this N cycling becomes very important in the surface layers when underlain by a strong pycnocline, which acts to restrict vertical fluxes of N. Therefore, if nutrient regeneration taking place at great depths gives rise to new production, only the part of the producers' biomass ingested by grazers and passing into the detritus fraction and being exported downwards would allow for new production. The part remaining in the herbivorous organisms that may be excreted near the surface would support regenerated production. This would be an important role of the herbivorous organisms which may turn out to control the nutrient uptake kinetics.

Nutrient limitation. Numerous reviews on the controlling role of nutrients for biological production in aquatic systems suggest that phosphorus (P) and/or nitrogen (N) compounds are normally the limiting factors. According to many authors algal biomass productivity is largely governed by the concentration of P compounds in the euphotic zone. Several recent reports, however, suggest that N is the most important growth-limiting factor under normal conditions as well as in eutrophic situations when P compounds are supplied in much larger proportion than N compounds (RYTHER and DUNSTAN, 1971). Silicon may also be a growth-limiting factor for diatoms and silicoflagellates, but, in general, silicon deficiency will cause changes in populations to non-siliceous species.

The self-regulatory effect of nutrient concentration on the rate of uptake has been shown to follow a Michaelis-Menten hyperbola when natural populations from eutrophic areas are studied (MACISAAC and DUGDALE, 1972)

$$V = V_{max} \frac{S}{K_S + S} \qquad (1)$$

where S is the ambient nutrient concentration and K_S the concentration at which the specific uptake rate V is 1/2 of the maximum attainable rate V_{max}. Populations adapted to low nutrient concentrations cannot react sufficiently fast to near-saturating levels, their kinetics resulting in truncated hyperbolae.

Nitrate and nitrite uptake seem to follow identical kinetics (CONWAY, 1974), both rates being equally suppressed by the existence of ambient ammonia. The effect is experienced by a lowering of V_{max} for nitrate that follows a linear relationship with ammonia concentrations, at least in the range 1 to 3 μg-at/ℓ of ammonia. A time lag on the order of 1/10 to 1 hour has been observed for this inhibitory effect. Phosphate uptake shows similar kinetics, with K_S ranging from 0.33 to 1.72 μg-at/ℓ. Phosphate is taken up in the dark when cultures grown in continuous light become P limited. Silicate kinetics, less well known, also follow a hyperbolic law with K_S ranging from 0.2 to 3.4 μg-at/ℓ of silicate. V_{max} for silicate seems to be affected by light intensity, but silicate uptake does not follow diel periodicity when populations are subject to alternating light-dark periods. Besides, quite high in situ uptake rates were observed at great depths relative to the depth of the euphotic zone (DUGDALE, 1967).

Light limitation. DUGDALE (1976) has reviewed the influence of light intensity on the rate of nutrient uptake by phytoplankton. Uptake of nitrate and ammonia is strongly dependent upon light. Experiments with ^{15}N show that actual uptake rates fit a Michaelis-Menten hyperbola when natural phytoplankton populations are exposed to light intensity gradients at nearly saturating nutrient levels

$$V = V_{max} \frac{I_z}{K_L + I_z} \qquad (2)$$

where $I_z = I_0 \exp(-Kz)$ is the ambient light intensity, K being the attenuation coefficient of light in water. K_L values obtained fall in the range 1 to 10% of the surface light intensity, depending on the origin of the phytoplankton population observed. Deep populations seem to be better adapted to low ambient light levels.

According to LORENZEN (1976), the vertical extent of the euphotic zone is approximated by the depth at which 1% of the surface light intensity exists. Changes in incident radiation are reflected in changes in the euphotic zone thickness since the compensation depth moves vertically in response to changes in surface light intensity. When computing the depth of the euphotic zone, not only decline in surface light intensity should be taken into account, but also the duration of the sunlit portion of the day, widely varying at high latitudes.

Attenuation due to the existence of phytoplankton organisms may strongly reduce the depth of the compensation depth. Although the amount of light back-radiated by eutrophic waters (green) is larger than that back-radiated by oligotrophic waters (blue), in general, shallow euphotic zones allow a larger proportion of incident radiation to be used in photosynthesis while in thick euphotic zones most of the radiant energy is absorbed by the water. LORENZEN (1976) also found a direct relationship between the radiant energy absorbed by phytoplankton and the chlorophyll standing crop of the integrated column. WALSH (1976) has proposed a depth-varying attenuation coefficient that takes into account the self-shading effect of the phytoplankton population at every location

$$I_z = I_0 \exp(-rz) \qquad (3)$$

$$r = 0.16 + 0.0053\,P + 0.039\,P^{2/3} \qquad (4)$$

P being the density of phytoplankton expressed in terms of nitrogen.

Multiple limiting factors. The actual photosynthetic rate is the result of the interaction between a number of factors: light, nitrate, ammonia, phosphate, silicate and others, some of which may be affected by other extrinsic or intrinsic factors. To solve such complex situations, two approaches may be taken involving (a) interaction among the limiting factors, or (b) Liebig's law of the minimum.

Taking a simplified example in which photosynthesis is assumed to be directly controlled by nitrate uptake and light intensity, the first approach would be considering that the light effect is a factor multiplying the maximum uptake rate, while a Michaelis-Menten hyperbola is controlling the nitrate uptake. The resulting photosynthetic rate would be

$$V = V_{max}\left[\frac{I_z}{K_L + I_z} \cdot \frac{NO_3^-}{K_N + NO_3^-}\right]. \qquad (5)$$

The second approach would be considering that the smallest of the two rates, produced by availability of light or by availability of nitrate, would control the actual photosynthetic rate, that is,

$$V = V_{max}\,\mathrm{MIN}\left[\frac{I_z}{K_L + I_z}, \frac{NO_3^-}{K_N + NO_3^-}\right]. \qquad (6)$$

WALSH (1976) used the second approach in his model of an upwelling ecosystem, selecting at every time from the various limitations, the factor giving the smallest value to the photosynthetic rate

$$V = \mathrm{MIN}\begin{cases} \dfrac{V_m\, NO_3^-}{K_N + NO_3^-} + \dfrac{V_s\, NH_3}{K_N + NH_3} \\[2ex] \dfrac{V_s\, PO_4}{K_P + PO_4} \\[2ex] \dfrac{V_s\, SiO_4}{K_S + SiO_4} \\[2ex] \dfrac{V_s\, I_z}{K_L + I_z} \end{cases} \qquad (7)$$

where V_s is the maximum specific uptake rate and V_m the specific uptake rate of nitrate in the presence of ammonia.

Effect of Pollution on Marine Ecosystems

Oil and petroleum products, synthetic organics, metals in excess of the amounts normally present in sea water, thermal or nuclear energy and many other categories of pollutants may have, and in fact do have, negative effects on the ecosystem. Perhaps the most dangerous of all kinds of pollution, as far as the ecosystem is concerned, is eutrophication. Eutrophication is the enhancement of the biological turnover by introduction of organic matter and/or nutrients into the marine environment. The term 'organic matter' is used in an ecological sense for the decomposable matter, thus shells and other hard skeletal parts of organic origin would not be 'organic matter.'

Most of the naturally occurring organic matter in the marine environment has its origin in planktonic detritus, forming relatively large aggregates with bacteria, and in fecal pellets that sink quickly to the bottom. Locally produced organic matter and humic compounds derived from the land are rapidly assimilated by the ecosystem. However, introduction with river runoff or sewage discharges of large amounts of organic matter (detritus) tends to encourage the development of the heterotrophic decomposers component while introduction of nutrient salts favors the growth of the producers component. The response of biological systems to increasing concentration of trophic materials is an increase in the respiratory demand in the waters below the euphotic zone and in the sediments.

Oxygen consumption in sea water. The chain of animal life in the deeper waters feeds mostly upon the rain of organic material, relying on the dissolved oxygen for respiration. Below the euphotic zone there is a net consumption of oxygen by respiration by animals and bacteria that decompose organic matter. These processes are accompanied by the release of CO_2 and nutrients to the water that are often re-utilized by photosynthetic producers. A useful term to express the amount of organic matter originally present in the sea water is the oxygen consumption of apparent oxygen utilization (AOU) given by the difference between the actual oxygen concentration and the equilibrium saturation value. AOU is used to estimate the changes in oxygen concentration which have taken place since the water left the surface layers where it was in equilibrium with the atmosphere. The rates of oxygen consumption estimated by RILEY (1951), WYRTKI (1962) and PACKARD et al. (1977) show an exponential decrease with depth

$$R = R_0 \exp(-az) \tag{8}$$

where $R_0 = 60$ to 140×10^{-10} ml/ℓ/sec, and $a = 3\text{-}4 \times 10^{-5}\ \mathrm{cm}^{-1}$.

In most of the world's ocean, circulatory processes replenish the depths with oxygen-bearing water at rates such that oxidative consumption does not exceed oxygen renewal, thus never losing all the dissolved oxygen. However, in special circumstances, generally where circulatory processes are restricted, and frequently where the rate of primary production or discharges of organic matter are high, the rate of oxygen consumption outstrips that of renewal and anoxic conditions arise.

Concurrent with anoxia, denitrification occurs and exhausts the supply of nitrate and nitrite ions, leading to the onset of sulphate reduction. Sulphide ion is produced during sulphate reduction, occurring in sea water mainly as undissociated H_2S and HS^-. The introduction of sulphite ion in the environment is a nearly catastrophic event, since sulphides are highly toxic and thus eliminate all organisms from the ecosystem except anaerobic bacteria. Sulphides form highly insoluble compounds with many metal ions at the pH of sea water, and thus not only do they tend to strip the water of ions of these metals, but they also enrich the sediments with their precipitates. Anoxic waters are by no means azoic or devoid of life. Although familiar forms are missing, life persists even in these most inhospitable regions of the sea.

Oxygen consumption in marine sediments. Most of the organic matter in marine deposits is mixed with fine particles of inorganic sediments which may have been trapped in quiet parts of the sea floor. Coarse sandy sediments tend to be poor in organic matter because they accumulate in agitated, well-ventilated waters, where the light organic matter is mostly washed away and the supply of oxygen is sufficient to result in swift decay. The organic carbon in coarse sediments is generally less than 1%. In finer sediments there is commonly a higher organic content, in many cases, of several percent units because light organic remains and clay both tend to come to rest in quiet regions of the sea floor where there is poor ventilation of the bottom water and a low rate of oxygen exchange with the sediment. Thus, below a thin cover of oxidized sediment, anaerobic conditions tend to develop, owing to bacterial activity and lack of oxygen supply by diffusion. However, various mud-feeding animals stir the surface stratum and burrow and plough through newly deposited sediment or seek protection by living below the surface. Plant roots (e.g., mangroves) also disturb the lamination of sediments in shallow water. As a result, decomposition of organic matter is facilitated by bioturbation of sediments.

Many marine sediments are anoxic. Natural conditions favorable for the formation of sediments rich in organic matter are found in regions of upwelling or near estuaries. In these areas, high primary production results in accumulation of detrital material on the sea floor and in development of anaerobic conditions. Much organic matter can thus be preserved, in spite of ventilation of the overlying waters. Contents of over 10% organic carbon in sediments are, however, rare, always being associated with anoxic conditions in the water (Black Sea). With the lowering of the redox potential (Eh), the thermodynamic drive is diminished, and organic materials tend to accumulate in the sediments rather than to be oxidized. Thus sediments laid down under anoxic conditions are considerably richer (up to 10 fold) in organic matter than are sediments deposited under oxygen-bearing waters.

When H_2S is produced in the sediments, the probability that lethal conditions occur for the fauna and flora in the overlying water is high. Sulphide also combines with the oxides of iron, blackening the anaerobic layer. The blackened sulphite-containing sediments can be oxidized rapidly in the presence of oxygen. The depth at which black sulphides occur indicates the depth to which significant amounts of oxygen penetrate, either by diffusion or by bioturbation.

Eutrophication. When large amounts of organic matter or nutrients are introduced by man into the ecosystem, the ecosystem adjusts to this perturbation. In the case of a discontinuous discharge, it tends to reestablish the equilibrium around the previous normal state. In the case of a continuous discharge, it will change into a new 'polluted' state. These changes may be advantageous to individual species or populations and proceed up to an optimum level, but thereafter, any increase in the concentration of the added substances merely produces a decline of the most sensitive species of populations. The self-purifying capacity of the marine waters is directly connected to the processes that control the oxygen balance. This balance may be easily broken, giving rise to an oxygen-producing surface layer and an oxygen-consuming bottom layer with downwards transport of oxygen being opposed by stably stratified water columns. The situation is further complicated by the fact that the oxygen produced in the shallow euphotic zone, greatly reduced by turbidity, tends to escape to the atmosphere, while the organic matter produced tends to settle, increasing the oxygen consumption of the deeper layers. Once the oxygen cycle is broken, the oxidation of organic matter proceeds through anaerobic pathways. When sewage is continuously discharged in excess of the self-purification capacity into a coastal zone with restricted circulation, the zone rapidly becomes a nuisance, turbid and foul-smelling. Essentially it is converted from an oxygen based system to a sulfur based one. Such a nuisance can be prevented by limiting the quantities of organic matter and nutrients discharged well below the self-purification capacity of the recipient water body.

Mediterranean waters are oligotrophic except perhaps in the neighborhood of the large rivers, and sediments have in general a low organic carbon content due to the low biological production of the waters and to the presence of high oxygen concentrations in deep waters. Therefore, local oxygen deficiencies are always connected with eutrophicating sources, mostly discharges of raw or treated urban effluents. Sources of eutrophicants in the Mediterranean Sea have been identified and their amounts and effects estimated by UNEP (1978). Their distribution around the region is uneven with a maximum in the northwest and in the Adriatic Sea and a minimum on the southern shores. Owing to the strong stratification of the surface waters, eutrophication is more acute in summer, when ambient natural nutrient concentrations are low and the oxygen transport through the thermocline is strongly reduced. Winter mixing allows for the required vertical transport of oxygen to keep the deep waters and the sediments mostly oxidized all over the Mediterranean Sea (CRUZADO, 1978).

Although the major effect of eutrophication is to change, if not to destroy, the equilibrium of the marine ecosystem, some of these effects are of direct concern to man, and therefore measures have to be and have been taken in some cases to avoid them. However, all of them are of a very limited nature. A consideration of the effect of necessary growth substances such as nutrients and organic matter upon biological systems yields a more lucid view of what is meant by eutrophication and gives a clear indication of the essentially complex nature of the ecosystems of which polluting sources must be considered integral parts.

Autotrophic Processes

Presentations on autotrophic processes were made in three lectures. The first two dealt with general principles and quantification of pelagic autotrophic processes, while the third dealt with those processes in a benthic system.

General Aspects of Autotrophic Processes

The growth of algae relies on factors such as irradiance and the nutrient concentration while phytoplankton abundance depends upon the growth rate of the algae minus the losses due to natural mortality, grazing, sinking, mixing, and advection. Phytoplankton populations are governed by two types of parameters. They are:

a. Physiological or functional parameters, knowledge about which is largely derived from experimental measurements, and

b. Environmental parameters, including the availability of light and nutrients, the hydrodynamic setting, and the behavior of the herbivore.

Experimental Measurements. Light intensity strongly affects the rate of photosynthesis. This relationship is positive until the optimum intensity is reached, at which point increases above the optimum result in no change (saturated) or become negative and photoinhibition occurs. The photosynthesis-light curve (P vs I curve) is characteristic of the different natural phytoplankton populations. The two important characteristics of the curve are its slope $\Delta P/\Delta I$ and the maximum photosynthesis rate, P_{max}, shown in Fig. 8. The initial slope is a function of the light reaction and is usually not governed by other factors. It can be expressed as number of oxygen moles evolved or carbon assimilated per unit light intensity, in einstein, as an assimilation index or quantum yield. P_{max} is a function of environmental limiting factors as nutrients and temperature (Figs. 9 and 10). Differences in the photosynthetic efficiency allow tropical phytoplankton species to utilize high light intensities at a higher efficiency, while phytoplankton from northern seas, adapted to lower light intensities, have depressed rates at the same intensities. However, the slope of the PI curves shows that the latter has a higher absolute rate at low light intensities (Fig. 11).

Two conclusions are generally accepted on the nutrient uptake dynamics of phytoplankton:

a. At low nutrient concentrations, the rate of uptake is proportional to the concentrations (i.e., uptake is concentration dependent).

b. The total yield of the phytoplankton is directly proportional to the initial concentration of the limiting nutrient, and independent of the growth rate of phytoplankton.

It was later shown (CAPERON, 1967; DUGDALE, 1967) that nutrient uptake could be described using enzyme kinetics (Michaelis-Menten)

$$V = \frac{V_m S}{K_s + S} \qquad (1)$$

where V = rate of nutrient uptake, K_s = substrate concentration at which $V = V_m/2$ or half saturation, V_m = maximum rate of nutrient uptake, and S = nutrient concentration. The half saturation constant, (K_s), appears to be an important parameter separating phytoplankton species. Survival depends upon the ability of a species to assimilate low concentrations of nutrients and on the minimum concentrations at which the species can grow.

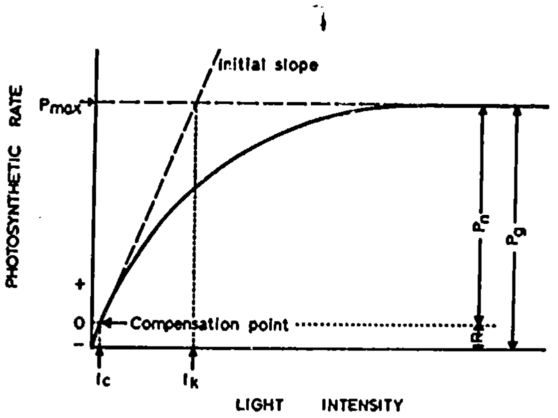

Fig. 8. Photosynthesis versus light relationship, P_{max} photosynthetic maximum, I_c light intensity at the compensation point, R respiration, P_n net photosynthesis, P_g grow photosynthesis, and I_k intersection of P_{max} and initial slope. From PARSONS and TAKAHASHI (1973), with permission of Pergamon Press.

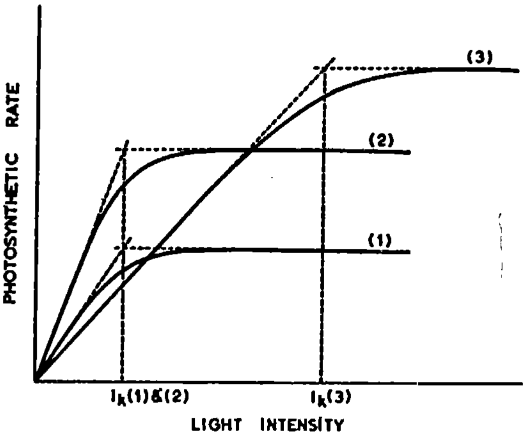

Fig. 9. PI curves for shade adapted communities (1,2) and sun adapted community. From PARSONS and TAKAHASHI (1973), with permission of Pergamon Press.

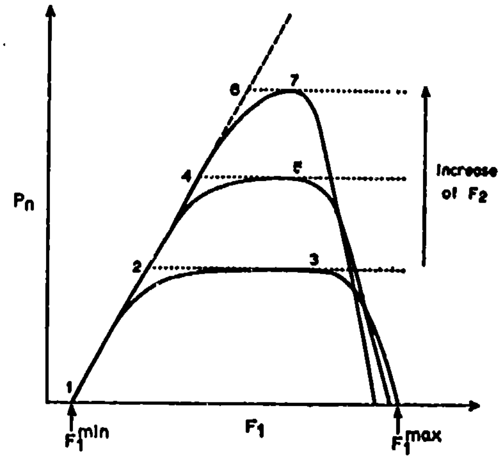

Fig. 10. Photosynthesis versus environmental factors, F_1 and F_2. From PARSONS and TAKAHASHI (1973), with permission of Pergamon Press.

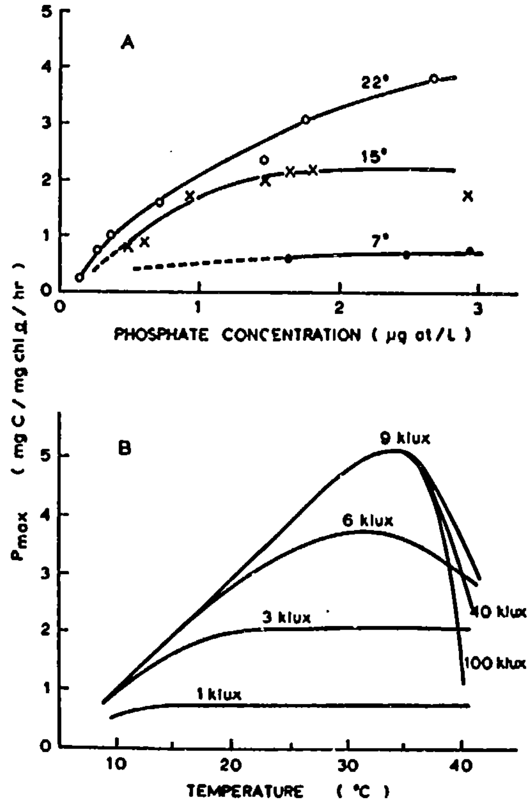

Fig. 11. Photosynthesis versus phosphate (upper) and temperature (lower). From PARSONS and TAKAHASHI (1973), with permission of Pergamon Press.

Several distinctions can be made based on nutrient uptake by phytoplankton cells (e.g., PARSONS et al., 1977):

a. Coastal phytoplankton communities have higher K_s values than the oceanic ones. Populations of the same species will have a different K_s depending upon their original environment.

b. Nutrient uptake is affected by light intensity. Under conditions of excess nutrients, the rate of uptake in response to light intensity is a hyperbola-shaped curve, and is analogous to the photosynthesis vs light curve, with an uptake inhibition at higher light intensities (above 10% or 25% surface illumination). On the other hand, in complete darkness, some nutrients can be taken up (ammonium more than nitrate).

c. Temperature also affects the rate of uptake. The value for K_s increases with increasing temperature. The nutrient threshold for growth is lower at lower temperatures.

d. K_s also increases with cell size. Smaller cells will still grow at concentrations limiting the growth of larger cells.

e. The ability to take up nitrate and ammonium at low concentrations differs with species. Some take up nitrate at lower concentrations than ammonium and vice-versa (Fig. 12). Such variability in the nutrient properties might throw light on some field observations and on succession of species with each species having a different optimal combination of light intensity and K_s.

The effect of temperature on algal growth rate in culture has been summarized by EPPLEY (1972). By plotting growth rate data vs temperature, he obtained an empirical relation for the maximum growth rate over a temperature range between 0° and 40°C under continuous illumination in the equation:

$$\log_{10} \mu = 0.0275T - 0.070 \qquad (2)$$

μ = the maximum growth rate in divisions/day, and T the temperature °C. Nutrient regulation of P_{max} is governed by the rate of the dark reactions through temperature.

Environmental parameters. The phytoplankton production cycles can vary in timing, amplitude, and spread, either in different areas or from year to year in the same area. Such variations are largely governed by two factors:

a. The 'production ratio' (CUSHING, 1975) or ratio of critical depth to depth of mixing, D_{cr}/D_m, which governs the start of production.

b. Grazing, and the delay period between the start of a bloom and the appearance of effective grazing.

A major factor in temperate latitudes is the depth to which the water column is mixed. At certain times, winds, and/or convective mixing in winter can cause phytoplankton cells to be mixed below the euphotic layer (i.e., compensation depth, D_c). During this time, a loss through respiration occurs and no net production takes place.

In addition to the compensation depth, another concept, the critical depth, D_{cr}, is used to refer to the depth at which total photosynthesis in the water column is equal to total respiration of the primary producers. D_{cr} can also be defined as the depth at which the average light intensity for the water column equals the compensation light intensity. SVERDRUP (1953) related the light compensation intensity to the compensation depth, D_c:

$$I_c = 0.5\, I_o \cdot e^{-kD_c} \qquad (3)$$

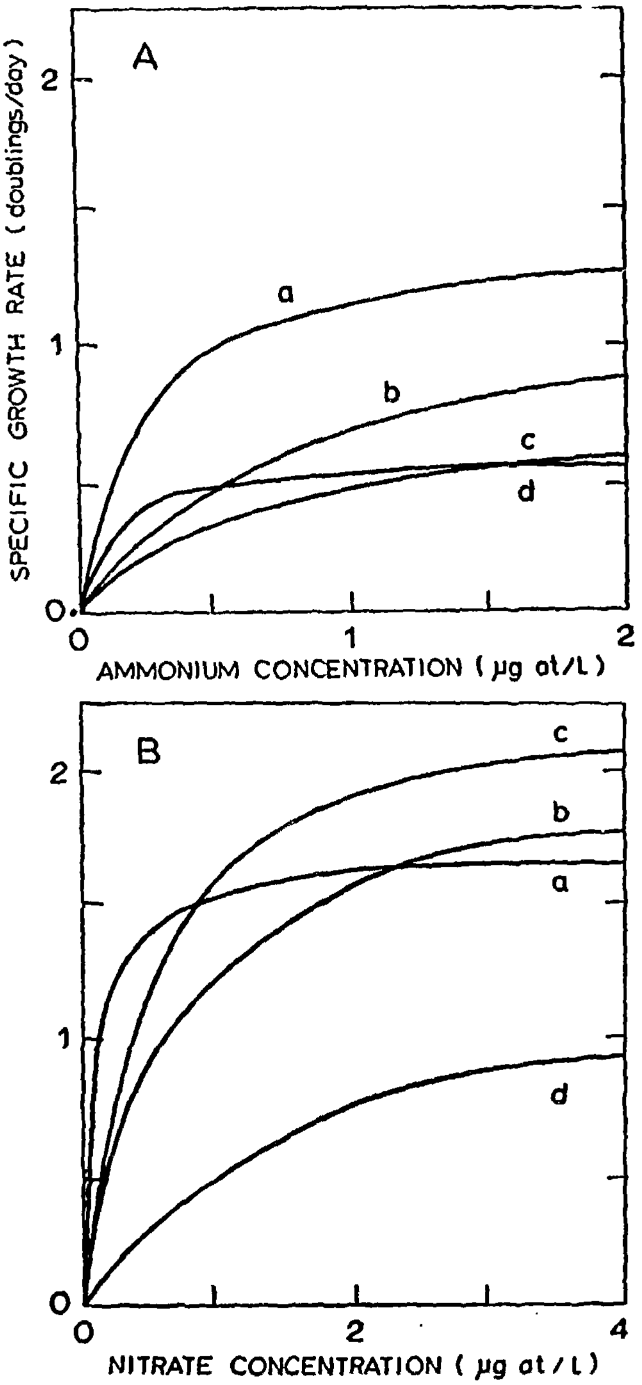

Fig. 12. Specific growth rate versus ammonium (A) and nitrate (B) concentrations. 'The light of (B) is approximately 4 times that of (A). a-*Coccolithius huxleyi*, b-*Ditylum brightwelli*, c-*Skeletonema costatum*, and d-*Dunaliella tertiolecta*. From PARSONS and TAKAHASHI (1973), with permission of Pergamon Press.

where I_c is the light intensity at compensation depth; I_0 is the surface radiation; 0.5 is a factor allowing for absorption of the longer and shorter wavelengths in the first meter, D_c is the compensation depth (m), and k is the average extinction coefficient. The relationship of D_{cr}, the critical depth, to I_c is obtained by integrating and dividing by D_{cr}:

$$I_c = 0.5\ I_0 \int^{D_{cr}} \frac{e^{-kz}\ dz}{D_{cr}} \qquad (4)$$

$$I_c = \frac{0.5\ I_0}{kD_{cr}} (1 - e^{-kD_{cr}}) \ . \qquad (5)$$

The critical depth (D_{cr}) can be obtained for any water column, knowing the extinction coefficient (k), incident light intensity (I_0), and assuming some value for I_c by the equation:

$$D_{cr} = \frac{0.5\ I_0}{I_c k} \ . \qquad (6)$$

When the depth of the mixed layer is greater than the critical depth, and photosynthesis in the water column is less than respiration for that area no net production can take place. On the other hand, when the critical depth is greater than the depth of mixing net production occurs and conditions for the onset of a bloom are favorable (Fig. 13). The lower limit of the mixed layer is often taken by the depth of the first pycnocline.

The validity of the 'production ratio' model depends upon several assumptions:

a. that the cells are uniformly distributed in the mixed layer,

b. that nutrients are not limiting,

c. that the extinction coefficient in the water column is constant (the average k can be used), and

d. that respiration is constant with depth.

With the development of the bloom, the first assumption becomes no more valid (Fig. 14) as self-shading will occur. LORENZEN (1972) gave a highly significant correlation between chlorophyll content and thickness of the euphotic zone in the equation:

$$\ln \overline{C} = 8.85 - 1.57 \ln D_c \qquad (7)$$

$\overline{C}$ being the total chlorophyll a in the euphotic layer in mg/m^2 and D_c equal to 1% light depth.

Grazing. After production has started in early spring, the availability of food and the rise in temperature induce the overwintered generation of herbivores to spawn. A new generation of grazers will appear after a lag period. A longer lag allows the bloom to develop to a higher amplitude and to last longer. In this case the transfer of energy to the following trophic levels is inefficient since much of the fixed energy is lost to the benthic system by sinking during the lag period. A shorter lag period is associated with continuous cycles of low amplitude and with more efficient transfer of energy. The grazing capacity of herbivores as measured by different authors appears to vary widely. In vitro measurements (MARSHALL et al., 1935) show the ratio per body weight per day or grazing intake for maintenance of planktonic herbivores to be about 7%.

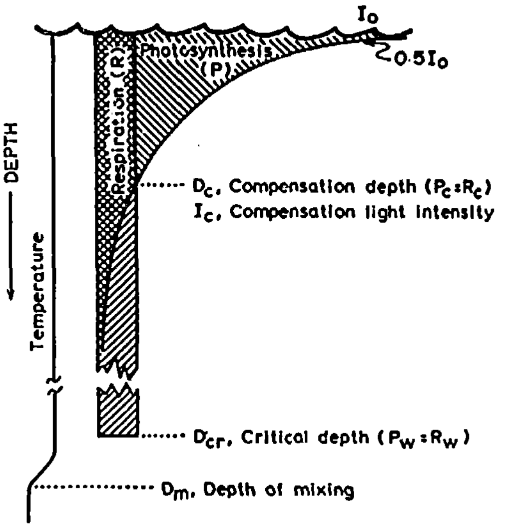

Fig. 13. Compensation and critical depth relationships. From PARSONS and TAKAHASHI (1973), with permission of Pergamon Press.

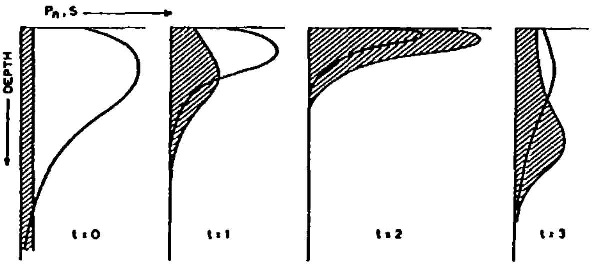

Fig. 14. Phytoplankton biomass versus photosynthetic rate after 3 time intervals (t) in shaded area as mg Chl a/m^3 and P_n as mg C/mg Chl a/day. From PARSONS and TAKAHASHI (1973), with permission of Pergamon Press.

LUCAS (1936) found a ratio of 40% in a flask of dense algal culture for Eurytemora hirundoides. In the field, HARVEY et al. (1935) and RILEY (1947a) estimated the ratio for short periods in the sea to be 30-40%. The value of 7% has been used to obtain algal mortality due to the grazing in a number of models, though it is now known that grazing capacity under experimental conditions is lower than might be expected from grazing observed in the field. 'Superfluous feeding' takes place at higher algal densities. During the Spring phytoplankton peak, the maintenance ratio (expressed in percent) could be as high as 350%, dropping to a few % at low algal density. According to

PETIPA (1966), this ratio is about 23% to 313% in the Black Sea.

From respiration measurements, it appears that the maintenance ratio for larger crustacean zooplankton averages 10-20% and 40-60% for the smaller ones. The most suitable prey density appears to be in the range 200-1000 µg carbon/liter. Inhibition of grazing occurred at higher prey density. A diel periodicity was also shown for zooplankton grazing, with bimodal maxima at dawn and dusk with the lowest feeding occurring at midday (BOUGIS, 1958). The filtration rate is a function of animal size:

$$\log F = n \log W + \log b. \tag{8}$$

where the filtration rate (F) is measured in units of ml swept clear per animal per hr, W is expressed in mg dry body weight per animal, and b is a filtering constant. The exponent n has been calculated for boreal (0-8°C), temperate (8-12°C), subtropical (12-20°C) and tropical (20-30°C) habitat temperatures, and is summarized in Table I (from CONOVER and HUNTLEY, 1980).

The b intercepts from these five regressions approximately fall along the exponential curve

$$b = 3.345\, e^{0.17T} \tag{9}$$

where b is the filtering constant, T temperature in °C and e the base of the natural log. Thus:

$$F = 3.347\, e^{0.172T}\, W^{0.824}\ . \tag{10}$$

Ecological efficiency is the ratio of the amount of energy extracted from one trophic level to the amount supplied to the next trophic level,

$$E = \frac{\text{energy extracted from a trophic level}}{\text{energy supplied to upper trophic level}}.$$

Ecological efficiency as defined does not take into account recycling processes. A 10% transfer of material between trophic levels implies a 90% loss to the system.

Quantification of Autotrophic Processes

The complex conversions of inorganic substances into organic matter by living marine plants are commonly termed 'autotrophic processes.' A quantification of these processes is paramount to any effort of ecosystem modelling. To date, the major emphasis has been directed towards measuring photosynthesis, nutrient uptake and assimilation by phytoplankton of pelagic systems in an effort to estimate their rate of growth. Notwithstanding the increasing sensitivity of methods, growth of phytoplankton has been a difficult parameter to measure. The difficulties in estimating autotrophic processes rests within the two major components required for quantification. These components, sensitive flux measurements and accurate biomass estimates are equally difficult to obtain and often are not done concurrently. This weakness leaves gaps which modellers fill with published data giving at best order of magnitude approximations.

While much work has been done in defining phytoplankton biomass in the past, only recently has the need for flux measurements been fully appreciated. The UNESCO SCOR publication entitled, "Mathematical Models in Biological Oceanography," by PLATT et al. (1981), stressed the following: "For understanding biological oceanographic systems it is necessary to have at least as much information on fluxes as on biomass." While measurements of all kinds of fluxes are currently being made with improved understanding, these measurements, like those for biomass, suffer uncertainties that make quantification, even of empirical facts difficult. Whenever possible, verification by more than one method is necessary to substantiate the rates measured.

A confusing terminology has developed along with the increased efforts in measuring primary production. CUSHING et al. (1958), and STRICKLAND (1960) took pains to clarify these terms, and it may be well to reiterate some of these pertinent definitions. STRICKLAND's (1960) term 'primary product' referred to all

Table I. Summary of regression analyses of log F (ml/animal/hr) on log W (mg dry weight/animal) at different habitat temperatures

Habitat	No. of data	Equation of the regression line log F = n log W + log b	Coefficient of Determination (r^2)	95% C.L. on slope, n
Boreal	128	log F = 0.820 log W + 0.67	0.884	0.052
Temperate	220	log F = 0.768 log W + 1.06	0.810	0.025
Subtropical	113	log F = 0.778 log W + 1.65	0.903	0.047
Subtropical*	483	log F = 0.868 log W + 2.01	0.846	0.033
Tropical	48	log F = 0.885 log W + 2.49	0.824	0.118

*Measurements between 12.5-15°C

the autotrophic plants in the sea. Some descriptors of the primary product are:

a. Standing stock, the quantity of plants present at any given time (CUSHING et al., 1958).

b. Biomass, the quantity of plant material as measured through cellular constituents as C, N, P, Chl-a, ATP, DNA, etc., in units of $\mu g/\ell$, mg, or g/m^3 or g/m^2 when integrated for the water column.

c. Plasma volume, the cell volume less skeleton and vacuoles, i.e., volume of living matter (LOHMANN, 1908) in units of μm^3.

Unlike the quantities just mentioned, 'primary production' refers to a rate measurement and should not be confused with measurements of standing crop or biomass. Its descriptors are:

a. Primary Productivity, the autosynthesis of inorganic constituents (carbon, nitrogen, phosphorus, etc.) into organic constituents. Units as $\mu g\ C/\ell$, $mg\ C/m^3$ or integrated as g/m^2.

b. Gross Primary Production, the photosynthesis before correction for respiration and excretion.

c. Net Primary Production, the net rate of production of plant organisms under the influence of all environmental factors including death and predation.

Autotrophic biomass. When growth is measured directly from a phytoplankton population, changes in cell number per unit of time are required to calculate the growth rate constants μ or k in equations 2 and 3. However, single phytoplankton counts can be used with appropriate flux measurements to calculate growth. This requires abundance values to be converted into biomass. If an electronic particle counter is used, counting is facilitated, and portions of the population can be quantified as having a known mean spherical diameter from which volume is easily calculated. Microscopic counts are more difficult to convert to biomass. LOHMANN (1908) introduced the concept that surface and volume relationships can be used to calculate volumes of 'living matter' or plasma volume (PV). He used the relationship:

$$PV = 1.10\ [(\text{surface area, } \mu m^2)(1\text{-}2\mu m) + (\text{protoplasmic bridge volume, } \mu m^3)] \quad (11)$$

A value between 1 and 2 was used for the thickness of the cytoplasm, and the volume of the protoplasmic bridge was measured (μm^3). SMAYDA (1965 and 1978) modified this equation to read:

$$PV = (\text{surface area, } \mu m^2)(\text{cytoplasmic layer, } 1\text{-}2\mu m) + 0.10\ (\text{total cell volume, } \mu m^3) \quad (12)$$

This equation results in less than 10% error from the former and reduces the number of measurements considerably. In either case the method of conversion to plasma volume is cumbersome but highly accurate for final carbon content. This method can be used when there is a concomitant taxonomic study requiring precise measurements of species in a natural population. Conversion from plasma volume to cellular carbon can be made using the equations of STRATHMANN (1967):

$$\log C = 0.892\ (\log PV) - 0.610. \quad (13)$$

When only cell volume is available, a short cut, less accurate estimate can be obtained from:

$$\log C = 0.758\ (\log V) - 0.422\ (\text{diatoms}), \quad (14)$$

$$\log C = 0.866\ (\log V) - 0.460\ (\text{other species}). \quad (15)$$

EPPLEY (see SMAYDA, 1978) slightly modified these equations giving greater precision as:

$$\log C = 0.76\ (\log V) - 0.35\ (\text{diatoms}), \quad (16)$$

$$\log C = 0.94\ (\log V) - 0.60\ (\text{other species}). \quad (17)$$

Converting phytoplankton into carbon biomass allows an estimation of a carbon based growth rate when coupled with primary production rates.

Phytoplankton carbon can be measured directly from natural populations providing the in carbon content. In some instances, differences of three orders of magnitude were found in this ratio. However, a judicious usage of C/Chl a ratio may prove a useful, if not entirely accurate, means of estimating phytoplankton carbon.

Within relatively stable environments, as central oceanic gyres, a relationship between carbon and chlorophyll a biomass may occur allowing Chl a measurements to estimate phytoplankton carbon directly. Since chlorophyll is unique to plants, Chl a measurements do allow a rapid conversion to carbon biomass, providing that a relatively constant carbon/chlorophyll a ratio exists. BANSE (1977) reviewed some problems in coupling Chl a fluctuations with changes in carbon content. In some instances, differences of three orders of magnitude were found in this ratio. However, a judicious usage of C/Chl a ratio may prove a useful, if not entirely accurate, means of estimating phytoplankton carbon.

An alternate method involves the measurement of phytoplankton ATP as described by HOLM-HANSEN and BOOTH (1966). Since ATP is associated only with living organisms and transiently with inert material, a C/ATP ratio can be effectively used to estimate carbon. A C/ATP ratio of 250 was measured for a large number of different oceanic species by HOLM-HANSEN and BOOTH (1966). Evidence that this ratio is not constant and can vary with the nutritional state of the phytoplankton has also been noted (SAKSHAUG, 1977 and HOLM-HANSEN, 1970). BANSE (1980) also reviewed potential errors in ATP measurements, and KARL (1980) has recently given a complete review of ATP and its application in biomass measurements. Again, with judicious usage and in tandem with other methods for estimating carbon, ATP can be an effective means for converting to phytoplankton carbon.

An interesting alternative method was proposed by EPPLEY (1968) using 24 and 48 hr incubations of phytoplankton exposed to ^{14}C-bicarbonate. Initial cell carbon (P_o) could be calculated from ^{14}C incorporated into phytoplankton from the equation:

$$P_o = \frac{\Delta P_1^2}{\Delta P_2 - \Delta 2P_1} \qquad (18)$$

where ΔP_1 = ^{14}C taken up over 24 hr and ΔP_2 = ^{14}C taken up over 48 hr. This method allows for the measurement of carbon biomass and an estimate of growth (k) based on carbon turnover. The errors in this method are those commonly given for ^{14}C incubations (see GIESKE et al., 1978; HARRIS, 1978; or PETERSON, 1980).

Autotrophic flux measurements. The growth constant (μ or k) of a phytoplankton population can be obtained directly through cell counts or indirectly by the use of biomass and an appropriate flux measurement. The direct measurement involves detecting changes in cell numbers with time. These values can then be applied to equations such as those given by GUILLARD (1973) to calculate maximum growth. In the ocean, however, this method is only practical in relatively stable waters, in situations in which the sampling of the same population is insured by drogue tracking. Entrainment of natural populations can be accomplished by dialysis culture (SAKSHAUG, 1977; and KOSSUT and MAESTRINI, 1977) or plankton cages (SAKSHAUG and JENSEN, 1978). These methods are most accurate in measuring growth.

Indirect calculations of growth can be made using observations of dividing cells. SWIFT and DURBIN (1972) used this method for obtaining 'in situ' growth of oceanic dinoflagellate *Pyrocystis*. WEILER and EPPLEY, 1979, and WEILER, 1980 obtained growth rates of *Ceratium* species by observing the frequency of division stages to obtain a mean frequency maximum and then applying the equation below:

$$F = (a+b)/(a+b+c) \qquad (19)$$

where a is the number of nondividing cells, b is the number of cells containing 2 nuclei, and c is the number of recently divided cells. From this growth was calculated as:

$$\mu_1 = 1/t \ \ln(1 + \overline{F}_{max}). \qquad (20)$$

WILLIAMS (1965) used observations of cellular dimensions of salt marsh diatoms to derive a relationship between volume, area and maximum growth rate (K_{max}). His equations are:

$$K_{max} = 3.75 - 0.7 \ (\log \text{cell volume}) \qquad (21)$$

$$K_{max} = -0.01 + 1.64 \left[\frac{\text{cell area}}{\text{cell volume}}\right]^{1/2}. \qquad (22)$$

Although highly accurate, measurements employing direct observations are slow, labor intensive, and at certain times, applicable to only certain species. SUTCLIFF et al. (1970) developed a method using an electronic particle counter to determine production and standing stock of particulate matter in surface waters. This method has not been fully evaluated, but of course the particle counter does not discriminate between living and inert particles nor between species having similar sizes. Use of a counting device having a fluorometric detector may greatly improve this method.

Formulations for estimating growth of phytoplankton indirectly have also been proposed. CUSHING (1959) used the following equation for estimating growth (R) as divisions in the mixed layer:

$$R = R_p \cdot \frac{D_c}{D_m} \qquad (23)$$

where R_p = division in the euphotic zone, and D_c and D_m are the compensation and mixed layer depths, respectively.

The ^{14}C incubation of EPPLEY (1968) mentioned previously could also be used to calculate growth (μ) as follows:

$$\mu = 1/t(\text{days}) \ \ln \ \frac{\Delta P_2 - \Delta P_1}{\Delta P_1} \ . \qquad (24)$$

The elements are the same as those noted previously.

An empirical formulation for growth (μ) was given by EPPLEY and SLOAN (1966) by

$$\mu = \frac{I_L \ [10^{0.036T-0.28}]}{0.015 + I_L} \qquad (25)$$

where $I_L = I_o \ [4.3 \ I_o + 0.18] \ [1-10^{-100(\text{Chl-}\underline{a})}]$, T = temperature (°C), I_o = incident radiation (g cal./cm^2/min.), and Chl-*a* = cell chlorophyll-*a* picograms/μm^3). THOMAS (1970) calculated a specific growth rate for phytoplankton using a carbon/Chl-*a* ratio and ^{14}C production measurements as follows:

$$\mu = \frac{\log_2(R \cdot \text{Chl-}\underline{a} + \text{Prod.}) - \log_2(R \cdot \text{Chl-}\underline{a})}{1 \ \text{day}} \qquad (26)$$

where R = C/Chl-*a* ratio and Prod. = daily ^{14}C uptake.

The theory of nutrient limitation proposed by DUGDALE (1967) and discussed in a previous section stimulated much work to quantify the effect of nutrient limitation, particularly nitrogen, on phytoplankton growth rate. EPPLEY and THOMAS (1969) proposed the following equation for calculating growth as doublings of cell nitrogen (v) as:

$$v = \frac{\log_2 10}{\text{uptake period (days)}} \cdot \tag{27}$$

$$\log_{10} \frac{\mu\text{Moles cell-N} + \mu\text{Moles } NO_3^- \text{ uptake}}{\mu\text{Moles Cell-N}} \cdot$$

The same equation can be applied to the uptake of any limiting nutrient to determine the growth based on the doubling time of that nutrient. Enzyme activity such as nitrate reductase and nitrite reductase can be used to calculate growth of nitrate limited populations of phytoplankton in the following equation:

$$k = \log_2 \cdot \left(\frac{N_o + \Delta N}{N_o}\right) \cdot \frac{1}{t} \tag{28}$$

where N_o = particulate phytoplankton nitrogen, ΔN = amount of nitrate or nitrite reduced/day, and t = time (days). To accurately estimate growth through nutrient uptake or enzyme activity in the previous equations, care must be taken to use that nutrient which limits growth thus dependent upon its supply. Earlier attempts to use nutrients in estimating growth such as those of RILEY (1956) for Long Island Sound and STEELE (1958a) for the North Sea were based primarily on phosphorus. These studies tried to relate biological change or production which were thought to be limited by phosphorus.

Light can also be considered as a limiting variable in formulating equations for predicting growth or production. GRAN and BRAARUD (1935) proposed the critical depth hypothesis which SVERDRUP (1953) quantified with numerous observations. RYTHER (1956) and RYTHER and YENTSCH (1958) used light saturated photosynthesis and chlorophyll to determine relative photosynthesis as

$$P = \frac{R_s}{k} \cdot P_{sat} \tag{29}$$

$$P_d = R_d \cdot C_d \cdot 3.7 \text{ g C/g Chl } \underline{a}\text{/hr} \tag{30}$$

respectively, where R = grams C fixed/m^3/day, R_s= Daily relative photosynthesis/m^2/day for appropriate I_o, k = extinction coefficient (m), P(sat)= gross photosynthesis at light saturation, R = relative daily photosynthesis (I_o;R=R_d at depth d), P_d= daily total photosynthesis, C = g chlorophyll/m^3, and C_d= g chlorophyll/m^3 at depth d.

When light is considered a limiting substrate for photosynthesis, the hyperbolic analogs of Michaelis-Menten kinetics can be applied. Photosynthesis rate can be calculated from:

$$P = P_{(max)} \cdot \left(\frac{\bar{I}}{K_i + \bar{I}}\right) \tag{31}$$

where P_{max} = photosynthesis at saturating light, $\bar{I}$ = mean daily photosynthetically available light, and K_i = saturating light intensity. The $\bar{I}$ in the above equation is calculated as

$$\bar{I} = \frac{I_o}{K_z} \cdot (1-e^{-kz}) \tag{32}$$

with k = the extinction coefficient of light, and z = depth.

The photosynthetic response to light by plants can be effected by the light prehistory as demonstrated by BORDMAN (1977). Recently FALKOWSKI (1980) discussed the role of light-shade adapted species of marine phytoplankton. A quantification of the light curve for photosynthesis will depend to some degree on the light conditioning of the phytoplankton population. JASSBY and PLATT (1976) and PLATT and JASSBY (1976) suggest that the slope (α) of the linear portion of the light saturation curve is most useful in predicting specific photosynthetic rates. They derived the following equation from a large data set:

$$P^B = P_M^B \tanh(\alpha \, I/P_M^B) - R^B \tag{33}$$

where P_M^B = specific rate of photosynthesis mgC/mg Chl a/hr), α = slope of the linear portion of light saturation curve, I = irradiance (W/m^2), and R^B = specific rate of respiration (mg C/mg Chl a/hr).

While this presentation was not meant to be an exhaustive review of all formulations proposed for describing autotrophic processes in the sea, it is hoped that through the discussion of those presented, an indication of the different approaches and the scope of the problem was given. Whether direct or indirect methods are used, the quantification of autotrophic processes remains an essential portion of any ecosystem model.

Benthic Autotrophic Processes

In shallow coastal marine waters the sea bottom and its associated organisms (the benthos) play a considerable role in the overall processes of the ecosystem. The benthic boundary is strongly coupled to the water column, exchanging organic and inorganic matter with it.

Sediments are deposited and may be resuspended. Active resuspension may affect the transparency of the overlying water. Nutrients entering the sea bottom, either in the form of organic matter or absorbed to inorganic particles, may be stored and released to the water column. Organic matter is produced on well-lit areas of the sea bottom sometimes in great quantities (e.g., inter- and sub-tidal sea grass beds on sediments or algae on rocky surfaces) of which a high proportion may be exported to the water column. Conversely, deep bottoms receive organic matter through deposition which is stored, decomposed, and subsequently released as nutrients to the overlying water.

The distribution of benthic biomes is largely controlled by the light and by the coastal inclination of the bottom and water movement at the coast (which are factors determining the sediment composition and stability). Unlike terrestrial systems, production often differs greatly from consumption. High fluxes across the boundaries of biomes are maintained by the transport qualities of water for organic matter and nutrients. At one extreme, we find highly productive systems (such as salt marshes, sea grass meadows, kelp beds or coral reefs) exporting organic matter, and at the other extreme we find the all-consumer systems, such as sea caves or the majority of deeper bottoms.

The main export pathways of organic matter from primary production are:

a. through soluble organic matter leaching through cell walls, a process which may remove up to 70% of the net primary production in algae (KHAILOV and BURLAKOWA, 1969; SIEBURTH and JENSEN, 1969) and which contributes to the pool of dissolved organic matter in the water column;

b. erosion of parts of thalli and leaves in algae and sea grasses which, depending on particle size, stay suspended as particulate organic matter in the water column or enter adjacent benthic systems;

c. leaf fall in sea grasses which mainly acts to export organics to other benthic systems; and

d. migrating stocks of consumers which come to feed in the benthic system. Higher trophic levels in the benthos may export a considerable part of their production through pelagic larvae.

Imports into benthic systems occur through the sedimentation of particulate organic matter which is consumed by deposit feeders; the transportation by water movements of dissolved and particulate organic matter to filter feeders; and the migration of benthic animals into the water column to feed there (Fig. 15).

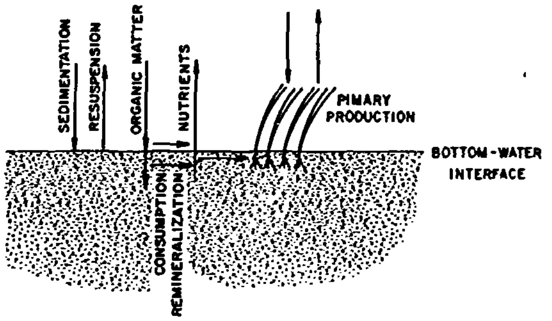

Fig. 15. Sketch of imports and exports from the benthic system.

Benthic systems are highly structured; benthic food chains are often complicated; close relationships between organisms, such as symbioses, are abundant; and many features of the benthos have a strong historical component. The large size and the relative longevity of organisms belonging to low trophic levels makes storages in the form of biomass with low respiration to biomass ratios an important feature (Table II).

Total community biomass is not simply dependent on the magnitude of energy flow (gross production, total assimilation) in a trend to maximize persistent biomass (ODUM, 1956 and O'NEILL, 1976) but may vary over a wide range of turnover-body size relationships (Fig. 16). This may have to do with the destructive effect of opportunistic flows discharging storages under severe perturbations. Stabilizing storages have a highly selective advantage for the system when input fluctuations are high and when concurrently the probability of perturbations exceeding the tolerance limits of the system is low. An example is found in the high biomass epifauna community developed in certain regions of the North Adriatic. This community, consisting of about 90% filter feeders (by biomass), is able to convert organic matter from the water column to benthic biomass with a high efficiency. Since its metabolism to unit body weight relationship is about 1/25 that of the water column organisms (including bacteria), it effectively damps input pulses that increase water column organic matter (OTT and FEDRA, 1977) (Fig. 17).

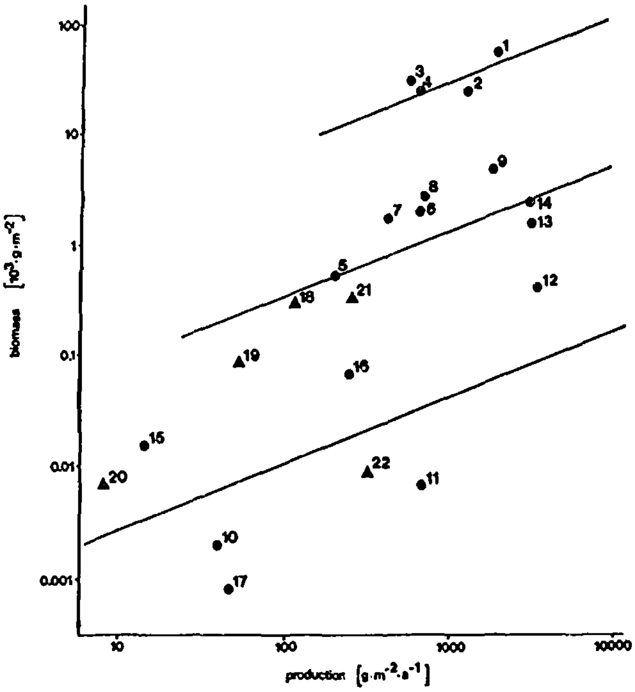

Fig. 16. Relationship between community biomass and an energy flow measure (net production producer dominated communities, respiration for consumer systems). Values for consumer systems (triangles) are per $10m^2$. Different levels of biomass are indicated by eye-fitted lines representing the energy flow dependency.

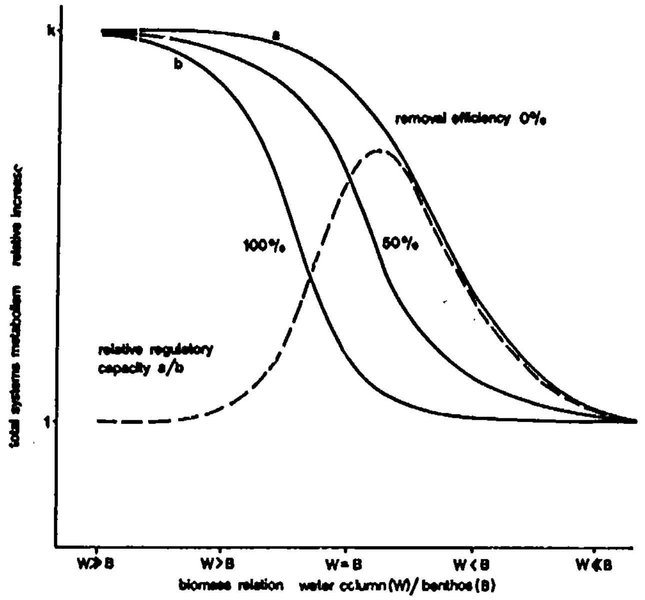

Fig. 17. Model of the regulatory properties of benthic macrofauna biomass on total system (benthic and pelagic) metabolism. The solid lines represent the increase in total system metabolism (e.g. respiration) after the pelagic component has been increased by a factor k over a variety of water column to benthic biomass relationships: (a) no removal of pelagic organic matter and incorporation by the benthos (b) the benthos crops pelagic organic matter down to its original density and all excess energy goes into benthic biomass increase. The regulative capacity (broken line, a:b) has a maximum at a certain biomass ratio depending on removal efficiency. From OTT and MAURER (1977).

Benthic primary production by macrophytes locally exceeds the production of the phytoplankton of the overlying water (MANN, 1972). However, very little of this high amount of organic matter produced enters the grazing food chain. Grazing in this context is defined as the consumption of living plant tissue that is active in the maintenance and propagation of the macrophyte stand or standing stock. For example, the animals feeding on those living parts of kelp thalli or sea grass leaves that have been detached by wave action are not considered grazers since that consumption does not influence plant growth).

Aquatic macrophytes either grow in places where the action of grazers is limited by other environmental factors (e.g., water movement in the case of kelp beds), or they are unpalatable or poisonous. Where the rate of nutrient regeneration within the system is critical (that is, when residence time of nutrients in the system is longer than turnover time of the plant for the respective nutrient) (Fig. 18), grazing plays a larger role and may even be enhanced (as it is in terrestrial grasslands). The loss of tissue to the grazers is proportionally paid back through the work done by grazers regulating the remineralization rates. Evolution of grazer defense mechanisms would in these cases disrupt the recycling processes and favor the replacement of the ecosystem by competing systems. In macrophyte stands a large proportion of the remineralization takes place outside the stand, and production is maintained by imports of nutrients from the water column. In this case a strategy of grazer defense is successful (Fig. 19). Benthic macrophytes can also supplement their nutrient requirements from the sediment depending on the nutrient availability in the interstitial water and their physiological capabilities to extract from this pool. Excess uptake of phosphorus and release of inorganic phosphate has been demonstrated for the sea grass <u>Zostera marina</u> (MACROY et al., 1972). The pattern of macrophyte production may be complicated by the translocation of storage products into special organs during times of highest carbon fixation. These storages may be used during times that are unfavorable to net carbon fixation (in winter at low light intensity and temperature) and thence be converted into photosynthetic biomass. By this mechanism, kelp and the sea grass <u>Posidonia oceanica</u> are able to incorporate N and P during the winter when phytoplankton and small annual epiphytes are limited by light and temperature (MANN, 1973). In <u>Posidonia</u> there is a net flow of carbohydrates into the rhizomes during spring to early summer, a time when the rhizomes and stems are packed with starch. During autumn and through winter, this flow is reversed to produce leaves until the storage is emptied by February (OTT, 1980). The pattern of leaf growth suggests that it is an adaptation to the overgrowth of older parts of the leaf surface by epiphytes. Both growth and production pattern have been fixed as a strategy in a circa-annual rhythm (OTT, 1979).

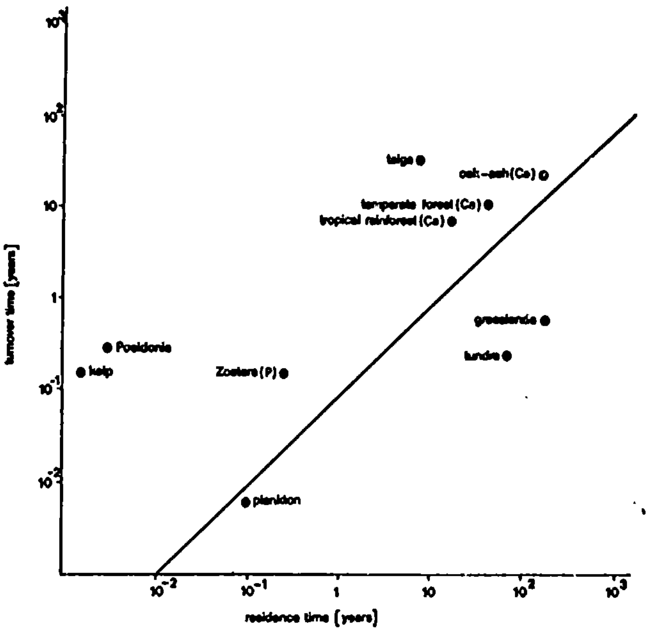

Fig. 18. Turnover time of the major primary producers versus residence time for mineral nutrients in various ecosystems. In the systems below the line, residence time of nutrients is more than 10 times the turnover time. In these systems high grazing rates are common.

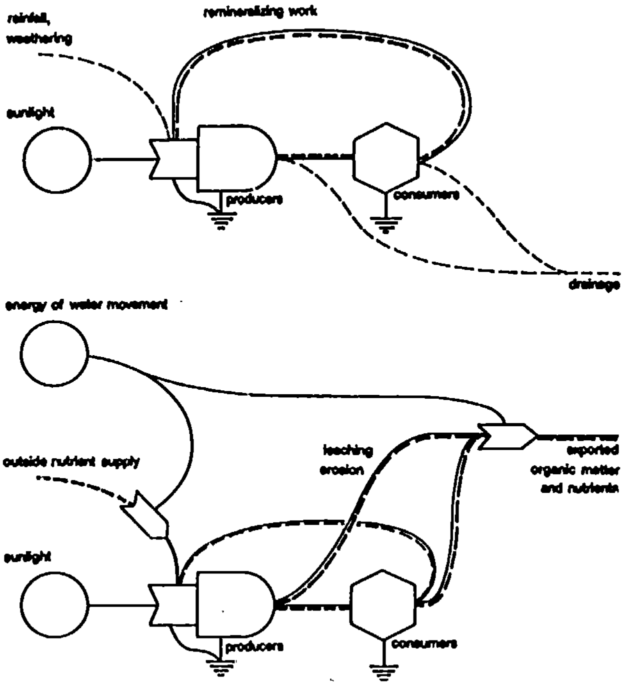

Fig. 19. Relative importance of remineralization within the ecosystem in a typical terrestrial system (upper graph) and an aquatic macrophyte system (lower graph). The terrestrial system remineralization in the system is the quantitatively more important process; the aquatic system however depends on large amounts of outside nutrient supply to compensate for losses through water transport. Modified from OTT and MAURER (1977).

Table II. Comparison between community biomass and an energy flow measure (production, respiration) for various terrestrial and aquatic communities.

	SYSTEM	BIOMASS(1)	PRODUCTION(2) RESPIRATION	SOURCE
1.	Tropical rain forest	45000-75000	1000-3500	
2.	Temperate forest	24000	600-2500	
3.	Boreal forest	20000-52000	200-1500	
4.	Mediterranean scrub	26000	250-1500	
5.	Tundra	100- 3000	200- 400	LEITH and
6.	Tropical grassland	1000- 5000	200-2000	WHITTAKER, 1975
7.	Temperate grassland	1000- 3000	100-1500	
8.	Cultivated annual crop	3500	100-4000	
9.	Marshes	2500-10000	800-4000	
10.	Oceanic plankton	1 - 5	20- 80	
11.	Neritic plankton	1 - 40	500- 900	
12.	Reefs, estuaries	40- 4000	2000-6000	
13.	<u>Posidonia oceanica</u>	1200- 1700	3200	OTT, 1980
14.	Seagrass (general)	800- 8000	1500-6000	
15.	Sublittoral sand	10- 30	10- 20	
16.	Intertidal sandflat	50- 80	210- 300	PAMATMAT, 1968
17.	Tropical benthic microflaur	0.3- 2	15- 160	BUNT et al., 1972a
18.	O-R-M community (macrofauna)	29.2	11.4	OTT and FEDRA, 1977
19.	Mudflat (macrofauna)	5- 15	2.1- 14	PAMATMAT, 1968
20.	Tropical sublittoral sand (macrofauna)	0.4-1.4	0.73-0.88	SMITH et al., 1972
21.	O-R-M community (total)	32	26	OTT and FEDRA, 1977
22.	Tropical sublittoral sand (total)	0.5-1.5	26.6-37.8	SMITH et al., 1972

(1) Biomass in g/m^2 (2) Net production in $g/m^2/a$ (1-17), respiration in mg $O_2/m^2/h$ (18-22).

Heterotrophic Processes

Introduction

The planktonic ecosystem will be mainly considered here, because it is much simpler to describe than the benthic one. In the latter, the presence of a substrate generates behavioral patterns which often overrule the elementary processes. Also because of the importance of settled organisms and of swimming planktonic larval components, any description must necessarily take into account the spatial structure of the benthic environment. Nevertheless, the following remarks can be applied to bottom fauna, because the elementary processes that control the terms of the energy balance have the same basis among all animals. In the planktonic field, a credible description can be rendered by assuming horizontal homogeneity. However, environmental variability cannot generally be ignored.

Secondary production is defined as the production of herbivores and tertiary production as the production of carnivores. Both are expressed in terms of an increase in biomass per unit time, where the biomass may be wet weight, dry weight, or carbon per unit volume. Whereas primary production is easy to measure, because the photosynthetic apparatus is a common characteristic of all plants, it is nearly impossible to delineate any measurable boundary between secondary, tertiary production or higher productions. This is because our concept of the food-chain is just an artifice that greatly simplifies the natural system, for which such boundaries are less distinct.

The relations between animals themselves, such as interactions between levels or competition, and those between animals and plants (or even detrital organics) constitute a complex network that must be translated into a simplified picture that can serve as the basis for a conceptual model of the system. The measuring of secondary production at sea is made difficult by our inability to separate the contribution of herbivores from that of heterotrophic organisms. A better approach to making this estimate might be to describe and to quantify the relationship between species or groups of species, to construct a model, and then to calculate the flow of matter going through the herbivore.

The Trophic Network

Herbivores. The flow of substances synthesized through photosynthesis is distributed among all plant species encountered at sea. However, herbivores are not strictly linked to living algal cells. It has been shown that they feed on suspended particles regardless of what they are, i.e., living organisms, flagellates, diatoms, etc., or remains of dead organisms. These animals are generally filter-feeders that generate water-currents to bring particles within the vicinity of their seizing organs or into their filtrating structures (nets, houses). They do not capture all the particles with the same efficiency, the differences being due either to the morphological characteristics of their seizing device, or to a deliberate selection controlled by the animal or by the particle's characteristics (e.g., motility). As a rough estimate, seizing efficiency can be considered as depending on the anatomical characteristics of the animal, but the deliberate choice operated by the animal or its filtration device must be taken into account as the second most important factor.

In the trophic network, the herbivores are related to all phytoplanktonic species and all kinds of particles, but the rate of food consumption will depend on two parameters: the maximum ingestion rate (specific to the animal) and the efficiency of capture (characteristic of both the animal and the particle involved).

Carnivores. In the trophic network, carnivores are found above the herbivores. They may be true carnivores or occasional ones, the latter being herbivores which seize animal prey when such an opportunity arises. This is also a definition of omnivores.

Considering what is known of the food habits of a group, it is possible to draw a graph with arrows connecting as many circles as groups considered in the ecosystem. It is at present impossible to draw a graph for all the species which have been identified at sea.

The study of gut contents does not often yield a solution to the problem, because the ingested organisms are digested at different speeds and some of them are impossible to identify. A better approach is to try to cluster species showing the same feeding behavior; this is quite convenient for some systematic groups (salps, siphonophores, chetognaths, ciliates), but it should be only a step towards a better representation of the trophic network. Each of these groups can then be represented by a 'mean organism' whose behavior and physiology is representative of the different species so associated.

When delineating and modelling the trophic network, it is important to bear in mind the relative role that a group or a species plays within the spatial and temporal context in which it is represented. The description of the network cannot practically extend to rare or occasional species; it seems obvious that there is little use in taking into account whales when representing the trophic network of a coastal bay. However, it may not be so with species which appear only during a few weeks in the year, but which are extremely abundant (medusae, pteropod molluscs, salps), or with organisms whose influence is intense, e.g., man through his various activities (fisheries, pollution, etc.). Indeed, these organisms can create impulses which may propagate throughout the trophic network.

Different Kinds of Heterotrophs

There are heterotrophs of all sizes. Among the smaller ones are bacteria that feed on the particulate organic matter or on dissolved organic matter resulting from the remains of dead organisms. The heterotrophs have two actions: they consume living or dead matter (complex organic molecules), and they regenerate nutrients, both of which increase their biomass. Usually they give back to the environment mineral elements (nutrients, CO_2): a process which is referred to as regeneration. Nevertheless, when the ratio of essential elements (N,P,C) is not correct in the organic matter, they can assimilate inorganic nutrients. This observation shows that it is necessary to consider elemental ratios in models. These processes are found among all heterotrophs in variable degrees. The smallest heterotrophs, bacteria, regenerate more matter than they use for their own growth. Of the matter consumed by a heterotroph, the proportion which is kept for growth and the amount regenerated depends on certain environmental controls (temperature, etc.).

Bacteria. Bacteria have a systematic diversity. Depending on what group they belong to, they have a primary metabolic activity (nitrate reduction, nitrification, methane production, etc.). A good proportion of species can adapt their activity to the most abundant substrate. The different kinds are:

a. those that break large organic molecules into smaller ones, keeping in the process the nutrients which they need for their growth (N,P,C, etc.); and if the organic matter does not have enough nitrogen in it, they can absorb ammonia from the environment;

b. those that use the smallest organic molecules and decay them while regenerating nutrients such as NH_4 and PO_4; and

c. those capable of oxidizing nitrogen (nitrifying bacteria); they use ammonia as an electron acceptor, and compared to the first two kinds they grow very slowly.

The bacteria which decay and mineralize the organic matter predominate in zones of intense biological activity (euphotic zone).

Nannoplankton. These species are generally ignored in conceptual models of the ecosystem, although these organisms are able to absorb organic compounds (dissolved organic matter). Some of them have no chloroplasts and can be considered as true heterotrophs. Others are occasional heterotrophs, utilizing these compounds when light energy is weak, or when the organic matter concentration is high.

Ciliates. These small organisms (5 to 40 μm) multiply very quickly. They are extremely motile and they can capture the particles which are the most adapted to the characteristics of their filtering cilia network. They compete with other microfilter-feeders, such as benthic organisms' larvae and salps. They develop when the nannoplankton, inefficiently captured by the copepods, grow up. They are efficiently captured by the copepods and in the process they realize a conversion of small particles to large ones.

Crustacea. Since they dominate phytoplankton dynamics, crustacea are usually taken as representative of heterotrophs. The most abundant are copepods. Some of them are real carnivores and their appendages can only seize large prey. The remainder are omnivorous and capture any kind of particle, dead or alive.

Tunicates. Tunicates include two important groups:

a. Appendicularians are organisms which build a house and can capture particles in a restricted size range. Their growth-rate is rather high compared to that of other animals. They have been taken into account very rarely in modelled ecosystems.

b. Thaliacea (salps and pyrosomes) are filter-feeders that are scarce during most of the year, but which may become very numerous at times. They tend to be discarded in ecosystem models because of their low abundance. Nevertheless, they are important in several respects. They are large organisms able to capture particles down to 2 μm in diameter with a mucous net. They produce dense fecal pellets that settle down rapidly creating an important vertical flux of organics. These animals can take a large part in the depletion of the total amount of mineral elements (N,P,C) in the euphotic layer. They can migrate vertically over long distances. Pyrosomes may be very numerous in limited layers of oligotrophic seas (e.g., in the Guinea Dome).

Carnivores (sensu stricto). Here can be put animals which exclusively feed on other animals. Some are capable of strong activity like chaetognaths, others keep generally still and capture prey by means of extendable appendages: tentacles, fishing filaments. These latter ones (medusae, siphonophores, ctenarians) are generally omitted as heterotrophs in ecosystem models, but their activity must be taken into account at certain times of the year. Depending on the abundance of prey, they can ingest up to 1000 percent of their body weight per day.

The above list is not exhaustive. Aside from the copepods it is absolutely necessary to consider the large heterotrophs that can have a considerable action. The development and feeding patterns of carnivores can damp or amplify the fluctuations induced in the primary level.

The Different Processes in the Heterotrophic Part of the Ecosystem

Anabolism. This covers the different processes by which the organisms can gain energy. Depending on the organisms concerned, this 'feeding process' will vary greatly.

a. Assimilation of dissolved components: This is the flow of the organic substances that go through the cell membranes. The assimilation rate of these molecules can be described with the same formulation as the assimilation rate of nutrients by the phytoplankton. Bacteria utilize organic compounds in such a way. A flow of regenerated matter is associated with the assimilation flow. Because of their speed of assimilation and their capability of acting through exo-enzymes, bacteria are often neglected. Instead, their regeneration effect alone is represented (flow of regenerated matter, proportional to the mass of dissolved substances). We must remember here that nannoplankton can assimilate organic molecules. However, at this time it is difficult to quantify their action.

b. Particle capture: We would call particles all the objects having a discrete shape, whether dead or alive. They range from one micron (bacteria) to several meters (siphonophores, salps-chains). Of course any given organism cannot capture all the particles in such a large range of size. Herbivores can capture the small particles, detritus, dead organic particles, living cells of the phyto- or nannoplankton. The larger particles, usually animals, are seized by carnivores. One can distinguish between organisms which seize one particle after the other (generally carnivores dealing with large-sized prey) from organisms that capture several particles together (generally herbivores and omnivores). Water currents are generated around them, and particles are swept clear by their filtering devices. Some algal particles are as large as animals (large diatoms as Rhizosolenia, and small animals like copepod nauplii and ciliates).

Herbivores, omnivores, and carnivores are arbitrary groups, and they are only loosely correlated with the kind of particles they ingest. The use of these categories in a model gives a first, but rough, approximation of the real structure of the food web. Each animal feeds on a size range: herbivores mostly on the small sizes, omnivores on the medium ones, and carnivores on the large ones.

A first approximate to represent the variation of the ingestion rate (R) versus the food concentration is to use an hyperbolic function analogous to the Michaelis-Menten equation:

$$R = \frac{R_{max} \cdot Food}{K + Food} \qquad (1)$$

where K is a half saturation constant. This function reaches a maximum when the concentration of food is very high (infinity). This kind of curve takes into account the fact that the animals' guts have a limited volume and that the mass of digestive enzymes is limited also. However adaptation must be taken into account: organisms living within a rich nutritional environment increase the mass of their digestive enzymes and their assimilation rate increases (the coefficient R_{max} increases). Other mathematical expressions might be used to represent this phenomenon.

When representing the various dimensional categories of particles, one should keep in mind that they are not captured with the same efficiency. The small ones are generally not so efficiently collected as the large ones. There is also a maximum beyond which overly large particles cannot be collected or ingested. The animals filter or sweep clear a volume of water, V, during a unit of time. From this volume the animal captures particles of different sizes with different efficiencies. Particles of diameter d(i) are collected with efficiency E(i) which can vary between 0 and 1. If E(i) is 1, and the measured ingestion rate is R(i) for these particles, then:

$$Ri = V \cdot Food(i), \qquad (2)$$

where Food(i) is the concentration of particles of size d(i). If the efficiency of particle i is different from 1, that is, there is some escape to the filtration apparatus of the organism, then the ingestion rate of these particles is:

$$R(i) = V \cdot E(i) \cdot Food(i) \ . \qquad (3)$$

The total ingestion rate for all kinds of particles is:

$$R = \sum_i R(i) = \sum_i V\ E(i)\ Food(i) \ . \qquad (4)$$

This quantity is to be compared to the volume of the gut, and the quantity of food that can be digested per unit time. The curve of efficiency of capture can be considered approximately as an asymmetrical bell-shaped curve.

When the animal seizes one prey at a time, its behavior and that of its prey become important. Chaetognaths, which are typical wait-hunting carnivores, are thought to detect their prey by means of the vibrations they emit. Siphonophores are much more passive: like medusae and ctenophores, they have filaments which, when expanded, act as a net in which prey are caught. The added effect of behavior can be introduced approximately in the capture efficiency coefficient relating the prey to the predator.

Another factor to keep in view when dealing with carnivores is a certain discontinuity in their nutrition. A gut repletion keeps the carnivore still during digestion. These feeding lags will only be important for the community as a whole if the organisms are synchronized. This could be stimulated by the light cycle, generating the vertical migration of some species.

Growth. With regard to smaller organisms, bacteria, ciliates, heterotrophic nannoplankton, one may consider that growth is a continuous process, similar to that of phytoplankton. This is based on the fact that asexual vegetative reproduction is the main rule for the population's growth.

For larger organisms, and particularly crustacea, the apparent developmental phases cannot generally be neglected. In many crustacea, the generation time is larger than the computation step of the models. Thus it must be considered that at certain times larvae will dominate, whereas at other times, the adults will dominate. Here again, this phenomenon can eventually be neglected if the population structure is constant, that is, if the percentage of young and adults is constant in time, so that a mean organism can be considered. However, it must be remembered that certain external stimuli can affect specifically certain stages of development. Another fact to keep in mind is that the young stages of numerous species do not migrate, whereas their adult stages do.

Catabolism. This comprises all the processes that develop as an energy loss for the organisms.

a. Excretion causes a flow of mineral substances (NH_4, PO_4) out of planktonic organisms. Ammonia represents 80% of the total nitrogen flow, the rest being composed of organic molecules that go back to the pool of dissolved organic matter (urea, amines, amino-acids). The excretion rate has been shown to be roughly proportional to the animal's weight which means that usually the molecules necessary to the metabolism of organisms are renewed at a constant rate. However, when food is abundant, the excretion rate of the animal is notably increased, but these conditions rarely occur at sea. The excretion of nitrogenous substances is generally linked with that of phosphorus products. The numerical ratio of the ammonia flow to the phosphate flow approximates 9. When the animal is starved, or when it hibernates in deep waters, its rate of nitrogen excretion decreases. Nevertheless, it never reaches zero, and after a period of starvation, the animal dies from having destroyed too much of its proteins. The excretion rate is connected with the respiration rate, which itself depends on the amount of stored products in the animal's body.

b. Respiration reflects the energy flow needed by the animal for its maintenance, and its growth, or its reproduction. It corresponds to the transformation of long staying energetic resources, such as lipids, into short-cycled energetic products like ATP. Krebs' cycle, which is responsible for oxygen consumption and CO_2 production, is constituted by an enzymatic chain whose activity depends on the amount of enzymes that can be utilized (the amount which can be modified by acclimatation), on the amount of carbohydrate and lipid substrate which can be utilized, and on temperature. The flow of carbon eliminated by respiration, measured by the associated oxygen flux (atoms), is generally 17 times as large as the flow of nitrogen eliminated by liquid excretion. However, when the animal has a lipid storage (e.g., in high latitude copepods, at certain times of the year), the O/N ratio reaches notably higher values.

Losses of matter other than those due to catabolism. Another category of negative processes in the energy budget of an animal corresponds to specific events. These are losses due to molting in crustacea; or related to nutrition when the animal builds a filtration apparatus, such as the house built by Appendicularians (this 'logette' is a mucous bubble produced by the animal who then gets into it and its openings are fitted with calibrated filters). The animal gets rid of the logette when disturbed or when the filters are clogged, and in either case, it immediately builds another one. At the present time, it is difficult to estimate this type of loss when formulating the dynamics of a zooplankton population as a whole. It could be included somehow into coefficients relative to growth efficiency.

Reproduction. This is certainly the most difficult process to represent in a model of an ecosystem. At present, zooplankton, and even heterotrophs as a whole, are thought to have an exponential growth, similar to phytoplankton. This hypothesis is relatively correct when dealing with a large water mass, when the zooplankton community is dominated by a given category of organisms (e.g., copepods), when presumably the environment varies slowly and without any important perturbations, and/or when the time scale is large. These conditions are not always fulfilled.

It is useful to consider that the development of copepods can proceed by cohorts. At certain times, the population is comprised of young stages only, consuming little phytoplankton, and unable to capture large particles. At some subsequent time, it is dominated by adults that are able to feed on large particles. This development-related phenomenon changes the total mass of zooplankton and also its functional characteristics. These biological processes must be retained, since they are responsible for delayed response. For instance, the growth of the whole population will depend on the food mass captured at a time which is linked with the generation-time.

In some species, whose longevity is large relative to the immature period, the different broods mix together and the population tends to a stable age distribution. In this case, it is possible to consider that the whole population is represented by a mean organism with mean characteristics.

Other species have very efficient reproduction patterns (vegetative reproduction, protection of larvae) which allow them to multiply very rapidly, so that they may dominate the dynamics of heterotrophs for short periods ranging from weeks to months. Salps have a vegetative multiplication, an oozoid being able to produce hundreds of blastozoids, with a similar nutrition type, by budding and without any important mortality. They are able to sweep out a phytoplankton bloom in a few weeks. Pelagic molluscs like Cavolinia and Creseis lay their eggs in a gangue, which protects the development of the embryos. This peculiarity allows the species to appear very suddenly in large numbers.

Unicellular organisms, such as ciliates, reproduce essentially by binary division; their development can thus be represented by a continuous exponential function similar to phytoplanktonic growth. It is not always possible to introduce this level of structure in a model, but it is advisable to do so for the most important elements when possible.

The reproductive rate (number of eggs or young larvae produced per female in unit time) depends critically on the amount of food and on the temperature. Planktonic animals such as copepods react very rapidly to variations in the amount of food by increasing or decreasing their breeding rate. Egg laying can thus be considered roughly as a continuous phenomenon in a constant or slow varying environment.

Relations between weight and metabolism. Quite a lot of the published research shows a link between the metabolic flows (excretion rate, respiration rate, and so on) and the size or weight of the organisms. Also, it has been demonstrated that the mean growth rate of an organism (expressed as its doubling-time) shows a good correlation with weight.

As a general rule, these metabolic flows are related to weight by the relation

$$F = aW^b \tag{5}$$

where F = rate/animal/time, and where the animal's weight (W) is given in the same mass units. The coefficient a expresses the flow intensity, whereas b shows its divergence from plain proportionality. A value for b of 0.75 is generally to represent respiration. There is no universal value for b to represent doubling-time, or growth, since in this application b must be specified for each environmental situation. In some cases there is an important variation on both sides of this relation, expressing the fact that the flows also depend on other factors (temperature, food). The flow of food-intake is one of those that does not follow this relation, because it depends too much on the amount of food available. However, this relation would be true for the maximum food intake, which is a characteristic of the animal. Small organisms always have higher weight-specific rates than large ones.

Action of the Physical Environmental Parameters on the Metabolic Flows

Temperature. Temperature is one of the most efficient parameters for the control of positive and negative terms of the budget. In some species, this parameter is quite important, while others are less sensitive to it (eurytherm species). At the scale of a population, it can be said that the best adapted species to environmental temperature will develop the best. Besides that first approximation, one should be conscious that the disappearance of a species due to high temperature can change the other gross characteristics of the population.

The relation between temperature and a given flow can be expressed by an approximate of Arrhenius' law:

$$Q_{10} = \left(\frac{K_2}{K_1}\right)^{10(T_2-T_1)} \tag{6}$$

where K_2 is the rate at temperature T_2 and K_1 is the rate at T_1, which translates the response of a physiological function to temperature. The factor Q_{10} is relatively high for respiration, whereas it is lower for excretion. This function has no maximum and is thus only valid in a restricted temperature range. When expressing extreme inhibition at temperatures, a different relation should be used, which expresses the fact that above a given temperature, a temperature increment accelerates the degradation of enzymes. Other, and more sophisticated, formulations exist, in which optimal, lethal, etc., temperatures clearly appear.

Light. Light may induce a periodicity in the activity of the zooplankton. Such a rhythm can appear in nutrition. In some planktonic organisms this nutritional rhythm is associated with a motion rhythm: the vertical migrations of copepods, euphausids, salps. It seems that the displacement which brings organisms from a poor feeding zone (where they stay during the day) into a richer one (by night) induces an acceleration of the nutritional rhythm, so that the ingestion rate is increased when the population first arrives in the richer zone.

Spatial heterogeneity. The importance of plankton swimming in the sea has been shown. It causes an heterogeneity in the distribution of algal and zooplanktonic biomasses, at the scale of some hundred meters. It is important to consider that the partition of food in smaller aggregates (some centimeters), as 'planktonic snow' in oligotrophic seas, can be an important parameter to consider when interpreting divergencies between a model and the observations.

MODELLING OF MARINE ECOSYSTEMS

Introduction to Modelling

Introduction

We are all 'modellers' in the sense that we are all constantly abstracting and simplifying the total world that our senses and their various technological extensions (telescopes, microscopes, elemental analyzers, etc.) have brought into our awareness. Models are tools for dealing with complexity - nothing more or less. For those of us attempting to understand and, perhaps, manage marine ecosystems, they are often useful and sometimes absolutely necessary.

The models used may take a variety of forms, including empirical relationships observed in the field, highly controlled single-variable laboratory experiments, flow diagrams, 'budgets' of energy or matter, mathematical equations, electrical analogs, computer algorithms for simulation, and micro or mesocosms. This workshop is devoted to the development of numerical simulation models, particularly those which are mechanistic and deterministic in approach. Such models will include a number of empirical relationships observed in the field as well as the results of many laboratory rate measurements. They will also involve the development of system flow diagrams, equations for describing those diagrams, and the design of an algorithm for solving those equations on a digital computer.

This approach to modelling is reductionist in the sense that it is largely dependent on information that has come from studying parts of nature more or less in isolation - for example, zooplankton excretion rates measured in the laboratory. But it is also an attempt to provide a conceptual and mathematical synthesis of a large amount of information that has been collected in this way - to see if some of the emergent properties of the whole system, for example the annual nutrient cycles, can be simulated by summing our best information on the behavior of the various parts of that system. This approach has been common in marine ecology, though other paths have been, and continue to be, pursued. The historical development of mechanistic ecosystem models given below is taken from a detailed description of the development of one such model by KREMER and NIXON (1978). A great variety of general ecological modelling approaches has been included in a recent book edited by HALL and DAY (1977), and a comparison of reductionist and holistic numerical models has just been published by UNESCO (PLATT et al., 1981).

The Evolution of Ecosystem Models[1]

The utility of numerical models in the study of marine ecosystems has been recognized for at least 35 years. In one of the earliest attempts to formulate aspects of the biological dynamics of the sea in mathematical terms, FLEMING (1939) examined seasonal changes in phytoplankton population levels in the English Channel using a simple differential equation:

$$\frac{dP}{dt} = P[a - (b + ct)]. \qquad (1)$$

Thus the rate of change with time of the phytoplankton population depended upon the biomass (P), a constant division rate (a), and a grazing rate composed of an initial value (b) and an arbitrary rate of increase (ct).

Except for the additional term, 'c,' Fleming's description was essentially identical to the basic exponential growth formulation given earlier by LOTKA (1925), VOLTERRA (1926), and others, for the change in a single population (N) as a function of a constant birth and death rate,

$$\frac{dN}{dt} = N(b - d). \qquad (2)$$

Fleming's treatment was modified somewhat by RILEY and BUMPUS (1946), who applied it to an analysis of phytoplankton growth on Georges Bank. As a logical improvement, they introduced another term, a_1, which represented the rate of change in phytoplankton division rate:

$$\frac{dP}{dt} = P[a + a_1 t - b(b + ct)]. \qquad (3)$$

In subsequent papers, RILEY (1946, 1947b) expanded the basic equation to include a number of mechanistic processes thought to be important in regulating phytoplanton populations on Georges Bank and in New England coastal waters. He obtained impressive agreement between calculated and observed populations using the formulation:

$$\frac{dP}{dt} = P[(p \cdot \bar{I})(1-N)(1-V) - R_0 e^{rt} - gZ]. \qquad (4)$$

The net rate (in brackets) includes a growth estimate balanced against losses due to respiration as an exponential function of temperature, as well as to zooplankton grazing. The growth estimate, in turn, includes a maximum as a linear function of the average light throughout the euphotic zone, which is reduced by two factors representing nutrient depletion of phosphorus and vertical turbulence.

As part of his study of plankton dynamics on Georges Bank, RILEY (1947b) also presented a preliminary formulation in this same manner for herbivorous zooplankton:

$$\frac{dH}{dt} = H(A - R - C - D). \qquad (5)$$

Here, too, increased biological detail was included, projecting the change in herbivores per unit biomass as the sum of a constant assimilation balanced against temperature-dependent

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[1] The remainder of the text of this lecture is from KREMER and NIXON (1978) Chapt. 1 with permission of the authors and Springer-Verlag.

respiration, carnivorous predation by chaetognaths, and a statistically estimated additional natural mortality. It should be pointed out that Riley projected the population changes using a mathematically exact method for successive two-week time intervals, rather than by the approximation methods used with many present digital computer models.

It was not until two years later that RILEY et al. (1949) coupled the mechanistic phytoplankton and zooplankton equations together in a feedback system that was used to calculate the steady-state phytoplankton population levels for various areas of the Western North Atlantic. While such a synthesis was conceptually straightforward, it represented an impressive mathematical and computational achievement in the days before high-speed digital computers. Nevertheless, the lack of time-varying solutions to the coupled equations severely limited their application in marine ecology for more than ten years after the initial advances of Riley and his coworkers. The full development of dynamic, mechanistic feedback models in ecology did not really begin until the application of analog and digital computers in the 1960s (WIEGERT, 1975). Throughout the 1950s, the few attempts to pursue this type of model reverted to more detailed analyses of primary production (RYTHER and YENTSCH, 1957; STEELE, 1958b; CUSHING, 1959) or grazing (CUSHING, 1968; HARRIS, 1968).

It is of historical interest that another group of marine ecologists working primarily in fisheries management joined with theoretical population ecologists from many backgrounds in using the much simpler Lotka-Volterra equations to study predator-prey-interactions.

$$\begin{aligned} \frac{dN_1}{dt} &= N_1(b_1 - d_1N_2) \qquad \text{prey} \\ \frac{dN_2}{dt} &= N_2(b_2N_1 - d_2) \qquad \text{predator.} \end{aligned} \tag{6}$$

Even in coupled form, it was possible to obtain dynamic solutions to the population growth equations by hand calculations, if the coefficients remained simple.

Thus, before the analog and digital computers became widely available, there was a tradeoff in ecological modelling. If one wanted to explore the behavior of one or two populations over time, then it was necessary to use simple equations with very general coefficients. However, if one wanted to use a model to do work in ecosystem analysis, it was critical to have coefficients with significant biological meaning and detail. Yet without the computer, such detailed equations could only be solved for steady-state conditions under various sets of assumptions. These different goals, methods of approach, and constraints produced a divergence between ecologists interested in ecosystem analysis and those interested in population dynamics. The increasing use of computers may eventually bring the two groups together, since the development of numerical techniques has made it possible to have an almost unlimited amount of mechanistic detail with time-varying solutions. For example, one of the active areas of investigation in fisheries modelling is the introduction of time-delay terms in population growth to more accurately describe recruitment (MARCHESSAULT, 1974). While this addition introduces nowhere near the complexity that has increasingly characterized models of lower trophic levels, it is following the same trend.

With the increasing availability of analog and digital computers in the 1960s, the removal of the steady-state contrating in mechanistic models stimulated renewed interest in their potential application to a great variety of ecological problems. As mentioned earlier, essentially all of these models are extensions of the historical trend toward increasing mechanistic detail. Of course, each particular model has its own variations. The literature on this subject is growing rapidly, and has been repeatedly discussed elsewhere. Historical reviews of mechanistic ecological models have been prepared by RILEY (1963), PATTEN (1968), MARGALEF (1973), STEELE (1974), WIEGERT (1975), and others. An introduction to the principles of ecological modelling with examples of various types of models is available in a series of volumes edited by PATTEN (1971-1975) and in a general text edited by HALL and DAY (1977). The proceedings of several recent conferences have emphasized the use of models in understanding estuarine (CRONIN, 1975) and marine (NIHOUL, 1975) ecosystems, as well as the role of models in ecosystem analysis and prediction (LEVIN, 1975). In the marine environment, most ecological models have been developed for pelagic systems such as the North Sea (STEELE, 1958b), the Continental Shelf off Florida (O'BRIEN and WROBLEWSKI, 1972), and upwelling regions (WALSH and DUGDALE, 1971; WALSH, 1975), though models have also been derived for kelp beds (NORTH, 1967), salt marshes (POMEROY et al., 1972; NIXON and OVIATT, 1973), and seagrass beds (SHORT, 1979). A recent volume of The Sea has been devoted to discussions of the numerical modelling of physical, geological, chemical and biological processes in estuarine and open ocean waters (GOLDBERG et al., 1977).

The Modelling Process

A mechanistic numerical model begins with observations of the 'real world.' From these observations emerge tentative answers to questions about the system which may be appropriate to a modelling analysis. What is our concept of the system? What are its physical and temporal boundaries? What are the major compartments in it and how do they vary in space and time? What flows of matter, energy, or information connect these compartments? What are the important forcing functions or inputs to and outputs from the system? What time scales are involved in the major processes of interest?

Over 20 years of laboratory and field work have made Narragansett Bay one of the most intensively studied and well-known marine ecosystems. As a result, we were able to draw on the data and experience of many scientists with specialized knowledge of various aspects of the system. A number of additional studies were carried out directly as part of the modelling effort, including a year-long sampling program of phytoplankton, zooplankton and nutrients at 13 stations around the bay. These data were collected specifically for use in verifying the model. The internal formulations of the model were based on general ecological and physiological principles combined with separate historical data and independent laboratory measurements.

Various techniques were used to organize this information, including verbal summaries, tables, graphs, budgets, and flow diagrams. The resulting conceptual model was much simpler than nature and yet far too complicated to simulate. For example, even a moderately detailed energy-flow diagram for Narragansett Bay on a summer day (see Fig. 23 in the next lecture) contains detail that would make a mechanistic model extremely cumbersome if all compartments were simulated. The decision of how much detail to include in a model is always extremely difficult. A model by definition is a simplification, and much of its utility is due to the fact that it lacks the bewildering complexity of the 'real world.' Yet there must also be sufficient detail to give the model credibility, to make it useful as a tool in synthesizing a variety of measurements, and to provide the parameters for a revealing sensitivity analysis of the system.

Conceptual Modelling

Introduction

Generally, the development of anything without some preconceived conceptual framework results in a disorganized and inefficient construction. To have a conceptual framework is almost equivalent to having a conceptual model. Often without recognizing it, we almost always have a conceptual model in our minds for anything we consciously do. This is true of driving, crossing the street, or anything else.

The main objective of a conceptual model is to demonstrate connections, causalities, feedback pathways, all between parts and components of the system of interest. This should be done in such a way that the final result is a help, not a hinderance, to understanding the functioning of the system. Every model is a drastic simplification of nature, and this is true even of the most comprehensive conceptual models. On the other hand, trying to present details of a particular model might result in a conceptual model which is too complicated and therefore missing its main characteristic, i.e., a clear picture of the real world.

The process of constructing a conceptual model is usually, by itself, a great educational exercise leading to a better understanding of the details and complex nature of a particular system. Besides, such a process results in a better understanding and an increased tolerance among specialists from different fields, as well as more appreciation for others' problems. It gives them the feeling that they belong to the same team, not the opposing one, as is often the case. Every conceptual model is in a way a mirror image of the group of people that constructed it.

Even when the conceptual model is the final step in the modelling process, it can have most beneficial results in identifying the specific points of an ecosystem where the most pronounced lack of knowledge and data base exist, but which are of extreme importance for understanding a particular ecosystem. This might lead to setting up laboratory and field work programs which in turn might yield important time, effort and financial savings.

Procedure

In order to prepare a conceptual model, it is necessary to follow some general scheme such as is presented in Fig. 20. In addition, it should be constantly kept in mind that numerical modelling is a highly iterative process, which means that the conceptual model should be changed according to the iterative cycle of the modelling procedure (Fig. 21).

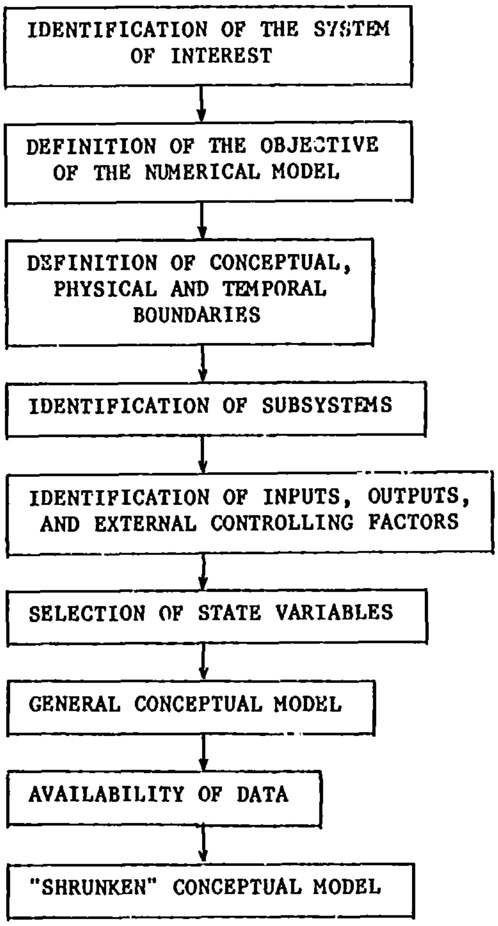


Fig. 20. General scheme for preparing a conceptual model.

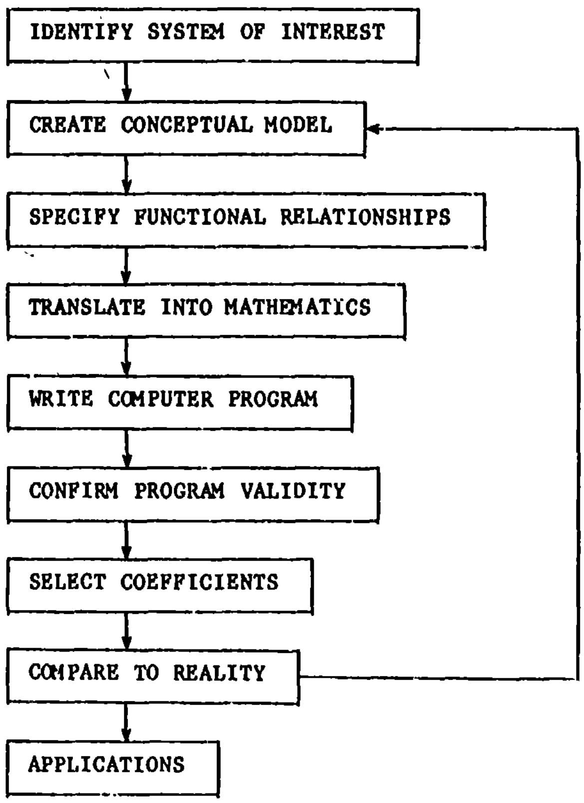


Fig. 21. Iterative processes involved in updating a conceptual model.

In the following text each of the suggested steps in the procedure of preparing a conceptual model will be discussed.

Identification of the system of interest. As the first step in the modelling procedure, a system of interest should be identified. The identification of the system will depend on many factors including scientific, social, political, financial, and other factors. In this step a system should be identified in a general way such as a trophic web of a certain area, or eutrophication of a region or mercury cycle in a particular location, etc. Detailed conceptual, physical, and temporal boundaries will be defined in the third step.

Definition of the objective of the numerical model. It is very important to define, as precisely as possible, the objective of the numerical model. It takes considerable experience and knowledge to set realistic objectives which are within reach of a group responsible for the numerical model. It is necessary to take into account: a) know-how of the modelling group; b) data availability; c) data relevance; d) competence and willingness of specialized experts to devote a part of their time and their intellectual capabilities to modelling efforts; e) availability of adequate computing facilities; and f) financial support. Only when all the components mentioned are well balanced, metals and the nutrients (N, P, Si) are generally more abundant than the same components in might it be possible to set a realistic objective which is small enough to be within reach and big enough to be worth losing time, mind, etc., for achieving it. Very often objectives are rather loose, and precise definition of the objective is pushed aside, eventually resulting in spending much money and effort with very little gain. An overambitious objective might be good for raising funds in the short run, but in the long run causes a loss of confidence in the modelling.

Definition of conceptual, physical, and temporal boundaries. Boundaries of the system which was identified in the first step in a general way should be determined in this step. Conceptual boundaries of the system are very important, and they will determine what is in the system and what is out of the system. Even the most comprehensive conceptual model, which would be impossible to handle even at the conceptual level, is still a simplification of nature. But in order to make a model a tool toward and not against reaching the objective, it is necessary to keep it at the level of manageable complexity. But, on the other hand, at least at the conceptual level, we can afford to include in the system some components which will be later excluded in the stage of mathematical formulation of the model.

Marine ecosystems are connected to the 'rest of the world' through three boundaries: the sea/air, the sea/land, and the sea/sediment boundary. Connection at these boundaries does not occur at a very precise place; it is rather a connecting zone which is called an interface.

Sea/air interface. In a broad sense this interface covers the zone where an intensive exchange of matter and energy, with pronounced changes of concentration between the sea and atmosphere, occurs. The size of the zone depends very strongly on meteorological conditions. In a stricter sense this transition zone is extremely reduced, less than a millimeter in thickness, and constitutes a microenvironment characterized by an accumulation of organic matter. It has only recently been recognized that atmospheric inputs to the ocean are in many cases comparable to those due to rivers. This interface is notable for both the input and the output of the matter. The surface microlayer of the sea plays a dominant role in the exchange rate of solid, liquid, and gaseous matter between the atmosphere and the sea.

Sea/land interface. This boundary consists essentially of estuarine areas. Most of the natural and man-made inputs to the sea pass through this boundary. This zone is of critical concern because of its nutritive resources. The estuarine environment, transition zones of highly variable dimensions, is the principal region of land/sea exchanges. They are zones of sharp chemical gradients, since it is here that seawater mixes with river water whose salt content, and often pH, is much lower. However, river water components, such as transition seawater. These materials are not always completely assimilated by organisms. The alteration of this organic matter represents an important source of chemical energy. Together with the availability of mechanical (winds and tide) and thermal energy, which are important at relatively shallow depths, the chemical energy can induce a large number of physico-chemical reactions. These may be homogeneous reactions, but the local abundance of sediment, tied to the presence of turbidity maxima and the closeness of the continental sources, favors reactions of the mixed type (solid-liquid). The most common phenomena affecting concentrations and speciation of major oligo-elements upon their contact with seawater include: adsorption and desorption, aggregation and precipitation, and the biological effects of metabolic assimilation and detritus formation. These same phenomena occur in the open ocean but are magnified in the estuarine environment. The continental margins, where great quantities of matter of continental origin accumulate, act as a buffer between the rivers and the ocean. The dimensions of this interface zone will vary from place to place, but examples may be cited of tidal estuaries, river deltas, shallow semi-closed seas, sea beds to whole shelf areas, depending on the nature of the events being considered and the scale of the ensuing impact.

Sea/sediment interface. This interface refers principally to the surface layer of the sediment, comprising about ten centimeters, where major transformations of organic matter, on the way to complete mineralization, take place. The time scales of the phenomena occurring at this interface are much shorter than those normally of interest to sedimentary geology. Like the sea/land interface, this interface occurs in an extremely critical zone in which gradients lead to intense exchanges between the solid and liquid media. Besides such exchanges there exist volcanic and hydrothermal inputs for which a good understanding of mechanisms and rates is necessary if we are to better evaluate marine mineral resources. It is also important to firmly understand the geochemistry of this environment because it is a potential site for the storage of industrial wastes. Budgets should be considered, since there exist both inputs and outputs of material.

The chemistry of this interface may be ascribed to a system of complex interactions between solid, dissolved, and living material. It is this living component which represents the most important energy source, and its dominant influence on the balance of sediment-water exchanges has been established for many constituents. Here, once again, the rates and flux directions are still not known with certainty. It is certain that phenomena such as bioturbation must be further studied since it appears that the continuous reworking of the top few centimeters of the sediment intensifies the exchange between interstitial and overlying waters beyond that which can occur through simple diffusion processes.

Taking into account what was written about interfaces, it is obvious that precise physical boundaries of the system cannot be determined, but they should be determined as close as possible. In addition, temporal boundaries have to be defined in order to know the period which is going to be covered in the modelling process.

Other Considerations

Identification of subsystems. Whenever possible it might be practical to identify subsystems within the system. Any larger part of the system which might be identified with logical conceptual boundaries should be identified as a subsystem. This approach is helpful for understanding the complexity of ecological systems; and at the stage of numerical modelling, it might be useful to have subprograms that correspond to subsystems. Any subsystem should actually gather a group of relevant parameters called state variables, with common characteristics representing a well-defined part of an ecosystem. Choice of subsystems will depend on the objectives, complexity of the model and the availability of data.

Determination of inputs, outputs, and external controlling factors. In order to follow the changes of mass or energy within the model it is necessary to know as precisely as possible the inputs and outputs of mass and energy through all the interfaces. Transfer of matter through any of the interfaces described is basically bidirectional, but flow rates in and out, which is commonly called the flux, are usually not the same. Such disproportion, comparing fluxes in and out, is very pronounced in the case of sea/land interface, where the amount of matter passing through the interface from sea to land is negligible in comparison with the amount of matter passing from the land to the sea.

External controlling factors such as light and temperature, winds, tides and currents, and others have to be determined in order to identify forcing functions which influence the dynamics of the system.

Selection of state variables. This is a crucial step in the modelling process. This is a step when the whole system is actually taken apart and then assembled back leaving out parts of secondary importance. It is probably easy to imagine what such a process would look like with an automobile.

There is no prescribed way for choosing most characteristic properties of a system. One extreme for the choice of state variables would be to use every chemical and biological species as a state variable. This would result in a model of absolutely unmanageable size, even for the smallest systems. Therefore, groups of organisms have to be combined into one state variable. The same applies to groups of chemical species and sometimes even whole classes of chemical compounds and organisms. Obviously, such a procedure is subject to a strong personal bias.

The number of state variables has to be kept at the manageable minimum. For instance, the model of KREMER and NIXON (1978), one of the best models produced so far, includes six state variables. Another detailed model (REDFORD and JOINT, 1980) includes eighteen state variables. Complexity of the model and choice of state variables should be in the closest connection with the availability of relevant data. Each state variable should be defined very precisely, showing not only what is included but also what is omitted.

Availability of data. When a general conceptual model has been prepared, it is necessary to screen the available data base very closely in order to be able to omit state variables which cannot be modelled because of the lack of relevant data. Also, grouping of some state variables into larger groups could be done at this stage for the same reason. In such a way a 'shrunken' conceptual model, suitable for the process of numerical modelling, will be produced.

General conceptual model. When the state variables are chosen, they should be presented in a form which would show all connections among them, as well as feedback loops and other details. For such presentation there are several approaches. This can be done with a different degree of accuracy depending on the problem and on the purpose of the conceptual model. One of the very popular ways of presenting conceptual models in ecology is ODUM's energy circuit language (ODUM, 1972). It is a sophisticated sign language using various symbols with which the flow of energy through an ecosystem is followed. Two examples are given in Figs. (22) and (23). This language is very constructive, but it tends to give too complicated a picture for very detailed models. A much more simple way of presenting a conceptual model is a simple box diagram showing only state variables and connections among them.

In the case of a large number of state variables it might be more practical to use binary connectivity matrix which will show only connections between each pair of any number of state variables and indicating with "1" or "0" signs existence or absence of the connection (Fig. 24).

Another way of presenting connections are Forrester's feedback dynamics diagrams which will show for each state variable connections to all other state variables (Fig. 25).

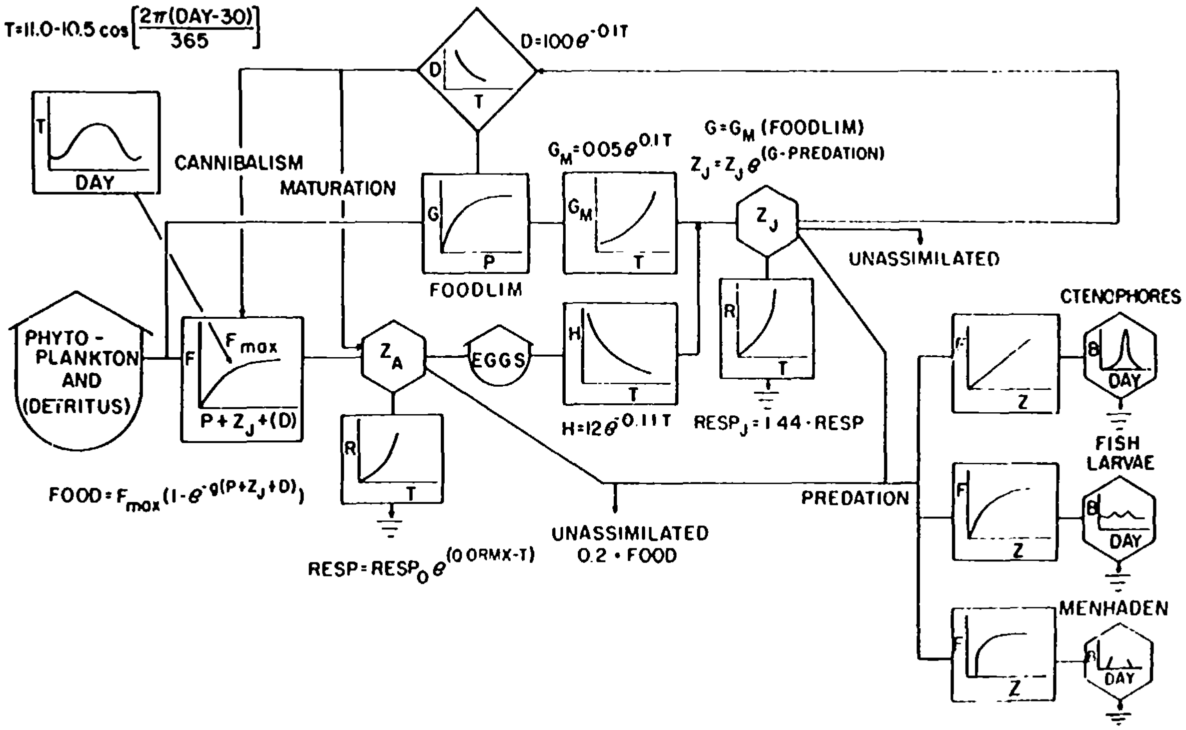


Fig. 22. A complex, but still greatly simplified energy flow diagram for the Narragansett Bay ecosystem on a summer day. This conceptual model was a first step in the process of abstraction that led to development of the numerical model. Symbols follow ODUM (1972) and have been used to synthesize past and on-going bay studies by a large number of people. From KREMER and NIXON (1978) with permission of Springer-Verlag.

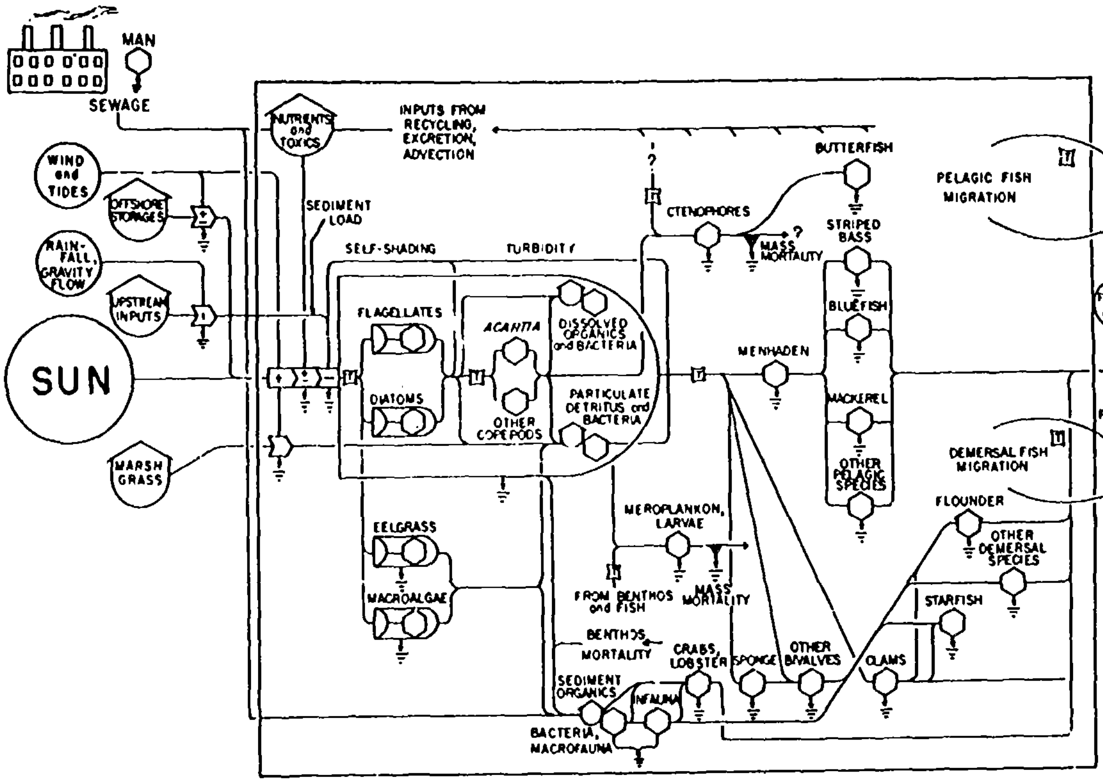
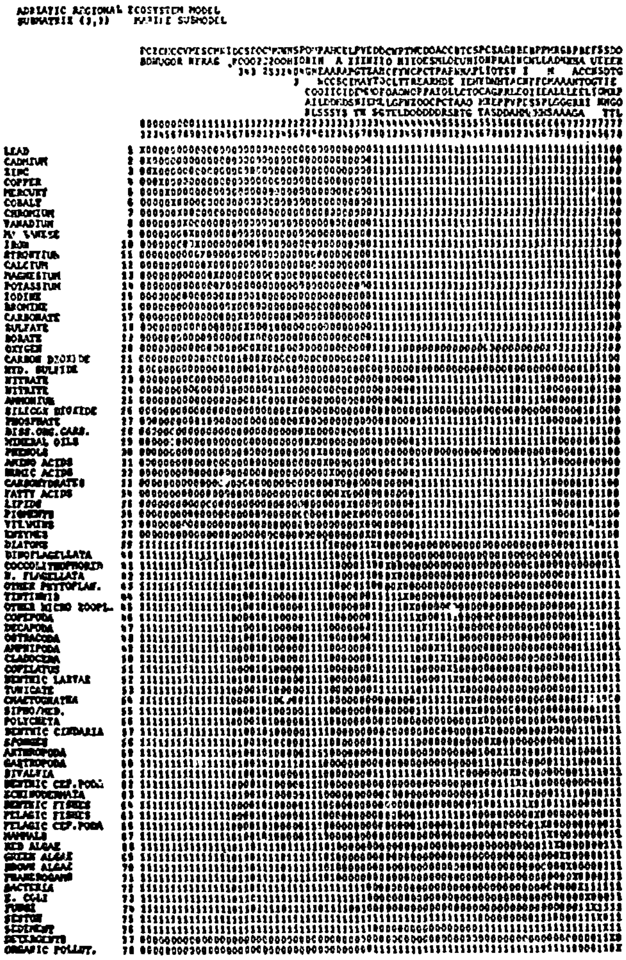


Fig. 23. Flow diagram for the zooplankton compartment showing relationships among the major equations described in text and a graphical representation of their behavior. From KREMER and NIXON (1978), with permission of Springer-Verlag.



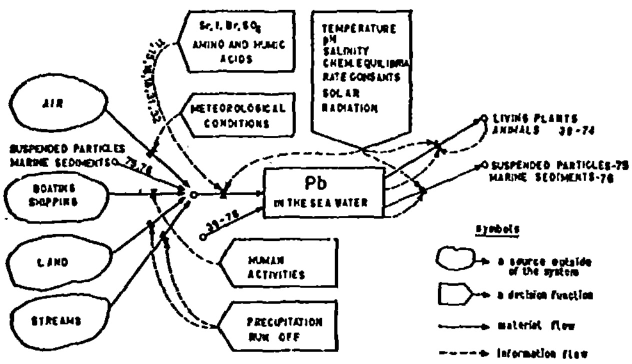


Fig. 25. Forrester diagram representing the inflow and outflow of Pb in sea water. From LEGOVIC, KUZMIC, JEFTIC, and PATTEN (1977), with permission of Thalassia Jugoslavia.

Fig. 24. Binary connectivity matrix of the marine submodel of the Adriatic Regional Ecosystem Model. The direction of the mass transfer is from the variable in the corresponding row to the variable in the corresponding column. From KUZMIC, JEFTIC, and POLICASTRO (1977), with permission of Thalassia Jugoslavia.

Problem Definition

The following lecture complements the previous one on conceptual modelling. Much of its content comes from UNESCO (1977a), which was considered again relevant to this workshop. Practical application of forming a conceptual model and defining a problem occurred in the model working sessions (see section on Modelling the Gulf of Naples).

Selection of a System

The improper delineation of the system can easily be the first pitfall in modelling methodology. Traditional research along purely biological, chemical, physical, or geological lines is inadequate in the sense that nature does not necessarily observe these subdivisions. Many such models of strictly biological or other processes have their intrinsic value from a scientific point of view, but often are not directly applicable to natural systems modelling because the subject process is not sufficiently separable. For example, in the modelling of primary production both the biological process of photosynthesis and the physical process of light transmission are relevant.

In applied problems there is also a chance of difficulty when the modelling goals are set by other than scientific criteria. For example, an environmental agency may want a model of a certain coastline that is either a geographic or political entity, but lacks continuity in a natural sense. Breaks between systems are best made where the coupling is the weakest. The criteria for weak coupling may be functional, spatial, or temporal. As a simple example, consider an automobile system. An analysis of the electrical subsystem as opposed to the braking subsystem would be a functional distinction; that of the right rear lamp versus the left rear lamp would be a spatial distinction; and that of wheel-hub lubrication (to be done every 50,000 km) as opposed to front-end lubrication (to be done every 5,000 km) would be a temporal distinction. This approach would contrast to other possible types of analysis which might consider all gaskets, all copper parts, and so forth, as separate subsystems.

Functional distinctions are made on the basis of activity within the system, for example, that between organic and inorganic suspended matter, that between planktonic producers and consumers, or that between surface heating and surface evaporation. Functional separation becomes extremely important in process modelling, where the cause and effect relationships of small functional components of a system are studied. The results of process modelling are general and hence applicable to other systems.

Spatial distinctions are perhaps the most obvious. Other distinctions are more complicated such as the photic depth, the spatial extent of which is not fixed but depends on the independent parameters of incident radiation and transmissivity of the water.

The difference in the time scales of natural processes also results in weak coupling permitting subdivision. Processes or components changing slowly with time can be considered independent of time with respect to those changing rapidly. Some examples of contrasting time scales are: a) phytoplankton biomass turns over within days, while some consumers require months; b) sea-level changes resulting from local wind set-up last from hours to days, while those from steric effects are more of a seasonal phenomenon; and c) planktonic eutrophication occurs within days, while benthic modification takes place on the order of years in the environs of a sewage outfall.

For problems concerning distributions of mass, we are primarily interested in length scales, i.e., those associated with the distribution. For patchy distributions we have short length scales, and vice versa. Each mass component has a 'reactive time' scale indicated by its half life in the system. The biological or chemical processes affecting the in situ mass determine its reactive time scale.

In the marine environment each mass distribution is set in a dispersive medium (see Lecture on Physical Processes). A comparison of the dispersive and reactive time scales indicates which physical (dispersive) processes are relevant; and a comparison of the reactive time scale and the dispersive velocity indicates which length scales are relevant.

When a system involves the dispersive effects on a mass component, then a careful inventory must be made of the reactive time scales and the relevant physical processes. Table III illustrates this point.

Connecting Conditions

Any selected system is always related to its environment, since there are no isolated or independent systems in nature. Among the criteria used for the selection of a system was that it be extracted from its environment at places of weak coupling. In doing so its connections are minimized in strength and/or number. Therefore, the connecting conditions specify how one system is related to another.

When the connection is from the modelled system to the external environment, it is referred to as the output. This is simply the consequence or solution of the modelled system. When the connection is from the external environment to the modelled system, it is referred to as the input or boundary condition. Usually the input is thought of as a forcing function, or an active connection driving the system from outside and often varying in space or time, as for example, the amount of solar radiation reaching the sea surface. The boundary conditions are often reserved to express the passive connections, as the reflectability of the light reaching the bottom. The special case for the condition at the beginning of modelled time is called the initial condition, as the temperature

Table III

The spatial and temporal scales characteristic of physical transport processes.

Time Scale	Survival water property in ecosystem	Horizontal Length Scale	Vertical Length Scale	Transport Processes
hours		1 cm	1 cm	diffusion small scale advection
	short			
			1 m	
days		10 m		coastal summer upwelling coastal winter convection
	meso		10 m	summer offshore frontal upwelling
		50 km		winter offshore convection
				meso-scale advection (local coastal flows) (summer offshore gyres)
weeks			100 m	(winter offshore gyres)
	long			
years		5,000 km	2,000 m	water mass exchange between basins

of the water when the model began. These distinctions are mostly a matter of usage and need not be discussed in detail here, the point being that these are the connections specified at the dimensional periphery of the system. Finally, two subsystems may be connected through an interaction connection. Interactions are considered internal, even though in some cases they may relate the output with the input.

The sensitivity of a system to its external connections varies. Fortunately we need only to concern ourselves with the stronger points of coupling, depending on the degree of accuracy we want in the output. For example, if we were modelling the salt content of the Eastern Mediterranean, the major connections are laterally through the straits of Sicily and vertically through the sea surface. Other connections through the Dardanelles, the Suez, the Adriatic and Egyptian runoffs are minor, and still others might be considered negligible. The output of the system may or may not be sensitive to its boundary conditions. For example, the production of a phytoplankton bloom is not so sensitive to the original population of phytoplankton, but it can be sensitive to the original population of zooplankton. The amount of dissolved O_2 in the surface water is much more sensitive to the atmospheric concentration of O_2 than to that of CO_2.

When the modelled problem is structured in space, or time, then certain information must be specified at these spatial or temporal boundaries, called boundary or initial conditions, respectively. As mentioned, we try to pose our problem such that the solution is insensitive to these conditions by defining them at points of weak coupling. However, this is often not possible; for example, in space we may be forced to draw boundaries that overlap other active domains, or in time there may not be a zero initial condition. There are several approaches to this problem, the most common being to extend the domain in a coarse dependency to a much larger domain (often referred to as grid nesting) such that the immediate boundary (initial) conditions can be generated.

The system is also sensitive to the type of interaction connections it may have internally. Three types of interactions are shown in Fig. (26): part a) shows a simple series connection of phytoplankton and zooplankton; b) a simple parallel connection between the phytoplankton species; and c) a nonlinear connection between the process of photosynthesis and that of light absorption. Thus the success of our model will depend strongly on an understanding and correct assessment of how our system is connected externally to its environment and how it is connected internally between component subsystems.

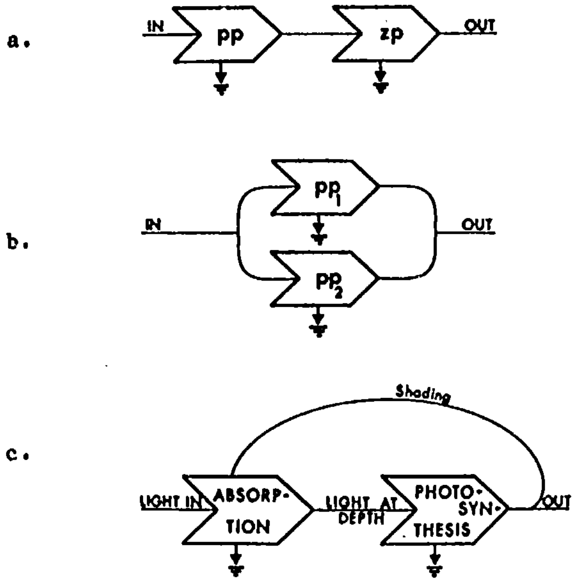


Fig. 26. Types of interaction conditions: a) series interaction, b) parallel interaction, c) non-linear interaction. From UNESCO (1977a).

Internal Dynamics

If we pose our problem as a case of a simple situation of

input —> transfer functions —> output

then we must work the problem in the reverse way in which nature does. For any desired output (e.g., distribution of mass after a certain time) we must select the relevant inputs and accurately represent the transfer function.

The inputs are chosen normally on the basis of scientific intuition or experience. Their relevance can be judged on the basis of scaling.

The first step in selecting the appropriate dynamics is to identify the relevant processes affecting individual components. This should be done using arguments similar to those of Table III for physical processes, and some corresponding scale guideline for biological processes.

The second step is to correctly formulate the processes (next lecture refers). This formulation, of course, relies on previous scientific knowledge. In a qualitative way the internal dynamics filter the input. For example, the input function has a frequency dependence, the transfer function another frequency dependence, and consequently the output has its own frequency dependence determined uniquely by those of the input and transfer. By evaluating these dependencies, certain simplifications in input and transfer functions are possible.

Formulation of Processes

Philosophy

As was emphasized in earlier lectures, models represent our perceptions of reality, including certain information at various levels of resolution. Some aspects are included only in a general way, others in a rather detailed way, and some may even be ignored as irrelevant and outside the scope of interest. This perspective is critical to the process of formulation in modelling, because the choices are never absolute. Rather, the choices depend on which aspects of the natural system are being considered. Within any arbitrary system of interest, the maze of detail must be organized into parts which we hope to understand in detail and 'black boxes' which we define as beyond (above or below) our level of interest (Fig. 27). The way we choose to describe the control mechanisms and processes within the system must necessarily gloss over many underlying processes. This may be perceived both as a strength and a weakness. It is clearly valuable to make simplifying generalizations and to test their adequacy in explaining natural processes. Yet, on the other hand, there will always be limitations in such a model, as some responses in nature may depend on processes not included in the model.

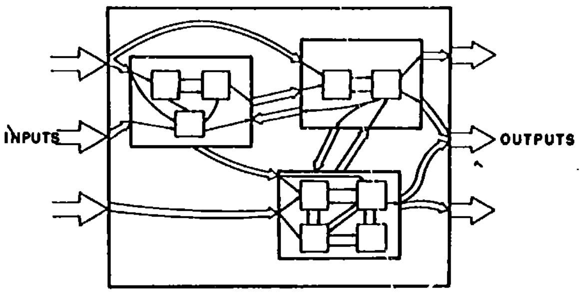


Fig. 27. Structural detail versus 'Black Boxes.' In any conceptual model, certain aspects of a system's structure or function may be arbitrarily considered beyond our level of interest. These processes may be modelled as forcing functions or as 'black boxes.' From ODUM (1972), with permission of Academic Press.

In this context, the similarity of modelling to traditional experimentation may be emphasized in research (Fig. 28). In a way quite analogous to the role of hypothesis and experiment, some models are complex sets of hypotheses, whose consistency with reality may be evaluated in the early stages of modelling. In particular, the formulation into mathematical form of ecological rates and mechanisms are the hypotheses. As with experimental science, the process must include many iterations, successively refining and evaluating the hypothesized relations.

Importantly, the analogy between modelling and experimentation is also strong in that 'good agreement' with observations cannot prove the hypotheses correct. This point of view is critical throughout the modelling process. During formulation, the expressions chosen to describe certain aspects of ecosystem function may appear to be crude approximations of the known complexity of nature. This is often the most difficult hurdle towards appreciating the usefulness of a model to those unfamiliar with the methods. But these apparently simplistic formulations are neither 'right.' nor 'wrong.' If used correctly, they are chosen because they express some aspects considered to be important or interesting for the present application. Whether the model agrees or disagrees with observations, useful information may be gained.

Finally, after extensive evaluation of a model, it may appear sufficiently predictive to be of use in management (Fig. 28). Even then (or perhaps especially then), the hypothetical nature of the formulations must continually be recalled. The possibility always exists that something in the natural system may change sufficiently that the adequacy of the assumption decreases. In such a case, the model (or rather modelling) can continue to be an important tool in management if such changes are, in turn, included and evaluated in the next iteration process.

Before focusing on the various approaches to formulation of processes, a brief mention of statistical modelling is in order. Many methods exist for establishing whether relationships exist among variables of interest in ecological systems. As early as 1946, Riley demonstrated that multiple linear regression could provide a good prediction of phytoplankton stocks off Georges Bank (RILEY, 1947). Recently, statistical methods of increased sophistication have been used to recognize patterns in varied and complex sets of data. In some cases, correlations discovered by statistical means may be useful predictive tools, yet it must be emphasized that the correlations need not be based on any direct causal relationship. For this reason, predictions based on such patterns are probably even more susceptible than mechanistic models to errors when some feature of the system changes.

The Spectrum of Formulation Strategies

Formulation is the step in the modelling process whereby hypotheses about the important patterns, controls, and rates included in the conceptual model are expressed in a mathematical form.

Depending on the available data, the goals, and the personal inclination of the individuals involved, various strategies may be used to derive the equations (Fig. 29a). While our main emphasis here will be on mechanistic formulations, it is important to recognize that other strategies exist that are equally valid, and even perferable in given situations. These methods span a continuum, and combinations of the examples presented here can well be used even in one model.

At one extreme of the formulation spectrum are the holistic methods (Fig. 29a). Based upon some assumptions about how the compartments interact at the ecosystem level, equations are chosen to interrelate the state variables of the model. Field data from the specific system are then used to select the values for coefficients. The important difference between this approach and the purely statistical descriptions is that the form of the equations is chosen a priori, based on ecological hypotheses.

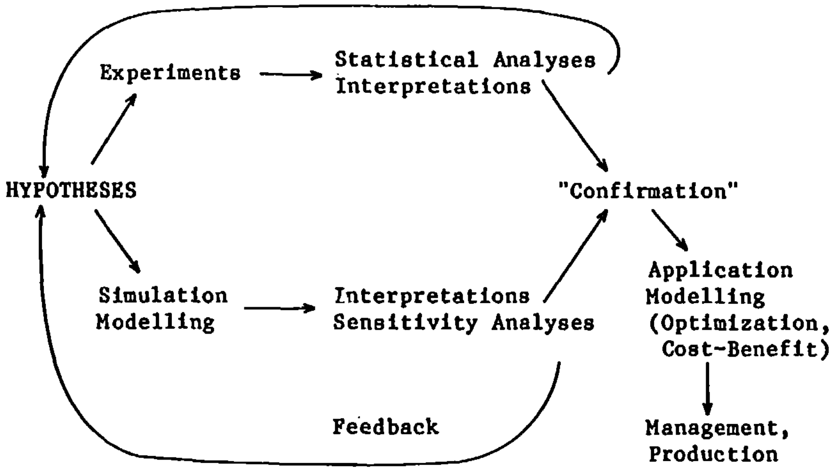
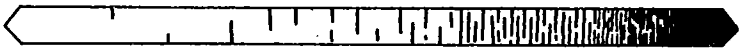


Fig. 28. The role of models in research. Modelling may be seen as analogous to traditional experimental science, with the predictions of the model testing the adequecy of the mathematical formulations (hypothesis) in explaining observations.

a. A SPECTRUM OF FORMULATION STRATEGIES

Holistic		Reductionist
Often Simple		Complex
Linear		Nonlinear
Empirical		Theoretical
No Mechanisms		Component Mechanisms
Formulation:	System Data	Component Data
Testing:	System Data	System Data
Inexpensive		Costly

b. EXAMPLES OF FORMULATION STRATEGIES



Donor Controlled	Phenomenological	Physiological Mechanistic
Linear	Nonlinear	Highly Nonlinear
Advocate:	Advocate:	Advocates:
Bernard C. Patten	Howard T. Odum	Very numerous

Fig. 29. Various strategies of formulation, whereby the conceptual model is stated formally as mathematical equations, are proposed to fall along a continuum from holistic to reductionist (a). Examples of three strategies along this continuum are presented in detail (b).

At the other end of the spectrum (Fig. 29a) are the highly reductionist formulations. Here the equations are chosen to represent presumed mechanisms, often at the physiological level. Functional responses of organisms to many different stimuli may be formulated as a complex set of equations. The coefficients for the equations are based on lab or controlled field experimental data, and may be drawn by necessity from literature on the same species, or even different species, from different regions. The assumption being tested in such a model is essentially how well are these mechanistic data able to explain the emergent properties of this ecosystem.

Examples of three formulation strategies (Fig. 29b) are discussed briefly below. Notice especially the different extent to which mechanisms underlying the responses of the ecosystem are included. Secondly, notice the different requirements for data: holistic models are formulated and evaluated by data at the system level, while mechanistic formulations use physiological data but are combined in the complete model to simulate system level responses.

Donor-controlled formulations. Patten has argued that natural ecosystems are best modelled by simple linear equations. The fluxes between compartments depend only on one variable. While the flux could technically depend on either of the compartments, more often the 'upstream' one is assumed to be driving the flow. Such formulations are called Donor-controlled (Fig. 30). Thus, the consumption of plants (P) by herbivores (H) would be a simple constant fraction (k) of the plants,

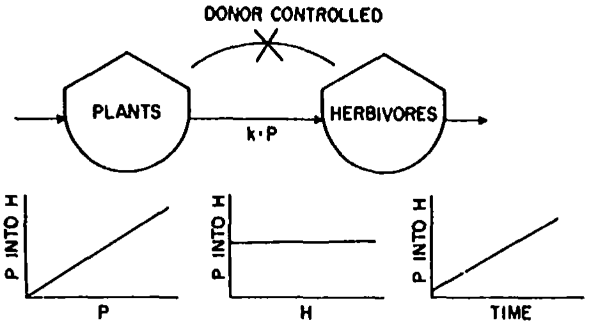


Fig. 30. Donor-controlled formulations assume that all fluxes are linearly dependent on a single compartment.

$$J_{p->H} = k \cdot P \; . \qquad (1)$$

Patten has presented formal arguments that such equations are reasonable ecologically, for example, since ecosystems exist near equilibrium where responses are linear (PATTEN 1975, 1979). Many biologists feel that even if these formulations have some basis, they seriously oversimplify the interactions that are personally of great interest. Yet the advantages in modelling are significant. Because of their simplicity, the number of state variables that can be included in a model is very large, and the mathematics for solving systems of linear equations is well defined.

Phenomenological formulations. This strategy of formulation is based on a basic law that relates the magnitude of any flux (J) to its driving force (X), i.e.,

J is proportional to X, or
$J = k \cdot X$

where k is the proportionality constant. This law can be used to describe all kinds of fluxes, whether physical, chemical, or ecological, if the true driving force X is understood. The difficulty in using this with ecological fluxes is to identify the force correctly. ODUM (1972) has presented a theoretical derivation concluding that ecological forces are proportional to concentrations and standing stocks of the interacting compartments. For example, the plant-herbivore interaction is expressed as a product of the two compartments (Fig. 31),

$$J_{p->H} = k \cdot P \cdot H \; . \qquad (2)$$

An important feature of this multiplicative interaction is that no flow occurs when either P or H is zero, which is ecologically sensible. Secondly, the response of the system is nonlinear. For example, herbivores are capable of exponential growth given sufficient plant food.

This strategy is readily expanded to include increased complexity. Thus sunlight (S) and nutrients (N) may be related to plant growth (J),

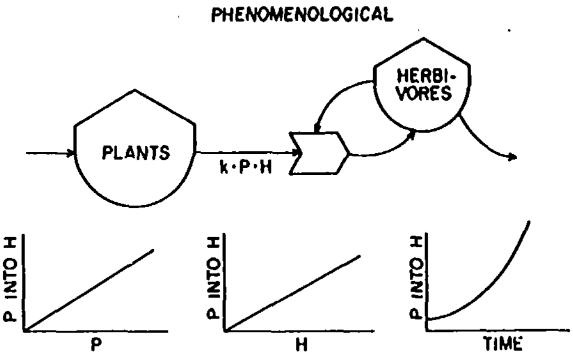


Fig. 31. Phenomenological Formulations express interactions that may take various linear or non-linear forms, based on asumptions about the forces driving each flux.

$$J = k \cdot S \cdot N \cdot P \; . \qquad (3)$$

In this case, the constant k is a composite of three interaction coefficients.

This approach is deceptively simple, and it is important to recognize the ecological basis in theory, and that these are not simply crude, convenient approximations. Odum argues that these formulations, when properly used to interconnect the important functional aspects of ecosystems, will model even very complex responses of systems. As with all models, the extent to which detail is omitted will limit the complexity of the responses. But the ease with which this strategy defines appropriate equations for very simple conceptual models and very complex ones is an important benefit.

A further advantage is that this strategy of formulation follows directly and explicitly from Odum's symbolic language, the Energy Circuit Language (ODUM, 1972). Once the conceptual model is diagrammed correctly using the various symbols, the appropriate mathematical equations are easily specified. The power that this provides in formulating even very complex systems is very great (see BAYLEY and ODUM, 1976). Often, the symbols of the circuit language are used loosely, and only in the diagramming step, so that many are unaware of their mathematical implications.

Mechanistic formulations. The two previously described strategies of formulation are based ultimately upon a holistic view of the ecosystem. The formulations are derived 'from the top down.' In mechanistic models, the formulations are derived 'from the bottom up' in that they are based on controlled experiments that define specific functional responses, often under laboratory conditions. For example, rather than specifying the flux of plants into herbivores based on the observed changes in those two compartments in the natural system (as is done in the holistic methods), the ingestion, assimilation, and respiration rates could be measured in the laboratory as a function of certain variables believed to control these fluxes. The result would be a series of experiments that would be used to specify, for example: a. ingestion rate as a function of available plant food and temperature, b. assimilation efficiency as a function of ingestion rate and feeding history, and c. respiration rate as a function of body size and temperature. These functional relationships are 'mechanistic' in the sense that they specify underlying processes that may contribute to the ultimate net fluxes observed in the field.

This is fundamentally a 'reductionist' approach. In fact, models of this type are clearly testing the extent to which our knowledge of these presumed mechanisms is capable of explaining changes we observe in the ecosystem. Here, again, the basic hypothetical nature of the modelling process is apparent. Of course, ingestion rate (continuing the above example) really varies in response to many more factors than we postulate. For example, food type, size, age, water turbulence (for plankton), light level, and many other variables might have to be included for a complete understanding of the control of herbivore ingestion rate. By omitting some, we are stating a hypothesis that food availability and temperature are the most important, and we proceed with the model to test this assumption.

Numerous examples exist to demonstrate this approach to the formulation step in modelling (see KREMER and NIXON, 1978 for one example and a review of others). It is the method most consistent with the great body of reductionist data on factors affecting marine organisms. And thus it is the method most often employed by many biologists not specifically trained as systems ecologists. Yet it is important to see this strategy as belonging to the spectrum that also contains the holistic methods. Examples can be readily found that fall between these extremes. Complex conceptual models using the Energy Circuit Language have been formulated into equations where some of the coefficients of interaction are replaced by functions of specified form (e.g., MITSCH, 1976). Thus, instead of the straightforward multiplicative equation (3), we might specify

$$J = k \cdot f(S) \cdot f(N) \cdot P \qquad (4)$$

where the functions f(S) and f(N) are defined empirically or a priori.

It might be more precise to refer to this strategy as 'pseudo-mechanistic,' since the form of the functional relationships proposed as 'mechanisms' are often based primarily on observations. In a few cases, formulations may be well founded on some principle or 'law' so that the expected form is fixed. Thus the effect of temperature on physiological rates is usually modelled as an exponential function based on the thermodynamic Arrhenius equation, even when the data are fit just as well by a straight line. But more often, the formulations are mechanistic only in the sense that they express observations at a lower level of organization than is being simulated, as is discussed below.

Coefficient Selection

Once the form of the equations has been chosen, using one or a combination of the strategies mentioned above, the coefficients must be selected. This is done based on data, and involves a statistical fitting of the data to the equation to achieve a satisfactory fit. Thus, if a straight line were assumed to express the rate of some process (J) depending on the value of some variable (X), a linear regression technique (Least Squares, or Functional Regression, see RICKER 1973, 1975) would determine the best choice of the slope and intercept,

$$J = mX + b \; . \qquad (5)$$

In some cases, especially using the mechanistic strategy, even the form of the equation may be based on observations, rather than on some a priori hypothesis about a mechanism. In this case, the formulation is simply a statistical model but at a lower level of organization (i.e., a statistical model of a process is used as a mechanistic part at the ecosystem level).

An important difference exists between the mechanistic formulations and the more holistic strategies in the area of coefficient selection. Mechanistic equations require laboratory data or carefully controlled field data to determine coefficients for the processes. Thus the coefficients for equations in Fig. (32) would be based on data relating herbivore ingestion to food availability, respiration rates as a function of body size, temperature, etc. These data might all be from lab experiments. Yet the final simulation results would be compared to descriptive data at the ecosystem level, i.e., seasonal abundances of plants, herbivores, nutrients, etc. Thus, with mechanistic models, the data required to build the model is very different from that used to evaluate the model.

With the phenomenological or linear formulations, the same type of system-level data is used to select the coefficients and to evaluate the simulation. It is therefore extremely important that independent data sets be used in the two phases of model development. This is

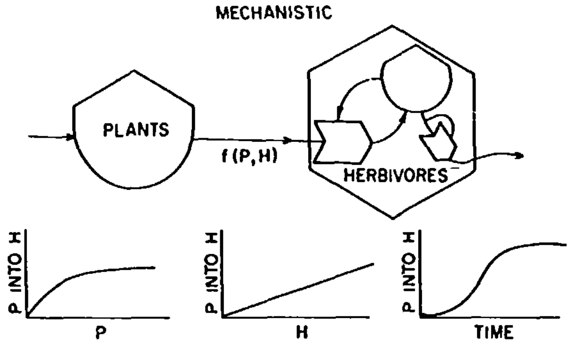


Fig. 32. Mechanistic Formulations express functional relationships between fluxes and the variables assumed to be important in determining the fluxes, based on controlled observations in the laboratory or in the field.

often a problem since complete sets of descriptive data are not easy to obtain, and, for example, only one year of adequate data may be available. Then the data must be used in parts to avoid the tautology of testing the model against the data used to develop it. For example, coefficients might be selected based on only a few months of data, while the rest of the data is kept for evaluating the results.

Contributing Errors in Formulation

Biologists, probably because of their general training in the reductionist approach, tend to emphasize the importance of increased complexity in understanding ecosystems. Aside from the question of whether this or a more holistic approach is more preferable philosophically, there is a methodological constraint on how much detail to include in numerical models. Two forms of error may contribute to general inadequacy of a model (O'NEILL, 1971; O'NEILL and RUST, 1979). Formulation error is introduced because the conceptual model, as formulated, is a poor analog of the real system. For example, if a formulation of herbivore grazing includes food availability and temperature but neglects feeding history of the organism, it may never provide satisfactory agreement with observations. Secondly, error is introduced when we attempt to select coefficients, each of which have measurement error and thus uncertainty associated with them. O'Neill has graphically demonstrated that formulation error is greatest with very simple conceptual models, whereas measurement error compounds itself as model complexity increases (Fig. 33). Theoretically, at least, some optimum exists where combined error is minimized, and there are suggestions about how to consolidate conceptual detail toward this goal (O'NEILL and RUST, 1979). For our purposes, the main point is that it is not always necessary or desirable to include more and more detail, even though available information suggests that factors may have some effect. Rather, the modeller should attempt to distill the complexity down to include only the factors most important in understanding the processes.

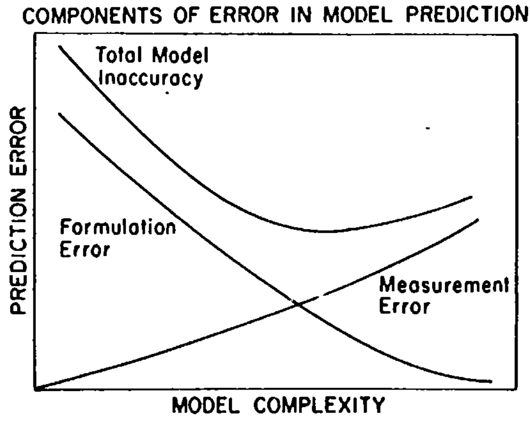


Fig. 33. Two components of error contribute to the inaccuracy of a model. One is due to formulations that inadequately represent the 'real system.' Another is due to errors inherent in measuring coefficients, and thus is increasingly important in complex, detailed models.

Verification, Calibration, Sensitivity Analysis and Validation

Introduction

During the last decade, the field of ecological modelling has, to a certain extent, developed towards application of more well balanced complexities of models. It has been realized that the complexity of the model should be selected in accordance with the objectives of the model, the characteristics of the ecosystem and the data available, and in most cases the data will limit the applicable complexity of the model (see also JEFFERS, 1978). During the coming years, we will get faster and faster computers which will make it possible to make simulations with more complicated models, but the calibration and validation of the models will require data, which in quantity (and partly in quality) are proportional to the squared complexity of the model. A comprehensive data collection is expensive, and in many ecological model studies the cost of data collection amounts to 80-90% of the total cost, making the use of complex models prohibitive. Validation must be distinguished from verification. The usage of the words is not consistent; however, verification is here regarded as the process of testing whether the general behavior of a model is in accordance with the intentions. Verification is therefore largely a subjective assessment of the behavior of the model, rather than an objective test of how well the model outputs fit the data--this is termed validation. To a large extent verification will inevitably go on during the play with the submodels and the total model before the calibration (Fig. 34).

Calibration is a crucial step in the modelling procedure, and the predictive value of the model is highly dependent on selection of realistic parameters, which ultimately will determine the agreement between model and observation.

Verification, sensitivity analysis, calibration and validation, the four last steps in the modelling procedure presented in Fig. 34, will be discussed in detail below.

The Application of Submodels

It is critical to include in the model - as already discussed in the introduction - submodels of importance to the problem in focus. This implies that the characteristic features of the ecosystem must be used as background knowledge.

It is possible to find in the literature descriptions of characteristic processes in aquatic ecosystems, but ecosystems are soft systems containing several feed-back mechanisms, suggesting that a rigid description in the form of an equation for a process is not valid, at least not with the same parameters in all ecosystems. Consequently, all general process descriptions must be questioned and verified for each case study, and the parameters must be calibrated against data from the modelled ecosystems, within ranges in accordance with the literature.

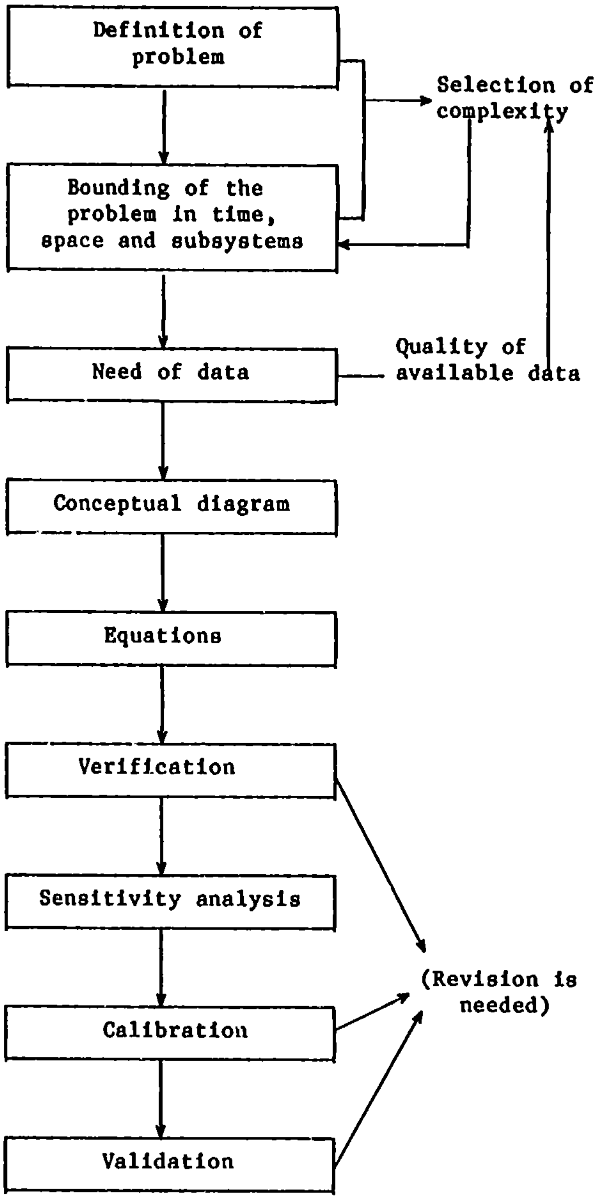


Fig. 34. Schematic of modelling steps emphasizing the importance of the junctures of the selection of complexity and of revision. See also JØRGENSEN and MEJER (1977) and JØRGENSEN (1980).

It is often advisable to examine suggested submodels for ecological processes either in situ or in the laboratory and base a calibration of these submodels on data from such an examination. It is of great importance to base such calibrations on high quality data. The growth of phytoplankton, for example, shall be used to illustrate these considerations.

In many studies data have been used based on measurements with too low frequency, e.g., twice a month. However, the dynamics of phytoplankton occur at too high a frequency to allow a reliable calibration on the basis of such measurements. As demonstrated in Fig. 35, the differential coefficient d(phytoplankton)/dt will be interpreted wrongly when a low measuring frequency is used, while measurements carried out 3-4 times a week will give a completely different picture of the phytoplankton dynamics during the spring or summer bloom. It implies that a reliable calibration should be achieved by use of intensive measuring periods. The details of the application of this technique is described in JØRGENSEN (1980) and JØRGENSEN and MEJER (1981). Further details are also given in MEJER and JØRGENSEN (1980) and some short notes on the procedure are given with Fig. (36), below. However, it should also be stressed in this context the possibility this procedure gives to test equations used in the model or submodel. If the measurements cannot be fitted to the model, it means that the parameters found are not constant, and there is every reason to question the equations.

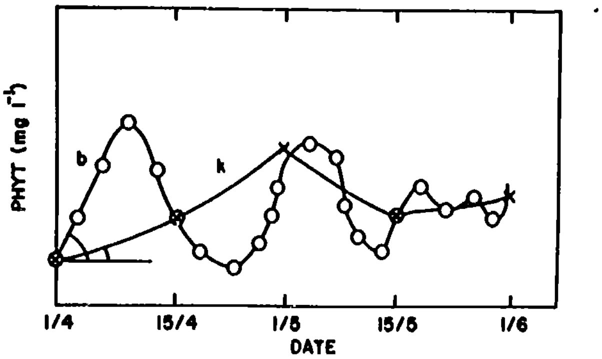


Fig. 35. Algae concentration plotted versus time, where k indicates a sampling frequency at twice a month (+), and b at three times a week (0).

The conclusion of this discussion can be summarized in the following outlines recommended for formulation of processes:

a. The processes included in the conceptual diagram are formulated in accordance with previous modelling experience and the literature. Possible alternatives are included at this stage.

b. The most crucial submodels (equations) are examined in the laboratory or in situ. An attempt will be made to get high quality data as a result of these examinations. The sampling frequency must be in accordance with the dynamic of the subsystem and the goals of the model (day by day prediction, annual average values only, etc.).

c. The data mentioned in point b are used to calibrate the model. If the parameter values are unrealistic or not constant, alternative descriptions of the processes must be tested.

Verification

Linkage of good and verified submodels does not necessarily lead to a good and well-working total model. It is necessary to verify the total model, meaning that it must be tested to see whether it reacts in accordance with expectations, e.g., higher nutrient concentration gives a higher degree of eutrophication, higher mercury concentration and more damage to the biological components of the model, etc.

If the verification is unsuccessful, it is necessary to examine whether a submodel is missing or the linkage of submodels must be changed.

The following steps, sensitivity analysis, calibration and validation are described below, but it is worth mentioning here that these three steps might also question the total model. If the sensitivity analysis shows that the model is very sensitive to a certain parameter, a more accurate submodel or a more accurate calibration of the submodel might be required. If the calibration or validation is found to give insufficient accuracy, this might also lead to considerations on how the total model can be improved.

Sensitivity Analysis, Calibration and Validation

Parameters can be considered constant for a specific ecosystem, or part of an ecosystem. In the causal models the parameters will have a scientific definition, for instance, the maximum growth rate of phytoplankton: that is, the rate at which phytoplankton grows under the best possible conditions (temperature, light, nutrient concentration, etc.). Many parameter values are known within limits. In JØRGENSEN et al. (1978) can be found a comprehensive collection of ecological parameters. However, only a few parameters are known exactly, and it is necessary to calibrate the parameters. The reasons for this can be summarized in the following points:

a. As indicated above the parameters are usually known only within limits.

b. Different species of animals and plants have different parameters which can be found in the literature (JØRGENSEN et al., 1978). However, most ecological models do not consider species but trophic levels, e.g., many eutrophication models do not distinguish between different species of phytoplankton, but consider phytoplankton as one state variable. In this case it is possible to find limits for the phytoplankton parameters, but as the composition of the phytoplankton species varies throughout the year, exact average value cannot be found.

c. The influence of the ecological processes which are of minor importance to the state variables in focus, and therefore not included in the model, can, to a certain extent, be considered by the calibration, where the results of the model are compared with the observations from the ecosystem. This might also explain why the parameters have different values in the same model, used for different ecosystems. The calibration can, in other words, take spatial differences and the ecological processes of minor importance into consideration, but it is, of course, essential to reduce the use of the calibration to this purpose. The calibration must never be used to force the model to fit observations if this implies that unrealistic parameters are obtained. If a reasonable fit cannot be achieved with realistic parameters, the entire model should be questioned. It is, therefore, extremely important to have realistic ranges for all parameters or at least for the very sensitive parameters.

Consequently, a calibration of the total model is almost always required, applying a set of measured data. However, a calibration of several parameters is not realistic. Mathematical calibration procedures for ten or more parameters are not available for most problems. Therefore, it is recommended:

a. to use good literature values for all parameters, and

b. to make a sensitivity analysis of the parameters (Fig. 34) before the calibration, and select the most sensitive parameters, as an acceptable calibration of 4-7 parameters is possible with the present technique.

A sensitivity analysis is carried out using the following definition:

$$S_x = \frac{\Delta x/x}{\Delta \mathrm{Param}/\mathrm{Param}} \qquad (1)$$

where S_x is the relative sensitivity, x is the state variable and Param is the considered parameter.

If it is necessary to calibrate 10 parameters, it is advantageous to use two different series of measurements for calibration of five parameters each, preferably by selecting measuring periods where the state variables are most sensitive to the parameters calibrated (MEJER and JØRGENSEN, 1980; JØRGENSEN et al., 1981). It is of great importance to make the calibration on the basis of good data for the total model as well as for submodels. An outline of the method is given in (Fig. 35).

Changes in Structure

Most ecological models are used to make predictions on the responses to changes in the external factors. Ecosystems are, however, soft systems, which are able to meet changes in external factors with only minor changes in the ecosystem due to a high flexibility in the structure.

This ability of the ecosystem can be quantified by means of the concept ecological buffer capacity which is defined as the change in external factors related to the change in a state variable:

$$\beta = \frac{\dfrac{\Delta(\text{ext. Factor})}{\text{ext. Factor}}}{\dfrac{\Delta(\text{st. variable})}{\text{st. variable}}} \qquad (2)$$

where β is the ecological buffer capacity.

A buffer capacity for each combination of external factors and state variables can be formulated, implying that a model with n external factors (precipitation, input of nitrogen, etc.) and m state variables (phytoplankton concentration, zooplankton concentration, soluble phosphorus concentration, etc.) will have m·n different ecological buffer capacities.

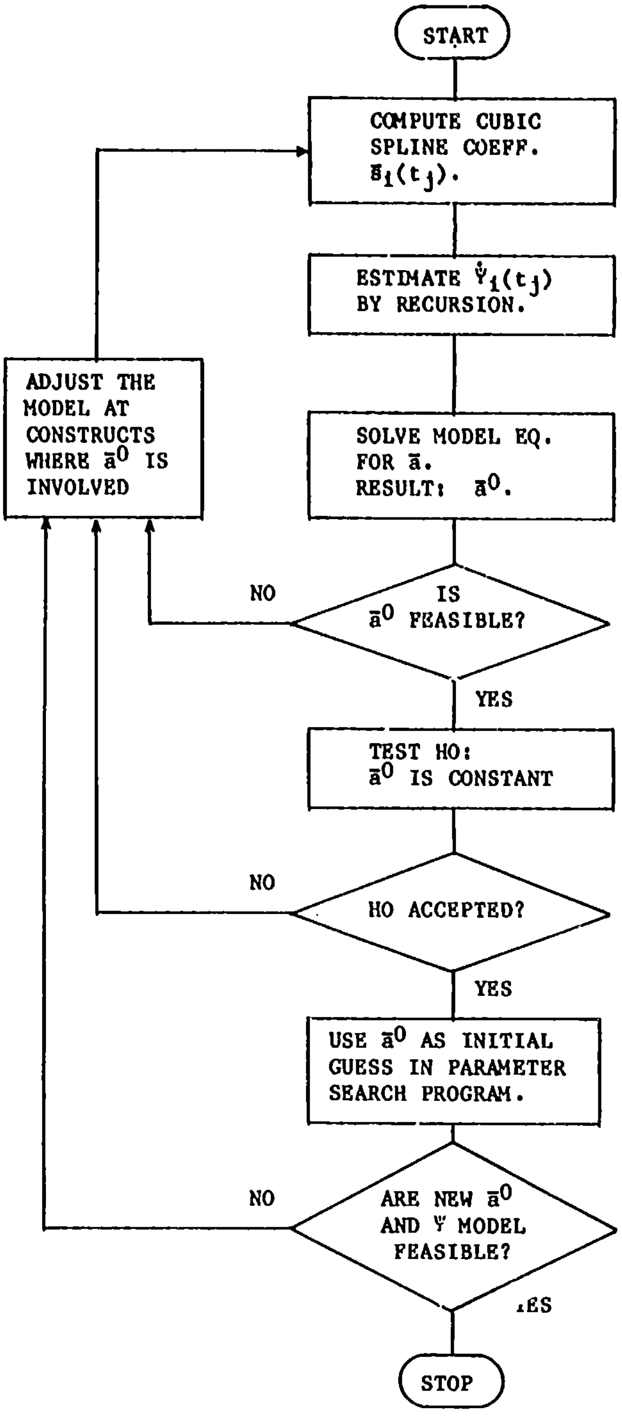


Fig. 36. Summary of method is as follows: (a) Find cubic spline coefficients $\bar{s}_i(t_j)$, i.e., second order time derivatives at time of observation, t_j, of the spline function $s_i(t)$ approximating the observed variable $Y_i(t)$. (b) Estimate $\hat{Y}_i(t_j)$ from the spline coefficients found in step a. (c) Solve for $\bar{a}$, or for a subset of the components of $\bar{a}$ regarded as unknown. (d) Evaluate the feasibility of the solution of $\bar{a}^0$ found in step c. If not feasible, modify the part of the model influenced by $\bar{a}^0$ and go to step a. (e) Choose a significance level, and perform a statistical test on constancy of $\bar{a}^0$. If the test fails, modify appropriate submodels and go to step a.

For further details on this concept, see JØRGENSEN and MEJER (1979) and JØRGENSEN et al. (1981). This consideration implies that a model constructed from an observed structure valid under a given set of external factors, might be insufficient to make predictions, if another set of external factors prevails. These ideas are conceptualized in Fig. 37. Impact on the system will imply that a new structure is developed.

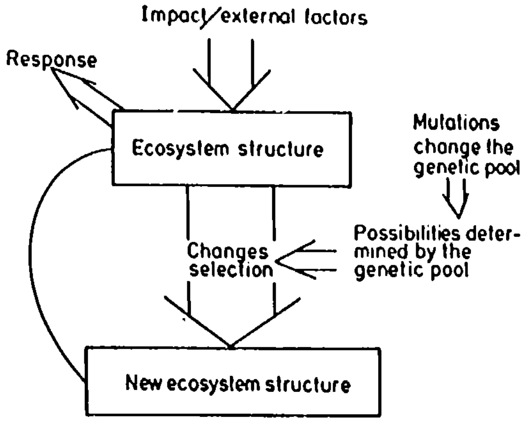


Fig. 37. Schematic of consequences of the impact due to external factors on an ecosystem structure.

It has been shown that the changes in structure, observed as a result of another set of external factors, are accompanied by an increase in the thermodynamic function energy, defined as:

$$\text{Energy} = T \cdot I. \qquad (3)$$

where T is the absolute temperature and I the thermodynamic information:

$$I = k \cdot P_j^* \cdot \ln P_j^*/P_j \qquad (4)$$

where P_j^* and P_j are probability distributions, a posteriori and a priori to an observation of the molecular details of the system, and k is the Boltzman constant.

Most models have a rather simple structure compared with the real ecosystem, but although this structure is valid for most combinations of external factors, the parameters, which are valid only for the species present at a certain system structure, will vary. The shift in parameters can, however, be taken into account by using the above-mentioned hypothesis.

The energy, which easily can be computed for a given model (see JØRGENSEN and MEJER, 1979; 1981), can be used to determine the parameters which are valid for any new set of external factors. The presented hypothesis is one method to build ecological principle into the model.

Further work on this general problem must be expected in the coming years, as it is crucial for further progress in ecological modelling to be able to take shifts in ecological structure into account, if the predictive value of our model is to be improved.

OCEANOGRAPHIC CHARACTERISTICS OF THE MEDITERRANEAN

Water Masses and General Circulation

The Mediterranean Sea, with its negative water balance, is a typical example of reverse estuarine dynamics. Since the time of the Danish Oceanographic Expedition (NIELSEN, 1912) which was the first modern oceanographic study of the entire Mediterranean Sea, a number of authors have described in part or in full the hydrography and circulation of the Mediterranean basin but none in such an enlightened manner as HOPKINS (1978). The process by which the incoming surface north Atlantic water, with salinity slightly above 36 ppt, is transformed into the outgoing deep Mediterranean water, with salinity above 38 ppt, is one of the most important oceanographical problems encountered in the Mediterranean Sea (LACOMBE, 1974). The dynamics of this process require not only large horizontal movements, covering the entire basin, but also a general net gain in density that often generates unusually large vertical velocities seldom found in other regions of the world's ocean.

During the passage through the different basins, the Atlantic Ocean water is subject to varying climatic conditions inducing wide temporal and spatial variations of its temperature and salinity, although these variations are confined mostly to the upper layers. The temperature of the water below the thermocline, characterized by an outstanding homogeneity, varies around 13°C (potential temperature) in the Western Mediterranean, while in the Eastern Mediterranean, the less homogeneous, intermediate and deep waters range in temperature between 13°C and 16°C. Changes in salinity of these subsurface and deep waters span from 38.35 ppt to 39.10 ppt (MILLER and STANLEY, 1965) with only 2 percent of the water being fresher than 38 ppt and 0.1 percent saltier than 39 ppt. The least saline waters are found in the Western Mediterranean and in the Adriatic Sea, and the saltiest in the Levantine Sea. These facts often make the distinction between the various water masses, especially those originated within the Mediterranean Sea, a rather sophisticated exercise. However, fairly steady-state conditions are reached, and various characteristic water masses may be identified, not without difficulty, by slight inversions in the vertical trend of the temperature and salinity distributions.

Water Masses

Surface. In the surface layers, the only obvious water mass is the North Atlantic Water mass (NAW). It is formed by mixtures of the relatively low saline water entering through the Strait of Gibraltar and the saltier subsurface waters forming a surface layer 150 m to 250 m thick. The characteristics of the incoming water at Gibraltar (Fig. 38) may be represented by a potential temperature of 15°C and a salinity of 36.25 ppt, although surface values in the area of the strait may range up to 20°C and 36.45 ppt (FRAGA and ESTABLIER, 1974). The values at the salinity minimum encountered in the surface layer increase eastwards, rapidly in the Alboran Sea as a consequence of intense recirculation, and then more slowly reaching the Sicilian (SANKEY, 1973) and Balearic channels (SALAT and CRUZADO, 1981a) with salinities around 37 ppt, thus containing a mixture with roughly 70 percent of the original Atlantic water and 30 percent of Mediterranean intermediate or deep water. The identity of the NAW may be tracked by the salinity minimum values found at or near the surface not only in most parts of the Western Mediterranean basin but also in the western areas of the Eastern Mediterranean basin as well (Fig. 39). A remnant of the NAW may also be detected as a subsurface layer of minimum salinity to the eastern end of the Levantine Sea (LACOMBE and TCHERNIA, 1960; OREN, 1971).

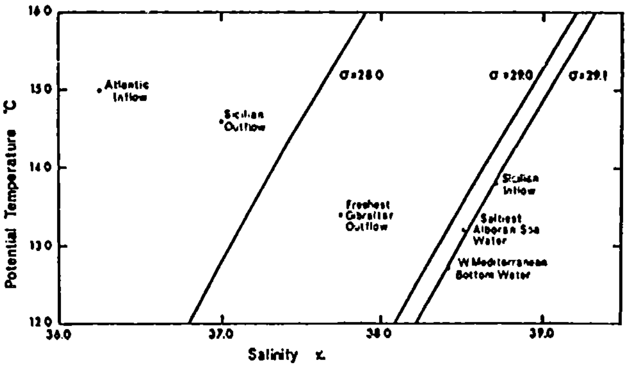


Fig. 38. The potential temperature versus salinity for the inflows and outflows from the Western Mediterranean Basin. From SANKEY (1973), with permission of Pergamon Press.

Recycling of the NAW, just at the entrance of the Mediterranean Sea, favors the mixing with outflowing intermediate and deep waters, contributing to the relatively low salinity of the outflow. The proportion of NAW in the Gibraltar outflow has been estimated as 23% (HOPKINS, 1978), or 35% (SANKEY, 1973). At the eastern Alboran Sea and in the southern Balearic Sea, the NAW flow produces meanders and deviations towards the north, the most important of which occurs in the vicinity of 1°W, 2°E and 7°E and reaches the northern part of the Balearic Sea and the southern part of the Ligurian Sea, the west of Corsica, and the Tyrrhenian Sea. Areas of the Mediterranean where the surface and subsurface salinities are never less than 38 ppt (Fig. 39) may be considered as not directly affected by the NAW. Often in these areas warmer winter deep or intermediate waters occupy the shallow layers as a result of the divergence existing in the zone (OVCHINNIKOV, 1966).

The evolution of the NAW is dependent on the climatic conditions encountered as it moves from west to east through the Western Mediterranean. The intensive solar heating of summer causes a strong thermocline to develop which, because of the lower salinity of this water mass, remains in a surface layer about 50 m to 10 m thick that spreads into a large part of the

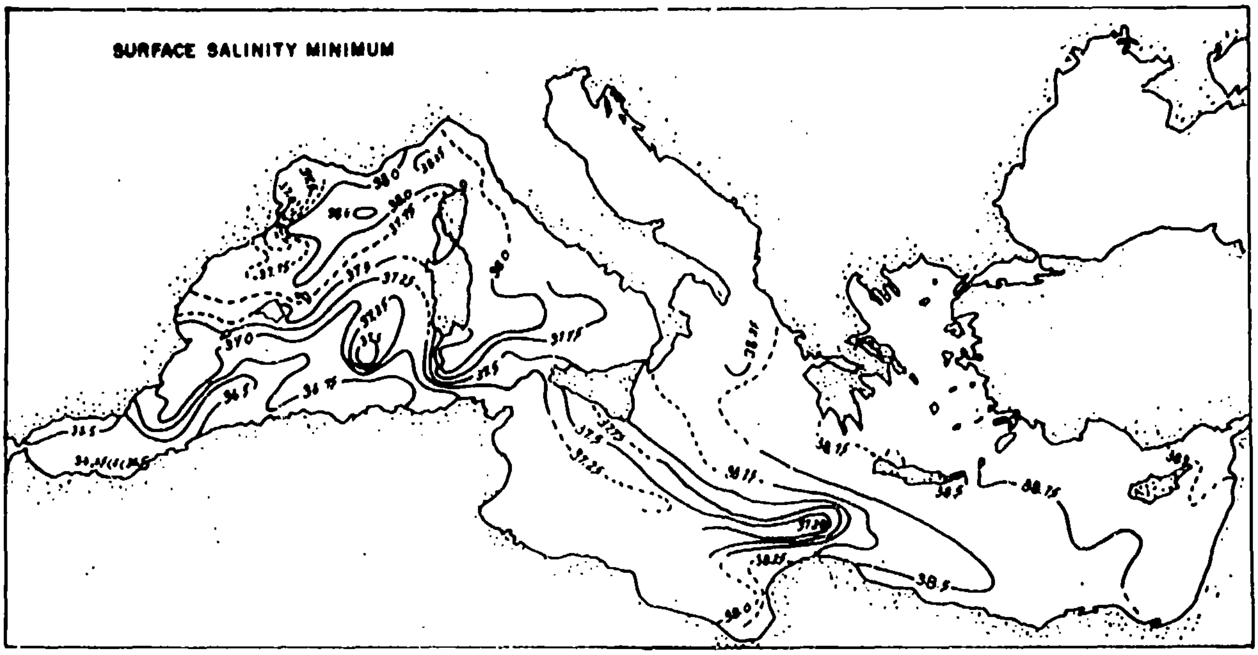


Fig. 39. The surface layer salinity minimum. From LACOMBE and TCHERNIA (1960), with permission of Cahiers Océanographiques.

eastern basin, especially the southern Ionian Sea, from the Sicilian Channel to the Cyrenaica peninsula. The salinity of the NAW after crossing the Sicilian sills (MOREL, 1971) is about 37.50 ppt and increases to about 38 ppt at 22°E (LACOMBE, 1974). During its transit into the Levantine, the NAW becomes heavier than the warmer, more saline surface water and sinks to a depth of 30 m to 75 m (OREN, 1971), where it remains and is marked by a salinity minimum value generally less than 38.6 ppt. On the other hand, the surface water is cooled during winter, often by the dry sirocco winds blowing from North Africa, causing an increase in density in this overlying surface water and consequently a destruction of the NAW by convective mixing. Thus the NAW entering the Eastern Mediterranean loses its identity in transiting the Ionian Sea.

The NAW may exert some influence on the surface water salinities in the northern portions of the Mediterranean Sea, but its effect is generally masked by other riverine sources of fresh water. In particular, the lowering of the salinity observed in the Golfe du Lion and along the coasts of Catalonia is basically produced by the discharges of the Rhone (FURNESTIN, 1960) although a small proportion of this water may have its origin in a branch of NAW which flows northward towards the eastern Balearic and Ligurian Seas and then turns westwards along the Provencal, Golfe du Lion, and Catalan coasts.

The Adriatic Sea is an exception among the Mediterranean basins in that it receives sufficient freshwater from the Po and other smaller rivers so that its annual water balance is positive. In the Aegean Sea, the slightly lower surface salinities, particularly along the Grecian Coasts, are a consequence of river discharges and of the fresher water entering from the Black Sea through the Dardanelles. In the southeastern Levantine, the Nile runoff used to play a role similar to that of the European rivers in the north; however, the effect has been strongly minimized since the Aswan High Dam became operative in 1965 (GERGES, 1976a).

Subsurface. The deeper water masses of the Mediterranean originated within the sea itself and are extremely homogeneous in their temperature and salinity characteristics. However, small but persistent features, such as maxima or minima in the vertical are used to identify different water masses. One of these water masses is the Deep Water mass (DW) that occupies depths greater than about 500 m in the western basin and 700 m in the eastern basin.

As a result of the relative isolation caused by the existence of a shallow sill across the Sicilian Channel and of a layer of warmer and saltier intermediate water that acts as a lid in the eastern basin, relatively important differences exist between the temperature and salinity of the DW in the eastern and western basins. The DW of the Western Mediterranean has a mean potential temperature of 12.7°C and a mean salinity of 38.4 ppt, corresponding to a sigma-t of 29.10 (SANKEY, 1973), while that of the Eastern Mediterranean, only slightly heavier with a sigma-t of 29.15, has a mean temperature of 13.6°C and a mean salinity of 38.7 ppt (HOPKINS, 1978).

Differences also exist within each basin. Small differences exist in the distribution not only of temperature and salinity but also of dissolved oxygen. An increase in the values of the first two properties and a decrease in the latter may be considered an indication of the

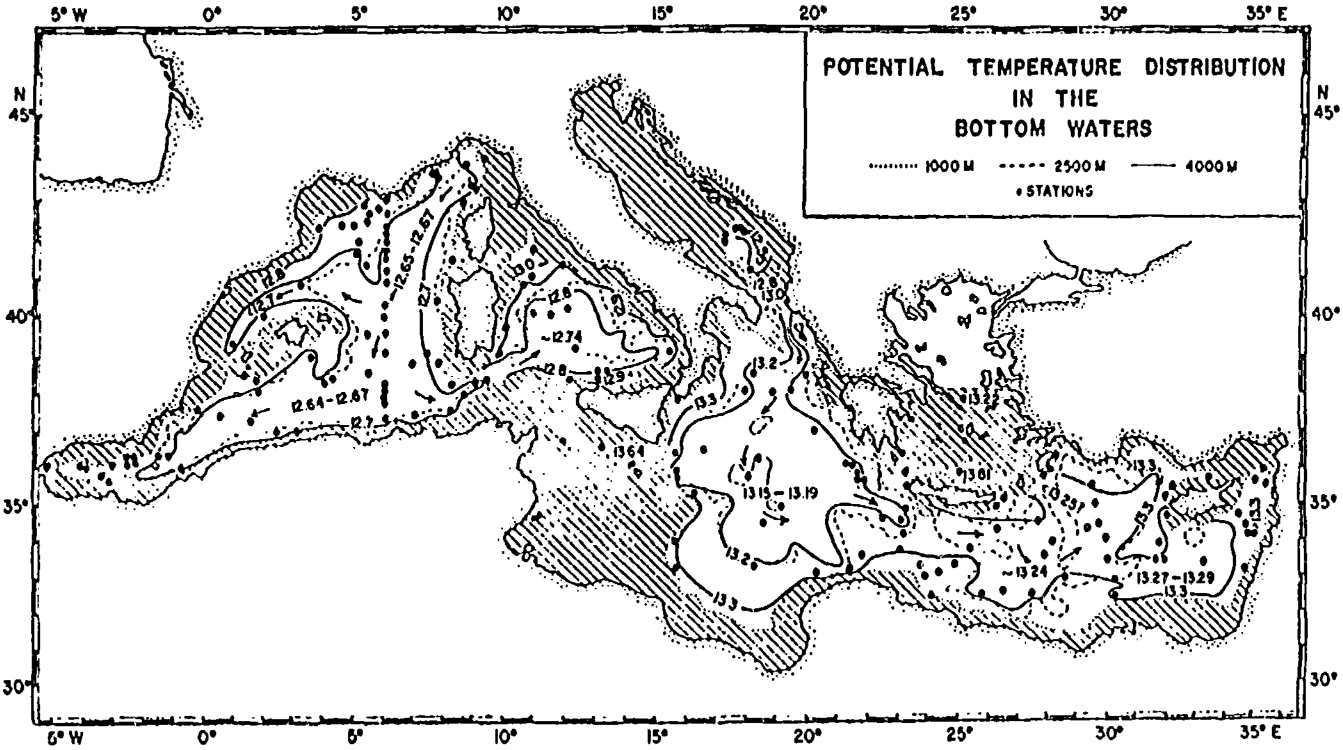


Fig. 40. Suggested bottom water flow based on potential temperature distribution. From WÜST (1961), with permission of Journal of Geophysical Research.

remoteness from the source region (Fig. 40), because the DW can only mix with the warmer and saltier intermediate waters above it and because lower oxygens are correlated with the age of a subsurface water.

In the Western Mediterranean, only the Tyrrhenian Sea deep water body departs from the characteristics of the main body of DW, with slightly higher temperature and salinity values. This is the result of the basin's relatively closed configuration, which restricts horizontal exchange of DW. The Alboran Sea deep water also differs from the main DW body through mixing with the intermediate water. It is this mixture that flows over the sills across the Strait of Gibraltar into the Atlantic Ocean.

The Aegean Sea deep water, with temperature of 14.5°C and salinity of 38.96 ppt, appears to be isolated from the bulk of the Eastern Mediterranean DW (POLLAK, 1951), and large or persistent outbreaks of Aegean deep water into the Ionian basin have not been reported so far (MILLER, 1974). The Adriatic Sea deep water, with 12.9°C and 38.57 ppt, the most important source of the Eastern Mediterranean DW (POLLAK, 1951), is formed in the southern Adriatic after vertical and horizontal mixing of winter cold surface water with warmer surface water entering through the Strait of Otranto. The small but consistent differences in the dissolved oxygen content, 0.15 ml O_2/ℓ, between the Ionian and the Levantine basins, suggests a DW age of about 200 years (HOPKINS, 1978).

Intermediate waters, generated within the Western Mediterranean by winter convection processes, often referred to as 'winter waters' (FURNESTIN, 1960), show lower temperature and salinity values than the DW. They are generally seasonal with only small portions remaining in summer identifiable as a temperature minimum layer. Their influence on the dynamics of the system as a whole is rather limited. Intermediate waters produced in the Eastern Mediterranean, on the other hand, have a quite different behavior as a consequence of their higher density and play a very important role in maintaining the salt balance of the two basins and of the Mediterranean Sea as a whole. They are formed by the winter cooling of the highly saline surface water (up to 39.5 ppt) and the mixing with the remains of the subsurface NAW. The process seems to take place preferentially south of Turkey and around Cyprus (LACOMBE and TCHERNIA, 1974) and also off the coasts of Egypt (MORCOS, 1972). This water mass, with temperatures ranging from 15°C to 18°C and salinities between 38.8 ppt and 39.1 ppt, is referred to as the Levantine Intermediate Water (LIW). MORCOS (1972) suggested that the LIW can also be formed in the Southern Levantine by winter convective mixing. The T-S diagram of Fig. (41) shows the seasonal transformation in the water column in the Southern Levantine. A vertically homohaline water mass of the winter occupies the depth range of 0 to 300 m. In the spring, it appears between 200 to 300 m as a vertical salinity maximum. From August to November it collapses to a well defined core layer represented by points, each of which retains the same density but becomes cooler and less saline. This dense homogenous water mass of relatively low temperature and high salinity occupies the broad continental shelf and part of the continental slope off Egypt. During the favorable winter conditions it can slope down and spread as an intermediate water to the north and south. From this and other evidence MORCOS (1972) concluded that a secondary source of formation of LIW exists in the southern Levantine. The LIW is more heterogenous in the eastern Levantine than in the other basins of the Mediterranean, which is further evidence that it is formed there. These waters become more homogeneous through mixing during their general westward flow through the Eastern Mediterranean (LACOMBE and TCHERNIA, 1960), where it everywhere occupies a layer between 250 m and 400 m deep under the surface NAW and is identifiable by a vertical salinity maximum. The LIW has been tracked in the various regions of the Mediterranean Sea by the core method (WÜST, 1961). As this water mass progresses away from its Levantine source, its water type changes due to mixing without any significant change in potential sigma-t giving rise to an isopycnal T-S regression (Fig. 42). During winter, the waters above and below the LIW are often colder and less saline, especially in the northwestern Mediterranean, the LIW layer appears as an elbow or 'scorpion's tail' (TCHERNIA, 1974) in local T-S diagrams.

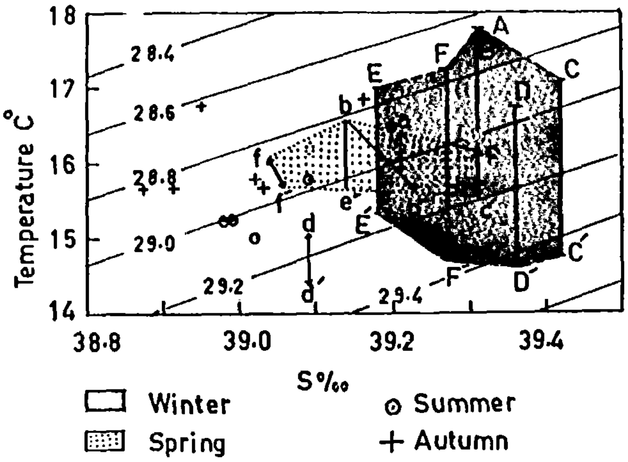


Fig. 41. T-S diagram of the core layer of the LIW in the six northernmost stations of the meridional sections of ICHTHYOLOG in the four seasons of 1966. Sections A to F are from east to west, respectively. From MORCOS (1972), with permission of Gordon and Breach.

On passage through the Sicilian channel, the LIW undergoes a drop in salinity to about 38.75 ppt as a result of the active vertical mixing with the overlying less saline surface NAW (MOREL, 1971). From there the LIW seems to spread to the north, a small portion entering the Tyrrhenian Sea, and a larger portion entering the Ligurian and Catalan Seas, where it appears in rather discontinuous tongues. Various authors have observed LIW on the African side also (COSTE, 1971). The properties of the LIW found in the southwestern Balearic Sea correspond to a much older water than that found between Sardinia and Tunisia, suggesting that most of the LIW circuits around the northern shores of the Western Mediterranean in a large cyclonic gyre back to the North African coast rather than proceeding there directly from the Sicilian Straits. In the eastern Alboran Sea, the LIW is well mixed with the DW, and the salinity maximum observed is only about 0.04 ppt above the values of the DW (FRAGA and ESTABLIER, 1974). This mixture flows over the Gibraltar sills along their northern channel, and is strongly exposed to admixture with the entering Atlantic surface water since the sills are exterior to the Mediterranean Sea (HOPKINS, 1978).

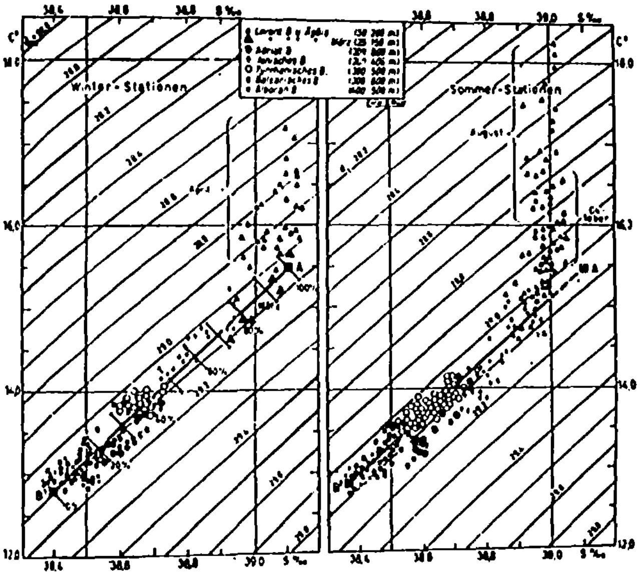


Fig. 42. T-S diagram for the LIW core in winter and summer. The left portion shows the winter stations and the right portion, the summer stations. The code for the various seas is given in the insert at the top. From WÜST (1961), with permission of Journal of Geophysical Research.

Circulation

Surface. The forces that drive the flow of the surface north Atlantic water into the Mediterranean Sea seem to be basically produced by a lower sea level in this basin with respect to that of the adjacent Atlantic Ocean, which is caused by a mean excess of evaporation over precipitation and runoff. In opposition there exists an internal pressure directed out of the sea which is caused by the heavier Mediterranean deep waters. Together these forces favor a mean circulation of in at the surface and out at the bottom, which is characteristic of negative thermohaline circulations (HOPKINS, 1978). This general trend, however, is modified by a number of transient forces that range from tidal to meteorological, contributing to important high-frequency fluctuations of the flow of water through the Strait of Gibraltar and making its quantification extremely difficult.

As a result of the weakness of the tidal forces in the Mediterranean Sea, tidal circulation is generally negligible except in the neighborhood of the Strait of Gibraltar and at the amphidromic points like those of the Sicilian channel, Sea of Crete, and in the northern Adriatic. Motions caused by wind stress and atmospheric pressure distribution generate important components of the velocity field. However, the thermohaline forces created by the hydrographic structure already described in the preceding section are more important in determining the net circulation in the Mediterranean; that is, the surface NAW flows eastward throughout, and the LIW and the western DW flow westward, and the eastern DW flows eastward.

Because of the rotation of the Earth (Coriolis effect) a general flow pattern of eastward to the south and westward to the north would be expected to produce a cyclonic (counter-clockwise) gyre in each of the basins. However, the large number of straits and sills, especially in the Eastern Mediterranean, complicates the actual circulation pattern not only of the surface layer but also of the deep and intermediate water layers. Based on the data gathered by the THOR expedition in 1908-1910, NIELSEN (1912) proposed a surface circulation pattern for the entire Mediterranean Sea (Fig. 43) which is still considered representative (LACOMBE, 1974; LACOMBE and TCHERNIA, 1972, 1974) although a large amount of research on this subject has been carried out in the last 70 years. In the Western Mediterranean in particular a number of authors have studied the current system and contributed to the improvement of the simple Nielsen scheme. ALLAIN (1960), taking into consideration previous works as well as his own dynamic computations, produced an improved version of the summer general circulation for the surface waters of the western basin. The main features are a number of cyclonic gyres found at the various parts of the basin, especially active along the northern shores of the Balearic, Catalan, Ligurian and Tyrrhenian seas. These gyres carry the largest part of the NAW all the way through the Balearic islands and into the Ligurian Sea. The remaining NAW, involved with the north African flow generating several weak clockwise (anticyclonic) gyres, enters the Tyrrhenian Sea which is circled in a cyclonic direction and, after crossing the Sicilian channel, flows into the eastern basin. OVCHINNIKOV (1966) also produced a composite charts of the surface currents for the entire Mediterranean.

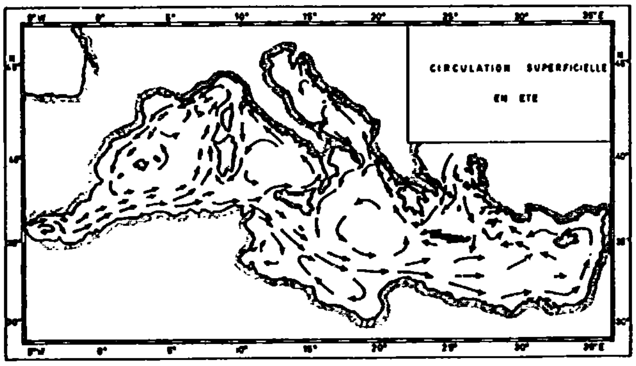


Fig. 43. Surface circulation in the summer. From NIELSON (1912), with permission of Report of the Danish Oceanographical Expedition, 1908-1910.

The surface circulation has been studied in greater detail in parts of the western basin. An excellent example is found in the Alboran Sea where the circulation (Fig. 44) is shown in much greater complexity than that in Fig. 43. The western Alboran Sea, under the strong influence of the Strait of Gibraltar inflow, shows a rather unusual anticyclonic gyre (ALLAIN, 1960; LANOIX, 1974) that is of interest in a number of ways. The flow of surface water, at the entrance of the Alboran Sea, would be expected to adhere to the Moroccan side by the Coriolis effect. Instead, it is directed to the northeast, towards the southern Spanish coasts, mostly due to the combination of the topography of the strait and a baroclinic radius of deformation larger than the radius of curvature of the Ceuta corner (HOPKINS, 1978). The eastward flow seems more intense on the northern side, with speeds up to 90 cm/sec, than the westward flow along the southern side, with speeds up to 60 cm/sec, while small cyclonic gyres appear in various places along the African shores. The gyre water, with salinities below 37.5 ppt, recirculates to a larger extent, producing a thickening of the surface layer in the central zone and a rising on both sides of the interface between the surface NAW and the deeper water, producing transient upwelling phenomena all along the northern shores and in some offshore locations as well.

As the gyre hits the Alboran island rise, it is partly deflected to the east, entering a cyclonic meander that drives most of the surface flow against the Algerian shores and then east of 2°W, towards the southeastern Spanish coasts south of Cabo de Palos (LANOIX, 1974). In the eastern Alboran Sea, the flow takes a more zonal direction along the shores of Algeria, with speeds up to 50 cm/sec (HOPKINS, 1978), but soon the flow splits into two branches, one following the direction of the Sicilian channel and the other that of the Balearic Islands. Axial instability of the zonal flow produces anticyclonic meanders that weaken the identity of the north African current. The flow directed towards the Balearic Islands, of about the same magnitude, joins a large cyclonic gyre that extends between the Catalan and Ligurian Seas. The speeds on the Catalan shelf were found to be persistent in direction and up to 50 cm/sec in magnitude, and they may still be higher on the opposite side along the western coast of Mallorca (ALLAIN, 1960; FONT, 1976). This alongshore flow on the mainland side constitutes a well defined western boundary current stretching from the Tuscany Islands to the eastern Alboran Sea.

The surface circulation through the Sicilian channel, of greatest importance to balance the water lost through evaporation in the eastern basin, is far from being well known. Most studies conducted earlier in this region were devoted to ascertaining the flow of water in the intermediate layers. The NAW that flows along the shores of northern Africa changes direction around Cap Bon in Tunisia, showing speeds on the order of 10 cm/sec (MOREL, 1971).

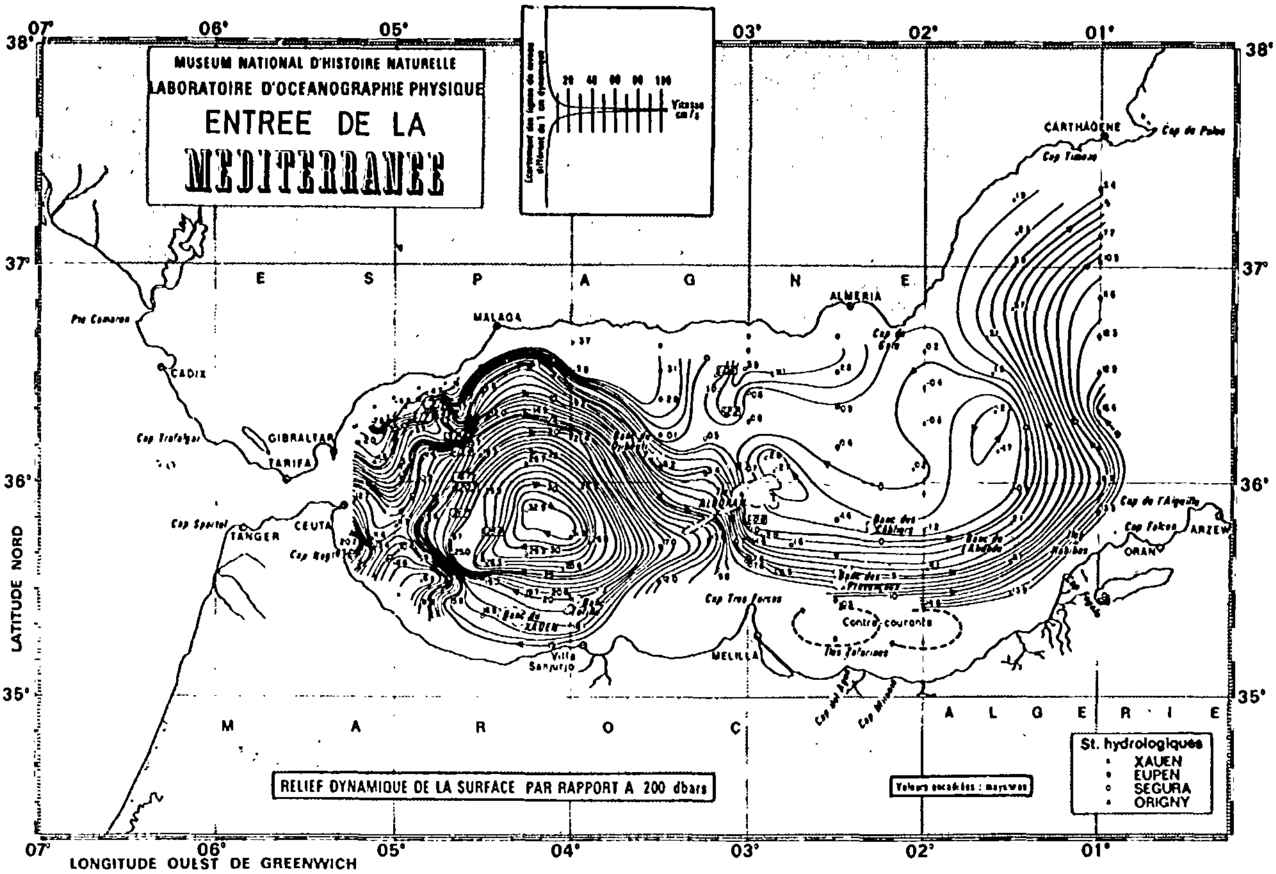


Fig. 44. The dynamic relief of the Alboran Sea for the surface relative to 200 dbars. The survey was conducted from 15 July to 15 August 1962 from the research vessels EUPEN, ORIGNY, XAUEN, and SEGURA. A geostrophic speed scale is located in the insert at the top. From LANOIX (1974), with permission of Rapport Technique (OTAN).

However, if the surface circulation follows the scheme proposed by GARZOLI and MAILLARD (1979), the main eastward flow is not located along the coasts of Africa but takes place through the middle of the channel, promoted by two opposite gyres set between Sardinia and Tunisia, the one to the south being anticyclonic (clockwise). This flow apparently splits into two branches at the entrance of the Ionian Sea, one directed eastward south of Malta, and the other, directed more southward into the Gulf of Sirte, along the Libyan shore, where it contributes to an anticyclonic circulation.

Unfortunately, it is much more difficult to draw a similar synthesis of recent knowledge on the surface circulation for the Eastern Mediterranean. Nielsen's scheme (Fig. 42) indicates a generally cyclonic surface circulation in summer, broken down in a number of smaller gyres of the same sign covering the central Ionian, Adriatic and Levantine Seas, while two smaller anticyclonic gyres are located in the Gulf of Sirte. Little more is known of the Ionian Sea circulation even though it is considered extremely important in the sense of controling the eastward flow of the NAW.

Subsurface. The circulation of the intermediate and deep waters in both the eastern and the western basins is even less well known than that of their surface waters. The general displacement of the intermediate waters is from east to west, and with the very few measurements of the velocity that have been carried out, no more than a rough estimate of 5 to 10 cm/sec may be given as the maximum mean velocities for the LIW (LACOMBE and TCHERNIA, 1972) which is presumed to follow a generally cyclonic circulation (Fig. 45). However, in certain critical places, such as in the lower layers of the Straits of Gibraltar and Sicily, lower layer speeds of up to 40 cm/sec have been measured (MOREL, 1971).

Geostrophic computations at 150 m and 500 m in the Levantine (OREN, 1970) show a meandering motion with a cyclonic gyre centered half way between Rhodes and Cyprus and an anticyclonic gyre located to the southwest of the former. The flow is southward along the shores of Lebanon and Israel, to the north along the western shores of Cyprus, to the south again between 31°E and 29°E, and then to the west and again north at the western end of the Levantine. This sort of vague circulation is the result of the lack of spatial structures of the deep and intermediate waters of this basin, whose salinities vary less than 0.2 ppt while the temperature range is only about 1°C at 150 m deep (OREN, 1970).

At intermediate depths in the Ionian Sea, the flow is cyclonic with a gyre in the northern part (LACOMBE and TCHERNIA, 1972; OVCHINNIKOV, 1966) affecting the water transport across the

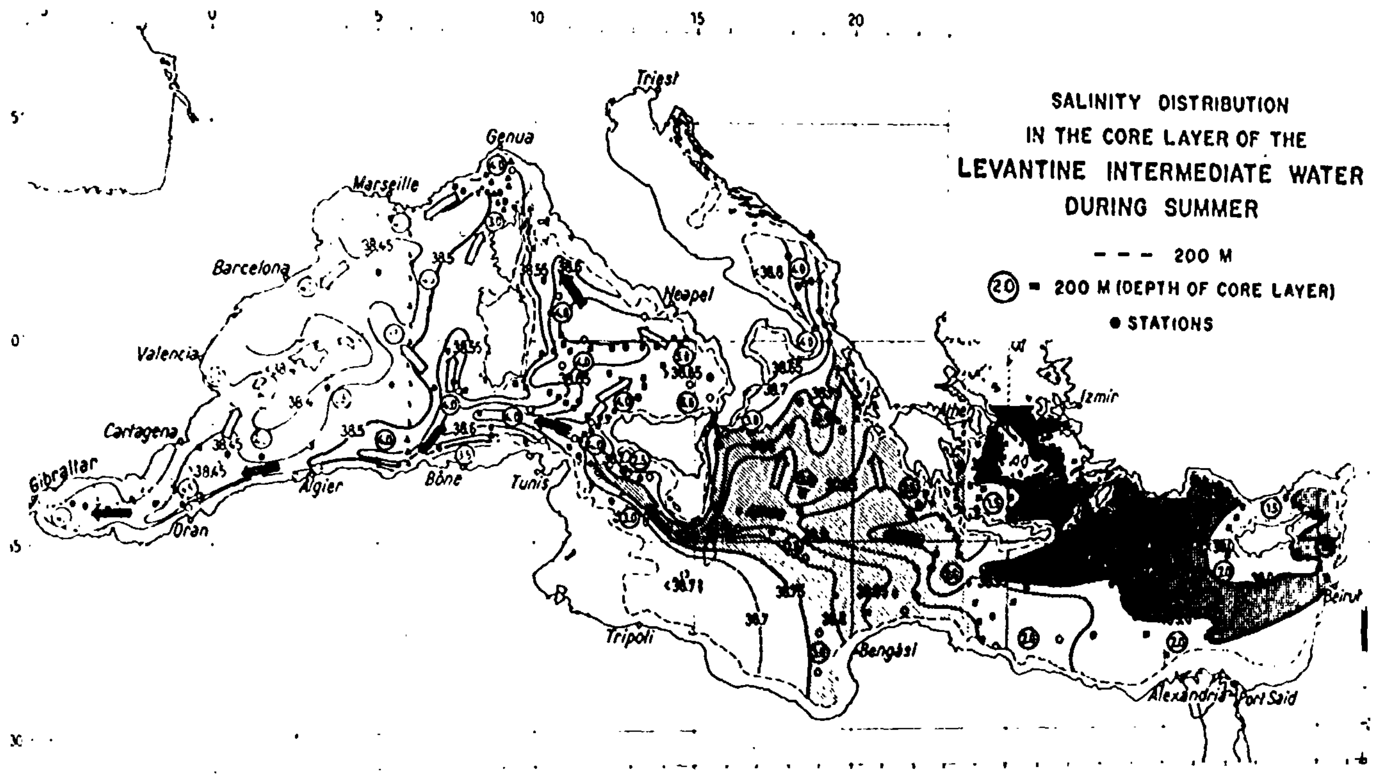


Fig. 45. The salinity maximums and the suggested circulation of the LIW during summer. From WÜST (1961), with permission of Journal of Geophysical Research.

Strait of Otranto, and a second gyre close to Cyrenaica (OVCHINNIKOV, 1966) that probably drives westward most of the Levantine water to the region of the Sicilian channel where the flow is definitely to the west. Intermediate water enters into the southern Adriatic favoring its eastern shores but does not penetrate to the northern Adriatic because of its shallowness. There is no evidence of substantial amounts of LIW in the Aegean.

In the western basin, the LIW flow seems to follow a cyclonic motion in the Tyrrhenian Sea and in the northwest, covering the northern half of the Catalan Sea, the eastern Balearic Sea and the Ligurian Sea (OVCHINNIKOV, 1966). The flow along northern Africa has been questioned on the basis of the continuity of the LIW core properties (KATZ, 1972) although it probably does exist along western Algeria. In the Alboran Sea, the flow is directed basically westward towards the Straits of Gibraltar, favoring the northern side.

Because of the strong homogeneity in the density of the Mediterranean deep waters, weak velocities are suspected in the deeper layers. The net movement is presumed to be away from the DW source, consequently eastward away from the Adriatic in the Eastern Mediterranean and southwestward away from the French coast in the Western Mediterranean. The main evidence of deep circulation is given by the potential temperature distribution of WÜST (1961) shown in Fig. (42).

Basic knowledge of the circulation in most coastal areas of the Mediterranean Sea is limited and fragmented. Many of the direct current measurements do not reach the current scientific literature either because they are made by private or military enterprises for specific purposes or because a complete scientific analysis of these large data bases is beyond the resources of local institutions. One of the main sources of information has been the release of drifters or drift cards in several regions carried out in the past 25 years (GERGES, 1976b). Some gross features of the western boundary current along the southern coast of France and the eastern coast of Spain were studied by a number of authors (BOUGIS, 1958; SUAU and VIVES, 1958; DUBOUL-RAZAVET, 1958) and recently by the DRIFTEX experiment carried out between Genoa, Nice and Corsica, within the framework of MED POL pilot project on Problems of Coastal Transport of Pollutants (MED VI). The circular motion in the Alboran Sea was studied by GAIBAR-PUERTAS (1967) although his conclusions were somewhat in contradiction to geostrophic computations made by ALLAIN (1960) and by LANOIX (1974). The north African current in the Western Mediterranean was also studied by GAIBAR-PUERTAS (1966) and the eastward flow along the southeastern shores of the Levantine Sea by GERGES (1978) using drifters and drift cards. Use of drifters in semi-enclosed bays was made by LOPEZ and ARTE (1973) in a coastal lagoon of the Ebro River delta, and by ILIC et al. (1978) in Rijeka Bay in the Adriatic Sea. However, there are great drawbacks in these procedures because of the trapping of the drifters in eddies between the shoreline and the general circulation, eventually producing results apparently contradictory to the known circulation patterns. The computer algorithm developed for DRIFTEX (SALAT and CRUZADO, 1981b) may allow previous data to be further analyzed with more reliable results.

Velocities in the coastal zone are mostly due to the transient disturbances caused by successive gusts of wind. Small-scale eddies, often trapped in the inner shelf, are caused by the existence of topographical features such as islands, capes or embayments, further complicating local coastal circulation patterns. The longshore component of velocity generally predominates over the onshore-offshore component (ÜNLÜATA et al., 1978) although point observations may often indicate the existence of important cross-shelf motions (SHARAF-EL-DIN et al., 1978). Measurements of this kind should always be looked upon critically since a number of high-frequency elements are normally included in the coastal velocity field without much effect on the transport of water. At any rate, coastal circulation is a local phenomenon likely to vary from hour to hour and from place to place, following the local meteorological conditions. In spite of the lack of in situ observations, several exercises have been conducted within MED POL, and consistent results are emerging from different coastal areas in the Mediterranean.

Deep-water Formation

Deep water formation depends on the local meteorology, on the basin's configuration, on the hydrographic conditions and on the surface circulation (HOPKINS, 1978). Buoyancy may be extracted from the surface water by the air over it, through cooling and evaporation processes, both of which are stronger during winter when the sea-air temperature differences are largest. River runoff in shelf areas can decrease the potential for buoyancy loss with the formation of a low salinity surface layer. This seems to be the case in the northern Adriatic where the circulation associated with northerly winds holds the Po runoff in a well defined plume along the Italian coast (HOPKINS, 1978). This could also be the case in the Golfe du Lion with the Rhone runoff. Also, a cyclonic offshore circulation may cause the exposure of the warm LIW to the surface where the relative temperature difference enhances the buoyancy loss and forms a very dense water (because of the high salinity of the LIW).

Buoyancy may be extracted, under the right conditions, anywhere in the basin, but a number of specific locations are known to be favored by their peculiar meteorological and hydrographic conditions. Some authors have considered the Aegean Sea as a possible source of Eastern Mediterranean DW, but the occurrence of consistent flow of Aegean deep water into the Ionian Sea has been practically ruled out (HOPKINS, 1978). The primary source of deep water for the Eastern Mediterranean is that formed in the north and middle Adriatic in winter (POLLAK, 1951), and for the Western Mediterranean that is formed off the Golfe du Lion (TCHERNIA, 1974). Dense water may be formed either on a large shallow area such as the north Adriatic or the Golfe du Lion shelves, or over a 'virtual shelf' produced by a front or pycnocline intersecting the sea surface (LACOMBE, 1974). In the case of nearshore formation, the dense water remains in a baroclinic geostrophic flow parallel to the coast, except in cases where troughs or canyons cut across the shelf and this water can escape to larger depths (HOPKINS, 1978). This seems to occur in the Golfe du Lion where shallow dense water sinks along the Lacaze-Duthiers canyon (FIEUX, 1971, 1974) or in the Adriatic Sea where it sinks into the central depression (ZORE-ARMANDA, 1969). The process of deep-water formation in offshore frontal areas seems to be more efficient. LACOMBE (1974) has pointed out the similarity between this and the nearshore process considering that the sinking of the dense water takes place along the pycnocline.

A number of authors have studied in great detail this process in the northwestern Mediterranean (see HOPKINS, 1978, for a review) and come to the conclusion that three phases may be identified: (1) a preconditioning phase, (2) a violent mixing phase, (3) a sinking and spreading phase. The preconditioning phase refers to previous exposure of surface water to buoyancy extraction which may have occurred by surface water during the autumn season, or it may be the result of upwelling of an intermediate water, particularly the LIW, to the surface. Such preconditioned water more quickly becomes unstable (forms dense water) on exposure to severe winter cooling events, such as the cold, dry mistral winds.

The violent mixing phase has been described as rather catastrophic, requiring the action of strong winds. Under the effect of the mistral, the water becomes vertically homogeneous to depths of more than 500 m and penetrates into the core of the DW. When this happens, the entire water column is filled with 'winter water' or deep water, and strong vertical motions both up and downwards, with velocities up to 2.5 cm/sec, develop (VOORHIS and WEBB, 1970). The extension of the dense water, reaching potential temperatures as low as 12.75°C and salinities of 38.45 ppt, is a patch of about 50 km in the north to south direction and 100 km in the east to west direction (MEDOC GROUP, 1970). However, water of the characteristics described may also be found as far south as 44°N, covering more than half the distance between the Straits of Bonifacio and Barcelona (CRUZADO and KELLEY, 1974). In fact, a long wedge of high-salinity water is maintained from about the latitude of the Ebro River (SALAT and CRUZADO, 1981a) to the Ligurian Sea, by a large cyclonic gyre (ALLAIN, 1960; OVCHINNIKOV, 1966; and FONT, 1978).

The sinking and spreading phase begins after relaxation of the mistral winds, normally in March. The surface layer, warmed by the increasingly strong solar radiation, regains some of its former stratification. The column of dense water spreads laterally giving rise to deep water, intermediate 'winter water' and surface water, and the LIW slowly recovers its original structure.

Formation of the Eastern Mediterranean DW has not been described in such detail but it may proceed through similar processes. During winter, the water in the north Adriatic, which is relatively fresh due to the Po runoff, experiences severe cooling because of the continental winds: the bora from the northeast and the tramontana from the north. These wind events cause buoyancy losses that increase its density above that of the Eastern Mediterranean DW (POLLAK, 1951). This water then flows southward into the middle Adriatic Sea, where it mixes with the overlying warmer and more saline intermediate water. During exit from the Adriatic it experiences some lowering of its dissolved oxygen content, because of in situ oxidation, to values characteristic of the Eastern Mediterranean DW (HOPKINS, 1978). The flow of Adriatic deep water through the strait of Otranto varies with the wind regime (ZORE-ARMANDA, 1969). With the prevailing northerly winds of summer, surface water is dragged out of the Adriatic Sea, and intermediate water flows in. Under these conditions, the flow out of the deep water is limited. During winter, southerly winds force an inflow of surface water, which together with an intermediate water inflow, requires a compensating outflow of Adriatic deep water into the Ionian Sea.

In the northern Ionian Sea sporadic circumstances may be right for the winter formation of DW departing from cooled NAW mixed with intermediate water whose characteristics approach those of the DW. Such mixtures may be converted into DW in this area after ten days of catastrophic conditions, resembling those of the northwestern Mediterranean, or after two months of severe winter conditions (HOPKINS, 1978).

Since the climatic conditions vary from year to year, the amounts of deep water formed in each of the basins must be small in order to account for the homogeneity shown. HOPKINS (1978) estimated that the overall residence time of the western DW would be somewhere on the order of 160 years. The residence time of the eastern DW, with a lower oxygen content in the Levantine than in the Ionian basin, has been estimated by the same author to be above 200 years, both being significantly greater than the overall residence time of about 90 years estimated by LACOMBE and TCHERNIA (1972) for the north Atlantic water in the Mediterranean basin.

Nutrient Distribution

The Mediterranean Sea is known for its oligotrophic character. Overall nutrient concentrations in the Mediterranean Sea waters are much lower than those found at equal depths in the Atlantic Ocean (MCGILL, 1969). This has been proposed as the main cause of the low primary production observed in the region (SOURNIA, 1973). Only a reduced number of areas receiving the discharges of the large European rivers, mainly the Rhone (COSTE, 1974) and the Po (SCACCINI-CICATELLI, 1973), or those experiencing upwelling such as occurring in the northwestern Mediterranean in winter (CRUZADO and KELLEY, 1974) or in parts of the Alboran Sea (BALLESTER et al., 1969), are relatively well fertilized. Vertical distribution of nutrients in most parts of the Mediterranean basin (MCGILL, 1969) shows a surface layer 50 m to 100 m thick with very low levels of nutrients at all times of the year, an intermediate zone in which nutrient concentrations increase with depth, and a deep zone in which they remain practically constant.

The general distribution of nutrients in the Catalan Sea and adjacent areas (CRUZADO, 1981) is taken here as an example of Mediterranean ecosystem. In the Catalan Sea, nitrate, phosphate and silicate show the same general distribution as the rest of the Western Mediterranean, with concentrations increasing with depth up to about 9 μg-at/ℓ for nitrate (Fig. 6a), 8.5 μg-at/ℓ for silicate (Fig. 6b) and 0.8 μg-at/ℓ for phosphate (Fig. 46a). Nitrite is extremely low in the entire water column, but generally has a maximum in the photic zone, which seldom exceeds 0.6 μg-at/ℓ (Fig. 46b). ammonia, an important component of the nitrogen cycle, is seldom determined and therefore is not considered here.

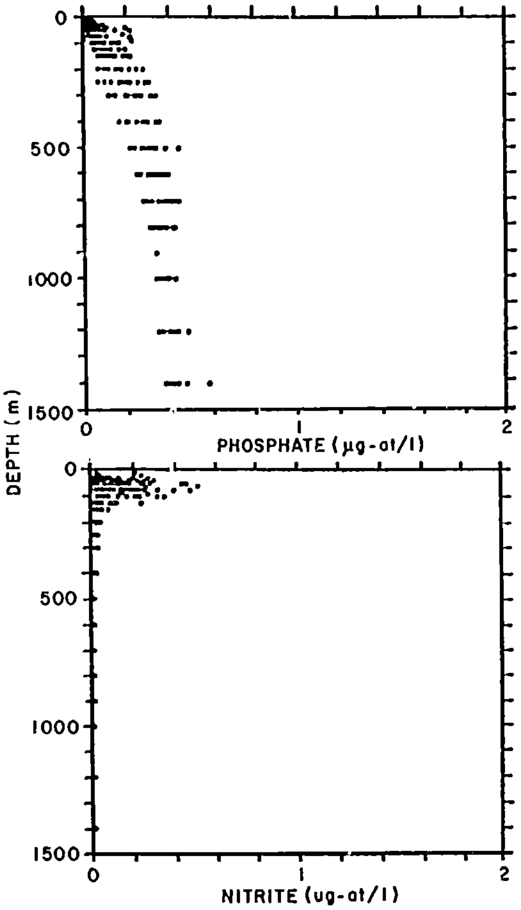


Fig. 46. Nutrient profiles in the Catalan Sea, a) Phosphate, and b) Nitrite. From CRUZADO (1981).

The transition between the depleted surface layer and the relatively rich intermediate layer is very sharp and is located below the thermocline during stratified conditions and is even found under conditions of no stratification (SALAT et al., 1978). At first glance, one would be tempted to say that this sharp nutrient gradient is a consequence of the different characteristics of the two water masses above and below the pycnocline and, in fact, the depth at which nutrient-rich water is found varies from place to place in relation to the thickness of the warm surface layer, which in turn is related to the existence of convergence or divergence areas (FONT, 1978). However, appreciable concentrations of nutrients, especially of nitrate, are generally found only tens of meters below the depth of maximum density gradient. This sharp gradient should be considered a consequence of the uptake of nutrients by the phytoplankton organisms in the surface layer, acting as a nutrient sink in the vertical, rather than as a consequence of the lateral water mass of nutrient depleted waters. This hypothesis is in agreement with the existence, in the open areas of the Western Mediterranean Sea, of an oxygen maximum layer (MINAS, 1970) and of a deep chlorophyll-a maximum (VELASQUEZ, 1981) between about 30 m and 100 m deep.

Strong indications are found that nitrate is the major nutrient controlling productivity. Phosphate concentrations away from the coasts are very low but, probably due to its high regeneration rate, are not limiting. This nutrient appears to play, except perhaps in polluted areas, a secondary role in controlling the photosynthesis. Light intensity limits the photosynthetic rates in the lower part of the photic zone. Nevertheless, enough light intensity must be reaching depths greater than 50 m for photosynthesis to take place at sufficient rates to overbalance the vertical diffusion of nutrients from underlying waters. This is certainly the case in summer when the very clear waters of the Mediterranean Sea show Secchi disk readings of 40 m and even higher.

Although there is little value in computing ratios among the various nutrients in surface waters, their concentrations being too low for these ratios to be given any confidence, the nitrate to phosphate and nitrate to silicate ratios suggest that nitrate is the limiting nutrient for photosynthesis in the region. Nitrate and silicate concentrations in the deep waters of the region show similar values, their ratio being close to unity. At intermediate depths, nitrate concentrations are always higher than those of silicate, this being rather surprising since the highest nitrate concentrations correspond to the saltier LIW, which at its eastern origin has a much lower nitrate-to-silicate ratio (MCGILL, 1969). On the other hand, maximum silicate concentrations appear at salinities that correspond to the Western Mediterranean DW. It may, therefore, be concluded that the relatively low silicate concentrations found at intermediate levels in the Catalan Sea are a consequence of local processes rather than of differences among the water types which form the LIW.

Biological action would be expected to be the main mechanism for the different dynamics of the two nutrients. Nitrate is taken up by all phytoplankton organisms while silicate is taken up only by diatoms. Differential uptake works also in favor of higher silicate relative to nitrate concentrations in the intermediate waters, contrary to observations. The explanation probably lies in the difference between the regeneration rates of the two nutrients within the water column. While silicate, incorporated into diatom frustules, sinks readily as undigested material in fecal pellets to be dissolved only at the bottom, nitrate, required for the production of herbivore biomass, is retained in the intermediate zone where it is excreted as ammonia or other reduced forms of nitrogen (WHITLEDGE and PACKARD, 1971) and then oxidized through nitrification.

Phytoplankton Distribution

Phytoplankton concentrations in the Mediterranean Sea waters are known to be very low throughout the year with the exception of spring and, to a lesser extent, of late fall. The causes of this poverty should be found in two opposite phenomena:

a. Winter cooling, resulting in vertical homogeneity, brings phytoplankton organisms to depths well beyond the compensation depth.

b. Summer heating, resulting in surface stratification, prevents a significant flow of nutrients from taking place through the photic zone.

The first situation results in very low winter phytoplankton densities concurrent with relatively important nutrient concentrations in the upper layers. This is especially true in the northern areas of the Mediterranean Sea where winter cooling is most important. Conditions for phytoplankton blooming are favored in spring by a slight warming of the surface water and stabilization of the water column still rich in nutrients, although this state is rather ephemeral. Summer stratification confines the development of phytoplankton populations to the lower parts of the photic zone where light and nutrient supply are low but significant (VELASQUEZ, 1981). The upper layers show very low Chl-a concentrations, but significant values are found, even in summer, between 50 m and 100 m (Fig. 7), coincident with the upper limit of the nitrate-rich waters and with the nitrite and oxygen maxima.

The process that leads to this particular distribution could be described in the following way: phytoplankton cells, especially diatoms, in the nutrient-depleted surface waters sink faster than the healthier nutrient-supplied cells in the lower layers of the photic zone. Any phytoplankton organisms present in the near-surface layer, if not grazed, readily sink through the thermocline into the nutrient-rich subsurface waters where barely enough light intensity allows photosynthesis to proceed, slowing down their sinking and thus giving rise to the chlorophyll-a, oxygen, and nitrite maxima found all over the Western Mediterranean open-sea waters. The existence of the nitrite maximum is a result of the partial reduction of nitrate which is carried out but not taken up by the phytoplankton cells under extremely low light conditions (BLASCO, 1972).

For the geographical distribution of phytoplankton in the Mediterranean the reader is referred to the excellent book of SOURNIA (1973).

A Simplified Numerical Model of the Lower Trophic Mediterranean Ecosystem

Nutrient and phytoplankton distributions suggest that local circumstances prevail over water mass history, that is, that the residence time of a water mass in a basin is large compared to the residence time in that water mass of a vertically cycling nutrient. Thus, a relatively simple one-dimensionl model should be suitable to simulate the low-trophic compartments of the ecosystem. Fig. (47) shows a simplified scheme of such a model in which the distribution of one nutrient (most likely NO_3^-) is controlled mainly by turbulent vertical diffusion, photosynthetic uptake and regeneration from herbivorous and saprovorous organisms both in the water column and in the sediments. Formulation of this simple model could follow the algorithm proposed in Table IV with the following assumptions:

a. Horizontal advection and horizontal turbulent diffusion are negligible due to, if nothing else, horizontal homogeneity.

b. Plants and detritus hydrodynamically behave as if they were dissolved properties, except when their vertical velocities are substantially different from water velocity.

c. Plants are produced by nutrient- and light-controlled photosynthesis and removed from the system only through grazing.

d. Part of the grazed plant material is egested as detritus, part is excreted as ammonia, and part is regenerated by bacteria.

A somewhat more complex scheme could arise if more than one nutrient, more than one species and more than one size of detrital particles were considered. Table V shows the formulation of such a model. In particular, it might be extremely interesting as an exercise to analyze the different behavior of N and Si by including in this model these two nutrients (NO_3^- and SiO_4^{-4}), two different groups of plants (diatoms and non-diatoms) and two detrital components with different particle size (fecal pellets and small particles).

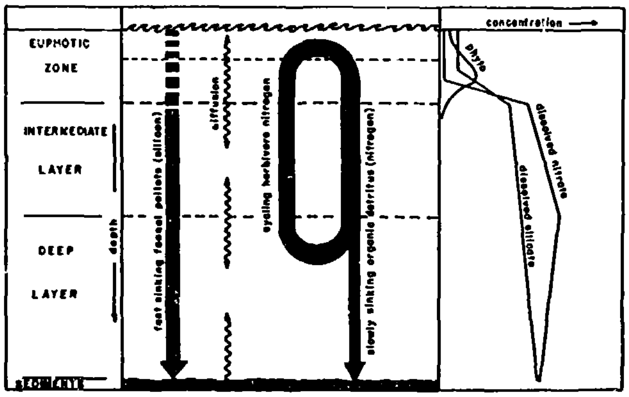


Fig. 47. Diagram of the main processes controlling the vertical distribution of nitrate and silicate.

Standing Stocks and Species Composition of Mediterranean Zooplankton

Introduction

The partial isolation of the Mediterranean confers a number of unique features to its zooplankton communities. The Mediterranean fauna, for example, is considerably poorer than that of the neighboring Atlantic Ocean and has few (if any) endemic pelagic species. Most species are of Atlantic origin, implying that in the past unlimited species exchange occurred through the straits of Gibraltar. At present, however, the Straits seem to act as an ecological barrier to the infusion of Atlantic species into the Mediterranean. Such migrations are probably limited to the Alboran regional though LAKKIS (1971) cites the presence of Atlantic species as far east as the Lebanese coast. The shallow straits also exclude the ingression of deep-water species into the Mediterranean. Deep Mediterranean waters are, in fact, populated by midwater species that descend to greater depths than in the neighboring ocean. The absence of a true abyssal fauna and the inability of the midwater fauna that replaces it to adapt itself to conditions of poor resources result in a strong decrease in biomass below the 1000 m depth (VINOGRADOV, 1968).

A relatively new source for species migration is the Suez Canal. The high salt content of the Bitter Lakes had always acted as a salinity barrier to the influx of Red Sea biota, but the salinity of the lakes has diminished over the years, and the present value is only 2% higher than the Red Sea proper (MILLER, 1972). The result has been that several Indo-Pacific species are no longer prevented from entering Mediterranean waters. In terms of biomass, however, these migrants probably do not play a major role in the pelagic ecosystem of the Eastern Mediterranean.

Knowledge of the zooplankton of the Mediterranean is sparse, fragmentary, and mostly descriptive. Most of the available information is for the Western Mediterranean, except for the Adriatic. In an extensive review paper, BERNARD (1967) summarizes information on Mediterranean zooplankton research up to 1965. The present section is not intended as a critical review of plankton research since then. Our own efforts will concentrate on analyzing the data bases available in recent years on Mediterranean net zooplankton. The first part of this report is mainly concerned with the distribution of standing stocks and geographic variations in zooplankton biomass. The latter part describes spatial and temporal variations of major zooplankters and presents a tentative list of key species of major importance for modelling Mediterranean secondary production. Although we recognize the importance of microzooplankton in the pelagic ecosystem, we have not referred to these latter organisms since there is no information on standing stocks for the Mediterranean and very little information on the faunistic composition.

TABLE IV

$$\frac{\partial N}{\partial t} = \frac{\partial}{\partial z}\left[A_z \frac{\partial N}{\partial z}\right] - w \frac{\partial N}{\partial z} - V_m P \left[\frac{N}{k_N + N} \text{ or } \frac{L}{k_L + L}\right] + rH + r'D$$

$$\frac{\partial P}{\partial t} = \frac{\partial}{\partial z}\left[A_z \frac{\partial P}{z}\right] - w' \frac{\partial P}{\partial z} + V_m P \left[\frac{N}{k_N + N} \text{ or } \frac{L}{k_L + L}\right] - g\ P\ H$$

$$\frac{\partial D}{\partial t} = \frac{\partial}{\partial z}\left[A_z \frac{\partial D}{\partial z}\right] - w'' \frac{\partial D}{\partial z} + e\ g\ P\ H - r'D$$

N = nutrient concentration
P = plant concentration
D = detritus concentration
H = herbivore concentration $H(z,t)$
L = light intensity $L(z,t)$
A_z = turbulent diffusion coefficient $A_z(z,t)$
w = vertical velocity of water $w(z,t)$
w' = vertical velocity of plants $w'(t,\text{species})$
w'' = vertical velocity of detritus $w''(t,\text{size})$

V_m = maximum growth rate of plants
r = rate of nutrient regeneration by herbivores
r' = rate of nutrient regeneration by detritus (after bacterial breakdown)
k_N = half-saturation constant for nutrient
k_L = half-saturation constant for light
e = 1 - assimilation/ingestion
g = ingestion rate

TABLE V

$$\frac{\partial N_i}{\partial t} = \frac{\partial}{z}\left[A_z \frac{\partial N_i}{\partial z}\right] - w \frac{\partial N_i}{\partial z} - \sum_j (V_m)_{ij} P_j \left[\text{smaller of } \frac{N_i}{k_{N_{ij}} + N_i} \text{ or } \frac{L}{k_L + L}\right] + r\ H + \sum_k r'_{ik} D_k$$

$$\frac{\partial P_j}{\partial t} = \frac{\partial}{\partial z}\left[A_z \frac{\partial P_j}{\partial z}\right] - w'_j \frac{\partial P_j}{\partial z} + \sum_i (V_m)_{ij} P_j \left[\text{smaller of } \frac{N_i}{k_{N_{ij}} + N_i} \text{ or } \frac{L}{k_L + L}\right] - g_j\ P_j\ H$$

$$\frac{\partial D_k}{\partial t} = \frac{\partial}{\partial z}\left[A_z \frac{\partial D_k}{\partial z}\right] - w'' \frac{\partial D_k}{\partial z} + \sum_j e_k\ g_j\ P_j\ H - \sum_i r'_{ik}\ D_k$$

Subindex i indicates the various nutrients.
Subindex j indicates the various phytoplankton species.
Subindex k indicates the various detrital size fractions.
All other symbols as in Table IV.

Western Mediterranean

The major subdivisions for the Western Mediterranean include the Alboran Sea, lying between Spain and Morocco, and the Tyrrhenian Sea, north of the Strait of Sicily and lying between Italy, Corsica, and Sardinia. The Western Mediterranean also includes several minor sub-regions which together comprise the Algero-Ligurian region. Included in this region are the Catalan Sea between the coast of Spain and the Balearic Islands, the Balearic Sea from the coast of Algeria to the Balearic Islands, the Gulf of Lions and the Ligurian-Provencal region which comprise the northeastern extension of the Balearic Sea.

The Alboran Sea forms the apex of the Western Mediterranean Sea. To the east, Atlantic surface waters enter the Mediterranean through the straits of Gibraltar. Inflowing currents transport unknown quantities of surface plankton into the Alboran region. Many Mediterranean zooplankton researchers focused much attention in the past on problems related to plankton indicators of Atlantic waters and on the role of Atlantic species in the Mediterranean pelagic ecosystem. According to VIVES et al. (1975), only a fraction of the species occupying the upper 150 m layer are transported from the Atlantic to the Alboran Sea. The number of migrants and the distance these migrants are transported away from their normal area of distribution ultimately depends on the tolerance limits for survival of individual species and on temporal fluctuations in the incoming flow of Atlantic waters. VIVES et al. (1975) also maintain that species occupy different depth ranges on either side of the straits. For example, species having a depth range of occurrence from 0-200 m in the Atlantic, occupy a reduced depth interval in the Alboran Sea (0-50 m). Since the boundary layer between surface Atlantic and deep Mediterranean waters probably acts as a barrier to the vertical dispersion of species, the plankton populations coming into the Mediterranean may not sink as deep in their vertical migration as in their original Atlantic waters. If they did penetrate into 'Mediterranean water,' its westward flow would transport and disperse them back again towards the Atlantic. In their continued migration, they would rise and come back into the Mediterranean with surface flow.

FURNESTIN (1968) suggests that differences in abundances and diversity of the plankton which characterize secondary basins in the Western Mediterranean are essentially due to the intensity of Atlantic inflowing currents. Following the main branch of the Atlantic stream and its subsequent ramifications, the author maintains that the greatest species abundance occurs in the Alboran region. The number of species is still relatively high along the North African coast and along the northern coast of Sicily as well as east of the Balearic Islands. In contrast, the number of species decreases in the northern Tyrrhenian and Ligurian Seas and also along the northern shores of the Gulf of Lions.

In our opinion, the distribution model proposed by FURNESTIN is too schematic since it is based on a limited number of observations and does not take into consideration the different time scales driving hydrographic and biological phenomena. Recent plankton investigations have demonstrated the relative species abundance of all Mediterranean subregions (KIORTSIS et al., 1969; LAKKIS, 1971; SCOTTO DI CARLO et al., 1975) and many species that were previously considered as indicators of Atlantic waters, such as the copepods *Mecynocera clausi*, *Ctenocalanus vanus*, *Lucicutia clausi* and others, are now known to be indigenous to the Mediterranean (HURE and SCOTTO DI CARLO, 1968). Furthermore, the various Western Mediterranean subregions have relatively distinct hydrographic regimes that are only partly driven by Atlantic inflowing currents (CRUZADO, this report). The question of plankton indicators of Atlantic waters therefore still remains very much open to debate.

Although the Alboran Sea may not have a distinctive species composition when compared to other Mediterranean subregions, it probably differs notably in plankton production. Values for nutrients, primary and secondary production suggest that the Alboran Sea is one of the most productive areas in the Mediterranean. The surface flow in the Alboran basin consists of a large anticyclonic gyre (LANOIX, 1974) which produces transient upwelling along northern shores. The resultant high nutrient levels (BALLESTER et al., 1969) and primary production (ESTRADA, 1981) in coastal areas give to annual zooplankton biomass values that are among the highest recorded for the Mediterranean as a whole (Table VI). Mean annual values for northeast Alboran coastal waters ranged from 20-60 mg/m^3 dry weight and were as high as 200 mg/m^3 in November 1978 and June 1979 at a coastal station subjected to the direct influence of upwelling waters (CAMIÑAS, 1981). Values for offshore waters are considerably lower. VIVES et al. (1975) report values of 3-26 mg/m^3 dry weight for June-July 1972.

The second major subdivision of the Western Mediterranean is the Algero-Ligurian region. Plankton studies in this area are more comprehensive than elsewhere in the Mediterranean. The structure of zooplankton communities, including spatial and temporal cycles in abundance of major taxonomic groups, have been studied quite extensively by French and Spanish researchers. Furthermore, in recent years zooplankton studies in this area have also focused on problems related to secondary production both of single dominant species and the zooplankton community as a whole. The cyclonic and anticyclonic gyres in various parts of this basin, particularly along the northern shores of the Ligurian and Catalan Seas and in the Gulf of Lions, are the main hydrographic event within the Algero-Ligurian region (CRUZADO, this report). The relationship between the hydrological regime of the area and the primary production is discussed extensively by SOURNIA (1973) who found higher values of primary production in areas of divergence. The highest values for primary production were those recorded for the Gulf of Lions which, according to COSTE and MINAS (1967) "apparait bien comme une région privilegiée de la Méditerranée, puisqu'il beneficie d'une double source de fertilite: par les apports fluviatiles au nord et par les apports profonds a l'extreme sud."

Estimates of total zooplankton production for the Algero-Ligurian region and differences in the areal distribution of biomass are somewhat harder to determine because of the lack of standardized sampling methods (Table VI). Quantitative data for an annual cycle of total zooplankton of Castellon Bay in the Catalan Sea are given by VIVES (1966). The author reports dry weights calculated using CUSHING et al.'s (1958) conversion for displacement volume whereby 1 ml = 160 mg dry weight. Annually, values ranged from 3 mg/m^3 in September to 11 mg/m^3 in February 1961. Zooplankton biomass from March to June 1966 in the vicinity of Barcelona (Vives, 1968) had values ranging from 6-21 mg/m^3 with a

TABLE VI. Regional abundance for total zooplankton in mg/m^3 dry weight.

Region	Period	Dry weight range mg/m^3	Average	Depth m	Net mesh μ	Reference
Alboran Sea						
NW coast	July '78-June '79	20-60	-	0-50	250	CAMIÑAS (1981)
Open waters	June-July '71	3-26	-	0-200	200	VIVES et al. (1975)
Algero-Ligurian						
Castellon Bay	Nov. '60-Oct. '61	3-11$^+$	5.9	0-bottom	250	VIVES (1966)
Barcelona	March-June '66	6-21$^+$	14.0	surface	100	VIVES (1968)
Gulf of Lions	Oct. '68-July '69	7.0-7.4	-	0-50	220	ARELLANO-LENNOX and MAZZA (1973)
Monaco	Sept. '67	1.77	-	0-50	160	RAZOULS (1969)
"	" "	1.43	-	50-100	160	" "
"	" "	0.55	-	100-200	160	" "
"	" "	0.22	-	200-600	160	" "
Sardinia and Corsica	Feb. '66	1.50-15.0	-	0-200	160	RAZOULS and THIRIOT (1973)
Between Sardinia, Tunisia and Sicily	" '68	0.58-5.66	1.91	0-200	160	RAZOULS and THIRIOT (1973)
W Basin	March '69	0.26-2.59	1.42	0-200	200	RAZOULS and THIRIOT (1973)
" "	" "	0.4-53.0	-	0-75	200	NIVAL et al. (1975)
" "	April '69	5.14-47.80	15.25	0-200	200	RAZOULS and THIRIOT (1973)
" "	" "	0.4-210.0	-	0-75	200	NIVAL et al. (1975)
Ligurian coastal waters	Feb. '63-April '64	1.57-35.96*	11.9	surface	158	GILAT et al. (1965)
Tyrrhenian Sea						
Gulf of Naples	Jan. '76-Jan. '77	0.7-9.0	3.2	0-50	250	CARRADA et al. (1980)
" " "	" " " "	0.3-4.4	1.9	0-300	250	" " " "
Adriatic Sea						
Gulf of Trieste	Oct. '72-July '74	8.0-40.0	15.03	0-15	200	SPECCHI et al. (1979)
Gulf of Venice	'74-'76 (4 cruises)	2.55-25.90	12.20	0-30	250	BENOVIC (1977b)
NE coast	'73-'74 (5 cruises)	0.88-17.26	7.22	0-bottom	250	" "
Mid Adriatic coast	'73-'74 (5 cruises)	2.12-20.58	6.59	"	250	" "
South Adriatic coast	March '73-Aug. '74	1.81-9.52	4.55	0-20	250	" "
Mid Adriatic offshore	(fall'74/spring '75)	5.39-14.46	8.99	0-30	250	" "
South Adriatic offshore	" " " "	2.25-17.83	8.30	0-30	250	" "
Aegean Sea						
Gulf of Saronikos	March'70,Dec.'72, Jan '73	2.0-17.2	-	0-bottom	240	YANNOPOULOS and YANNOPOULOS (1976)
Ionian Sea	Aug. '70	0.34	-	surface	200	GUGLIELMO (1974)
East coast of Sicily	" "	1.66	-	0-50	200	" "
Open waters	'59-'61 (6 cruises)	-	6.43*	0-200	?170	GREZE (1963)
Levantine Sea						
Israeli coast	Feb. '67-Dec. '68	2.93-10.90*	-	0-135	200	PASTEUR et al. (1976)
NE Levantine	May-June '68	-	4.38*	0-135	200	" " " "
Offshore	Sept. '68	-	1.67*	0-135	200	" " " "
	Dec. '68	-	2.02*	0-135	200	" " " "
Levantine Sea and Gulf of Sirti	Oct. '59	1.33-1.89*	-	0-200	?170	DELALO (1966)

$^+$Normalized by equation of CUSHING et al. (1958): 1 ml zooplankton = 160 mg dry weight

*Normalized by equations of WIEBE et al. (1975):

$$\text{Log (DV)} = -1.828 + 0.848 \text{ Log (DW)}$$
$$\text{Log (WW)} = -1.983 + 0.922 \text{ Log (DW)}$$

mean of 14 mg/m^3. For the Provencal region, RAZOULS (1969) reports dry weights of 1.77 mg/m^3 for coastal waters off Monaco in September 1967.

For offshore waters, RAZOULS and THIRIOT (1973) give dry weights that ranged from 1.40-15.0 mg/m^3 for 26 stations sampled from 0-200 m west of Sardinia and southern Corsica in February 1966 and mean values of 1.91 mg/m^3 dry weight for 105 stations sampled from 0-200 m between Sardinia, Tunisia and Sicily in the same period. Forty-eight stations were surveyed for primary and secondary production in 1969 during the Medripod I cruise north of the 40th parallel and west of Corsica. Stations were sampled during two 15-day intervals, the first when winter conditions ended in March, the second in spring conditions in April. RAZOULS and THIRIOT (1973) report mean biomass values of 1.42 mg/m^3 from 0-200 m during the first part of the cruise, and much higher values (15.25 mg/m^3) during the second part. For the same cruise, NIVAL et al. (1975) found values that ranged from 0.4-53.0 mg/m^3. Of the stations sampled, 94% had values less than 20 mg/m^3 (mean calculated for 4 depths: 0, 20, 50, 75 m). A tenfold increase in biomass was observed during the second part of the cruise when values as high as 210 mg/m^3 were recorded, mostly in central areas and near the surface. In this case, 90% of the stations had values from 10 and 100 mg/m^3 dry weight. The values recorded during the Medripod I cruise are the highest reported for the Mediterranean. COSTE et al. (1972) relate these findings to the hydrological features and the distribution of nutrients in the area. High biomass values were also reported by GILAT et al. (1965) for coastal Ligurian waters during an annual cycle in 1963-1964. Mean annual values for this area were 11.9 mg/m^3 with a maximum in spring of 35.9 mg/m^3.* Values as high as 114.8 mg/m^3 were reported for stations subjected to upwelling waters. Other biomass values are available for Calvi Bay, Corsica where mean annual biomass values were 1.06 mg/m^3 with a maximum in spring of 31.3 mg/m^3 (DAUBY, 1980).

The third major subdivision of the Western Mediterranean is the Tyrrhenian Sea. The limited data available for this region suggest that it is notably poorer in zooplankton abundance when compared to the rest of the Western Mediterranean. Annual biomass values for coastal waters are available only for the Gulf of Naples (CARRADA et al., 1980). Values for 0-50 m depth at a fixed station in the gulf ranged from 0.72 mg/m^3 dry weight in August to 8.98 mg/m^3 in June 1976 with an annual mean of 3.2 mg/m^3. The values recorded for 0-300 were much lower, ranging from 0.32 mg/m^3 in September to 4.37 mg/m^3 in March with an annual mean of 1.86 mg/m^3. CARRADA et al. (1980) also give biomass values for 27 stations sampled from 0-50 m throughout the Gulf of Naples in May 1975. Values in this case ranged from 2.3 to 11.4 mg/m^3, depending on the distance from the coast and proximity to the effects of industrial, fluvial and anthropogenic sources.

A map of the biomass distribution of 29 stations sampled from 0-200 m in Tyrrhenian open waters in September-October 1963 is given by VIVES (1967). Unfortunately, VIVES' data are not comparable with those given by other authors since the values are expressed as volume sedimented and therefore cannot be converted to dry weight using either the equations given by CUSHING et al. (1958) or WIEBE et al. (1975). Furthermore, the samples were collected at night when diel migrations of zooplankters are known to strongly affect the composition of the surface community. It is interesting to note, however, that we have found higher biomass values (770 cm^3/1000 m^3) for southwestern Tyrrhenian waters. The lowest values (160 cm^3/1000 m^3) were those recorded for northeastern waters between Corsica and the Italian mainland. According to VIVES, zooplankton biomass distribution more or less coincides with the distribution reported by MARGALEF et al. (1966) for nutrients and chlorophyll pigments. The latter authors suggest that southern surface waters are enriched by upwelling currents which would explain the higher standing stocks for zooplankton (VIVES, 1967).

Eastern Mediterranean

The Eastern Mediterranean encompasses four seas, namely, the Adriatic Sea between Italy and Yugoslavia, the Ionian Sea which lies south of the Adriatic from the southern tips of Sicily to the Greek mainland, the Aegean Sea between the coasts of Greece and Turkey, and the Levantine Sea south of the Aegean to the eastern extremities of the Mediterranean.

The most intensively investigated area in the Eastern Mediterranean is the Adriatic, a nearly landlocked and relatively shallow sea that is exposed to a considerable influence from the adjoining mainland. Of the numerous rivers and streams draining into the Adriatic, the Po River adds the largest quantity of freshwater (600-1950 m^3/sec, SCACCINI-CICATELLI, 1962), particularly in spring and summer with the melting of the snow in the Italian Alps. As a consequence of its morphology and hydrological regime, the Adriatic has a marked dual physiognomy. The shallow northern section is neritic in character, showing strong gradients influenced seasonally by variations in discharge of the Italian river complex. In addition to the resident neritic species, there are a number of pseudo-brackish water species including the copepods *Pseudocalanus elongatus* and *Temora longicornis*. These species normally reach weak abundances in summer when they extend southward following the plume of the Po River, and become an important component of the zooplankton biomass for the entire northern Adriatic and the Italian coast southwards to the Strait of

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*To normalize data for comparative purposes, original data were converted from displacement volume or wet weight to dry weight using equations of WIEBE et al. (1975) given below Table VI.

Otranto (HURE et al., 1980). It is worth noting that the northern Adriatic is presently the only area of the Mediterranean proper where the coastal community has a strong brackish-water component at certain times of the year.

In contrast, the southern Adriatic is a relatively deep basin with oligotrophic characteristics that is subjected to the seasonal incursion of different water masses originating in the Eastern Mediterranean (HOPKINS, 1978). It shows a notable richness in species number and is characterized by the presence of a large number of open water species that comprise relatively uniform but quantitatively poor populations. Temporal variations in the horizontal distribution of the open water community are extremely complex and depend on the coupling of several factors, most importantly production cycles of the single species, their vertical migration throughout the year, and the surface current regime (HURE et al., 1980).

The most complete data set for zooplankton biomass are those given by BENOVIC (1977a, 1979) who sampled 35 fixed stations during four seasonal cruises. Three distinct density zones were recorded: the northern Adriatic and all coastal Italian waters with values from 10.3 to 15.7 mg/m^3 dry weight (average for four cruises); open mid Adriatic and coastal Yugoslavian waters with values from 5.0 to 9.3 mg/m^3; and southern Adriatic waters where minimum values from 1.9 to 4.5 mg/m^3 were recorded. Maximum densitites were observed during the spring cruise whereas the lowest values were recorded in autumn.

Coastal Yugoslavian waters in the vicinity of Split have been continuously monitored since 1954, and long-term records are available for standing crop and species composition (VUCETIC, 1971, 1979). Mean annual values from 1954 to 1970 for three coastal stations were 7.7, 4.8 and 3.8 mg/m^3 dry weight. Biomass values for other Adriatic waters include those given by BENOVIC (1977b) for the northeastern Adriatic (0.88-17.26 mg/m^3 dry weight) and for Lokrum Canal, in the southern Adriatic (1.81-9.52 mg/m^3). Annual biomass values are also available for the Gulf of Trieste (northern Adriatic) where values from a minimum of 8.0 mg/m^3 in May 1973 to 40.0 mg/m^3 dry weight in July 1974 were observed (SPECCHI et al., 1979).

The Ionian Sea lies south of the Adriatic. Few quantitative data are available for this region. GREZE (1963) gives biomass values for different depth levels from 0-2000 m. For the first 200 m, the value recorded was 6.43 mg/m^3 dry weight. According to GREZE, this value is of the same order of magnitude as those recorded for the Gulf of Sirte (7.07 mg/m^3), Aegean (6.01 mg/m^3) and Levantine Seas (5.6 mg/m^3). Mean biomass decreased rapidly with depth, and below 1000 m the values recorded were about 100 times less than those for surface waters. Biomass values are also available for Sicilian and southern Italian coastal waters (GUGLIELMO, 1974). Mean dry weight values for August 1970 were 0.34 mg/m^3 for surface waters and 1.66 mg/m^3 for 0-50 m.

The Aegean Sea lies to the north of the Levantine Sea. The topography of this region is very complex as a result of the high irregular coastline and the numerous islands which fill the two major basins. The Aegean is generally divided into two subregions; a neritic northern section having a broad continental shelf which is subjected to the incursion of low salinity waters from the Black Sea and a deeper southern section which is probably very similar to other oligotrophic Eastern Mediterranean waters (MORAITOU-APOSTOLOPOULOU, 1976).

Information on zooplankton is particularly scant for this region as a whole. Plankton surveys were conducted by KIORTSIS et al. (1969) during the course of six cruises in the north Aegean from 1963-1965 and four cruises in the south Aegean in 1966 and 1967. A species list is available and relative proportions for dominant zooplankters are given using a 'biomass factor,' based on the measurement of the surface area of projected camera lucida drawings of individual copepods. According to MORAITOU-APOSTOLOPOULOU (1976), northern coastal waters are characterized by the presence of several Black Sea species. The number of migrants increases in late spring and summer because of an increased surface outflow from the Black Sea. However, the influence that these migrants have on the local fauna is limited.

One of the most intensively investigated areas in the Aegean Sea is the Saronikos Gulf where zooplankton biomass in winter 1972-1973 was reported by YANNOPOULOS and YANNOPOULOS (1976). Values ranged from 2.0 to 17.2 mg/m^3 dry weight for open surface waters in Saronikos Gulf and from 25.0 to 96.1 mg/m^3 for the polluted Elefis Bay area. YANNOPOULOS and YANNOPOULOS (1976) also give biomass values from 0.5-2.9 mg/m^3 dry weight for other (unspecified) Aegean waters in winter.

The easternmost section of the Mediterranean includes the Levantine Sea. POR (1978) defines this basin as a "subtropical saline cul de sac of the warm-temperate Atlanto-Mediterranean zoogeographic area." Since JESPERSEN's (1923) observations for Mediterranean macrozooplankton of the Dana expedition, the general rule of thumb has been that standing crops of Western mediterranean zooplankton are as much as three times higher than those recorded for the Eastern Mediterranean. Recent zooplankton data confirm this general trend although differences between the two basins are not as marked as those originally reported by Jespersen. According to DELALO (1966), biomass for 28 station sampled in 1959 throughout the Levantine Sea ranged from 1.33-1.89 mg/m^3. These values are somewhat higher than those recorded for the open Aegean and Tyrrhenian Seas but lower than those recorded for the Alboran Sea, Adriatic Sea, and the Algero-Ligurian region. GREZE et al. (1968) give values of 1.81 mg/m^3 dry weight for the Levantine Sea as compared to 3.5 mg/m^3 for the Ionian and 1.38 mg/m^3

for the Aegean Seas. STIRN (1973) gives dry weight values for zooplankton collected from 0-150 m during the ATLANTIS II cruise in May-June 1969 between Rhodes and Cadiz. Unfortunately, his data are not comparable with others since they are expressed per unit tow and flowmeter data are not included. STIRN concludes that plankton biomass during this period was significantly higher in Eastern Mediterranean waters. Only central Western Mediterranean waters, between the Balearic Islands and Sardinia, and east Tyrrhenian waters were similar in order of magnitude to those recorded for the Eastern Mediterranean. The highest absolute values were recorded in the north Levantine Sea and in the Straits of Messina. The lowest values occurred in the Alboran Sea and along the Algerian coast. It is interesting to note that STIRN himself admits that his results are strange and are opposite to those expected for the Mediterranean as a whole.

Seasonal variations in zooplankton biomass collected in Israeli coastal waters are given by PASTEUR et al. (1976). Values ranged from a maximum of 10.94 mg/m^3 dry weight recorded in April to minimum values of 2.93 mg/m^3 in July 1968. Values for offshore zooplankton are given by the same authors for three cruises in May-June, September and November-December 1968. Mean biomass values for the three cruises were 4.38, 1.67 and 2.02 mg/m^3 dry weight, respectively.

Species abundance is difficult to document for the Eastern Mediterranean. The most complete set of data for Mediterranean zooplankters dates back to the DANA expedition (1908-1910) which reported a sharp decrease in species abundance from west to east. For example, 46 plankton hyperiid amphipods were recorded for the Western Mediterranean as compared to 10 species for the Eastern Mediterranean (STEPHENSEN, 1924). More recently, GODEAUX (1974) documented the same paucity with respect to thaliaceans and ALVARIÑO (1974) with respect to siphonophores. However, DOWIDAR and EL-MAGHRABY (1973) cite 132 copepod species from 0-100 m for Egyptian waters. Such values are comparable to those recorded for the Gulf of Naples by HURE and SCOTTO DI CARLO (1968). DELALO (1966) found 141 copepod species from 0-2000 m for the Levantine Sea and the Gulf of Sirte. LAKKIS (1981) identified 300 zooplankton species in Lebanese coastal waters, 90 of which were copepod species. These data support an alternative hypothesis that the Levant basin may be one of the richest regions in the Mediterranean, second only to the Alboran Sea in species abundance. Several of the copepod species recorded along the Israeli and Lebanese coasts are considered to be of Red Sea origin such as Calanopia elliptica, C. media, Acartia centrura (BERDUGO, 1968, 1974) and Labidocera madurae, L. detruncata, Acartia fossae (LAKKIS, 1981). The number of Red Sea species cited for the Eastern Mediterranean has increased in recent years probably because of the combination of two factors: on the one hand, as HALIM (1976) suggests, the closing of the Aswan Dam has favored the passage of less euryhaline forms giving rise to more active and successful immigration of Red Sea species to the Eastern Mediterranean; on the other hand, plankton research has notably increased in this region over the last ten years. Data on zooplankton of Egyptian coastal waters, particularly with regard to differences prior to and after the Nile floods, are given by DOWIDAR and EL-MAGHRABY (1971, 1973) and EL-MAGHRABY and DOWIDAR (1973). The general problems related to the influx of Red Sea biota to the Eastern Mediterranean were critically reviewed by POR (1978).

Composition of the Zooplankton

The species composition, temporal and spatial fluctuations of dominant Mediterranean zooplankters have been studied by numerous authors. The following section summarizes the available information for the various subregions. References to earlier sources of information relating to individual taxa or to the zooplankton community as a whole are available in several bibliographies (BERNARD, 1967; FURNESTIN, 1968; biannual reports of the Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee C.I.E.S.M.), or in synoptic surveys in specific areas (MAZZA, 1966; CASANOVA, 1977). The taxa which are presented are those which the authors consider significant either in terms of biomass or in terms of defining or characterizing specific areas of the Mediterranean.

The most striking feature of Mediterranean zooplankton composition is its relative uniformity throughout the various coastal subregions so that a relatively small number of species (about 10) comprise the bulk of the zooplankton population throughout the year. Copepods constitute the major proportion of the total zooplankton throughout the year and cladocerans rank second in importance (Table VII). Cladocerans have a seasonal periodicity, reaching peak abundances in summer and disappearing shortly afterwards. Appendicularians are also important the year round. Two peaks in abundance are generally observed, one in winter when a Fritillaria spp. maximum occurs and one in summer due to Oikopleura spp. Gelatinous organisms, such as Thaliaceans, occur sporadically in the plankton when swarms of the two species Thalia democratica and Doliolum nationalis can represent an important fraction of the overall coastal zooplankton biomass. At the secondary consumer level, chaetognaths are probably the most important zooplankton group although little information is available on the role played by other predators such as ctenophores, siphonophores and schyphomedusae. At times, these latter organisms can occur in large numbers over Mediterranean shelf areas.

Species considered to be dominant by various Mediterranean investigators are listed in Table VIII. Notwithstanding differences in sampling methods as type of net used, mesh size employed, depth sampled, method of haul (vertical, horizontal, oblique), sampling time of

TABLE VII. Relative percentage composition of dominant zooplankton groups (copepods, cladocerans, appendicularians, chaetognaths) for the various Mediterranean subregions.

Region	Cop.	Cla.	App.	Cha.	Reference
Alboran Sea					
NW coast	60	19	6	-	RODRIGUEZ (1981)
Algero-Ligurian					
Castellon Bay	55	7	6	2.6	VIVES (1966)
Marseille	81	4	5	0.9	GAUDY (1971)
Ligurian Sea	80	8	4	1.7	GILAT et al. (1965)
Tyrrhenian Sea					
Gulf of Naples	85	4.8	5	0.7	GONEP (1979)
Adriatic Sea					
Gulf of Trieste	71	13	3	0.6	SPECCHI et al. (1981)
North Adriatic	40	31	2	2.3	HURE and SCOTTO DI CARLO (1969)
South Adriatic	83.5	-	-	3.1	HURE (1955)
Levantine Sea					
Lebanon coast	65	4.5	3.3	3.0	LAKKIS (1981)
Egyptian coast	76.9	-	3.9	1.7	EL-MAGHRABY and DOWIDAR (1973)

year and, most important of all, location of the sampling sites (i.e., distance from the coast, proximity to continental runoff sites, sewage outfalls, etc.), few dominant species were observed throughout the year. Among the copepods, dominant species are *Paracalanus parvus*, *Acartia clausi*, *Centropages typicus*, *Temora stylifera*, *Ctenocalanus valus*, *Clausocalanus furcatus*, *C. arcuicornis*, *Oithona* (*O. nana*, *O. helgolandica* and *O. plumifera*). Important cladocerans are *Penilia avirostris* and *Evadne spinifera*, and the appendicularians *Oikopleura longicauda*, *Fritillaria pellucida* and *F. borealis*. Two species of chaetognaths are dominant, *Sagitta enflata* and *S. setosa*. Regional exceptions are *Ctenocalanus vanus* in the Adriatic as a whole and *Pseudocalanus elongatus* and *Temora longicornis* in the north Adriatic (HURE et al., 1980), the absence of *Centropages typicus* in Levantine coastal waters (LAKKIS, 1971), the substitution of *C. typicus* by the congeneric Atlantic species *C. chierchie* in the Alboran Sea (VIVES et al., 1975), the substitution of *Sagitta setosa* by the congeneric Atlantic species *S. friderici* in the Levantine Sea (HALIM, 1976).

Seasonal changes in zooplankton abundance have been studied for the various subregions. Three peaks were observed by RODRIGUEZ (1981) in Alboran coastal waters. The largest peak occurred in summer (June-July) mainly due to the copepod *A. clausi* and the cladocerans *P. avirostris*. The autumn peak in September was due to *Clausocalanus* sp. and *P. avirostris* whereas the one observed in February-March was due to *A. clausi*, *Clausocalanus* sp. and *C. chierchie*. Three peaks were also recorded in Ligurian coastal waters by GILAT et al. (1965). The spring peak in this case occurred from March to May and was caused mainly by the presence of *A. clausi*. The summer peak in July-August was caused mainly by large numbers of *C. arcuicornis* and *P. parvus*. A smaller peak was recorded in October-November due to *T. stylifera* and *Euterpina acutifrons*. Appendicularians were particularly important in Ligurian coastal waters in February (*Fritillaria*) and in July and August (*O. longicauda*). Cladocerans were abundant during the summer and early autumn months. Three peaks were again observed in the Gulf of Naples, Tyrrhenian Sea (GONEP, 1979). The March peak was the result of an increase in the number of copepods (*Clausocalanus paululus* and *C. arcuicornis*), doliolids (*D. nationalis*) and appendicularians (*F. pellucida* and *F. borealis*). The maximum in June was mainly due to the presence of the copepods *P. parvus* and *A. clausi* whereas the one observed in October was due to *A. clausi*, *C. furcatus* and to a lesser extent to *C. typicus* and *T. stylifera*. Other dominants were cladocerans (*E. spinifera*) in June and appendicularians (*Oikopleura fusiformis* and *O. longicauda*) in October.

For Eastern Mediterranean coastal waters, the only data on annual cycles of abundance for total zooplankton are those given by PASTEUR et al. (1976) who recorded two peaks in Israeli coastal waters. The spring peak in April-May was due to the copepods *P. parvus*, *Centropages kroyeri*, *Isias clavipes*, *A. clausi*. The autumn peak in December was due to *P. parvus*, *C. furcatus* and *T. stylifera*. Two peaks were also observed by SPECCHI et al. (1981) for the Gulf of Trieste. The spring-summer peak from April to July was due mainly to *A. clausi* and *P. avirostris*, *A. clausi* and *T. stylifera*.

TABLE VIII. Annual relative percentage composition of dominant copepods for the various Mediterranean subregions

Region	Period	Depth m	Net mesh µ	Pp	Ac	Ct	Ts	Cv	Cl	Oi	Reference
Alboran Sea											
Open waters	Jun - Jul 72	Sur.	200	34.8	26.8	7.9	-	-	8.9	-	VIVES et al. (1975)
Algero Ligurian											
Castellon Bay	Nov 60- Dec 61	0-60	250	21.8	-	7.6	9.6	-	35.0	-	VIVES (1966)
Marseille	Nov 64- Dec 65	0-25	250	12.3	14.1	23.5	13.8	-	18.7	-	GAUDY (1971)
La Spezia	Oct 49- Mar 51	Sur.	333	-	8.8	16.6	17.5	-	34.1	-	DELLA CROCE (1952)
Genova	May 55- Jun 56	Sur.	166	16.3	1.7	1.9	1.3	-	6.1	17.4	SERTORIO (1956)
Algers	Nov 55- Jun 56	0-50	200	15.2	-	3.6	3.7	-	26.2	22.1	BERNARD (1958)
Tyrrhenian Sea											
Gulf of Naples	Jan 76- Jan 77	0-50	250	37.9	23.7	1.7	1.0	-	13.0	9.3	GONEP (1979)
Adriatic Sea											
North Adriatic	Jan - Dec 65	0-bot.	333	15.8	18.9	8.3	5.3	12.7	-	-	HURE and SCOTTO DI CARLO (1969)
South Adriatic	Oct 65- Sep 66	0-30	250	7.5	11.2	9.4	10.6	-	-	-	HURE and SCOTTO DI CARLO (1968)
" "	" "	0-100	250	3.4	0.5	2.4	7.6	14.6	10.9	4.9	HURE and SCOTTO DI CARLO (1968)
Ionian Sea											
Saronikos Gulf	Aug 77- Jul 78	Sur.	180	9.9	33.8	-	-	-	12.4	-	MORAITOU-APOSTOLOPOULOU (1981)

(Pp = Paracalanus parvus; Ac = Acartia clausi; Ct = Centropages typicus; Ts = Temora stylifera; Cv = Cetnocalanus vanus; Cl = Clausocalanus spp.; Oi = Oithona spp)

Regional data on species abundance are given by KIORTSIS et al. (1969) for the Aegean Sea. In order of abundances, dominant species were T. stylifera, C. typicus and Nannocalanus minor for the North Aegean and T. stylifera, C. arcuicornis and O. plumifera for the South Aegean.

Changes in zooplankton density focus attention on breeding cycles of dominant zooplankters. Comparatively few studies have been conducted on the life cycles of Mediterranean species. Information is available mostly for copepods, in particular for Calanus helgolandicus, N. minor, C. furcatus, P. parvus, T. stylifera and C. typicus of the Gulf of Marseille (GAUDY, 1962, 1972); T. stylifera and C. typicus of Banyuls-sur-Mer (RAZOULS, 1973a, b, 1974); T. stylifera of Algerian coastal waters (Bernard, 1970). Comparative studies of vicarious copepod species have been conducted by LE RUYET-PERSON et al. (1975) for T. stylifera and C. typicus from the Gulf of Lions and T. longicornis and C. hamatus from the English Channel. The available data suggest that most copepod species produce several broods over the entire year, with intensification of breeding in particular periods. Different species are abundant at different times so that overall yearly fluctuations in total biomass are comparatively small. Brood numbers are relatively high, ranging from 3 to 6, with a maximum of 7 recorded for C. typicus and T. stylifera. Only C. helgolandicus seems to show seasonal breeding over restricted periods of the year. A single breeding period seems to be characteristic of several other zooplankton groups, particularly for cladoceran species (SPECCHI et al., 1974; SPECCHI and FONDA-UMANI, 1974; THIRIOT, 1968).

Little information is available regarding open Mediterranean zooplankton communities. Data on regional abundance for the Alboran Sea include zooplankton data collected during the Spanish-Moroccan cruise in June-July 1972 which sampled discrete depths from 0-1000 m at 16 stations in the Atlantic in the vicinity of the Straits of Gibraltar and 10 stations in the Alboran Sea. Data for dominant zooplankters such as copepods, amphipods, euphausiids and other groups are given by VIVES et al. (1975) whereas ALCARAZ et al. (1975) describe the cladoceran and ostracod populations. Dominant surface zooplankton in this period were the copepods P. parvus, Clausocalanus sp., T. stylifera, C. typicus, A. clausi, O. helgolandica, and O. plumifera. Other dominants were the appendicularians Oikopleura dioica, O. longicauda, F. pellucida, F. borealis, the cladocerans Evadne nordmanni, E. spinifera, P. avirostris, the ostracods Conchoecia rotundata and C. elegans, and the pteropods Spiratella inflata and S. tronchiformis. Intermediate depths were characterized by euphausiids (Euphausia krohnii, and Nematoscelis megalops) and copepods (Eucalanus monachus, Pleuromamma gracilis, Lucicutia flavicornis).

For the Tyrrhenian Sea, copepods were sampled at 58 stations at discrete depths from 0-700 m in September-October 1963 during the Italian-Spanish cruise of the R.V. BANNOCK (VIVES, 1967). According to VIVES, dominant species for 0-200 m were N. minor, Mecynocera clausi, T. stylifera, C. arcuicornis, C. typicus, Acartia negligens and O. plumifera. Intermediate depths (200-700 m) were characterized by the copepods Pleuromamma abdominalis, P. gracilis, L. flavicornis and Haloptilus longicornis. The vertical distribution of deep-sea copepods was studied 10 miles off the island of Ponza (Tyrrhenian Sea) by SCOTTO DI CARLO et al. (1975). Discrete depths were sampled from 0-2000 m in June 1973 and 1974. The authors give data on numerical abundance and depth range of occurrence for 116 copepod species. Dominant surface copepods in this period were C. arcuicornis, C. vanus, P. plumifera, C. typicus. Intermediate layers were mainly characterized by the presence of Clausocalanus pergens, Euchaeta acuta, Spinocalanus longicornis, P. gracilis, H. longicornis and O. setigera. Copepod abundance and number of species were found to be extremely low below 1000 m. Only 0.3 (1973) and 0.94 (1974) individuals/m^3 were recorded from 1000-1500 m and the respective values for 1500-2000 m were 0.08 and 0.26 individuals/m^3. With regards to species abundance, only 18 species were recorded from 1000-1500 m and 10 from 1500-2000 m. Dominant copepods for 1000-1500 m were Mormonilla minor, Oncaea ornata, Scaphocalanus invalidus and Monacilla typica. From 1500-2000 m, dominant species were Lucicutia longiserrata, M. minor and Gaetanus kruppi.

Recently, IANORA and SCOTTO DI CARLO (1981) reported biomass and species distribution for copepods sampled from the surface to 3000 m in the central Tyrrhenian Sea. The authors noted a sharp decrease in biomass and total number of individuals with depth, with over 80% of the biomass occurring in the upper 200 m. Below 1000 m, copepod biomass was only 1% of the total recorded for the entire water column, and copepod density was less than 1.0 individual/m^3. The decrease in total number of species was less marked. Twenty-two species were still present below 2000 m, but not one of these copepods was a deep-sea species.

VAISSIERE and SEGUIN (1980) gave the depth range of occurrence for 112 copepod species sampled to the 2000 m depth in the Tyrrhenian and Ionian Seas. Affinities between the two basins were discussed on the basis of faunistic composition and distribution range of individual species. GREZE (1963) reported the depth range of occurrence and relative abundances for 122 copepod species sampled at discrete depths from 0-3000 m at 14 stations in the Ionian Sea from 1959-1961. Dominant surface species were M. clausi, P. parvus, C. arcuicornis, A. negligens, and Corycaella rostrata. Intermediate depths were mainly characterized by P. gracilis, P. abdominalis, Heterorhabdus papilliger, H. longicornis, M. minor and O. setigera. Only G. kruppi and Lucicutia lucida were dominant below 1000 m. DELALO (1966) gave the depth range of occurrence from 0-2000 m for 139 copepod species sampled at 27 stations in the Levantine Sea from August-October 1959 and November 1960. PASTEUR et al. (1976) gives relative abundances for major species sampled at 17 stations in the Levantine Sea in May-June 1968. Dominant surface species recorded in this period were C. furcatus, T. stylifera, P. parvus, Corycaeus sp., Oithona sp., Euchaeta marina, L. flavicornis and Oncaea sp.

Conclusions

To attempt a synthesis or comparison of zooplankton standing stocks and species composition for the various Mediterranean subregions is a difficult task. One of the main problems in attempting such a comparison is that of integrating data expressed in different units of biomass derived from different sampling strategies and methods. On the basis of the available information, we conclude that:

a. The Mediterranean is relatively uniform in terms of species composition. Major differences seem to occur only between inshore and offshore waters and not among the various subregions. Regional exceptions are the Alboran, eastern Levantine and northern Adriatic Seas. The former two areas are partially subjected to the influx of Atlantic and Red Sea species, whereas the latter region comprises the only slightly brackish water environment known for the Mediterranean proper.

b. Marked variations for standing stocks are generally observed for the different subregions. The available data corroborate JESPERSEN's (1923) observations for Mediterranean macrozooplankton. The Eastern Mediterranean seems to be somewhat poorer in biomass than the Western Mediterranean. Exceptions in our opinion are the Adriatic Sea which is as rich as, or richer than, the Western Mediterranean and the Tyrrhenian Sea which seems to be as poor as the Eastern Mediterranean.

c. Coastal waters generally have higher standing stocks than offshore waters. Areas of divergence, as the northern shores of the Alboran Sea and the Algero-Ligurian Basin, as well as those subjected to considerable land runoff, as the northern Adriatic, are the richest for the Mediterranean as a whole.

d. Copepods comprise the bulk of the zooplankton of neritic waters. About ten species dominate all coastal Mediterranean areas throughout the year. Of the zooplankters, only cladocerans contribute significantly to the overall biomass of coastal areas, especially in summer. Detailed studies on the biology of these species are of utmost importance for understanding plankton dynamics in Mediterranean ecosystems.

e. Production cycles for the Mediterranean are similar to those recorded in other temperate seas, with a late winter or early spring maximum and a smaller peak in late summer or autumn. Production is continuous throughout the year with maximum standing stocks ranging from three to ten times the minimum.

f. The life cycles of Mediterranean zooplankters have been poorly studied. The available information indicates that the main reproductive strategy for copepods is a succession of broods spread out during the year, with intensification of breeding only over restricted periods. Brood numbers are generally high (up to seven generations for Temora stylifera and Centropages typicus) implying high turnover rates for Mediterranean coastal areas. The tendency for species to show only one breeding period appears to hold true for other zooplankton groups such as cladocerans and probably thaliaceans which reach peak abundances in summer and spring, respectively, only to disappear shortly afterwards.

g. Offshore waters are characterized by the presence of a large number of open-sea species that comprise relatively uniform but quantitatively poor populations. Seasonal changes in abundance are less marked than those recorded for coastal areas. Copepods comprise the bulk of the population of surface waters throughout the year, whereas intermediate layers are dominated by large copepods and euphausiids that are known to undergo ample diel vertical migrations. Below 1000 m, the plankton fauna is drastically reduced due to the absence of deep-sea species. Deep waters are populated by several midwater species (aboubt 15) living unusually at great depths.

By way of a coda, we wish to add a final comment on the relative poverty of the Mediterranean. The marked spatial heterogeneity in terms of quantity of zooplankton, and the limited information available to date on production mechanisms for the various subregions make it rather hazardous to attempt a comparison between the Mediterranean and other oceanic regions. According to GREZE (1963), the values recorded for open Eastern Mediterranean waters are of the same order of magnitude as those given by Russian authors for vast expanses of the tropical and subtropical Pacific and Indian Oceans. Based on plankton surveys covering the entire North Atlantic, BE et al. (1971) conclude that values grater than 200 ml/1000 m^3 characterized boreal and neritic waters of the North Atlantic. Values ranging from 50 to 200 ml/1000 m^3 were recorded in the boundary currents, and values less than 50 ml/1000 m^3 in central waters. The corresponding dry weight values using the equation in Table VI of WIEBE et al. (1975) are 21.4 and 4.2 mg/m^3, respectively. The similarities of these values to those reported in Table VI places in question the 'orthodox' view of the quantitative poverty of the Mediterranean Sea, especially in regards to its euphotic zone. In our opinion, one of the main drawbacks in Mediterranean plankton ecology has been that of approaching the Mediterranean as a more or less uniform entity and not as a mosaic of subregions of uneven spatial scale in which different hydrographic patterns result in strikingly different production levels. In the prospect of future modelling efforts it is therefore evident that a model of any Mediterranean subregion will 'suffer' for the inadequate coverage in space and time of those processes which are the basis of pelagic production.

THE GULF OF NAPLES AND ITS DATA BASE

Geographical Description

The Gulf of Naples is one of the most prominent and well defined embayments to be found along the Italian Tyrrhenian coast (Fig. 48). Centered around 40°45' N and 14°15' E, it has an area of 870 km^2, a mean depth of 170 m and a volume of 150 km^3. Its main access to the open sea is to the southwest, through a passage with a 9.5 km^2 cross section, between the islands of Ischia and Capri. This passage is characterized by the two deep canyons of Ammontatura and Procida Trough which extend well into the Gulf and provide its main access to external deep waters. Additional connections with the Tyrrhenian are found to the south and to the north. Bocca Piccola, between Capri and the tip of the Sorrentine Peninsula, has a sill of 74 m, a cross section of 0.4 km^2 and connects the Gulf of Naples with the deeper portion of the Gulf of Salerno. To the north, the passages on either side of Procida Island provide the Gulf with an access to external coastal waters. Both of these have shallow sills of 24 m (cross section 0.04 km^2) and 12 m (cross section 0.03 km^2), to the southwest and northeast of Procida, respectively.

The continental shelf extends over most of the inner part of the Gulf. A number of rocky banks, scattered along the northern shores and rising up to 30-20 m from the surface, further contribute to the complicated bathymetry of the basin. The three bays of Pozzuoli, Mergellina, and Castellammare, which indent the coastline from north to south, represent important subregions of the Gulf. The presence of dense urban and industrial settlements in this area impose a need for understanding the status of most of the Gulf's marine environment. The resident population of the territory, draining directly or indirectly through rivers and channels into the Gulf of Naples and adjacent waters, amounts to about 2,700,000 inhabitants.

Metropolitan sewage is presently discharged for the most part at Cuma, outside the Gulf, four miles north of Procida Island. Many minor outfalls are nevertheless found along the shores of the Gulf proper, except for the Sorrentine Peninsula where the sewage is mostly treated before discharge.

EUROSTAFF (1973) has calculated the daily rate of total waste discharge in the Gulf and adjacent waters as 534,667 kg BOD_5, 131,707 of which are of domestic origin and 402,960 industrial. The areal distribution can be summarized as follows:

Cuma outfall	domestic	53,450 kg/day
	industrial	77,745 "

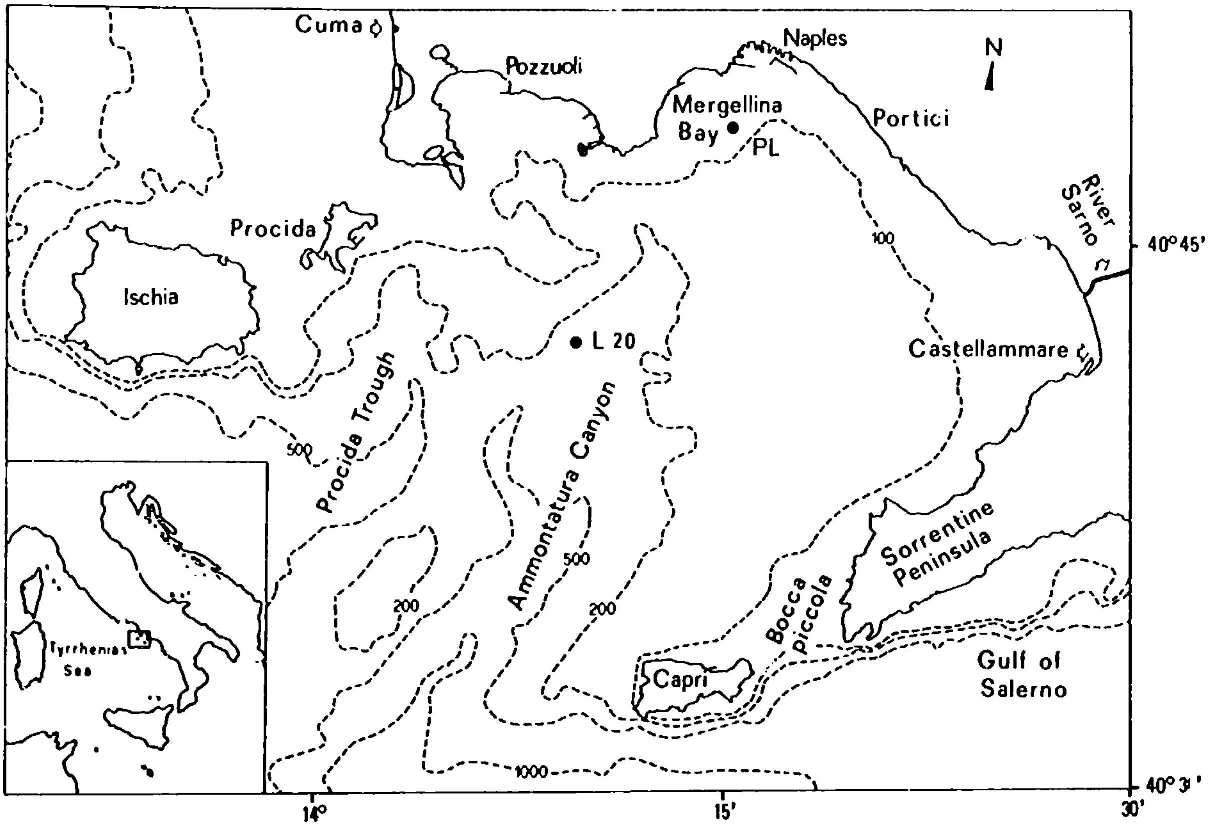


Fig. 48. Topographical map of the Gulf of Naples, showing location of L20 and coastal primary productivity station (PL) (CARRADA et al., 1980).

Pozzuoli Bay	domestic	6,928	"
	industrial	12,657	"
Naples Harbor to Castellammare Bay	domestic	62,611	"
	industrial	260,635	"
Sorrentine Peninsula	domestic	4,399	"

The differential discharge of urban waste and land runoff in the three bays of Pozzuoli, Mergellina, and Castellammare accounts for their distinctiveness in ecological terms, but the degree of overlap between these systems appears to be increasing. Furthermore, the bay of Castellammare receives the effluent of the Sarno River, which has only a slight hydrographical effect, but acts as an important additional source of nutrients for the eastern part of the Gulf.

Data Set

Despite the activity of the Stazione Zoologica for more than a century in the Gulf of Naples, the ecological information available on its ecosystem is still scarce and fragmentary. A review of the available information on the Gulf ecosystem can be found in MONCHARMONT (1977) and CARRADA et al. (1980).

In 1975, following the launching of the National Programs for Oceanography by the National Research Council (CNR), the Stazione Zoologica was granted financial support to start a five-year program on the Gulf of Naples.

A research group, designated GONEP, including both staff members and scientists from foreign institutions, was established to deal with the hydrographic and pelagic compartments of the Gulf. A second team, dealing with problems of benthic ecology, was also activated at the Ischia Marine Ecology Laboratory of the Stazione Zoologica.

Since 1975, GONEP has conducted seven major cruises, sampling hydrographic and biological parameters within the Gulf and adjacent waters. An average of 30 stations were sampled on each cruise. During cruises GONEP I, III, IV, V, and VI surface contour maps of the surface distributions of temperature, salinity, nutrients, and chlorophyll were made.

In January 1976 an annual cycle of biweekly samplings was started at the fixed station L20 (Fig. 48) providing a complete time series for temperature, salinity, dissolved oxygen, nutrients, transparency, chlorophyll a, phytoplankton and zooplankton. Physical and chemical parameters were sampled at hydrographic standard depths, chlorophyll a and phytoplankton at five depths (0, 5, 10, 25, 50 m) and zooplankton at two depth intervals (300-0; 50-0). A total of 178 phytoplankton species and 204 zooplankton species, 123 of which were Copepods, were found to be present at L20 throughout the year.

Sixteen cruises, at monthly intervals, have also been conducted in the inner portions and including the eutrophied areas of the Gulf in order to provide information on spatial and temporal trends of surface, temperature, salinity, nutrients, and chlorophyll.

Primary productivity measurements have been carried out biweekly during six months at two coastal stations (L20 and PL in Fig. 48) including chlorophyll, number of cells and ^{14}C uptake.

Additional samplings for water movements via current meters and drogues and meteorological parameters have also been conducted in varying degrees of completeness. The sampling activities and the parameters measured are summarized in Table IX. A sampling grid was used as reference for the horizontal positioning of stations.

Water Mass Characteristics

By virtue of its depth, the Gulf of Naples is exposed to three Tyrrhenian water masses: Tyrrhenian Surface Water (TSW), Tyrrhenian Intermediate Water (TIW), and Levantine Intermediate Water (LIW). The LIW originates in the eastern Levantine Sea (MORCOS, 1972; HOPKINS, 1978) as a result of winter atmospheric buoyancy extraction processes. During formation, its water type varies about 15.5°C and 39.1 ppt. As it moves westward, it conforms to a fairly consistent T-S regression (WÜST, 1961) such that on reaching the straits of Sicily it is characterized by a water type of 14.2°C and 38.7 ppt. Entry and distribution of the LIW in the Tyrrhenian has not been thoroughly described. The work of LACOMBE and TCHERNIA (1960) and the data of ALIVERTI et al. (1968) show the LIW to completely occupy the Tyrrhenian although the thickness and value of the salinity maximum vary. Its presence in the Ammontatura Canyon in the Gulf of Naples has been demonstrated by HOPKINS and GONEG (1977), where it has a water type of ~14°C and ~38.65 ppt. The depth of its upper limit (38.6 ppt isohaline) varies from >200 m in summer to >300 m in winter. The LIW does not directly affect the TSW, but it does act as an upper bound to salinities reached in the TIW.

The TIW is itself a winter water being formed as a result of local buoyancy extraction processes. Because the atmospheric conditions are not so severe, nor the circulation so favorable off the west coast of Italy, as they are off the south coast of France, no Tyrrhenian winter water is formed which is more dense than the LIW. Consequently, the TIW lies above the LIW and is characterized by fresher water of nearly the same temperature (13.6-14.2°C and 37.8-38.6 ppt), and during the warming portion of the year, by a temperature minimum. Its production and distribution in the Tyrrhenian are less well described than the LIW (e.g., LACOMBE, 1974). For the Gulf of Naples the TIW plays an important role since about 3/4 of the volume of the Gulf is occupied by this water.

Table IX. GONEP Sampling Activity

Cruises	Area	Number of stations	Depths sampled	Parameters
GONEP I March 28- April 1, 1975	Gulf of Naples and adjacent waters	35	Standard hydrographic	T, S, oxygen, pH, transparency, NH_4, NO_2, NO_3, PO_4, SiO_2, Chl *a* (surface), zooplankton, (qualitative and quantitative) 50-0 m at 29 stations.
		93	Surface	Contour mapping (April 1) of T, S, NH_4, NO_2, NO_3, PO_4, SiO_2, Chl *a*.
GONEP II April 28- May 26, 1975	" "	27	50-0 m bottom-0 m	Zooplankton (qualitative and quantitative).
GONEP III March 20- April 13, 1976	" "	37	Standard hydrographic	T, S, oxygen, pH, transparency, NO_2, NO_3, PO_4, SiO_2, Chl *a* (4 depths), zooplankton (bottom-0 m; 50-0 m).
		50	Surface	Contour mapping (March 3) of T, S, NO_2, NO_3, PO_4, SiO_2, Chl *a*.
		50	Surface	Contour mapping (April 13) of T, S, NO_2, NO_3, PO_4, SiO_2, Chl *a*.
GONEP IV June 8-24, 1976	" "	23	Standard hydrographic	T, S, oxygen, pH, transparency, NO_2, NO_3, PO_4, SiO_2, Chl *a* (surface).
		46	Surface	Contour mapping (June 9) of T, S, NO_2, NO_3, PO_4, SiO_2, Chl *a*.
		33	Surface	Contour mapping (June 24) of T, S, NO_2, NO_3, PO_4, SiO_2, Chl *a*.
GONEP V July 14-15, 1977	Gulf of Naples and adjacent waters	51	Surface	Contour mapping of T, S, NO_2, NO_4, PO_4 SiO_2, Chl *a*, phytoplankton (6 stations).
GONEP VI October 26- November 6, 1977	" "	47	Standard hydrographic	T, S, oxygen, pH, transparency, NO_2, NO_3, PO_4, SiO_2, Chl *a*, phytoplankton.
		31	Surface	Contour mapping (Nov. 6) of T, S, NO_2, NO_3, PO_4, SiO_2, Chl *a*.
GONEP VII February 7-18, 1979	" "	20	Standard hydrographic	T, S, oxygen, pH, transparency, NH_4, NO_2, NO_3, PO_4, SiO_2, Chl *a*, phytoplankton (surface).
Station L20 January 1976 to June 1977, Biweekly	Gulf of Naples 40° 42.1'N 14° 10.2'E		Standard hydrographic	T, S, oxygen, transparency, NO_2, NO_3, PO_4, SiO_2, Chl *a*, phytoplankton (qualitative and quantitative), zooplankton (qualitative and quantitative).
December 1977 to May 1980, Biweekly			Five light levels	Primary production: ^{14}C uptake, Chl *a*, nutrients, species composition and abundance.
CONTOUR CRUISES February 1976 to June 1977	Gulf of Naples Inner northern area.	40	Surface	Contour mapping of T, S, oxygen, NO_2, NO_3, PO_4, SiO_2, Chl *a*.

T = temperature; S = salinity; NO_2 = nitrite; NO_3 = nitrate; PO_4 = phosphate; Chl *a* = chlorophyll; NH_4 = ammonia; SiO_2 = silicate.

The annual cycling of the water masses can be well demonstrated on a T-S diagram (Fig. 49), where the 20 m and 75 m values from station L20 are compared. The column becomes isopycnal (to 75 m) around the first of January but retains some salinity structure until the first of March when the entire column to 75 m is homogeneous. From March to September the 20 m warms with little increase in salinity; during September it salts to maximum October salinities as fall overturn begins and salt is mixed in from deeper layers. From October to March, the 20 m values are representative of the entire surface layer, and they follow a T-S cooling slope of 8°/0.25 ppt. Winter runoff more than compensates for increases in salinity due to evaporation and convective mixing. As a consequence the TIW (at 75 m) has a salinity minimum (and temperature minimum) in March. The 75 m water type remains stable during the stratified period until October when it drifts to warmer, fresher values in response to convective admixtures of TSW. By the time of maximum convective mixing, it is at its temperature minimum.

The TSW is very strictly seasonal, being distinguishable from the TIW only during the stratified season as the superficial water mass above the thermocline. It has no stable water type although its summer T-S values are about 26°C and 38 ppt. Closer inshore the variability increases; in fact, CARRADA et al. (1980) have defined a Coastal Surface Water (CSW) as having distinct properties (mostly chemical) from the TSW. Coastal freshwater discharge and effluents are primarily responsible for the greater variability of the CSW. The water mass characteristics are summarized in Fig. 50.

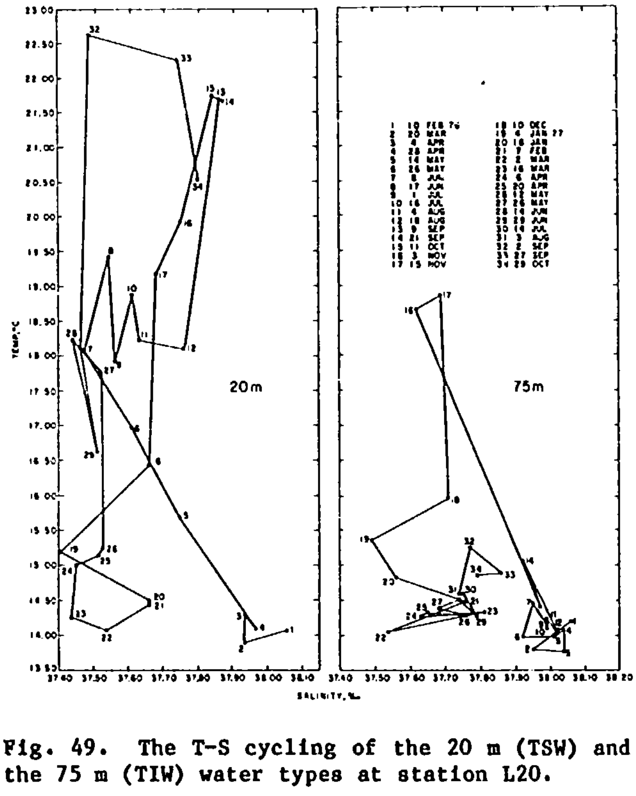


Fig. 49. The T-S cycling of the 20 m (TSW) and the 75 m (TIW) water types at station L20.

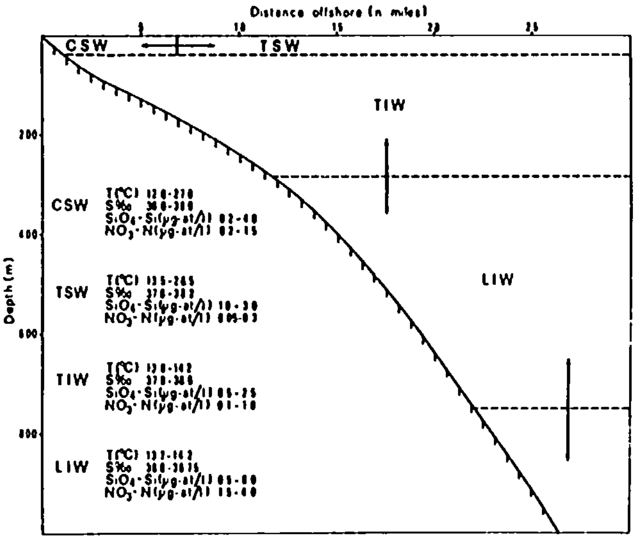


Fig. 50. Schematic distribution and physicochemical characteristics of the water masses within the Gulf of Naples (CSW: Coastal Surface Water; TSW: Tyrrhenian Surface Water; TIW Tyrrhenian Intermediate Water; LIW: Levantine Intermediate Water).

Nutrients

The distribution of nutrients in the Gulf shows pronounced variations both in space and time. Strong offshore gradients are usually present throughout the year in the inner area, where the influence of urban discharge and runoff is stronger. Within this general pattern, different distributions are often observed among the three inner bays of Pozzuoli, Mergellina and Castellammare. As already mentioned, these bays are affected by differential discharge of domestic and industrial wastes as well as by different microclimatic regimes which can result in significant variability in rainfall, and hence runoff, between the coastal regions of the Gulf. In addition, the connection of the northern part of the Gulf with external coastal waters through the channels of Ischia and Procida, allows the plumes of the Volturno River and Cuma outfall to enter the Gulf and influence the channel areas, and, at times, as far within the Gulf as station L20 (CARRADA et al., 1980, 1981a,b). Figs. (51), (52), and (53) are an example of the temporal and spatial distribution of surface nitrates, phosphates and silicates in the northern part of the Gulf.

At the fixed station L20 the observed values of the same nutrients fall within the range known for open Tyrrhenian waters (Fig. 50). The waters of L20 may then be considered to represent the hydrographic characteristics of the 'open waters' of the Gulf, where oligotrophic conditions, driven by the seasonal succession of external water masses, can be considered as constant. Only occasionally, strong plumes originating in the bay of Pozzuoli, or the already mentioned advection of external coastal waters, may raise the surface concentration of nutrients at L20 (CARRADA et al., 1980, 1981a,b).

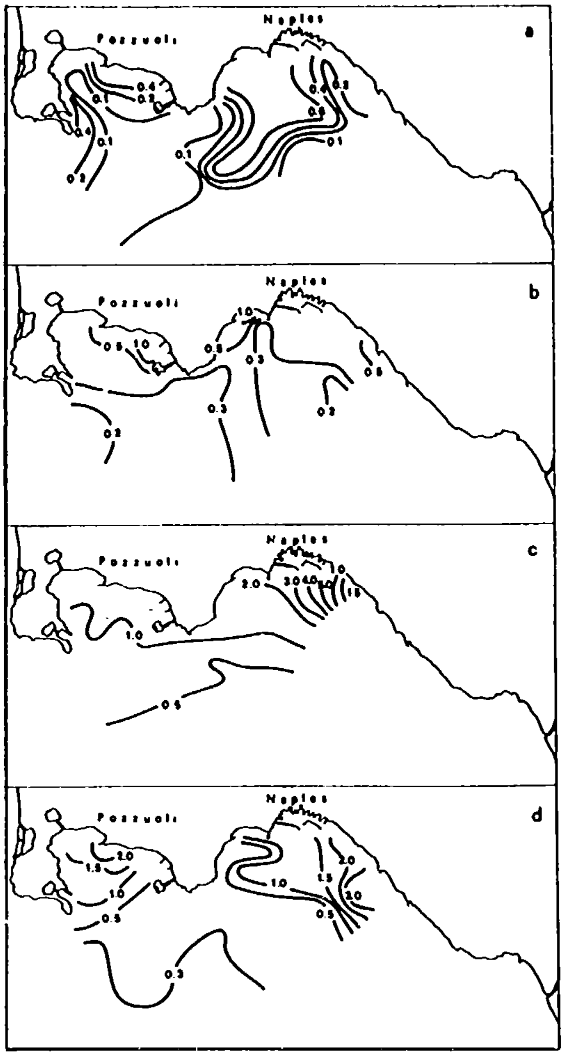


Fig. 51. Surface contours of nitrate (μg-at/ℓ) on (a) July 1, 1976, (b) October 11, 1976, (c) January 18, 1977, (d) April 6, 1977. From CARRADA et al. (1980).

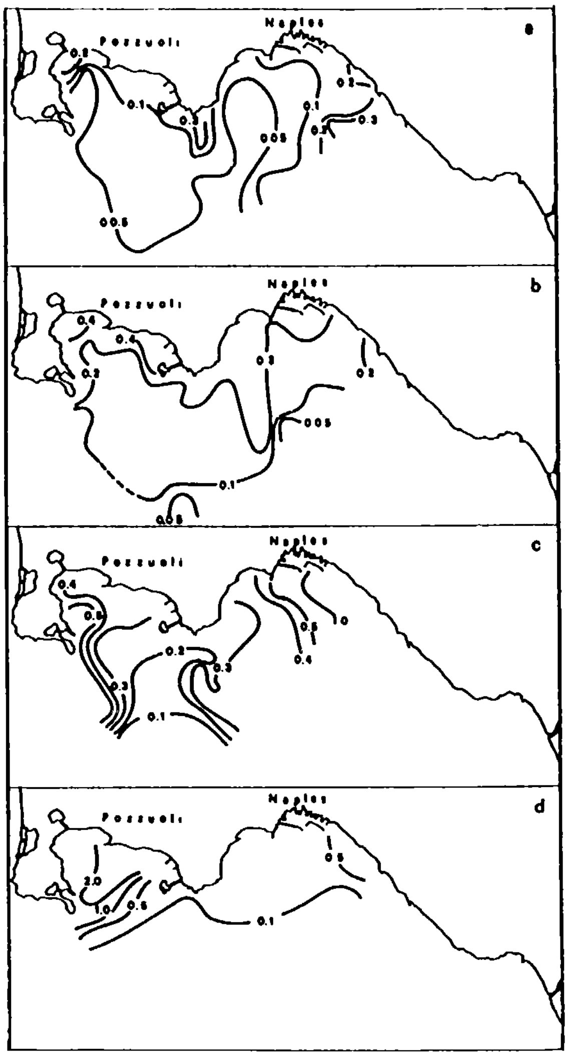


Fig. 52. Surface contours of phosphate (μg-at/ℓ) on (1) July 1, 1976, (b) October 11, 1976, (c) January 18, 1977, (d) April 6, 1977. From CARRADA et al. (1980).

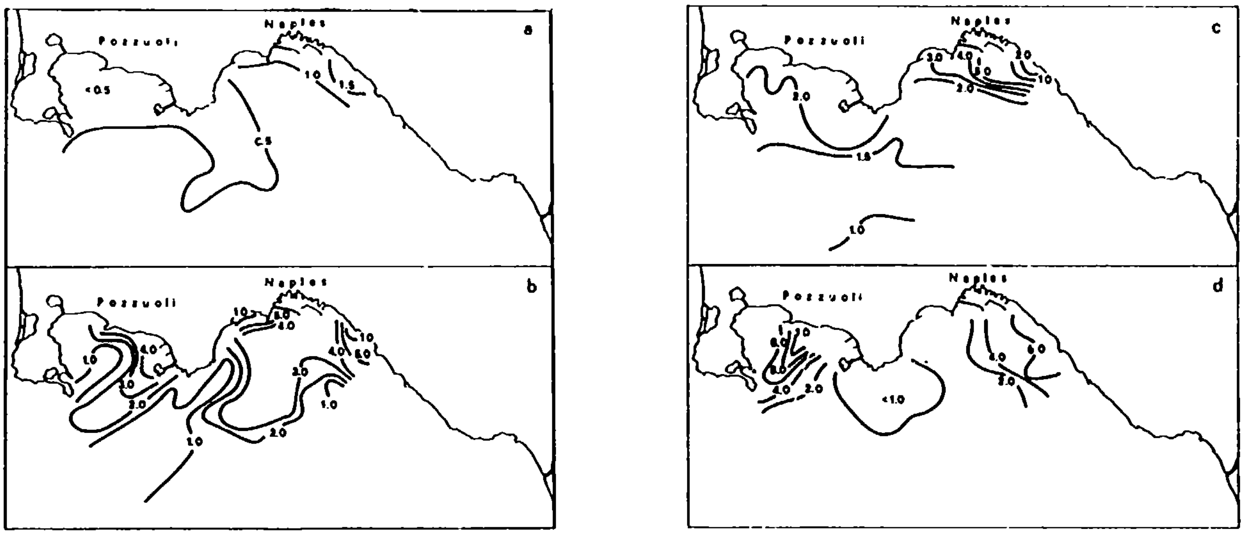


Fig. 53. Surface contours of silicate (μg-at/ℓ) on (a) July 1, 1976, (b) October 11, 1976, (c) January 18, 1977, (d) April 6, 1977. From CARRADA et al. (1980).

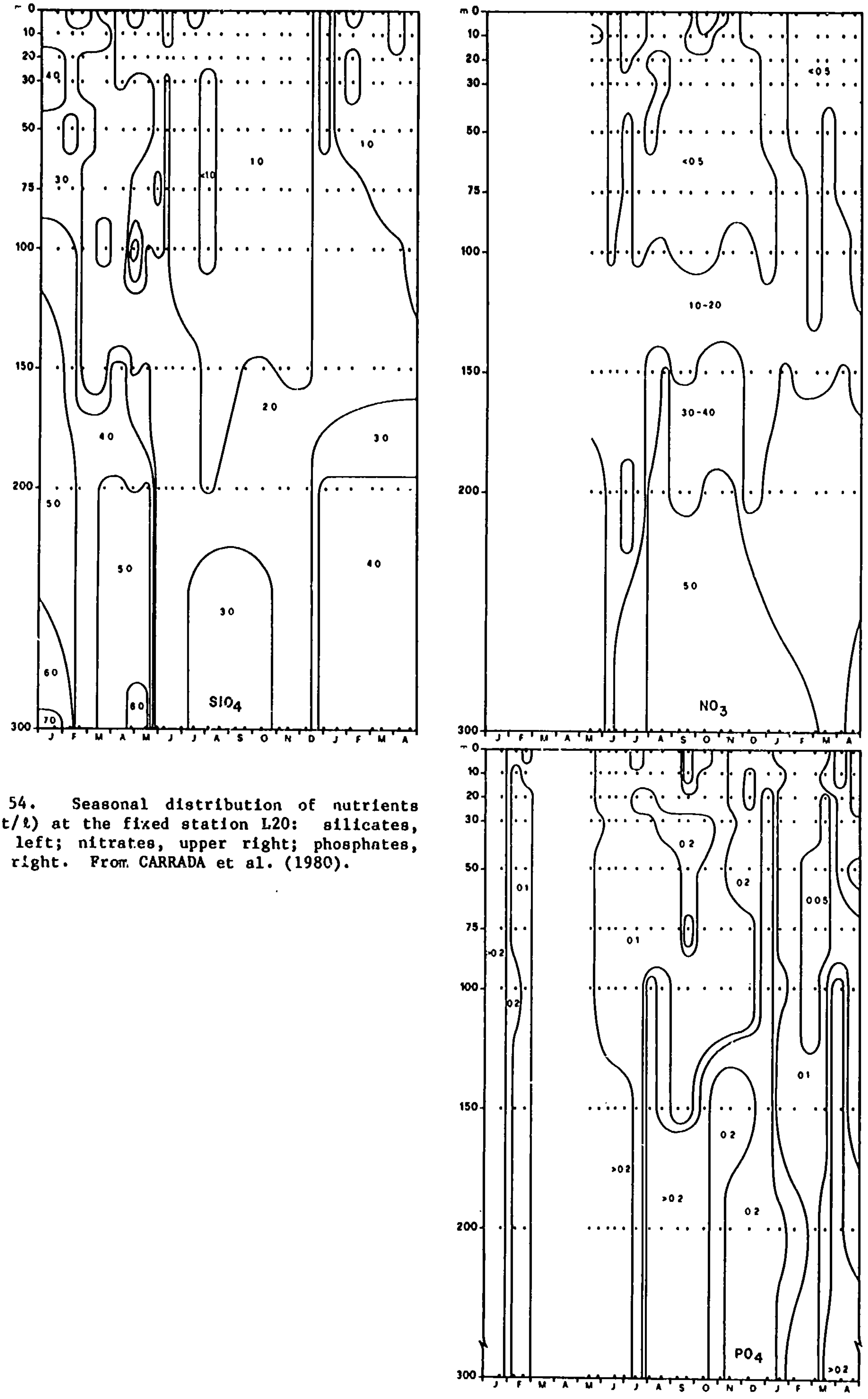


Fig. 54. Seasonal distribution of nutrients (µg-at/ℓ) at the fixed station L20: silicates, upper left; nitrates, upper right; phosphates, lower right. From CARRADA et al. (1980).

Chlorophyll and Phytoplankton

The contour mapping of surface chlorophyll concentrations has revealed pronounced spatial variations within a range from up to 20 mg/m^3 alongshore to an average of 0.3 mg/m^3 for the mid-Gulf.

Fig. 55 shows the spatial distribution of surface chlorophyll a in March 1976 and July 1977 for the entire area of the Gulf; and Fig. 56 for the inner areas in the different seasons. Both the concentrations and periods of occurrence of the peaks are uncorrelated in time for the different sub-areas of the coastal region. The same trend has been observed for the temporal and spatial distribution of nutrients. This suggests that the dynamics of production processes in the littoral section of the Gulf are likely to be driven primarily by the quality, quantity, and uneven distribution of land runoff, more than by the circulation patterns or by seasonal water mass differences (CARRADA et al., 1980).

The high concentrations of chlorophyll at the coast decrease toward mid-Gulf, to the average Tyrrhenian values so that, at the fixed station L20 (three miles offshore) concentrations are about 0.2-0.5 mg/m^3.

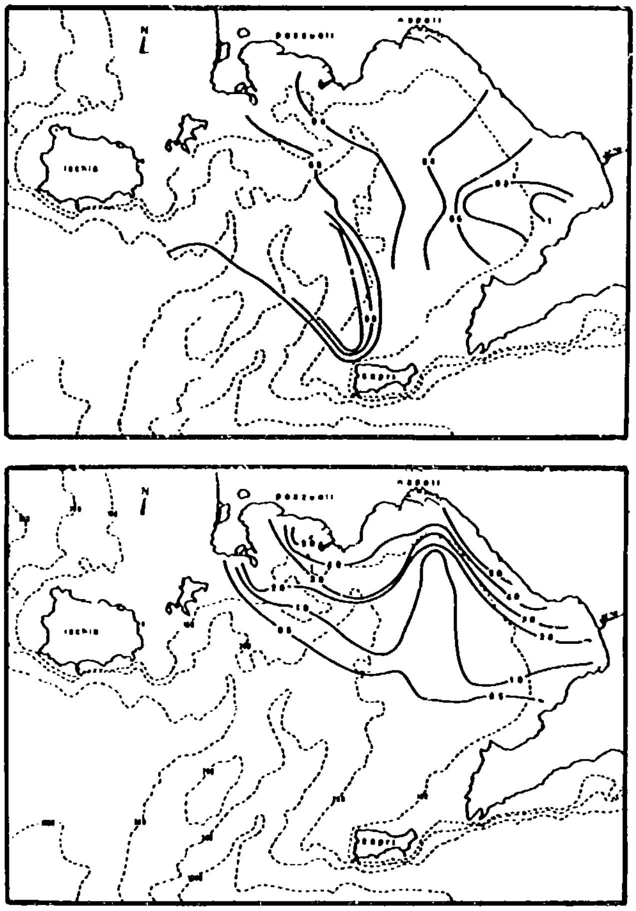


Fig. 55. Surface contours of chlorophyll a (mg/m^3) on March 22, 1976, upper; and on July 14, 1977, lower. From CARRADA et al. (1981b).

Fig. 57 compares surface chlorophyll annual concentrations at two littoral stations (Pozzuoli and Mergellina) and at station L20. Fig. 58 shows the annual variation of chlorophyll a in the euphotic zone at station L20.

The most coherent information on the phytoplankton of the Gulf comes from the time series of biweekly samples collected at L20. The series recorded 93 Diatoms, 75 Dinoflagellates, 3 Coccolithophores and 3 Silicoflagellates. An annotated checklist of the phytoplankton Diatoms for the Gulf is being published by MARINO and MODIGH (1982).

On a quantitative basis (CARRADA et al., 1979 and GONEP, unpublished data), the spring peak (204,000 cell/ℓ) is mostly due to Diatoms (64%) followed one month later by another peak (113,000 cell/ℓ) mostly due to Dinoflagellates. In this period the dominant species of Diatoms are Nitzschia closterium (78%), Nitzschia longissima (4%) and Chaetoceros compressum (4%);

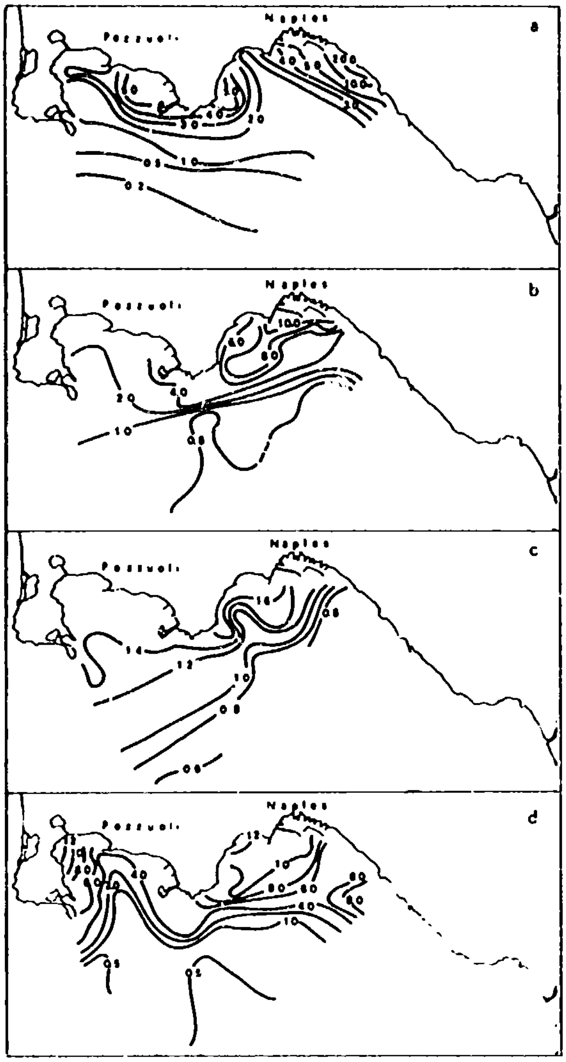
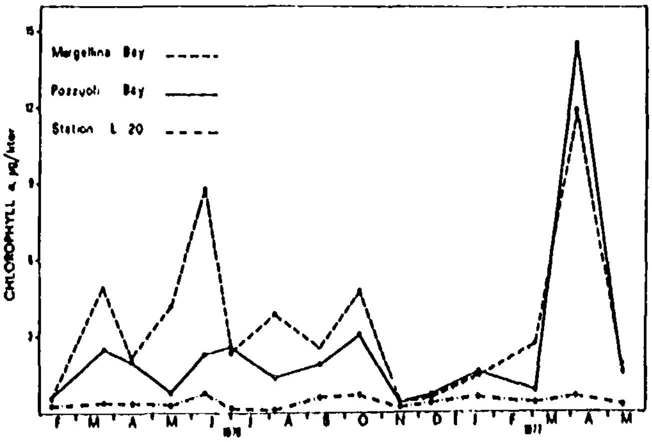


Fig. 56. Surface contours of chlorophyll a (mg/m^3) on (a) July 1, 1976, (b) October 11, 1976, (c) January 18, 1977, (d) April 6, 1977. From CARRADA et al. (1980).



[illegible]g. 57. Seasonal variations of surface chlorophyll a (mg/m^3) at Pozzuoli and Mergellina Bays and station L20. From CARRADA et al. (1980).

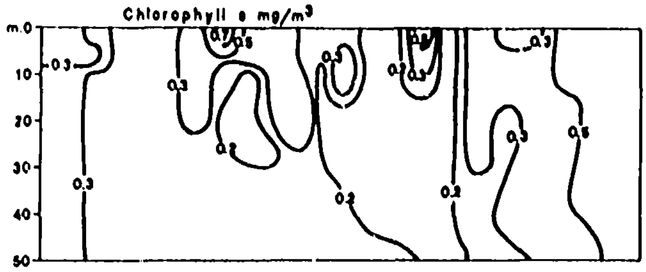


Fig. 58. The annual variation of chlorophyll a (mg/m^3) at Station L20, from January 1976 through January 1977. From CARRADA et al. (1979).

of Dinoflagellates, Gymnodinium sp.p. reached 80%, Prorocentrum micans 4% and Amphidinium acutissimum 3%.

The autumn peak (241,000 cell/ℓ) was largely due to Dinoflagellates (43%), followed by Coccolithophores (28%) and Diatoms (10%). Among the Dinoflagellates the dominant elements were again Gymnodinium sp.p (84%), while several species of Peridinium and Exuviella baltica comprised 1.5%.

During winter a smaller peak (99,000 cell/ℓ) was observed, mostly due to Coccolithophores, the dominant species being Emiliania huxley. Fig. 59 gives the annual quantitative variation of Diatoms, Dinoflagellates and Coccolithophores at station L20.

Primary production was measured by TOMAS (1981), at biweekly intervals for a winter-spring period, at the shelf station PL in the bay of Mergellina (Fig. 40) and at station L20. Production values at Mergellina varied between 2.40 and 6.30 mgC/m^3/d at various depths in the water column. Integrated values varied from 0.62 to 8.2 gC/m^2. Chlorophyll a values were from 0.21 to 5.76 mg Chl a/m^3 and light intensities at 50 m rarely below 10% incident surface intensities. Total production for the winter-spring period has been calculated at 55.1 gC/m^2.

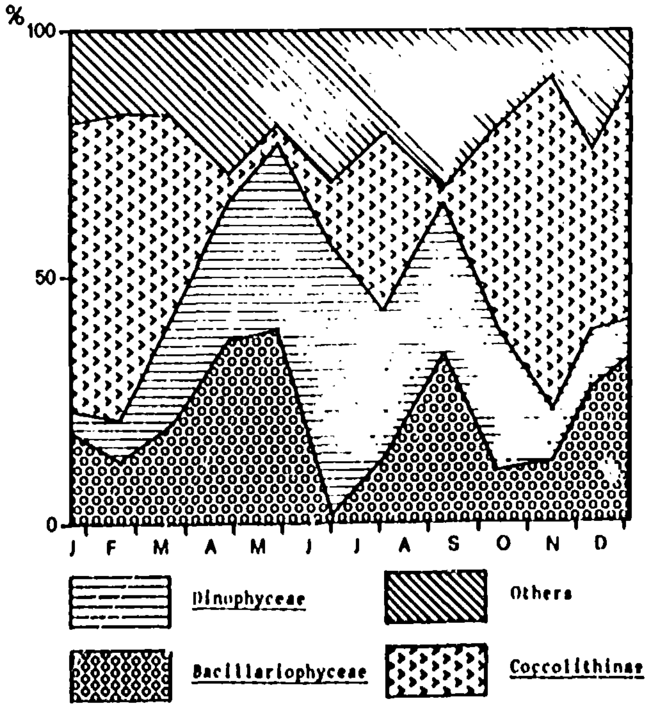


Fig. 59. Seasonal succession of phytoplankton group at station L20. Percent composition in the entire water column.

At station L20 production varied between 1.4 and 111 g mgC/m^3/d with maximal values at surface and at 50% light intensities. Integrated values were between 0.33 and 5.7 gC/m^2 for a total of 31.39 gC/m^2 for the winter-spring period. Chlorophyll a varied between 0.11 and 1.77 mg/m^3 at the surface, whereas depth values of <1.14 mg/m^3 were observed. Total inorganic nitrogen varied between 0.59–7.12 µg-at/ℓ and was undetectable during April and May, suggesting a limiting role for this parameter.

Zooplankton

The spatial and temporal structure of zooplankton communities within the Gulf is rather heterogeneous. On the basis of the qualitative and quantitative data collected during the GONEP II cruise, in May 1975, at 27 stations from 50-0 m, four communities have been identified (Fig. 60a):

a. Ischia and Procida Channels, occupied by a community characterized by Evadne spinifera, Oithona helgolandica, Oikopleura dioica;

b. Pozzuoli Bay to Naples Harbor with a community based on Decapod larvae, Podon polyphemoides, Acartia clausi and Oikopleura dioica;

c. the southeastern coast, from Naples Harbor to Capri Island, characterized by Evadne spinifera, Centropages typicus and Oithona helgolandica; and

d. the central portion of the Gulf, characterized by Paracalanus parvus, Centropages typicus, Oithona helgolandica and Decapod larvae.

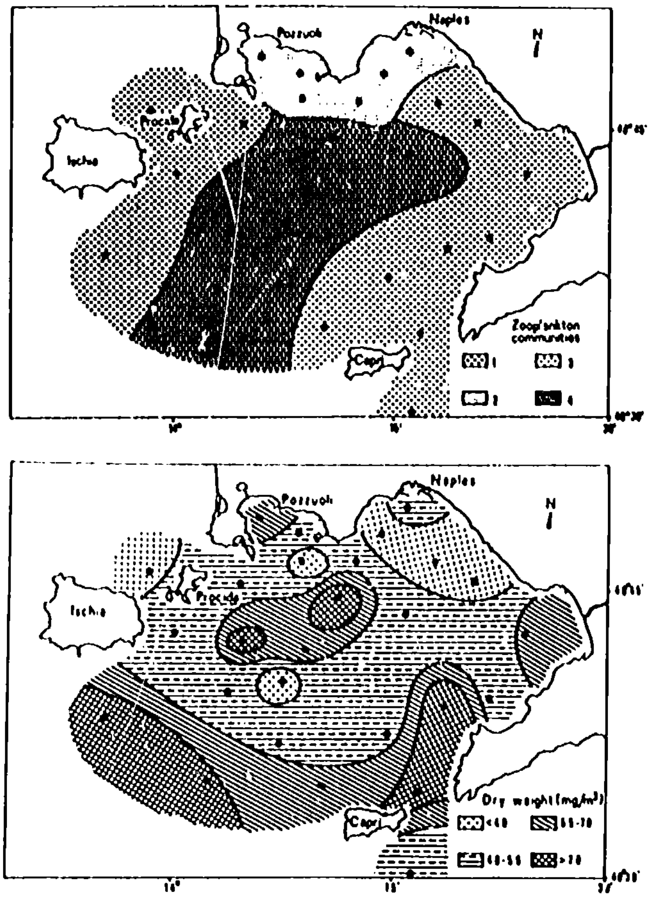


Fig. 60. Zooplankton community structure (a), and zooplankton biomass distribution (b) from 50-0 m in May 1975. (Black dots indicate sampling sites.) From CARRADA et al. (1980).

In terms of quantities, dry weight estimates of biomass increased offshore, whereas the total number of individuals decreased (Fig. 60b), indicating a preference offshore for higher standing stocks of fewer individuals of larger size (namely Copepods) and inshore for lower standing stocks with dominance of Cladocerans, meroplankton and small filter-feeding Copepods.

The time series at the fixed station L20 has provided information on the annual cycle of zooplankton communities. In the 50-0 m interval three peaks were noted. The peak in March was due to Doliolids and Appendicularians; the June maximum was due to Copepods and Cladocerans; the October peak was almost entirely due to Copepods and Appendicularians. Other minor groups characterized specific periods of the year: Siphonophores were abundant in March; Chaetognats and Cirripede larvae in April and May; Decapod larvae in October.

In terms of numbers, Copepods constituted the major portion of the total zooplankton biomass, both in the 50-0 m and 300-0 m levels, with an annual mean of 85.8% and 85.5%, respectively. For the greatest part of the year they comprised more than 80% of the total zooplankton in both levels. This percentage decreases in late winter-early spring to 50% for the increment of Appendicularians, Doliolids and Cladocerans. Fig. 61 shows the seasonal biomass distribution at the two depth intervals.

Two subsystems are present in the Gulf: coastal and open water. The coastal subsystem, including the Bays of Pozzuoli and Mergellina,

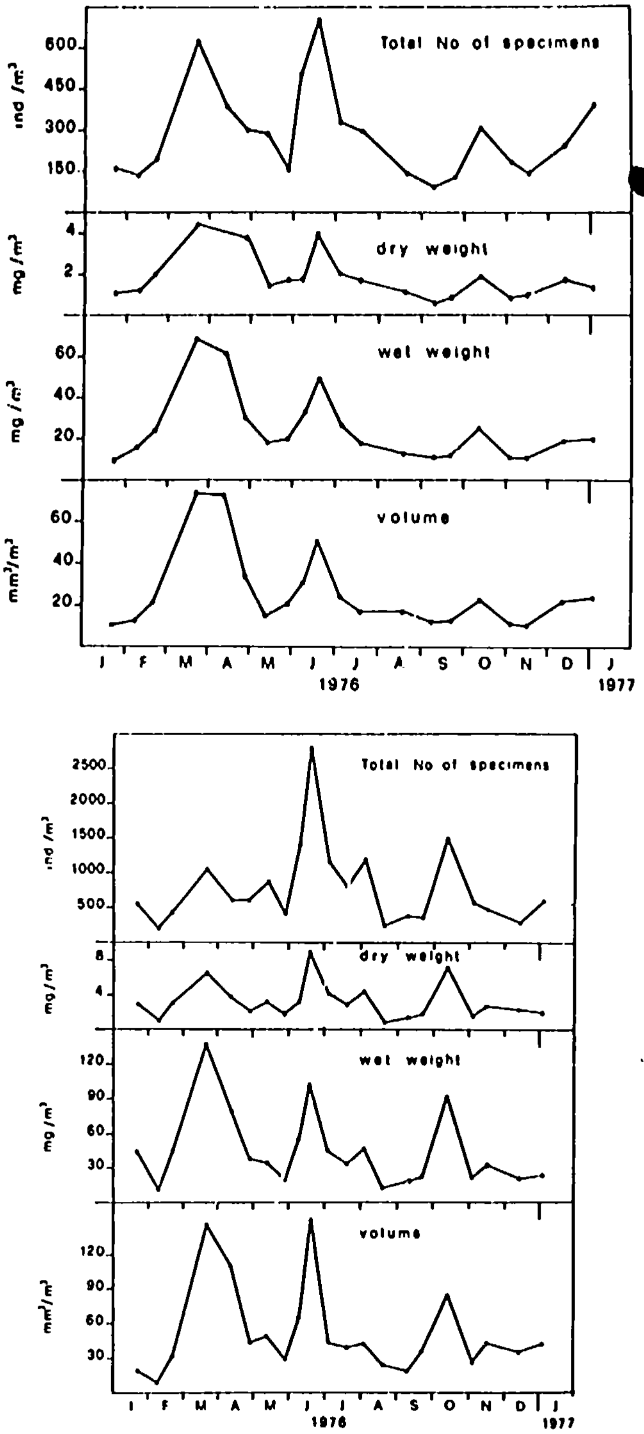


Fig. 61. Seasonal variation in zooplankton biomass at station L20: from 50-0 m (upper), and from 300-0 m (lower).

the Naples Harbor area and the Vesuvian shore down to Castellammare Bay, is essentially characterized by a permanent condition of eutrophication. Within the coastal subsystem, particularly in the Bays of Pozzuoli and Mergellina, the distribution pattern of chemical and biological parameters appears strictly linked to local runoff both in its variability and in its composition, a dependence that generates strong time dependent offshore gradients in the distributions. The exchange between coastal and open water occurs over short spatial scales. Marked gradients of the same parameters can also be found alongshore due to the complicated bathymetry and to the mentioned uneven distribution of land discharge, which explains the areal independence in timing and succession of phytoplankton biomass. A comparison of the values of the chemical and biological parameters inshore and offshore provides a means to evaluate the relative level of eutrophication of the coastal area: for chlorophyll, the values at Pozzuoli and Mergellina Bays show a mean seven to nine times that for L20 station.

The open water subsystem has oligotrophic characteristics and is essentially driven by the seasonal succession of external water masses. Station L20 is permanently characterized by nutrient and chlorophyll concentrations consistent with those reported in the literature for the open Tyrrhenian Sea. Only episodically were higher levels of nutrients and chlorophyll observed at L20 due to the presence of coastal water. The analysis of the structure of the phytoplankton and zooplankton communities, based on the L20 time series and on the areal surveys of GONEP II and GONEP VII cruises, provided additional evidence to the dual character of the ecosystem of the Gulf of Naples.

From the faunistic point of view, Copepods were the most abundant and dominated the group, both in quantity and number of species, with a total of 123 species (85 of which were from the 50-0 m level). Paracalanus parvus and Acartia clausi comprised 63.4% of the total Copepod population. Appendicularians (19 species) were the second most abundant group both in quantity and number of species, representing 4.01% of the total population from 50-0 m and 5.76% from 300-0 m. Cladocerans ranked third with five species, and their contribution to the total zooplankton biomass was particularly evident in spring and summer. Other groups did not represent quantitatively important fractions but contributed significantly to the faunistic variety of zooplankton populations: Chaetognaths with 3 species; Siphonophores, 19 species; Thaliaceans, 3 species of Salps and 3 species of Doliolids; Euphausiids, 6 species; Amphipods, 9 species; Pteropods, 5 species; Hydromedusae, 4 species. A variety of meroplankton forms were found the year round, particularly Decapod larvae.

Conclusions

The data base available to date for the Gulf of Naples is essentially descriptive and represents the output of a research program focusing mainly on the problems caused by anthropogenic loading. As a result, most of the available information deals with the inner area of the Gulf where the effects of man-made environmental alterations are most obvious. The time series at the fixed station L20, situated at the boundary of the eutrophied area, has nevertheless provided significant information also on the structure of the open part of the Gulf. It is therefore already possible to identify some general features of the ecosystem of the Gulf.

MODELLING THE GULF OF NAPLES

CONCEPTUAL MODEL

The purpose of this session of the workshop was to set the stage for the construction of the numerical model of the Bay of Naples. Based on the step by step modelling procedure that was presented during the introductory lectures, the objectives, boundaries, subsystems, state variables and forcing functions were discussed.

Objectives

After a thorough discussion of the objectives of the numerical model of the Gulf of Naples, and taking into account the available data base, it was concluded that the most realistic objective was to construct a mechanistic numerical model which would simulate the pathways and feedbacks of the coastal and offshore ecosystems and show the influence of the polluted coastal area to the offshore region.

Boundaries

Geographical boundaries of the ecosystem of interest were determined as: coastline from Punta di Fumo to Punta Campanella, line connecting Ischia with Capri and both islands with the mainland.

Conceptual boundaries were determined as: nutrients, phytoplankton, and zooplankton as parts of the pelagic trophic web, and the interaction of the benthic communities (including macrophytes) and sediments with the overlying water.

Subsystems

In order to develop a simulation model of the Gulf of Naples, the ecosystem was divided for practical and conceptual reasons into two parts, that involving the circulation or 'physical model,' and that involving the biology and chemistry or 'biological model.' The two models acted as submodels of the general model. The physical model supplied the biological model with the mass exchanges due to the circulation.

State Variables and Forcing Functions

State variables for the biological model were chosen on the basis of general knowledge and specific knowledge of processes, concentrations, biomasses, and fluxes of the most important components of the Gulf of Naples. The following state variables were chosen as most important and suitable for the numerical modelling procedure: nitrate, ammonia, phosphate, silica, diatoms, other phytoplankton, ciliates, filterfeeders, carnivorous zooplankton, juvenile zooplankton, benthic macrophytes, dead organic matter, and sediments.

The workshop split into two working groups which were devoted to the construction of these two models. The persons leading the discussions were T. Hopkins for the physical model, and S. Jørgensen, J. Kremer and S. Nixon for the biological model. Both groups started to work with the elaboration of the conceptual model agreed upon in plenary sessions and then proceeded with the numerical stages of their models.

In order to make the presentation of the model construction phase as understandable as possible, the elaboration of both physical and biological conceptual models will be presented in their corresponding sections of the following text (Figs. 61 and 65).

PHYSICAL MODEL

Introduction

It was felt that the purpose of the working session should be to proceed as far as possible towards completing a numerical model. The exercise was considered valuable and instructive even though the hardware limitation prevented a numerical output. None of the participants had quite experienced such an activity and, consequently, all were pleasantly surprised by the outcome. The normal modelling experience involves on the order of one to ten man-years for a complete model, so that the various modelling stages are normally not experienced over such a short time interval as occurred in the working session. This provided a really valuable perspective for those involved. It was felt that this type of activity should precede any serious modelling endeavor. The restriction of time at the workshop was perhaps a little too severe and was exaggerated by the necessity to prepare certain routine software.

It was hoped that this modelling exercise would have a value apart from that derived from participating in the exercise itself. To that end the model was constructed as generally as limitations would allow. The applicability to other systems was noted in discussions and appears to some degree in the following description. Every attempt was made to make the included software code generally applicable, although it should be considered as an instructive example, with possible errors, rather than as a packaged program for use without modification.

The schematic shown in Fig. 61 was used for the basis of the conceptual model discussion. It was very useful in conceptualizing the various interactions and processes. For example, if one wished to consider only barotropic waves, one would deal mainly with the BT PE and BT KE storages and their mutual transfers. However, at some scales the effects of depth, Coriolis, continuity, and friction all must be considered. In the figure, these connecting lines act as a visual reminder.

Forces and Boundary Conditions

Considerable discussion was spent on various types of models and their applicability to Mediterranean coastal ecosystems. The objective primarily was to evaluate the relative importance of the various forcing functions. Except

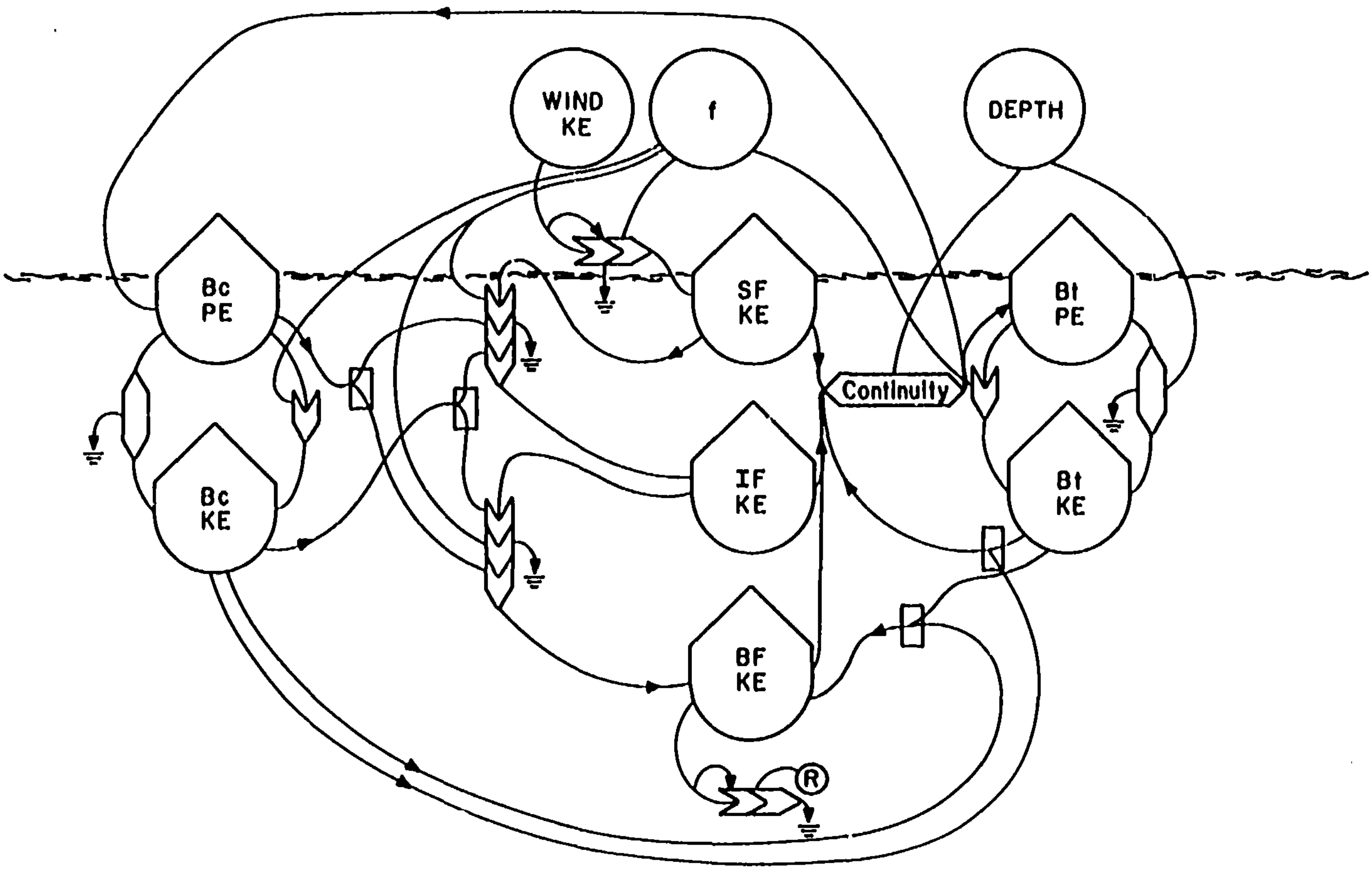


Fig. 62. Conceptual model for coastal dynamics, including barotropic (Bt) forcing, baroclinic (Bc) forcing, wind, and friction (SF=surface friction, IF=internal friction, and BF=bottom friction). KE, PE, R, and f stand for kinetic energy, potential energy, bottom roughness and the Coriolis parameter, respectively.

for the northern Adriatic, the effect of tides is small and need not be modelled. Forcing by the baroclinic pressure field may or may not be included depending on depth and season. Coastal systems generally have a strong summer pycnoclines at about ~20 to 30 m, the depth being dependent on the extent of wind mixing (e.g., KRONFIELD and HOPKINS, 1976). Stratification is derived primarily from the thermal difference which is fairly consistent Mediterranean-wide, on the order of 14 to 25°C . The resulting pycnocline may be on the order of > 3 sigma-t units. However, in coastal systems the vertical stratification can be exaggerated due to warmer surface temperatures or due to lower salinities caused by local runoff. In any case, considerable internal potential energy is available to dampen barotropic motions in the lower layer and, consequently, must be included in summer circulation models. Winter baroclinicity may also be significant when small horizontal density gradients are persistent over deep water columns.

Barotropic pressure gradients inevitably are present in coastal systems, being generated primarily by wind transport divergences/convergences against coastal boundaries. With irregularities in coastal topography, appreciable wind stress variations may occur even over short spatial length scales and drive divergences/convergences in the interior through the wind stress curl.

The inclusion of some dissipative force is necessary for coastal circulations where frictionless dynamics are apt to be poor approximations. Particularly bottom stress should not be excluded in shallow or in bathymetrically rough regions.

Representing the proper boundary conditions is one of the greatest difficulties in developing a coastal circulation model. For semi-enclosed bays such as the Gulf of Naples, the condition of no momentum flux at the coast can be imposed. This is a simpler boundary condition than that representing the momentum flux at one of the open boundaries. Even so, the solid boundary condition becomes increasingly approximate, in practice, for gradually sloping near-shore bathymetry where the frictional forces are not well understood and poorly formulated. The open boundary condition is facilitated, if it exists along a zone of dynamic uncoupling (Lecture on Physical Processes).

It is difficult to justify the construction of a steady state model on any other basis than that it is simple and instructive. Coastal circulations invariably have considerable energy in the meso-scale portion of the spectrum (~1 to 40 hours). The significance of this portion is enhanced when one of the main purposes of the circulation is to feed into a biochemical model. However, steady models are very useful in terms of the low frequency framework that they describe. They are not so sensitive to inaccuracies in the solid boundary condition, but they can depend strongly on the open boundary condition. Yet for this very reason they are a requisite step toward time dependent models, since they provide an instructive mechanism to calibrate the open boundary condition against low frequency (days to weeks) observations of the circulation. For these reasons, and because of obvious computation limitations, a time dependent model was not attempted for the Gulf of Naples case study.

One concession to simplicity that was not made was to include a mechanism to recover the z-dependency from the integrated flow field. Vertical fluxes to the surface layer and its differential movement with respect to the underlying water column are essential to the accuracy of a biochemical model.

Equations for Sea Level Model

The problem was formulated in the following way. The full time dependent equations of motion (e.g., NEUMANN and PIERSON, 1966) were reduced to the relevant forces

$$-fv = -\phi_x - P_x + (Au_z)_z \qquad (1)$$

$$fu = -\phi_y - P_y + (Av_z)_z \qquad (2)$$

$$u_x + v_y = -w_z \qquad (3)$$

where the derivatives are indicated by subscripts. A is the kinematic viscosity. The complex potential function ϕ is the barotropic pressure gradient,

$$\phi_x + i\phi_y = -g(e_x + ie_y) \qquad (4)$$

where g is the gravitational acceleration and e the sea level displacement. The complex baroclinic pressure gradient is written as

$$\nabla P = P_x + iP_y \text{ and } P = \frac{g}{\bar{\rho}}\int_0^z \rho\,dz\ . \qquad (5)$$

The coordinate system is oriented such that the y-axis lies parallel to the coast, the x-axis extends offshore, and the z-axis is positive downwards.

Equations (1-3) can be integrated over the water column depth, d,

$$-fV = -d\phi_x - \Psi_x + \tau^{sx} - \tau^{dx} \qquad (6)$$

$$fU = -d\phi_y - \Psi_y + \tau^{sy} - \tau^{dy} \qquad (7)$$

$$U_x + V_y = 0\ . \qquad (8)$$

The transports are defined as $(U,V) = \int_0^d (u,v)dz$, and the complex baroclinic transport potential as

$$\nabla\Psi = \int_0^d (P_x + iP_y)dz, \qquad (9)$$

or we can express its components as

$$\Psi_x = R_x - d_xP^d, \quad \Psi_y = R_y - d_yP^d$$

where $R = g\int_0^d\int^z \rho dz$ and $P^d = g\int_0^d \rho dz$.

The surface stress, τ^s, and the bottom stress, τ^d, result from the vertical integration of the vertical friction terms in (1) and (2).

If equations (6) and (7) are cross differentiated and subtracted, then

$$J(d,\phi) + J(d,P^d) = \mathrm{curl}(\tau^s - \tau^d) \qquad (10)$$

where use was made of equation (6) and that

$$\phi_{yx} = \phi_{xy},\ \Psi_{yx} - \Psi_{xy} = d_xP^d{}_y - d_yP^d{}_x = J(d,P^d)$$

Equation (10) includes three unknowns, ϕ , P^d, and τ^d. It is assumed that the distribution of τ^s is known, and of course that d is known everywhere. In order to solve (10) for ϕ , we must make approximations of τ^d and P^d, and we must express the boundary conditions for ϕ.

Transport Components

Before proceeding with the input information and boundary conditions for equation (10), we discuss equations (6) and (7) in terms of the different forcing functions. This can be done by a linear decomposition into transport components of the left-hand side, each of which is driven by a corresponding forcing term on the right-hand side, as for example from (6)

$$f[V_{BT} + V_{BC} + V_{SEK} + V_{BEK}] =$$

$$\underset{\overset{\uparrow}{BT}}{d\phi_x} + \underset{\overset{\uparrow}{BC}}{\Psi_x} - \underset{\overset{\uparrow}{SEK}}{\tau^{sx}} + \underset{\overset{\uparrow}{BEK}}{\tau^{dx}} \qquad (11)$$

where BT = Barotropic, BC = Baroclinic, SEK = Surface Ekman, and BEK = Bottom Ekman.

It is quite important to point out that these are not truly linearly separable by virtue of vertical friction which gives rise to the third and fourth terms. However, a look at the response to various combinations of these forcing terms is essential to understanding their behavior. One can find a more complete discussion in the literature, e.g., FOFFONOF (1962), KUNDU (1976), or HOPKINS and SLATEST (1982). We note here a few points germane to our modelling approach.

a. Water columns deeper than ~30 m can be characterized by the three dynamic layers corresponding to SEK, BT and/or BC, and BEK. For shallower depths the two frictional layers begin to overlap, making the parameterization of bottom friction more difficult. This separation depends on the magnitude of the eddy viscosity, A (e.g., MADSEN, 1977, or HOPKINS and SLATEST, 1982)

b. The bottom stress is ultimately a function of the interior flow and the bottom roughness. From the top of the constant stress layer, proceeding down to the bottom, the stress remains constant and the velocity decreases logarithmically to zero; and proceeding up through the bottom Ekman layer, the stress decreases and the velocity increases to their respective interior values.

c. In the event of baroclinic forcing, the barotropic interior velocity will be reduced, and in the event of complete pressure adjustment between the barotropic and baroclinic fields at some depth at or above the bottom, the flow at the bottom will be negligible and consequently also the bottom stress. In such situations, the kinetic energy of the flow is dissipated internally rather than at the bottom. Near the coasts, complete adjustment is unlikely, but strong baroclinic shears may result due to large displacements of the pycnocline within the coastal boundary layer (see CSANADY, 1977, or ALLEN, 1980). The baroclinic forcing is derived from the density field which often has sharp variations in the vertical. In the presence of vertical friction, these in turn result in large baroclinic shears which in turn generate frictional ageostrophic flows, HOPKINS and SLATEST (1982).

Input Information

Bottom Stress

We represent the velocity at the bottom (z=d) as q_d. This is in fact ~1 m above the bottom but taken to be in the constant stress region,

$$\tau^d = u_*^2 \qquad \text{and} \qquad u^{*2} = \left[\frac{k\ q_d}{\ln \dfrac{z_{100}}{z_o}}\right]^2 \tag{12}$$

where the units of stress are cm^2/sec^2 , where k = 0.4 is von Karmen's constant, and

$$q_d = \frac{u^*}{k}\ \ln \frac{z_{100}}{z_o} = q_{100} \tag{13}$$

The parameter z_o is a bottom roughness parameter and is not well quantified. It is a length scale associated with the origin of the z coordinate for the logarithmic profile and is related to the physical bottom roughness; but it may be enhanced in the presence of high frequency motions (GRANT and MADSEN, 1979). The bottom stress is conventionally written in terms of a drag coefficient, C_d.

$$\tau^d = C_d \left|q_d\right| q_d \tag{14}$$

For the purposes of numerical quantification for the Gulf of Naples C_d was related to z_o by the following approximation for $0.2 \lesssim z_o \lesssim 10$ cm:

$$C_d = \left[\frac{k}{\ln \dfrac{100 + z_o}{z_o}}\right]^2 \simeq 0.0041 + 0.0028\ z_o; \tag{15}$$

and z_o values were assigned according to bottom type: for a deep, smooth bottom $z_o \simeq 0.2$ cm, for a nearshore, smooth bottom $z_o \simeq 0.2$ to 2 cm, and for an uneven or rocky bottom, $z_o = 2$ to 5 cm. The values of z_o were enhanced around the solid grid boundary to simulate additional lateral friction. The values of z_o that were used are in the code listed in the appendix to this section.

The bottom stress is clearly nonlinear since it has the quadratic dependence on the velocity at the bottom which in turn depends on the solution to (10). The bottom stress is linearized through several conventions, for example

a. $\tau^{dx} = r\bar{u}$ where $\bar{u} = U/d$ and r is a specified resistance coefficient.

b. As in (a) except that r is approximated by $C_d\left|\bar{u}^2 + \bar{v}^2\right|^{1/2}$. This is more recommended when there exists considerably high frequency energy, as with waves and tides, that may have a non-zero contribution to a quadratic dependence (e.g., WINANT and BEARDSLEY, 1979). Neither of these two formulations consider the effects of

- the variations in bottom roughness,
- the veering of the velocity through the bottom Ekman layer, or
- the differences between the depth-averaged flow and the bottom flow.

c. $\tau^{dx} = ru_d$ or $C_d\left|u_d^2 + v_d^2\right|^{1/2} u_d$. This is more accurate but requires additional information on q_d. Some options are

- to numerically lag τ^d by one time step (t) such that q_d is known, i.e., $(\tau^d)^t = f[\phi^t, (\tau^d)^{t-1}]$,
- to use an empirical relationship to relate q_d to (below), or
- to compute q_d separately, with a z-dependent model.

d. For shallow water columns $\lesssim$30 m, the stress at the bottom may contain a contribution from the surface stress, that is, stress put in at the surface which is not dissipated internally by the depth of the bottom. This complication was not considered here, in part, because the Gulf of Naples is generally deeper than 30 m. For a treatment of this problem see HOPKINS and DIETERLE, 1982.

For the purpose of the workshop example, the following procedure was used:

a. Assume that q_d is reduced and rotated in the bottom Ekman layer (as in HOPKINS, 1974)

$$q_d = \mu e^{i\theta} q_I \tag{16}$$

where μ is an amplitude reduction, θ is veer angle, and q_I is the interior velocity at the top of the bottom Ekman layer, or at $z = I$.

b. In strictly barotropic situation (and $d > 30$ m)

$$q_I \simeq \frac{i}{f} \left[\nabla\phi \right] . \tag{17}$$

In the case of baroclinic shear the geostrophic velocity at

$z = I$ will be

$$q_I = \frac{i}{f} \left[\nabla\phi + \nabla\Psi \right] . \tag{18}$$

However, we can express $\nabla\Psi$ in terms of $\nabla\phi$, such that

$$\nabla\Psi = - \nu\nabla\phi \qquad \text{at } z = I. \tag{19}$$

Where ν is the fraction of pressure compensation at depth $z = I$.

$\nu = 1 \Rightarrow$ total adjustment

$\nu = 0 \Rightarrow$ zero adjustment

In general $\nu = f(z)$, and deeper water columns tend to be more completely compensated. For the purpose of the exercise we have used the following dependency for the depth interval $20 < d < 545$ m:

$$\nu = 1 - \left[\frac{6.3 - \ln d}{5}\right] . \tag{20}$$

This represents 34% compensation at $d = 20$ m and 98% at $d = 500$ m. For a purely barotropic problem, $\nu = 0$ such as might occur in winter. Note that in reality ν will not be uniform in x and y for a given d.

c. Now we can express the bottom stress as

$$\tau^d = C_d \left| q_d \right| q_d \quad \text{or}$$

$$\tau^{d} = i e^{i\theta} \gamma \nabla\phi \tag{21}$$

where $\gamma = C_d \left[\frac{\mu}{f} (1 - \nu) \right]^2 \left| \nabla\phi \right| .$

For the purpose of the exercise we choose $\left| \nabla\phi \right| = 1.5 \times 10^{-3}$ cm/sec^2, $\mu = 0.8$, and $\theta = 20°$.

Appropriate estimates for other situations might be obtained from observations or from the literature. Equation (21) may be decomposed into components as

$$\tau^{dx} = -\gamma\, \phi_y - \gamma\, \phi_x \tag{22}$$

$$\tau^{dy} = \gamma'\, \phi_x - \gamma\, \phi_y \tag{23}$$

where γ' and $\gamma \cos \theta$ and $\gamma = \gamma \sin \theta$. These two expressions can now be included into equation (10)

$$\gamma' \nabla^2 \phi + (\gamma'_x + \gamma_y - d_y)\phi_x + (\gamma'_y - \gamma_x + d_x)\phi_y = \text{curl } \tau^s - J(d, P^d) . \tag{24}$$

Field of Mass

The Jacobian term in (24) can be generated in a diagnostic sense, that is by assuming that the observed P^d field is steady and applies throughout the steady period being modelled. In fact as mentioned before, a steady representation is imprecise, but since the baroclinic bottom pressure changes more slowly than the barotropic pressure field, a diagnostic estimate of P^d can be used with some success even for quasi-time dependent models (HAN et al., 1980; HSUEH, 1980).

The distribution of P^d was taken from the GONBP-6 data report. An interpolation/extrapolation scheme was devised so that P^d values could be generated for grid points and grid depths near a sampled station. Note that the sampled P^d field cannot be simply extrapolated to other grid points because P^d is a function of the depth indirectly through the z dependency of the density (e.g., GALT, 1975).

After solution of (24) for ϕ, the transport components of (6) and (7) must be evaluated. This requires an evaluation of $\nabla\Psi$. We note that an exponential density distribution of the form

$$\rho = \rho_d - (\rho_d - \rho_o) e^{-\alpha z} \tag{25}$$

gives a Ψ_x from (9) with $\alpha = 3/d$ of

$$\Psi_x = \frac{5}{9} g d d_x \left[\rho_d - \rho_o\right]_x + \frac{g d^2}{18} \left[11\rho_d - 2\rho_o\right]_x . \tag{26}$$

For the model we simplify this by assuming that $\rho_o = 1.0268$ and is spatially constant, and that

$$\Psi_x = \left[\frac{gd}{2\Delta x} \; (\bar{\rho} - \rho_o)\Delta d + d\Delta\bar{\rho}\right] . \tag{27}$$

We note that the first term on the right accounts for an increased baroclinic pressure gradient when the depth is increasing horizontally coincident with the density increasing vertically. The second term accounts for what might be considered a decreased isosteric height as the density increases horizontally.

Wind Stress

The other parameter functions needed in equation (24) are the wind stress and depth. The wind occurring during the GONEP-VI cruise was typical for the summer situation. A value of 4 m/sec from 200°T was used, and it was converted to stress by the relationship

$$\tau^s = C_a \frac{\rho_a}{\rho_w} W^2 \qquad (28)$$

from RUGGLES (1969), where $C_a = 2.5 \times 10^{-3}$, $\rho_a = 1.23 \times 10^{-3}$ gm/cm^3 and W is in cm/sec. The ρ_w is required to convert τ^s to kinematic dimensions (cm^2/sec^2). For a constant wind there is no contribution in equation (24). However, the curl τ^s is potentially a significant forcing in the Gulf of Naples where for certain wind directions considerable variations are caused by the steep and irregular coastlines. Very little, good data exists for evaluating curl τ^s for coastal systems. For larger systems (e.g., the Aegean or eastern Levantine) it is significant, but again difficult to observe or to estimate.

Depth

The grid depths, d(x,y), were obtained by a coarse smoothing of the charted depths within each grid, given in the code. The range of d relative to the grid size was ultimately the obstacle for obtaining a numerical solution (see below). The total depth range is more limiting in a numerical solution than large variations in depth which could be removed by more smoothing.

Boundary Conditions

Equation (24) is meant to apply over some domain thereby requiring a set of conditions on ϕ about the boundary of the domain, which can be either a specification of ϕ and/or its normal derivative. The primary difficulty in posing this problem for coastal domains, as opposed to lakes or bounded seas, is that little or no information exists about the sea level along the boundaries. In this regard the straight coast is the most difficult to model; however, even in the Gulf of Naples with approximately one open boundary, there is difficulty in specifying the sea level about its coastal perimeter because no sea level observations are available.

For the purpose of the modelling exercise, ϕ was estimated about the entire domain to provide a Dirchlet condition on all boundaries. The reader is reminded that this approach was used out of expediency and should not be considered generally applicable. The procedure is outlined as follows and the boundary ϕ values are given in the code:

a. A reference point was chosen from the GONEP VI data set (Station 6) located approximately at grid point 84 in Fig. 62. This location is the deepest along the open boundary and assumed to be most nearly pressure adjusted at a nominal reference depth of 500 m.

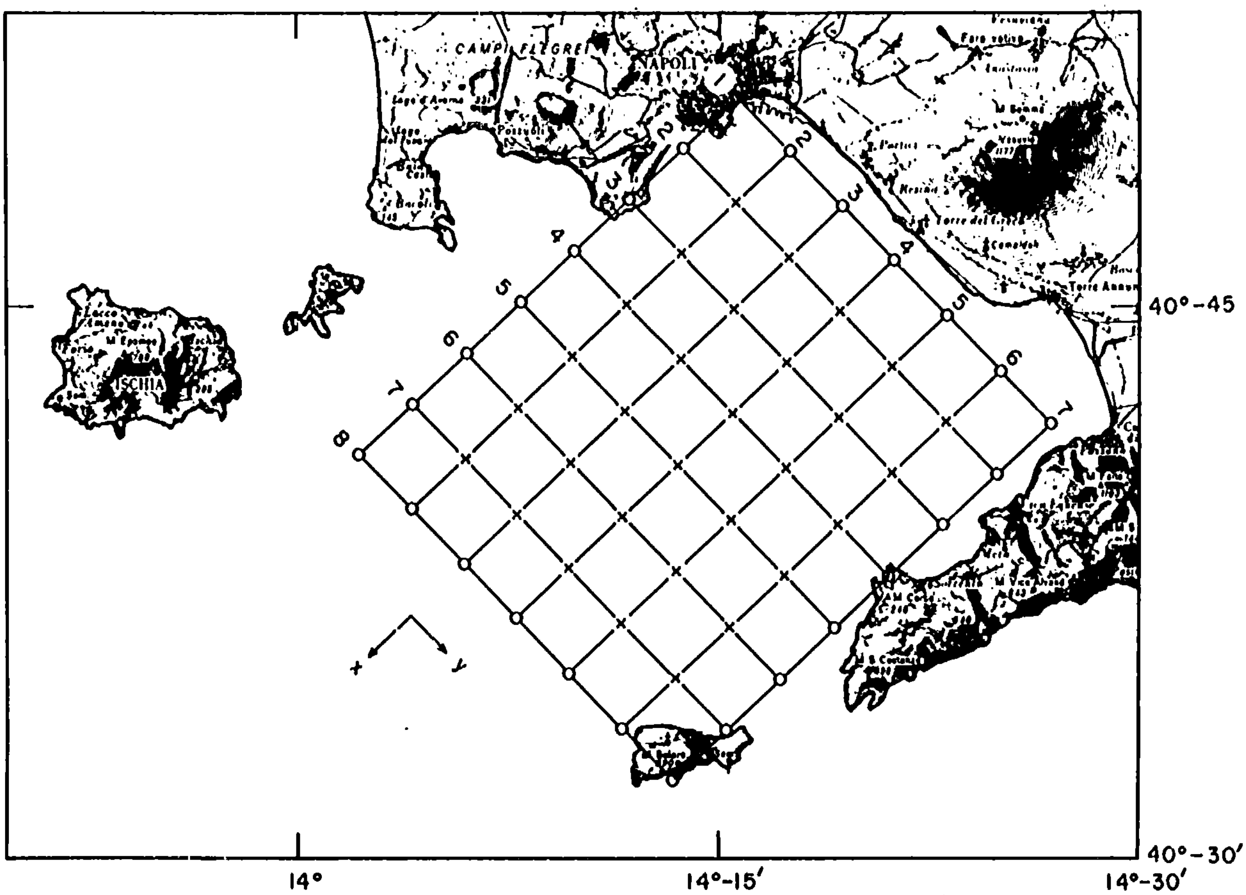


Fig. 62. The grid used for the Gulf of Naples physical model. The i index runs in the x direction to the southwest, and the j index to the southeast.

b. It was assumed that the sea level, or ϕ, along the open boundary could be determined from the distribution of the dynamic height along that boundary. For points along this boundary shallower than 500 m, the dynamic heights were computed by integrating to the bottom and then along the bottom to 500 m.

c. Along the three lateral boundaries, the condition of no normal flow was used to determine the tangential gradient of ϕ, which was then integrated along the boundary to provide a Dirchlet condition. For example, along the Sorrentine boundary y = constant, V = 0, and equation (6) applies

$$0 = -d\phi_x - \Psi_x + \tau^{sx} - \tau^{dx}.$$

But $\Psi_x = - \nu\phi_x$ and $\tau^{dx} = -\gamma'\phi_y - \gamma\phi_x$ which gives

$$\phi_x = \frac{\gamma'\phi_y + \tau^{sx}}{d - \nu - \gamma} \tag{29}$$

from which an integration in x gives ϕ. The value of ϕ_y (normal derivative) is extrapolated between its values at the corners.

d. The determination of ϕ along the boundary in this way requires some iteration to match ϕ at either ends of the open boundary. In the case of the Gulf of Naples, some freedom was allowed in matching due to the uncertainty generated by the Ischia and Procida Channels. For the treated southwest wind case, it was assumed that the sea level rises to the southwest, hence simulating some inflow ($V \neq 0$) and thereby simplifying the iteration scheme.

Equations for the Vertical Model

The biological model requires some vertical resolution in the flow field, in particular it is desirable to separate the dynamics of the euphotic mixed layer from that below it. To provide this resolution, a subroutine was constructed to compute the 0 to 20 m flow, the 20 m to bottom depth flow, and the vertical flow between them. The following formulation is not necessarily so restricted. More detail can be found in (HOPKINS, 1974, or HOPKINS and SLATEST, 1982).

From equations (1) and (2) an ordinary differential equation acting on the complex velocity of $q = u + iv$ is formed:

$$q_{zz} - \alpha^2 q = \nabla\phi/A \tag{30}$$

where $\alpha^2 = if/A$. The boundary conditions are:

$$q_z = -\tau^s/A \qquad \text{at } z = 0 \tag{31}$$

$$Aq_z + rq = 0 \qquad \text{at } z = d$$

where r is a resistance coefficient with dimensions of speed.

The solution is written as

$$q(z) = \left[\frac{\nabla\phi}{Ad^2}\,\frac{r\cosh\alpha z}{A\alpha\sinh\alpha d + r\cosh\alpha d} - 1\right]$$

$$+ \frac{\tau^s}{A\alpha}\left[\frac{A\alpha\cosh\alpha(d-z) + r\cosh\alpha(d-z)}{A\alpha\sinh\alpha d + r\cosh\alpha d}\right] \tag{32}$$

where the first portion represents the contribution to q due to the barotropic and bottom Ekman dynamics and the second that due to the surface Ekman dynamics.

Equation (32) may be integrated between any two depths. We require the integral be evaluated from z = 0 to h = 20 m.

$$Q = \int_0^h q(z)dz = U_h + iV_h\,. \tag{33}$$

This becomes

$$Q = \frac{\nabla\phi}{A\alpha^2}\left[\frac{r\sinh\alpha h}{A\alpha^2\sinh\alpha d + r\alpha\cosh\alpha d} - h\right]$$

$$- \tau^s\left[\frac{\sinh\alpha(d-h) - \sinh\alpha d}{A\alpha^2\sinh\alpha d + r\alpha\cosh\alpha d}\right]$$

$$+ \frac{\tau^s}{A\alpha}\left[\frac{r\cosh\alpha(d-h) - r\cosh\alpha d}{A\alpha^2\sinh\alpha d + r\alpha c p s h\alpha d}\right]. \tag{34}$$

The value of $\nabla\phi$ is supplied by the main program which also computes the total transports, U and V. By subtraction the lower layer flow is obtained.

$$U_d = U - U_h \text{ and } V_d = V - V_h\,;$$

and by using the continuity equation (3) the vertical velocity at z=h is given,

$$w_h = \frac{\partial U_d}{\partial x} + \frac{\partial V_d}{\partial y}\,. \tag{35}$$

Numerical Procedures

The model formulated during the workshop consists of five programs as indicated in Table X. The use of these programs is illustrated in the flowchart of Fig. 63.

The input data of bathymetry, bottom roughness, and integrated pressure gradients are read in by the program COEF2 and transformed to the format of equation (24), which becomes

$$G(\phi_{xx} + \phi_{yy}) + A\phi_x + B\phi_y = C \tag{36}$$

where
$G = \gamma' \cos\theta$
$A = (\gamma'_x + \gamma_y - d_y)$
$B = (\gamma'_y - \gamma_x + d_x)$
$C = \operatorname{curl}\tau^s - J(d, P_d)$

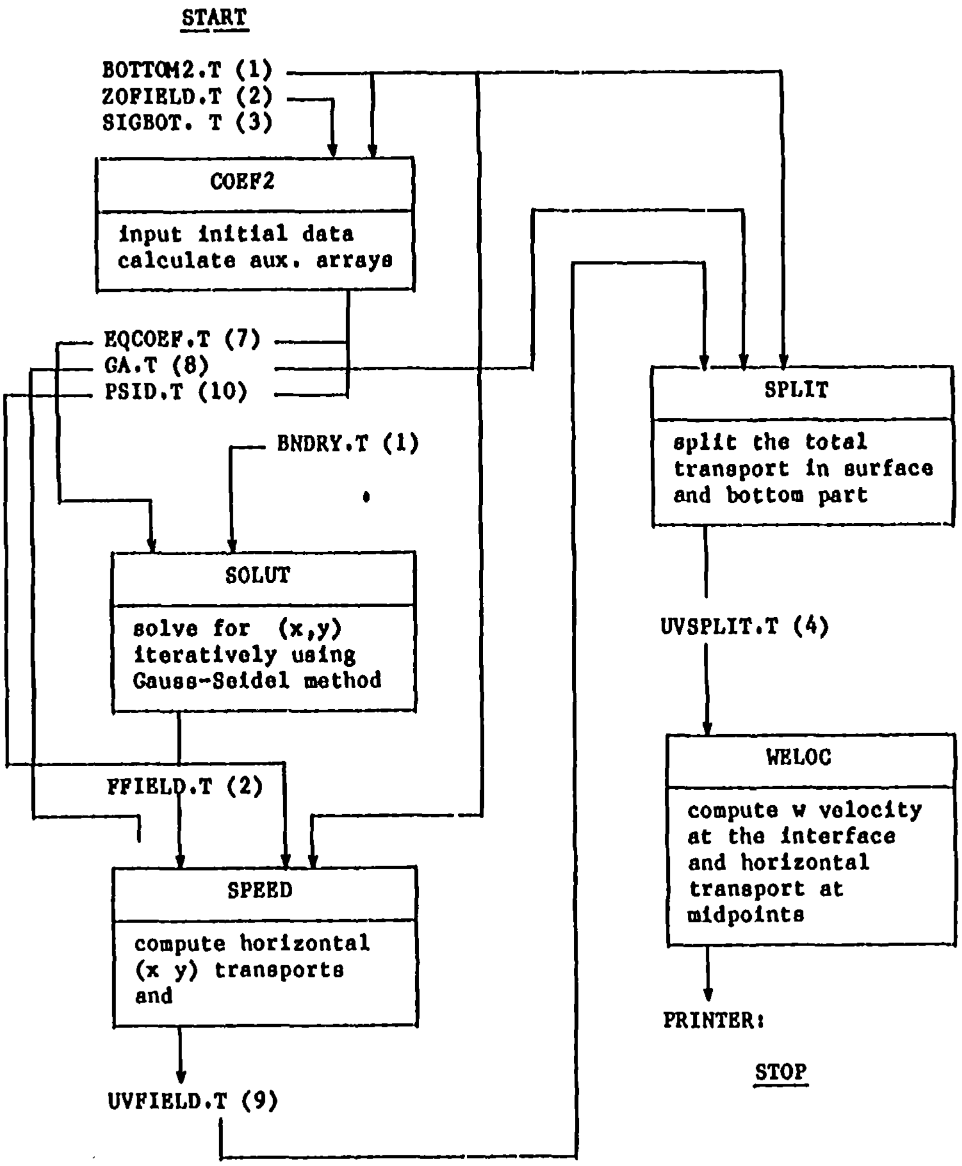


Fig. 63. Program flowchart for physical model.

The data matrices thus obtained are further transformed in the SOLUT program to conform to a particular numerical scheme, namely, using the Taylor's expansion one obtains:

$$\phi_x(i,j) = \frac{1}{2\Delta}\,[\phi_{i+1,j} - \phi_{i-1,j}] + O(\Delta^2) \quad (37a)$$

$$\phi_y(i,j) = \frac{1}{2\Delta}\,[\phi_{i,j+1} - \phi_{i,j-1}] + O(\Delta^2) \quad (37b)$$

$$\phi_{xx}(i,j) = \frac{1}{\Delta^2}\,[\phi_{i+1,j} - 2\phi_{i,j} + \phi_{i-1,j}] + O(\Delta^2) \quad (37c)$$

$$\phi_{yy}(i,j) = \frac{1}{\Delta^2}\,[\phi_{i,j+1} - 2\phi_{i,j} + \phi_{i,j-1}] + O(\Delta^2) \quad (37d)$$

where Δ is a spatial resolution. Using equation (31), the equation (30) becomes:

$$\alpha_1\phi_{i+1,j} + \alpha_2\phi_{i-1,j} + \alpha_3\phi_{i,j+1} + \alpha_4\phi_{i,j-1} - \alpha_o\phi_{i,j} = \alpha_5 \quad (38)$$

where $\alpha_o = 4G_{ij}$,

$\alpha_1 = G_{ij} + \frac{\Delta}{2} A_{ij}$, $\alpha_2 = G_{ij} - \frac{\Delta}{2} A_{ij}$,

$\alpha_3 = G_{ij} + \frac{\Delta}{2} B_{ij}$, $\alpha_4 = G_{ij} - \frac{\Delta}{2} B_{ij}$,

and $\alpha_5 = C_{ij}\Delta^2$ but with the condition

$$0 < \Delta < \min\left[\frac{2G_{ij}}{|A_{ij}|}, \frac{2G_{ij}}{|B_{ij}|}\right]$$

Table X

System of programs to run the model

1. **Files:**

Input files:

BOTTOM2.TEXT	10X9 Matrix of depths
ZOFIELD.TEXT	10X9 Matrix of bottom roughness parameters
SIGBOT.TEXT	10X9 Matrix of depth-averaged densities
BNDRY.TEXT	A file containing boundary conditions for the barotropic potential

Intermediate files:

GA.TEXT	10X9 Matrix of gamma values
EQCOEF.TEXT	4X8X7 Matrix of the coefficients of the equation
PFIELD.TEXT	7X8 Matrix of the barotropic potential
UVFIELD.TEXT	4X8X7 Matrix of the gradients of phi function and horizontal transports
UVSPLIT.TEXT	4X8X7 Matrix of horizontal transport in every layer
PSID. TEXT	8X7 Matrix of the baroclinic potential gradients

2. Programs

Input

COEF2	Input to the model
SOLUT	Solution of the partial differential equation
SPEED	Compute the horizontal transport
SPLIT	Split the total flow into two layers
WELOC	Compute the vertical velocity and centered horizontal transports

This equation is then solved iteratively using the Gauss-Siedel method for which one obtains:

$$\phi^{(k)}_{i,j} = \frac{1}{\alpha_0}[\alpha_1\phi^{(k-1)}_{i+1,j} + \alpha_3\phi^{(k)}_{i-1,j} + \alpha_2\phi^{(k-1)}_{i,j+1} \alpha_4\phi^{(k)}_{i,j-1} - \alpha_5] \qquad (39)$$

The equation is solved in a rectangular region defined by $1 \leq i \leq 8$ and $1 \leq j \leq 7$ (Fig. 62). Superscript k is an iterative pointer. The equation (30) defines a computational molecule repeatedly evaluated at each grid point. The grid size has been reduced to 8x7 in the x and y directions, respectively, due to the limited capacity of the Apple II computer.

Zero condition is assumed initially for all the interior points and the Dirichlet conditions are prescribed at both solid and open boundaries. After an interative solution is obtained, the baroclinic part is added to complete the potential field solution.

Program SPEED is then used to calculate horizontal transports from the results obtained by the SOLUT program. Another program (SPLIT) is used to calculate transport in the upper 20m. This 20-meter flow is then subtracted from the total flow in order to obtain two-layer prediction. Finally, program WELOC is used to compute vertical velocity between the two layers. These are illustrated in Fig. 64.

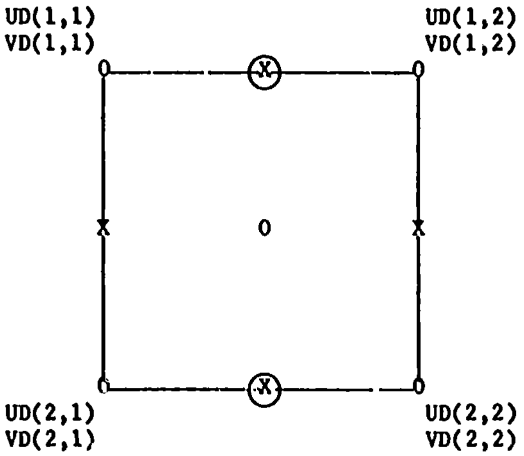


Fig. 64. Scheme for computing w from the transport at each grid element. The UHX and UDX are averaged at mid-points marked X and VHY and VDY are averaged at mid-points marked ⓧ, and W is calculated at grid center marked 0.

Appendix to Physical Model

Table XI. List of Variables used in physical model program.

INPUT

Code Variable	Math Variable	Identification
D(10,9)	$d(x,y)$	depth
ZO(10,9)	$z_o(x,y)$	bottom roughness parameter
PD(10,9)	$P^d(x,y)$	integrated pressure at bottom
GA(10,9)	$\gamma(x,y)$	bottom stress parameter
TSX(10,9)	$\tau^{sx}(x,y)$	x component of wind stress
TSY(10,9)	$\tau^{sy}(x,y)$	y component of wind stress
F	f	Coriolis parameter
FNU	$1-\nu$	baroclinic reduction factor
DFI	$\lvert\nabla\phi\rvert$	barotropic pressure gradient
DELTA	Δs	integration step
PSI(8,7)	$\Psi(x,y)$	baroclinic transport potential
NB(8),SB(8),EB(8),WB(8)	$\phi(x,y)$	barotropic potential at the boundaries
H	h	depth of surface layer
AF	A	vertical eddy viscosity
ALFA	α	Ekman length scale
EMME	μ	bottom Ekman reduction factor
SINFI,COSFI	$\sin\theta,\cos\theta$	bottom Ekman veer factors
RE	$r = \dfrac{\gamma}{\mu(1-\nu)}$	bottom resistance coefficient
RHO	ρ_o	representative ambient density
GHLF	$g/2$	acceleration of gravity halved
	INTERMEDIATE OUTPUT	
X,Y	ϕ_x,ϕ_y	x y components of barotropic pressure gradient
U(8,7),V(8,7)	$U(x,y),V(x,y)$	x y components of the vertically averaged horizontal transports
UH(8,7),VH(8,7)	$U_h(x,y),V_h(x,y)$	x y components of transport for upper layer
UD(8,7),VD(8,7)	$U_d(x,y),V_d(x,y)$	x y components of transport for lower layer
	FINAL OUTPUT	
UHX(7,6),VHY(7,6)	$\overline{U}_h,\overline{V}_d$	x y components of transport for upper layer at grid box centers
UDX(7,6),VDY(7,6)	$\overline{U}_d,\overline{V}_d$	x y components of transport for lower layer at grid box centers
W(7,6)	W	vertical transport between layers at grid box centers

Data Inputs

Bottom depths (BOTTOM2) in m.

j i	1	2	3	4	5	6	7	8	9
1	0	0	0	0	0	0	0	0	0
2	0	5	29	70	83	55	53	63	0
3	0	10	58	114	141	146	134	99	0
4	0	10	55	144	165	165	140	111	20
5	0	70	150	205	189	179	141	115	25
6	0	80	86	228	208	180	140	115	25
7	20	100	135	293	299	279	149	111	30
8	90	170	258	335	388	432	176	117	35
9	160	250	470	390	450	520	228	200	120
10	250	400	600	500	600	600	450	400	200

Bottom roughness (ZOFIELD) in cm.

j i	1	2	3	4	5	6	7	8	9
1	9	9	7	6	6	6	6	6	6
2	9	8	6	5	5	5	5	5	6
3	9	8	5	4	3	3	4	5	6
4	7	6	4	2	1	1	3	5	6
5	6	5	6	3	1	1	3	5	6
6	6	5	4	0.5	0.5	1	3	3	4
7	4	3	2.5	0.5	0.2	1	1	3	4
8	4	3	2	0.5	0.2	0.2	0.5	3	4
9	4	3	1	0.2	0.2	0.2	0.5	3	4
10	4	2	1	0.2	0.2	0.2	0.5	2	3

Depth-averaged sigma-t (SIGBOT)

i \ j	1	2	3	4	5	6	7	8	9
1	27.10	27.20	27.30	27.40	27.45	27.45	27.35	27.30	27.25
2	27.20	27.25	27.35	27.50	27.50	27.50	27.40	27.35	27.30
3	27.25	27.30	27.50	27.80	27.65	27.55	27.45	27.45	27.40
4	27.30	27.50	27.80	27.90	27.80	27.65	27.50	27.30	27.20
5	27.10	27.70	28.10	28.08	27.95	27.70	27.50	27.30	27.10
6	27.25	27.50	28.20	28.25	27.95	27.70	27.40	27.25	27.00
7	27.40	28.00	28.40	28.35	28.00	27.75	27.50	27.20	27.10
8	27.75	28.40	28.55	23.45	28.25	27.95	27.65	27.45	27.25
9	28.00	28.50	28.60	28.52	28.35	28.10	27.85	27.60	27.45
10	28.10	28.60	28.65	28.59	28.44	28.20	27.95	27.75	27.90

Sea level potential on boundary (BNDRY) in cm/^{2}sec^2 x 10^3

i \ j	1	2	3	4	5	6	7	8	9
1									
2			2.36	2.68	2.14	1.46	1.33		
3		1.17						2.02	
4		1.54						2.06	
5		1.98						2.05	
6		1.77						2.00	
7		1.83						1.91	
8		2.24						2.42	
9			1.08	0.3	0.0	0.84	1.32		
10									

Computer Program Listing for Physical Model

```
C -
C      PROGRAM COEF2
C -    NEW VERSION 9-04-1981
C -
C -    D=BOTTOM TOPOGRAPHY, RHO=DENSITY FIELD, TSX & TSY=WIND STREESS
C -    F=CORIOLIS PARAMETER, DELTA2=GRID SIZE, DELTA=2.*DELTA2
C -    (Z0,RNU, DFI, EMME, FI) TO COMPUTE BOTTOM STREESS FACTORS
C -
C -   WIND STRESS COEFF'S NOT USED IN THIS SUB.
C -   WIND IS UNIFORM --> CURL(...) = 0.
       REAL D(10,9), RHO(10,9), GX(10,9),PDX(10,9),PDY(10,9)
       REAL GY(10,9), RHOX(10,9), RHOY(10,9), DX(10,9), DY(10,9)
       REAL G(8,7), A(8,7), B(8,7), C(8,7), GA(10,9),PD(10,9)
       REAL PSIX(8,7),PSIY(8,7),Z0(10,9)
        EQUIVALENCE (Z0(1,1),GA(1,1))
C -
       DATA GX, GY, DX, DY/360*1.0/
       DATA G, A, B, C/224*1./
       DATA DFI,EMME,F,FI,DELTA/1.5E-5,.8,.93E-4,.349066,7200./
       DATA GAMIN, GBMIN/2*1.E+20/
C -
C -    SUMMER RNU(D)=(6.30-ALOG(D))/5. WINTER RNU(D)=1.
C -
       SINFI = SIN(FI)
       COSFI  = COS(FI)
       RHO0=1.0268
       GHLF=9.81/2.
C -
       OPEN (1, FILE ='BOTTOM2.TEXT')
       OPEN (2, FILE ='Z0FIELD.TEXT')
       OPEN (3, FILE ='SIGBOT.TEXT')
       OPEN (6, FILE ='PRINTER:')
C
       OPEN (7, FILE ='EQCOEF.TEXT')
C
       OPEN (8, FILE ='GA.TEXT')
C -
        OPEN(10,FILE='PSID.TEXT')
C      READ PRIMARY VARIABLES
C -
       DO 10 I=1,10
       READ (1,1000) (D(I,J), J=1,9)
       READ (2,2000) (Z0(I,J), J=1,9)
       READ (3,3000) (RHO(I,J), J=1,9)
10     CONTINUE
       PAUSE 'STEP1'
C -
C -    COMPUTE SECONDARY VARIABLES
C -
       DO 20 I=1,10
       DO 19 J=1,9
C -    SUMMER RNU
       RNU=(6.3-ALOG(D(I,J)))/5.
       GA(I,J)=(.0041+.0028*Z0(I,J))*EMME*EMME*RNU*RNU*DFI/F*F
       RHO(I,J)=1000.+RHO(I,J)
       PD(I,J)=9.81*D(I,J)*RHO(I,J)
19     CONTINUE
       WRITE (8,9000) (GA(I,J), J=1,9)
       WRITE (6,9000) (GA(I,J), J=1,9)
20     CONTINUE
       CLOSE (8)
C -
C -    COMPUTE SPACE DERIVATIVES
C -
       DO 21 I=2,9

       DO 21 J=2,8
       GX(I,J)=(GA(I+1,J)-GA(I-1,J))/DELTA
```

```
      GY(I,J)=(GA(I,J+1)-GA(I,J-1))/DELTA
      DX(I,J)=(D(I+1,J)-D(I-1,J))/DELTA
      DY(I,J)=(D(I,J+1)-D(I,J-1))/DELTA
      RHOX(I,J)=(RHO(I+1,J)-RHO(I-1,J))/DELTA
      PDX(I,J)=(PD(I+1,J)-PD(I-1,J))/DELTA
      RHOY(I,J)=(RHO(I,J+1)-RHO(I,J-1))/DELTA
21    PDY(I,J)=(PD(I,J+1)-PD(I,J-1))/DELTA
      DELTA2=DELTA/2.
C -
C -   COMPUTE COEFFICIENTS
C -
      DO 30 I=2,9
      DO 30 J=2,8
      G(I-1,J-1)=GA(I,J)*COSFI
      A(I-1,J-1)=(GY(I,J)*SINFI+GX(I,J)*COSFI)-DY(I,J)
      B(I-1,J-1)=(GY(I,J)*COSFI-GX(I,J)*SINFI)+DX(I,J)
      C(I-1,J-1)=DX(I,J)*PDY(I,J)-DY(I,J)*PDX(I,J)
      PSIX(I-1,J-1)=D(I,J)*GHLF*((RHO(I,J)-RHO0)*DX(I,J)+
     #D(I,J)*RHOX(I,J))
      PSIY(I-1,J-1)=D(I,J)*GHLF*((RHO(I,J)-RHO0)*DY(I,J)+
     # D(I,J)*RHOY(I,J))
C*
C*    CONTROL OUTPUT
C*
      WRITE (*,6000) I,J
      GAM=G(I-1,J-1)/ABS(A(I-1,J-1))
      IF(GAM-GAMIN) 31,31,32
31    GAMIN=GAM
32    GBM=G(I-1,J-1)/ABS(B(I-1,J-1))
      IF(GBM-GBMIN) 33,33,30
33    GBMIN=GBM
30    WRITE (6,6666) GAM,GBM
6666  FORMAT (2F30.6)
C 30  CONTINUE
      SMALL=AMIN1(GAMIN,GBMIN)
      ORCO=DELTA2/SMALL
      WRITE (6,7000) ORCO
C-
C-    END OF CONTROL OUTPUT
C-
C -
C     WRITE COEFFICIENTS
C -
      DO 40 I=1,8
      WRITE(7,8000)(G(I,J),A(I,J),B(I,J),C(I,J),J=1,7)
40    WRITE(6,5000)(G(I,J),A(I,J),B(I,J),C(I,J),J=1,7)
      WRITE(10,9900)(PSIX(I,J),PSIY(I,J),J=1,7)
      CLOSE (7)
       CLOSE (10)
      STOP 'READY'
C -
1000  FORMAT (9F4.0)
2000  FORMAT (9F3.1)
3000  FORMAT (9F6.2)
4000  FORMAT (9F3.U)
5000  FORMAT (7(4E15.7/)/)
6000  FORMAT ('STEP I,J', 2I3)
7000  FORMAT ('ORCO = ',E20.7)
8000  FORMAT (7(4E15.7))
9900  FORMAT(7(2E15.7))
9000  FORMAT (9F8.2)
```

```
ISC.SO T=00003 IS ON CR CN   USING 00018 BLKS R=0000

      PROGRAM SOLUT
C***********************************************************************
C     PROGRAN TO SOLVE PDE OF THE FORM:
C
C     C1(D2U/DX2+D2U/DY2)+C2(DU/DX)+C3(DU/DY) = C4
C
C     USING CENTER DIFFERENCING AND GAUSS-SEIDEL METHOD
C
C     WITH DIRICHLET BOUNDARY CONDITIONS
C
C  A0(I,J) TO A4(I,J) ARE THE ATOMS OF  +Y    A3
C                                             I
C     THE COMPUTATIONAL MOLECULE              I
C                                        A2-- A0 --A1
C     REF: W.F. AMES                          I
C                                             I
C     NONLINEAR PDE IN ENGENEERING            A4     +X
C
C     ACAD. PRESS 1965 PP 370-378
C
C***********************************************************************
      REAL A0(8,7),A1(8,7),A2(8,7),A3(8,7),A4(8,7),
     1  NB(6),SB(6),EB(5),WB(5),FINEW(8,7),FIOLD(8,7)
      REAL G(8,7),A(8,7),B(8,7),C(8,7)
      DATA D2/3600./
C-
      OPEN(6,FILE ='PRINTER:')
      OPEN (1,FILE ='BNDRY.TEXT')
C     OPEN (2,FILE ='FFIELD.TEXT')
      OPEN (3,FILE ='EQCOEF.TEXT')
C-
      READ (1,70)(SB(I), I=1,6)
      READ (1,70)(NB(I), I=1,6)
      READ (1,70)(WB(I), I=1,5)
      READ (1,70)(EB(I), I=1,5)
70    FORMAT (6F7.4)
C-
      DO 99 I=1,8
99    READ(3,7000)(G(I,J),A(I,J),B(I,J),C(I,J),J=1,7)
7000  FORMAT (7(4E15.7))
      PAUSE 'READ'
C-
      DO 100 I=1,8
      DO 100 J=1,7
C-    SET UP CONPUTATIONAL MOLECULE
      A1(I,J) = G(I,J) + D2*A(I,J)
      A2(I,J) = G(I,J) - D2*A(I,J)
      A3(I,J) = G(I,J) + D2*B(I,J)
      A4(I,J) = G(I,J) - D2*B(I,J)
      A0(I,J) = 1./(4.*G(I,J))
      C(I,J)=C(I,J)*D2*D2
100   CONTINUE
999   WRITE (*,50)
      WRITE (6,50)
50    FORMAT ('PUT OMEGA, EPS, ITERMAX')
      READ (*,60) OMEGA, EPS, ITERMX
60    FORMAT (2(F10.8/), I4)
      WRITE (6,60) OMEGA, EPS,ITERMX
C
C-    ZERO INTERIOR POINTS
C
      ITER = 0
      DO 110 I=1,8
      DO 110 J=1,7
110   FINEW(I,J) = 0.
C-    SET UP DIRICHLET BOUNDARY CONDITIONS
      DO 120 I=2,7
      FINEW(I,1) = SB(I-1)
```

```
120   FINEW(I,7) = NB(I-1)
      DO 130 J=2,6
      FINEW(1,J) = WB(J-1)
130   FINEW(8,J) = EB(J-1)
      DO 135 I=1,8
      DO 135 J=1,7
135   FIOLD(I,J) = FINEW(I,J)
150   CONTINUE
C-    BEGIN ITERATION PROCEDURE
      TOTEPS = 0.
      ITER = ITER + 1
900   FORMAT('NUMBER OF ITERATION',I4,'TOTEPS',E15.7)
      DO 140 J=2,6
      DO 140 I=2,7
      FIOLD(I,J) = FINEW(I,J)
      FINEW(I,J)=(1./A0(I,J))*(A1(I,J)*FIOLD(I+1,J)+A2(I,J)*FINEW(I
     #-1,J)+A3(I,J)*FIOLD(I,J+1)+A4(I,J)*FINEW(I,J-1)-C(I,J))
      TOTEPS = TOTEPS+ABS(FINEW(I,J)-FIOLD(I,J))
140   CONTINUE
      WRITE (6,900) ITER, TOTEPS
      DO 1001 JJ=1,7
      J=8-JJ
      WRITE (6,2000)(FINEW(I,J), I=1,8)
1001  CONTINUE
2000  FORMAT (8E10.2)
      IF(TOTEPS.GE.1.E30) THEN
      GO TO 401
      ELSEIF(ITER.LT.ITERMX.AND.TOTEPS.GT.EPS) THEN
      GO TO 150
      ELSEIF (ITER.GE.ITERMX.AND.TOTEPS.GT.EPS) THEN
      WRITE (*,200) ITERMX
200   FORMAT(5X,'NO SOLUTION AFTER',I4,'ITERATIONS'/)
      GO TO 1023
C     STOP
      ELSEIF (ITER.LE.ITERMX.AND.TOTEPS.LE.EPS) THEN
      WRITE (*,300) ITER
300   FORMAT(2X,'CONVERGENCE AFTER',I3,'ITERATIONS'//)
C     STOP 'PROVA'
      DO 160 JJ=1,7
      J=8-JJ
160   WRITE(6,400)(FINEW(I,J), I=1,8)
400   FORMAT (2X,8F8.2)
      ENDIF

401   WRITE(*,800)
800   FORMAT ('CHECK! POSSIBLE ERROR')
1023  WRITE (*,500)
500   FORMAT(2X,'HIT ZERO TO REPEAT,ONE TO QUIT')
      READ (*,600) JPAR
600   FORMAT (I1)
      IF (JPAR.EQ.0) GO TO 999
      DO 170 JJ=1,7
      J=8-JJ
  170 WRITE (2,400)(FINEW(I,J), I=1,8)
      CLOSE (2)
      STOP 'CIAO'
```

```
      PROGRAM SPEED
C-    COMPUTE VELOCITY FIELDS
      REAL GA(10,9), FI(8,7), D(10,9),S(8,7),T(8,7)
      REAL X(8,7),Y(8,7),U(8,7),V(8,7)
C-   X,Y ARE DERIVATIVES OF POTENTIAL FUNCTION FI
C-    S,T ARE DERIVATIVES OF POTENTIAL FUNCTION PSI
C-    U,V ARE THE HORIZONTAL VELOCITIES (TRANSPORT)
      DATA DELTA/7200./,FFI/20./,F/.93E-4/,TSX/-.34/,TSY/-.34/
      FFI=FFI*3.14159265/180.
      SINFI=SIN(FFI)
```

```
        RHO0=1.0268
        COSFI=COS(FFI)
        DELTA2=DELTA/2.
C-
        OPEN(1,FILE='BOTTOM2.TEXT')
        OPEN(2,FILE='FFIELD.TEXT')
        OPEN(3,FILE='GA.TEXT')
        OPEN(4,FILE='PSID.TEXT')
        OPEN(7,FILE='PRINTER:')
        OPEN(9,FILE='UVFIELD.TEXT',STATUS='NEW')
C-
        DO 50 I=1,10
        READ(1,2000)(D(I,J),J=1,9)
        READ(3,4000)(GA(I,J),J=1,9)
50      CONTINUE
        DO 55 I=1,8
55      READ(4,9900)(S(I,J),T(I,J),J=1,7)
        DO 60 JJ=1,7
        J=8-JJ
        READ(2,3000)(FI(I,J),I=1,8)
60      CONTINUE
C-
        DO 100 I=2,7
        DO 100 J=2,6
        X(I,J)=(FI(I+1,J)-FI(I-1,J))/DELTA
        Y(I,J)=(FI(I,J+1)-FI(I,J-1))/DELTA
100     CONTINUE
        DO 200 I=2,7
        Y(I,1)=(FI(I,2)-FI(I,1))/DELTA2
        Y(I,7)=(FI(I,7)-FI(I,6))/DELTA2
        DO 200 J=1,7,7
        X(I,J)=(FI(I+1,J)-FI(I-1,4))/DELTA
200     CONTINUE
        DO 300 J=2,6
        X(1,J)=(FI(2,J)-FI(1,J))/DELTA2
        X(8,J)=(FI(8,J)-FI(7,J))/DELTA2
        DO 300 I=1,8,8
        Y(I,J)=(FI(I,J+1)-FI(I,J-1))/DELTA
300     CONTINUE
C-
        DF=1./F
        DO 400 I=1,8
        DO 401 J=1,7
        FNU=1.-(6.3-ALOG(D(I+1,J+1)))/5.
        V(I,J)=DF*(D(I+1,J+1)*X(I,J)+S(I,J)-TSX -
       #G(I+1,J+1)*(Y(I,J)*COSFI+X(I,J)*SINFI))
        U(I,J)=DF*(-D(I+1,J+1)*Y(I,J)-T(I,J)+TSY -
       #G(I+1,J+1)*(X(I,J)*COSFI-Y(I,J)+SINFI))
        U(1,J)=0.
401     CONTINUE
        U(I,1)=0.
        U(I,7)=0.
400     CONTINUE
C-
        WRITE (7,1000)((X(I,J),J=1,7),I=1,8)
        WRITE (7,1000)((Y(I,J),J=1,7),I=1,8)
        WRITE (7,1000)((U(I,J),J=1,7),I=1,8)
        WRITE (7,1000)((V(I,J),J=1,7),I=1,8)
        WRITE (9,1000)((X(I,J),J=1,7),I=1,8)
        WRITE (9,1000)((Y(I,J),J=1,7),I=1,8)
        WRITE (9,1000)((U(I,J),J=1,7),I=1,8)
        WRITE (9,1000)((V(I,J),J=1,7),I=1,8)
        CLOSE (9)
C-
1000    FORMAT (8(7E11.3/)/)
2000    FORMAT (9F4.0)
3000    FORMAT (2X,8F8.2)
4000    FORMAT (9F8.2)
5000    FORMAT (8F10.2)
9900    FORMAT(7(2E15.7))
        STOP 'FINE'
```

```
         PROGRAM SPLIT
C-    TO SPLIT VELOCITY IN TWO LAYERS
C-    H IS THE DEPTH OF THE UPPER LAYER
      REAL D(10,9),X(8,7),Y(8,7),U(8,7),V(8,7)
      REAL UH(8,7),VH(8,7),UD(8,7),VD(8,7)
      REAL TSX(8,7), TSY(8,7), GA(10,9)
      DATA UD,VD/112*0./
      DATA H,F,AF/20.,.93E-04,1./
C-
C-    WIND STRESS: TSX=TSY= - .34 M2 SEC2
      DATA TSX,TSY/112*-0.34/
      DATA EMME/.8/
      ALFA = .707*SQRT(F/AF)
      A1 = SINH(ALFA*H)
      B1 = COSH(ALFA*H)
C-
C-    SUMMER RNU(D)=6.30-ALOG(D))/5. WINTER RNU(D)=1
C-
      OPEN (9,FILE='UVFIELD.TEXT')
      OPEN (1,FILE='BOTTOM2.TEXT')
      OPEN (4,FILE='UVSPLIT.TEXT', STATUS='NEW')
      OPEN (6,FILE='PRINTER:')
      OPEN (8,FILE='GA.TEXT')
C-
      READ (1,1000)((D(I,J),J=1,9),I=1,10)
      READ (8,8000) ((GA(I,J),J=1,9),I=1,10)
      READ (9,9000) ((U(I,J),J=1,7),I=1,8)
      READ (9,9000) ((V(I,J),J=1,7),I=1,8)
      DO 100 I=1,8
      DO 100 J=1,7
C-    SUMMER RNU
      RNU=(6.30-ALOG(D(I+1,J+1)))/5.
      R=GA(I+1,J+1)/(EMME*RNU)
      D1=D(I+1,J+1)-H
      IF(D1) 99,99,1
1     A=SINH(ALFA*D(I,J))
      B=COSH(ALFA*D(I,J))
      A2=SINH(ALFA*D1)
      B2=COSH(ALFA*D1)
      AA1=TSX(I,J)*ALFA*(B*B+A*A)-F*B*A
      AA2=TSY(I,J)*ALFA*(B*B+A*A)
      BB1=TSX(I,J)*ALFA*(B*B-A*A)+F*B*A
      BB2=TSY(I,J)*ALFA*(B*B-A*A)
      E2=(AA1+BB1)*(AA1+BB1)+(AA2+BB2)*(AA2+BB2)
      G1=TSX(I,J)/E2
      G2=TSY(I,J)/E2
      GRO1=G1*R/(2*ALFA*AF)
      GRO2=G2*R/(2*ALFA*AF)
      P11=R*(AA1+BB1)*A1*B1-H*E2
      P12=R*(AA2+BB2)*A2*B1
      P21=R*(AA1-BB1)*A1*B1
      P22=R*(AA2-BB2)*A1*B1
      S11=AA1*B2*B2+BB1*A2*A2
      S12=AA2*B2*B2+BB2*A2*A2
      S21=BB1*B2*B2-AA1*A2*A2
      S22=BB2*B2*B2-AA2*A2*A2
      S31=AA1*A2*B2+BB2*B2*A2
      S32=AA2*A2*B2+BB2*B2*A2
      S41=AA1*A2*B2-BB1*B2*A2
      S42=AA2*A2*B2-BB2*B2*A2
      SS11=-AA1*B*B-BB1*A*A
      SS12=-AA2*B*B-BB2*A*A
      SS21=-BB1*B*B+AA1*A*A
      SS22=-BB2*B*B+AA2*A*A
      SS31=(-AA1-BB1)*A*B
      SS32=(-AA2-BB2)*A*B
      SS41=(-AA1+BB1)*A*B
      SS42=(-AA2+BB2)*A*B
C-
      UH(I,J)=((Y(I,J)*P11+X(I,J)*P21)+(X(I,J)*P11-Y(I,J)*P21))/E2*
     # (G1*(S31+SS31)+G2*(S32+SS32))-(G1*(S41+SS41)+G2*(S42+SS42))+
```

```
       # GR01*(S11+SS11+S21+SS21)-GR02*(S12+SS12+S22+SS22)+
       # GR01*(S21+SS21-S11-SS11)+GR02*(S22+SS22-S12-SS12)
C-
        VH(I,J)=((Y(I,J)*P12+X(I,J)*P22)+(X(I,J)*P12-Y(I,J)*P22))/E2*
       # (G1*(S32+SS32)+G2*(S31+SS31))-(G1*(S42+SS42)+G2*(S41+SS41))+
       # GR01*(S12+SS12+S22+SS22)+GR02*(S11+SS11+S21+SS21)+
       # GR01*(S22+SS22-S12-SS12)-GR02*(S21+SS21-SS1-SS11)
C-
        UD(I,J)=U(I,J)- UH(I,J)
        VD(I,J)=V(I,J)- VH(I,J)
        GO TO 100
99      UH(I,J)=U(I,J)
        VH(I,J)=V(I,J)
100     CONTINUE
        WRITE(4,9000)((UH(I,J),J=1,7),I=1,8)
        WRITE (4,9000)((VH(I,J),J=1,7),I=1,8)
        WRITE (4,9000)((UD(I,J),J=1,7),I=1,8)
        WRITE (4,9000)((VD(I,J),J=1,7),I=1,8)
        WRITE (6,9000)((UH(I,J),J=1,7),I=1,8)
        WRITE (6,9000)((VH(I,J),J=1,7),I=1,8)
        WRITE (6,9000)((UD(I,J),J=1,7),I=1,8)
        WRITE (6,9000)((VD(I,J),J=1,7),I=1,8)
        CLOSE (4)
C-
        STOP 'READY'
1000    FORMAT (9F4.0)
9000    FORMAT (8(7E11.3/)/)
8000    FORMAT (9F8.2)
```

```
        PROGRAM WELOC
C-      THIS PROGRAM COMPUTES THE VERTICAL VELOCITY BETWEEN TWO LAYERS
        DIMENSION UD(8,7),VD(8,7),W(8,7),UDX(8,7),VDY(8,7)
        DIMENSION WX(8,7),WY(8,7)
        DIMENSION UH(8,7),VH(8,7),UHX(8,7),VHY(8,7)
        DATA DELTA2/3600./
        OPEN (6,FILE='PRINTER')
        OPEN (4,FILE='UVSPLIT')
        READ (4,4000)((UH(I,J),J=1,7),I=1,7)
        READ (4,4000)((VH(I,J),J=1,7),I=1,8)
        READ (4,4000)((UD(I,J),J=1,7),I=1,8)
        READ (4,4000)((VD(I,J),J=1,7),I=1,8)
C-
        DO 1 I=1,8
        DO 1 J=1,8
        UHX(I,J)=(UH(I,J+1)+UH(I,J))/2.
1       UDX(I,J)=(UD(I,J+1)+UD(I,J))/2.
        DO 2 J=1,7
        DO 2 I=1,7
        VHY(I,J)=(VH(I+1,J)+VH(I,J))/2.
2       VDY(I,J)=(VD(I+1,J)+VD(I,J))/2.
        DO 3 I=1,7
        DO 3 J=1,6
3       WX(I,J)=UDX(I+1,J)-UDX(I,J)
        DO 4 I=1,7
        DO 4 J=1,6
4       WY(I,J)=VDY(I,J+1)-VDY(I,J)
        DO 5 I=1,7
        DO 5 J=1,6
5       W(I,J)=(WX(I,J)+WY(I,J))/DELTA2
C-
4000    FORMAT (8(7E11.3/)/)
        WRITE (6,6666)((W(I,J),J=1,6),I=1,7)
6666    FORMAT (7(6E12.4/)/)
        WRITE (6,6666)((UHX(I,J),J=1,6),I=1,7)
        WRITE (6,6666)((VHY(I,J),J=1,6),I=1,7)
        WRITE (6,6666)((UDX(I,J),J=1,6),I=1,7)
        WRITE (6,6666)((VDY(I,J),J=1,6),I=1,7)
        STOP
        END
```

BIOLOGICAL MODEL

Introduction

During the workshop an attempt was made to consider a modelling problem that was relevant to the participants yet one that was limited enough to be tractable within the brief time available. We then proceeded through the steps of developing a model, attempting to strike a balance between these two considerations. Were a model of similar scope and objectives to be undertaken as a serious research project, much of what was done at Ischia could be valid, but all of the formulations and supporting data would have to be critically reevaluated.

The guiding objective for this model was: to formulate major processes necessary to describe the consequences of nutrient discharge in the Bay of Naples. Additionally, the form the model could take was constrained by the data available for evaluating the model, and the specific characteristics of the ecosystem. The latter constraint is critical. The perception of certain physical and biological features as important in characterizing the system limits the formulations that are chosen and determines the literature that can be relied upon when local data are not available. In this case, the Bay of Naples was physically characterized as a large volume with long residence time and weak currents. Biologically, the Gulf is a system capable of high turnover with a spectrum of different sized organisms within the functional groups of primary producers and zooplankton. In some shallow areas the production is dominated by Posidonia seagrass beds and detrital food webs.

Conceptual Diagrams, State Variables, and Forcing Functions

The decision of how much detail to include in a model is always difficult. A model by definition is a simplification, and much of its utility is due to the fact that it lacks the bewildering complexity of the 'real world.' Yet there must also be sufficient detail to give the model credibility, to make it useful as a tool in synthesizing a great deal of information, and to include the parameters necessary for a revealing sensitivity analysis of the system.

Once the physical dimensions of the Gulf of Naples model area were defined, we still had to decide which compartments or state variables were going to be simulated. While it was generally agreed that phytoplankton and zooplankton should be simulated, it was not clear at the start if the phytoplankton compartment should be further divided into large and small cells or if carnivorous and herbivorous zooplankton should be separated, or if large and small animals could be 'lumped' together, or if different life stages would require separate treatment. These kinds of decisions were made on the basis of the information that various members of the group had obtained from many years of experience in studying the Gulf of Naples. After much discussion, the following state variables were chosen for simulation:

(1) dissolved phosphate
(2) dissolved silica
(3) dissolved ammonium
(4) dissolved nitrate
(5) diatoms
(6) other phytoplankton species
(7) omnivorous zooplankton
(8) carnivorous zooplankton
(9) detritus
(10) sediment
(11) benthic macrophytes
(12) ciliates (microzooplankton)

Note that the model contains two phytoplankton classes and three zooplankton classes. The three classes are: filter feeders which feed on diatoms and detritus; ciliates (microzooplankton) which feed on smaller diatoms, other phytoplankton categories, and detritus, but which have a faster metabolic rate than the filter feeders; and carnivorous zooplankton, which feed on the two other zooplankton categories. Together these functional groups open the possibilities for a high turnover rate. Higher trophic levels are not included; they are treated as a simple sink on the zooplankton classes.

Sea grasses might be of importance in Naples Bay and are therefore included at this stage. Our formulation includes two state variables: a carbohydrate pool and a tissue compartment. The first is increased by photosynthesis and the input rate is controlled by the tissue compartment and by temperature and light. The transfer from the carbohydrate pool to the tissue is controlled by temperature and the amount of tissue present. This process is accompanied by uptake of nutrients.

Once the state variables had been selected, decisions were required concerning the forcing functions (the information that would be input to the model rather than simulated within the model). For example, while it might be possible to simulate the water temperature using solar radiation and various physical laws and some empirical coefficients in a thermal energy budget, little would be gained from such a computation, and some errors would be introduced. It is much simpler and more direct to input measured water temperature data to the model. This procedure was adopted whenever it was felt that feedback processes within the system did not influence the value of a given parameter, or that the response of the parameter to changes in the simulated system were long relative to the time frame of the simulations.

Forcing Functions

The primary forcing functions which were considered are listed below. No distinction was made between waste water and tributary input of nutrients, the latter being insignificant for the Gulf of Naples.

(1) solar radiation
(2) precipitation (mm of rainfall N, P)
(3) other external sources (NO_3^-, NH_4^+, P, Si, organic matter)
(4) temperature
(5) the physical model (input, output for boxes)
(6) zooplankton mortality
(7) background transparency, excluding phytoplankton.

With the state variables and forcing functions identified it was necessary to represent the various relationships among them in a conceptual model. Fig. 65 shows a conceptual representation of the model, using H.T. ODUM's ecological circuit language.

While this symbolism is at first glance complicated, it is important to note that this scheme presents not only the state variables and their interconnections, but also information on the mechanisms for each of the flows. The model includes nitrogen, phosporous, and silica, though separate pathways are not shown in all cases.

Another type of diagram for the conceptual model is shown in Fig. 66. Here the state variables and interconnections are more simply presented through the single variable of nitrogen and no further information on mechanisms is included. The processes associated with each path are numbered for easy reference and are specified in Table XII.

Based on the conceptual model, as stated symbolically in diagrams such as these, the next step was to formulate equations for each of the processes.

For each state variable a differential equation can be written including the inputs and outputs. For example, in its simplest form, the differential equation for ammonium is:

$$\frac{d(NH_4)}{dt} = \text{input} - \text{output}. \qquad (1)$$

In both diagrams, the separate flows that compose the inputs and outputs are shown as lines entering or leaving a compartment; for example, from Fig. 66 it is seen that input includes the processes (1), (27), (28), (29) and (30), and output includes the processes (4), (5), (7) and (30). For each of the processes an equation must be defined that quantifies the process.

Formulation and Coefficient Selection

Formulation is the process of expressing the fluxes and interactions included in the shrunken conceptual model into specific mathematical equations. Numerous techniques exist, some of which were summarized in the introductory lectures, and their use depends on the objectives, available data, and background of the scientists. For this case study of the Gulf of Naples, a mechanistic model based on our conceptualization of the important factors controlling phytoplankton production was our goal. Thus we focused in detail on certain compartments, and handled others quite crudely. All of the selected equations are summarized in Table XIII (in the appendix to this section). The following discussion will present some of the rationale behind these choices. The mathematics are for the most part simple. The reader may find it helpful to sketch graphs of some of the formulations for arbitrary values of the coefficients in order to better understand their shape and meaning, for example, equations 5-11 below.

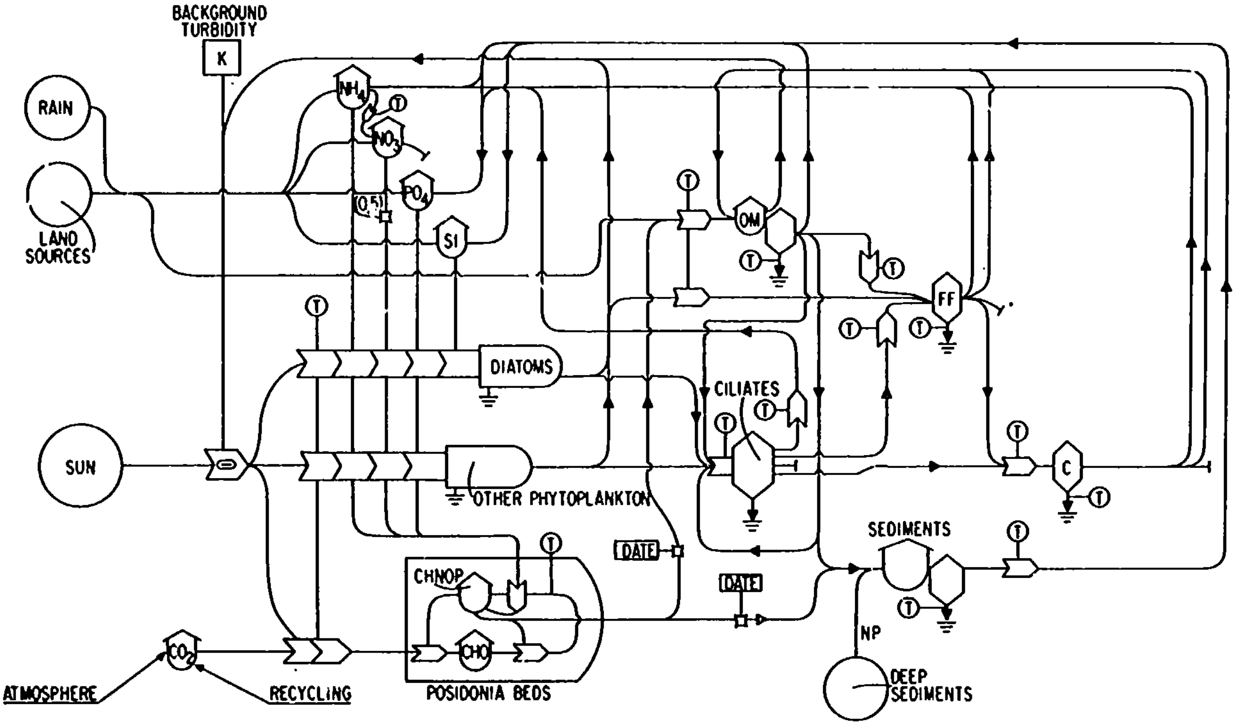


Fig. 65. The conceptual model for the biological model.

TABLE XII
Nitrogen Processes for Fig. 67

NUMBER	NAME
(1)	Input of ammonia by external sources
(2)	Input of nitrate by external sources other than by precipitation
(3)	Input of nitrogen by precipitation
(4)	Uptake of ammonium by diatoms
(5)	Uptake of ammonium by other phytoplankton categories
(6)	Uptake of nitrate by diatoms
(7)	Uptake of ammonium by benthic macrophytes
(8)	Uptake of nitrate by other phytoplankton categories
(9)	Uptake of nitrate by other phytoplankton categories
(10)	Grazing of filter feeders on diatoms
(11)	Defecation of filter feeders feeding on diatoms
(12)	Grazing on other phytoplankton categories by filter feeders
(13)	Defecation of filter feeders feeding on other phytoplankton categories
(14)	Excretion of ammonium by carnivorous zooplankton
(15)	Sinking of diatoms
(16)	Sinking of other phytoplankton categories
(17)	Consumption of detritus by filter feeders
(18)	Defecation of filter feeders feeding on detritus
(19)	Mortality of filter feeders
(20)	Predation on filter feeders by carnivorous zooplankton
(21)	Defecation of zooplankton feeding on filter feeders
(22)	Mortality of carnivorous zooplankton
(23)	Carnivorous zooplankton predating on ciliates
(24)	Defecation of zooplankton predating on ciliates
(25)	Feeding of ciliates on detrital-N
(26)	Defecation of ciliates feeding on detrital-N
(27)	Mineralization of detrital-N
(28)	Mineralization of sediment-N
(29)	Excretion of ammonium by filter feeders
(30)	Nitrification
(31)	Excretion of ammonium by ciliates
(32)	Mortality of benthic macrophytes
(33)	Release of benthic macrophytes to water
(34)	Predation on filter feeders by fish
(35)	Predation of carnivorous zooplankton by fish
(36)	Predation of ciliates by fish
(37)	Settling of detrital-N

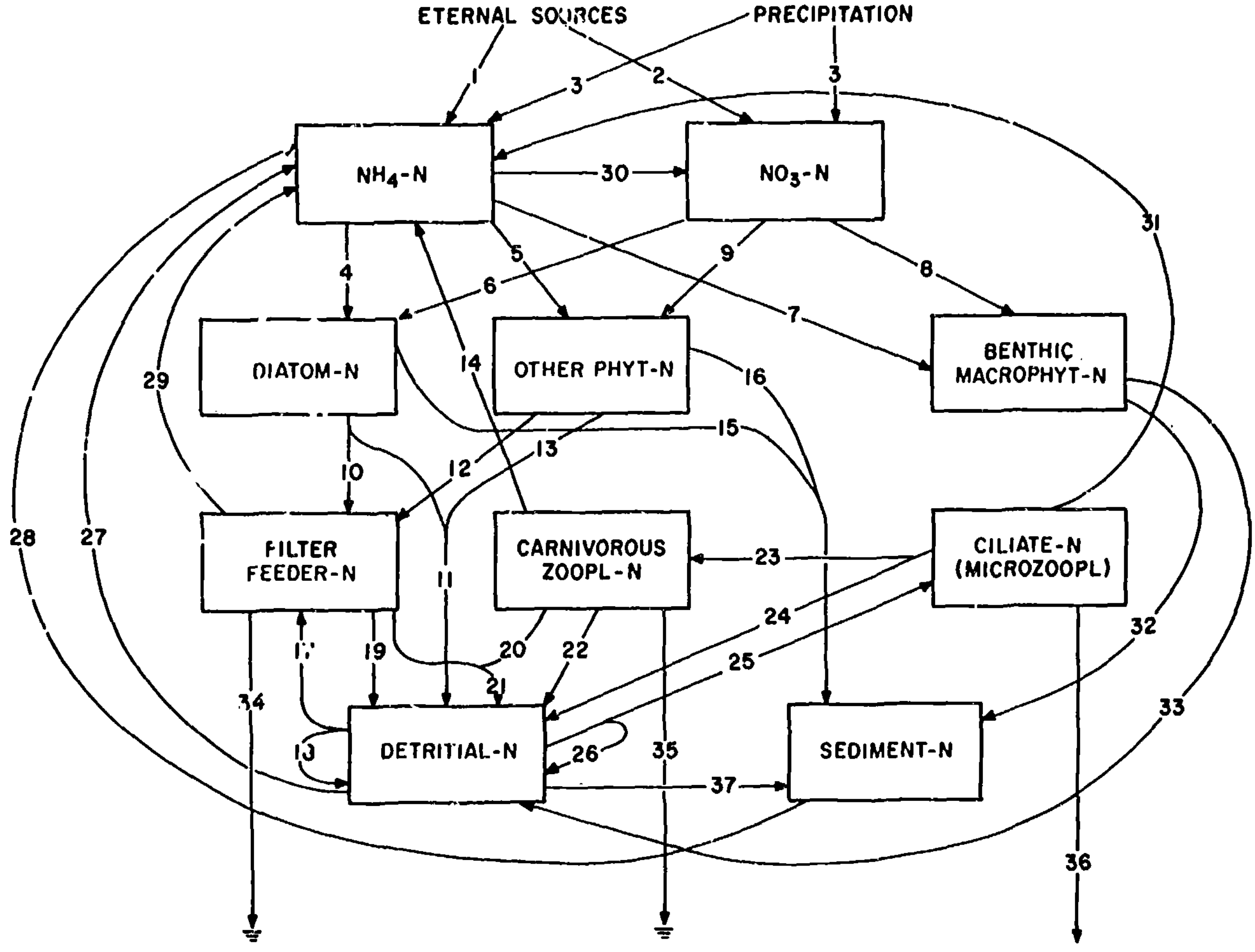


Fig. 66. Conceptual model using only the state variable of nitrogen. The numbers on the flow arrows correspond to the processes listed in Table XII.

Phytoplankton Formulations

From the diagram, it can be seen that the phytoplankton biomass changes due to various processes. For this, as well as the other state variables, we may express this simply as:

$$\frac{dP}{dt} = \text{Inputs} - \text{Outputs} \quad (2)$$

In the case of phytoplankton, the only input is growth. (Advective mixing from other regions may increase or decrease the stock, but this is independent of the biological fluxes. It is discussed in the physical model, and will not be dealt with further here.) The losses include respiration, grazing by filter feeders and ciliates, and natural mortality. We may write a more complete equation (see Table XIII):

$$\frac{dP}{dt} = \mu P - G - M - \pm A \quad (3)$$

Each of these terms must now be specified. The growth depends on the biomass, P(mg C/ℓ) and the instantaneous rate of growth, μ(day^{-1}). If we consider only growth (i.e., net primary production), the respiration term is implicit and need not be specified separately. The growth rate μ is, in turn, affected by light, temperature, and nutrients. One approach for expressing multiple interactions such as this is to propose a maximum rate under optimal conditions, and to reduce this maximum by unitless fractions based on less-than-optimum conditions:

$$\mu = \mu_{max} \text{ (light limitation)(temperature limitation)(nutrient limitation)} \quad (4)$$

EPPLEY (1972) proposed an equation defining the maximum daily division rate for a variety of phytoplankton cultures depending on temperature. We chose this expression to formulate the temperature limitation factor and the maximum rate. By rewriting the original EPPLEY equation in exponential form, μ_{max} is defined as:

$$\mu_{max} = 0.59\ e^{0.0633T} \quad (5)$$

where T is temperature °C. The unit of μ_{max} is day^{-1}. To be more consistent with the idea of a unitless temperature limitation factor, we may define the rate relative to the rate at the maximum temperature in the ecosystem, TMAX (°C). Thus, for any temperature:

$$\text{Temperature limitation} = \frac{e^{0.063 \cdot T}}{e^{0.063 \cdot TMAX}} . \quad (6)$$

We must select a value for μ_{max}, based either on experimental data for species or populations from the region, or we may use the prediction of Eppley's original equation. (In this case, the two expressions clearly are identical.)

The temperature formulation includes the constant 0.063, which may be called PK1, so that it may be adjusted to represent the temperature response of the species represented by the state variables Diatoms and Other Phytoplankton.

The mechanism of limitation of growth due to insufficient nutrients is a topic of active research. Numerous models of varying complexity have been proposed to help understand the role of uptake of dissolved inorganic nutrients into internal storage pools. For this model, we chose to consider the effect relatively crudely, ignoring internal pools and conversions, and relating growth directly to ambient concentrations. The equation widely used for this is the hyperbola, called Michaelis-Mentin kinetics in enzyme studies and the Monod equation in microbial growth (see KREMER and NIXON, 1978 for other references).

$$\text{Nutrient limitation} = \frac{[\text{Nutrient}]}{PK + [\text{Nutrient}]} \quad (7)$$

The constant PK, which is different for different species, and variable due to many factors, is called the half-saturation constant. It is defined as the nutrient concentration at which growth is half the maximum.

When more than a single nutrient is considered, the question of how they may interact to control growth must also be considered. Few data exist for any phytoplankter that specify clearly the nature of this interaction. Most evidence has been interpreted as supporting the most-limiting factor hypothesis (Liebig's Law), and we used this assumption. Based on half-saturation constants for growth for nitrogen, phosphorus, and silicate, three terms are calculated, each expressing the extent to which one nutrient would limit growth if it were considered alone. The smallest of these fractions is selected, and it alone is used to quantify the nutrient limitation effect.

Perhaps the most complicated of the terms in the phytoplankton growth expression is the light limitation factor. Again, much recent research has focused on understanding this effect, and various scientists have emphasized different approaches, from controlled lab studies of photosynthetic pigment biochemistry to descriptive studies of natural populations in situ. Some models have used the hyperbola mentioned above for nutrient limitation to express the light response (in fact, the Posidonia model does this). However, because 24-hr ^{14}C uptake experiments in the Gulf of Naples often demonstrate the phenomenon of surface inhibition, we chose an equation that allows this response. Originally proposed by STEELE (1962), the following equation has proved remarkably flexible in describing the photosynthesis-light response of various phytoplankton (see discussion in KREMER and NIXON, 1978), although recent work suggests more complex and flexible equations.

$$\frac{\mu}{\mu_{max}} = \frac{\bar{I}}{I_{opt}} \exp\left(1 - \bar{I}/I_{opt}\right). \qquad (8)$$

$\bar{I}$ is the average light in the water, and I_{opt} is the level for optimum growth. The equation passes through the origin (i.e., zero production at zero light), and so is not well-suited for predicting net photosynthesis, or growth. For this reason, a slight modification was added, allowing a decrease in biomass below a critical light level. We assumed that growth would be zero at a light level of 1% of the optimum light. The value of the Steele equation at $I/I_{opt} = 0.01$ is 0.027, and by subtracting this value from the equation, the function predicts zero growth at the 1% level. However, the maximum of the function, at $\bar{I} = I_{opt}$, is also reduced to 1.0 - 0.027 = 0.973, so the function must be multiplied by the factor (1.028) to assure a value of 1.0 at $\bar{I} = I_{opt}$. While these modifications are arbitrary, the rationale is that the expression is only a means to describe in a statistical way the functional response of the phytoplankton. It need not have any inherent meaning or mechanistic interpretation to be useful in the model.

The modified equation then defines a unitless factor from -0.027 to +1.0 which is multiplied by the other two factors and μ_{max} to predict the daily growth rate (or loss) of phytoplankton

$$\text{light limitation} = \frac{\bar{I}}{I_{opt}} (1+r) \exp\left(1-r-\frac{\bar{I}}{I_{opt}}\right) \qquad (9)$$

where r = 0.028.

The light level, $\bar{I}$, is the average intensity for the water column, or a layer of the water column. For example, if the column is divided into two layers, 0-20m and 20m-bottom, $\bar{I}$ would be calculated for each layer, as an average throughout the depth range.

$$\bar{I}_{o-z} = \frac{I_o \left(1 - e^{-Cz}\right)}{Cz} \qquad (10)$$

where z is the depth range in meters of the layer, and C is the extinction coefficient. The extinction coefficient, also called the diffusion attenuation coefficient, expresses the rate at which light is reduced with depth in the water column, according to the familiar exponential equation:

$$I_z = I_o e^{-Cz}. \qquad (11)$$

The coefficient C represents the combined effects of all dissolved and particulate material in the water. The use of a single constant value for C over a specific depth range implicitly assumes a uniform water column. This is often not the case, as can be seen in the analysis of a vertical light profile from the Gulf of Naples (Fig. 67a). Note that the log-transformed plot (Fig. 67b) is not a straight line, as would be the case if the extinction coefficient were constant in the top 30 meters. Rather, there is evidence of a high rate of absorption in the ranges 0-10m and 20-30m. This might be indicative of high concentrations of material in these parts of the water column. Nevertheless, the linear regression with a value of C=0.062/m provides a good prediction overall (r^2=0.95). Thus, while the detailed analysis reveals some complexity, the simplified assumption that C is constant within a given layer is satisfactory in this case.

The value of C may be taken from field data, such as in the example above, but to use the measured values directly omits a potentially important feedback on phytoplankton growth. As their biomass increases, the absorption of light also increases reducing the light available deeper in the water. Since our modelling objective focuses on phytoplankton productivity, it may be important to include this self shading. To do this, we need to express the extinction coefficient as the sum of component parts:

$$C = CBL + CKP\,(P) + CKOM\,(OM). \qquad (12)$$

Here, the contributions of phytoplankton and dead organic matter to the extinction coefficient are separated from a 'baseline' value (CBL) that includes all other effects, since the conceptual model includes these as state variables. Equations for the phytoplankton contribution have been derived from field data, and have been widely used in plankton productivity models. In this case, data for the Gulf of Naples allow the specific relation in this region to be investigated. A plot of extinction coefficient, determined from Secchi disk depths, and chlorophyll concentrations at the same stations suggests that the formulation of a baseline value plus a linear function of chlorophyll provides a useful prediction (Fig. 68). Were complete data on dead organic matter also available, a multiple regression might provide the coefficients necessary to support the complete formulation. Finally, since the regression uses chlorophyll as the indicator of phytoplankton biomass, and since chlorophyll is not one of the state variables, a conversion to carbon or nitrogen is required before this equation can be used in the model.

This derivation of the formulation for the extinction coefficient serves as a good example of the formulation step of modelling. In many cases, the equations, and even suggested values for coefficients, are available in the literature. If data were not available for the specific ecosystem, then published formulations may be used. However, if data are available, it may

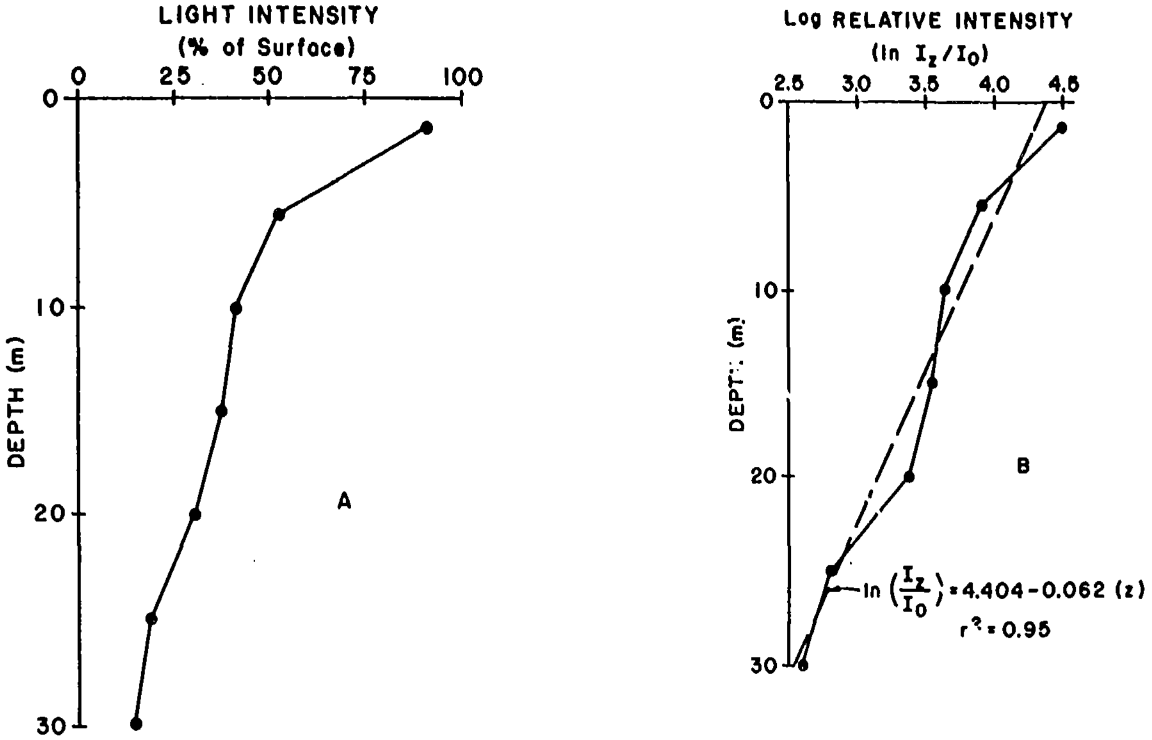


Fig. 67. The vertical light profile for the Gulf of Naples during GONEP 6. Panel (A) shows the light intensity in terms of percentage of surface value, and panel (B) gives the same information in terms of the natural logarithm of the relative intensity I_z/I_0.

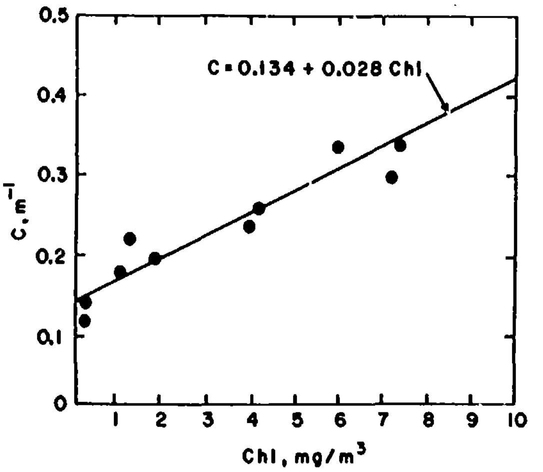


Fig. 68. Extinction coefficient values from the Gulf of Naples plotted against chlorophyll values. The intercept (CBL = 0.14) and the slope (CKP = 0.028) of equation (12) may be determined from field data.

be used. However, if data are available, it may be preferable to incorporate these patterns into the equations. In either case, of course, the model serves to test the adequacy and usefulness of the assumptions underlying the formulations, whether they are specific to the ecosystem, or a general pattern observed in other systems.

The remaining terms in the phytoplankton differential equations are grazing, mortality, and advective change specified via the physical model. Mortality is formulated as a simple fractional loss from the phytoplankton compartment. While this flux is certain to occur, few data are available, so it was not possible at this time to select a value for the parameter.

Grazing by herbivores is a process that has been intensively studied for many years. Numerous complex and simple approaches have been used to model this process (see discussion in KREMER and NIXON, 1978). From the point of view of the phytoplankton formulation, most of these grazing expressions reduce to a simple loss representing the total ingestion of the grazers. In our model, two groups of grazers were included, so the equation specifies both independently; and each rate, in turn, would depend on the detailed formulations for the zooplankton compartments,

$$G = F_{\text{filter feeders}} + F_{\text{ciliates}} \qquad (13)$$

The above discussion demonstrates how the conceptual ideas about specific ecological mechanisms may be expressed in mathematical form. Similar rationales were used to propose the formulations in the other ecological compartment: zooplankton, Posidonia and nutrients (Table XIV in the Appendix to this section).

The Computer Program

Because of the time constraints of the Ischia Workshop, it was not possible to write a computer program for the entire model. In order to demonstrate as much of the modelling process as possible, a partial program was completed including only the growth rate formulations for the two phytoplankton groups considered. The flow chart (Fig. 69) describes the sequence of operations performed in the program, and a complete listing is included in the Appendix to the biological model. The program was written in FORTRAN, and most statements are standard. In a few cases, especially input/output operations, system-dependent syntax was used.

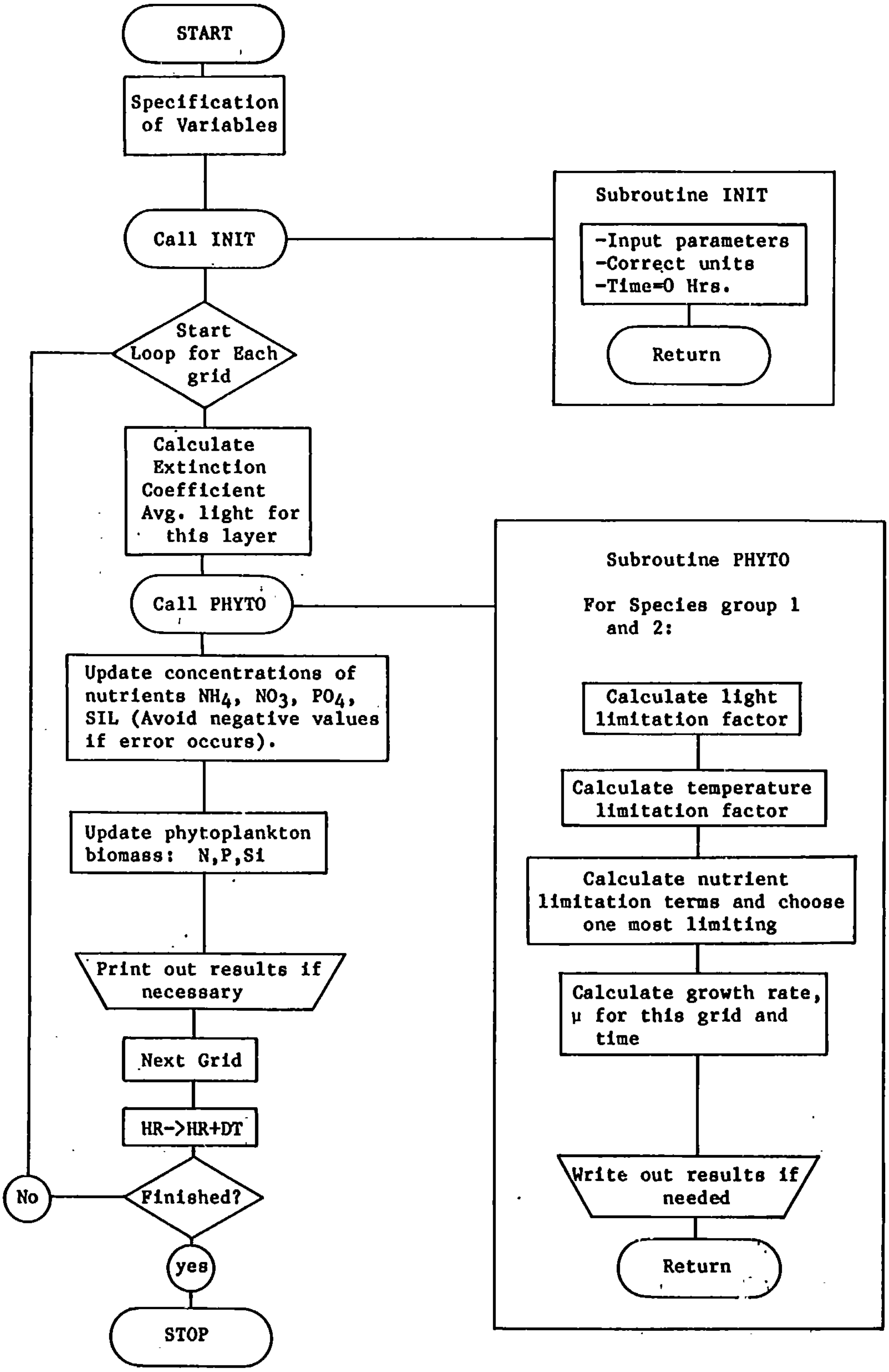


Fig. 69. Flowchart for the Computer Program NAPOLI

Computer Facility

A small portable minicomputer system was available during the workshop. The main computer was an Apple II+ with 48K bytes of core. The language used for the physical and ecological models was FORTRAN, and BASIC was used for some demonstrations. The system included two 5 1/4" floppy disk drives, so that data and programs could be stored and modified efficiently. A quiet thermal printer and a 12 inch black and white TV monitor with graphics capabilities were used for output. While larger computers are faster and can accept much larger programs, it is noteworthy that even on today's very small and inexpensive computers, useful simulations are possible.

The Phytoplankton Program

During the workshop, participants were able to study the complete program, virtually line-by-line. It is beyond the scope of this report to discuss the program in such great detail. However, a few points may prove useful in demonstrating how the formulations are provided to the computer.

The SUBROUTINE PHYTO determines the growth rate based on temperature, light and nutrients. Two indices are important in interpreting the FORTRAN statements. S indicates the species group; when S=1, the calculations relate to diatoms, and S=2 for the other phytoplankton. G indicates the grid in the physical structure of the model, and taken together, S and G can specify a single state variable in one small region of the model.

Consider the following lines taken from Subroutine Phyto:

```
1.  X = AVGLT/IOPT(S)
2.  LTFACT = X * EXP(1.-X)-R(S)
3.  PLIM = PO4(G)/(PKP(S) + PO4(G))
4.  U(S) = UMAX(S)*LTFACT*TFACT*
           AMIN1(NLIM,PLIM,SILIM)
```

(These are taken from the complete program listing in the appendix to this section. Note that some lines are not listed here, especially comment lines which are designated by a "C" in the first column.) In line 1, X is an intermediate value, calculated as the average light (AVGLT, computed earlier in the main program, and passed to this sub-program) divided by the optimum light for growth for each species (IOPT(S)). In line 2 the light limitation factor, called LTFACT, is calculated using the intermediate value of X (see Table XIV, eq. I.3). Small details such as this make the program run more quickly, since the division is only performed once, the result stored as X, and then used twice in the next line. In line 2, the EXP refers to a function supplied within the computer, to exponentiate what is within the parenthesis, i.e., $e^{(1-X)}$. R(S) is the parameter used in the light formulation to allow decreases in biomass at very low light levels. Again, the subscript S specifies diatoms or other phytoplankton. Line 3 computes the nutrient limitation factor for phosphate (PLIM) from the ambient concentration in each grid, PO_4(G), and the half saturation constant for each species, PKP(S). Finally, in line 4, after all other calculations for species S are complete, the growth rate, U(S), is calculated as the product of four terms (see Table XIII, eq. I.2). The function AMIN1 is also supplied by the system, and automatically chooses the minimum of the three nutrient limitation factors included within the parentheses (see Table XIII, eq. I.5).

After looping through all the growth rate computations for S = 1 and then 2, the two values of U (i.e., U(1) and U(2)) are passed back to the main program where nutrient uptake and the appropriate changes in biomass are computed. Although the growth rates were originally specified in the unit of day^{-1}, we must update the standing stocks and concentrations more frequently. Thus, the rates have been converted to an hourly basis. The variable DT is the time-step in hours, and all rates are multiplied by this during the numerical integration. The following statements from the main program NAPOLI demonstrate this process.

```
 1.        NH4(G)=NH4(G)-(U(1)*DIAT(1,G)
                 +U(2)*OTHERP(1,G)*DT
                 + OTHER FLUXES WHEN INCLUDED...
 2.        IF(NH4(G).GE.0.)GO TO 100
 3.        NO3(G)=NO3(G) + NH4(G)
 4.        NH4(G)=0.
 5.        IF(NO3(G).GE.0)GO TO 100
 6.           NO3(G)=0.
 7. 100    CONTINUE
 8.        NO3(G)=NO3(G) + OTHER FLUXES WHEN
              INCLUDED
 9.        DDIAT=U(1)
10.        DOTHER=U(2)
11.        DO 250 I=1,3
12.        DIAT(I,G)=DIAT(I,G)
                  +DDIAT*DIAT(I,G)*DT
13.        OTHERP(I,G)=OTHERP(I,G)
                  +DOTHER*OTHERP(I,G)*DT
14. 250    CONTINUE
```

In line 1, the uptake of ammonia due to phytoplankton growth is accomplished. First, it should be emphasized that in a computer language like FORTRAN, the equals sign does not mean algebraic identity--clearly the two sides of the equation in line 1 are not equal. Instead, the equals sign causes the previous value of the variable to be replaced by a new value calculated according to the right side of the equation. Thus, line 1 updates the value of ammonium concentration in the specific grid defined by the value of G. Next, the program checks to assure that excessive uptake has not exceeded the supply (lines 2-6). Normally, in that case, the predicted growth rate should be altered, or the simulation rerun with a shorter time step. But here, a simple correction allows the program to continue running (lines 4 and 6). The same process must be repeated for PO_4 and Si, although all these steps are not shown here. A FORTRAN 'Do Loop' allows some lines of the program to be repeated easily. The loop enclosed by lines 11 to 14 repeats statements 12 and 13 three times, integrating the growth rates calculated earlier (lines 9 and 10) for the three measures of phytoplankton standing stock: N, P and Si.

Appendix to Biological Model

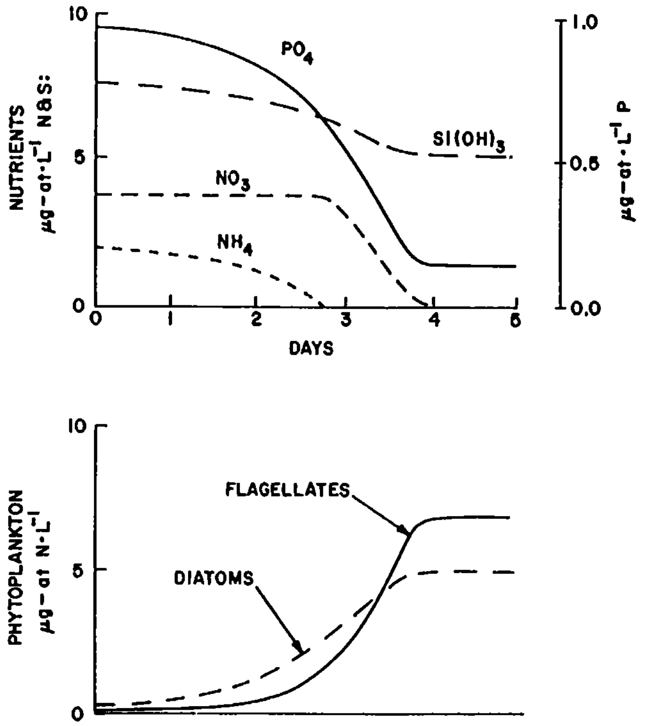


Fig. 70. Sample simulation of the phytoplankton model written during the Ischia Workshop. While the main program NAPOLI has provisions for physical circulation and other ecological compartments, these were not completed during the workshop. Thus this result demonstrates the phytoplankton compartment only, SUBROUTINE PHYTO. The model simulates the standing stock of 2 phytoplankton groups, perhaps diatoms and flagellates, and the concentrations of PO_4, $Si(OH)_3$, NO_3 and NH_4 (µg-at/ℓ) during a 5 day run. The model shows the initial increase of diatoms in response to high nutrients. As nutrients become limiting, the other phytoplankton group surpasses the diatoms, due to lower nutrient requirements. Note the preferential uptake of ammonium, followed by the switch to nitrate; growth of both phytoplankton groups stops when nitrogen is depleted.

Table XIII

Input file used by the PROGRAM NAPOLI. This data file is read from the Subroutine INIT to set the value of the various coefficients in the Golfo de Napoli ecosystem model. The resulting simulation is shown in Fig. 70. A description for the coefficients is given in the text.

Coefficient	Value					
DT	1					
OUTINT	12					
NX	1					
NY	1					
NZ(2G)	2					
FINTIM,Z(2G)	5.	20.	20.			
DIAT N(2S)	0.1	0.1				
OTHERP N(2S)	.01	.01				
N:P,SI(2S)	5.	1.0	10.	0.		
UMAX(2S)	1.6	2.0				
R(2S)	.027	.027				
TEMP(2G)	26.	13.				
TMAX(2S)	26.	26.				
PK1(2S)	.05	.06				
ISFC	200.					
IOPT(2S)	50.	50.				
CBL(2G)	.134	.134				
N:CHL	.476					
CKP SLOPE	.028					
PKN,P,SI(2S)	3.	0.2	2.	0.7	0.1	0
NH4(2G)	2.	4.				
NO3(2G)	4.	8.				
PO4(2G)	1.	2.				
SIL(2G)	8.	10.				

(2S = 2 phyto species; 2G = 2 vertical grids)

Table XIV

Equations of the preliminary Gulf of Naples biological model. The values for the parameters are given in the succeeding Table XIV.

I. PHYTOPLANKTON

1. $\frac{dP}{dt} = \mu P - G - M \pm A$

where: P = phytoplankton biomass, mg C/ℓ
μ = instantaneous daily growth rate, per day

2. $\mu = \mu_{max} \cdot$(Light Limitation)·(Temperature Limitation)·(Nutrient Limitation)

where: μ_{max} = maximum daily growth rate, per day

3. Light limitation = $\frac{\bar{I}}{I_{opt}} \exp(1 - \bar{I}/I_{opt}) - r \quad (1 + r)$

where:
$\bar{I}$ = mean light in the water column, calculated from $\bar{I} = \frac{\bar{I}_s \, (1 - e^{-Cz})}{Cz}$

$\bar{I}_s$ = average visible light at the surface, which may be taken directly from field measurements or obtained by multiplying an estimate of total incident solar radiation (Ly/day) by 0.85 to correct for reflection, and by 0.45 to eliminate long-wave radiation.
C = diffuse attenuation coefficient (or extinction coefficient), per meter
z = thickness of the water layer, m
I_{opt} = light intensity at which phytoplankton growth is maximum, Ly/day
r = a correction factor allowing for a negative change in biomass at very low light levels, $\bar{I} < 0.01 \; I_{opt}$

4. Temperature limitation =

$$\frac{e^{PK1 \cdot T}}{e^{PK1 \cdot T_{max}}}$$

where: PK1 = slope of the growth rate as an exponential function of temperature, $^{o}C^{-1}$
T = water temperature, per ^{o}C
T_{max} = maximum water temperature, ^{o}C

5. Nutrient limitation = $\frac{[NH_4 + NO_3]}{PKN + [NH_4 + NO_3]}$ or $\frac{[PO_4]}{PKP + [PO_4]}$ or $\frac{[Si(OH)_4]}{PKSi + [Si(OH)_4]}$

where: The lowest of these three values is used
[ ] = concentration of ammonium and nitrate, phosphate, or silicate in the water, μmol/ℓ^{-1}

PKP, PKP, PKSi = half saturation constant for each nutrient; the concentration at which growth is reduced to half the maximum

6. $G = F_f + F_c$

where: F_f = ingestion by filter feeding zooplankton, mg C/d
F_c = ingestion by ciliates, mg C/d

7. $M = m \cdot P$

where: m = a fractional daily death rate
P = phytoplankton biomass

8. A = advective exchanges according to the physical circulation model

II. MACROPHYTES (Posidonia)

1. $$\frac{d(\text{CHO-C})}{dt} = P_{max} \; \frac{T}{T_{opt}} \exp(1-T/T_{opt}) \; \frac{I_z}{k_{PI} + I_z} \; \text{CHNOP} - \text{TR}$$

2. $$\frac{d\ \text{CHNOP-C}}{dt} = \text{TR} - \text{M} - k_d\ (\text{CHNOP-C})$$

3. $$\text{TR} = 0.022\ (\text{CHNOP}) \; \frac{T}{T_{opt}} \exp(1-T/T_{opt})$$

where: CHO-C = standing crop of Posidonia carbohydrate, g C/m^2
P_{max} = the weight specific maximum carbon fixation rate of Posidonia, g C/g C/d
T = bottom water temperature, ^{o}C
T_{opt} = the optimum temperature for Posidonia photosynthesis, ^{o}C
I_z = visible light reaching the bottom, Ly/d
R_{PI} = visible light intensity at which Posidonia photosynthesis is half the maximum, ly/d
CHNOP = the standing crop of Posidonia tissue, gdw/m^2
CHNOP-C = the standing crop of Posidonia tissue carbon, g C/m^2
TR = the input of carbon from carbohydrate storage, g C/m^2/d
M = 0.85 (CHNOP-C) on day 270, g C/m^2
k_d = fractional daily loss to the detrital pool, per day on days 1-270.

III. ZOOPLANKTON

1. $$\frac{dZ}{dt} = Z(F - R) - U - D$$

where: Z = zooplankton biomass, mg C/ℓ
F = feeding rate, weight specific per day
R = respiration rate, weight specific per day
U = unassimilated food, weight specific per day
D = mortality, weight specific per day

2. $F = F_{max}$ (Food Limitation)(Temperature Limitation)

where: F = feeding rate
F_{max} = maximum feeding rate, mg C/mg C/d
$$\text{Food Limitation} = \frac{\text{Food Concentration, mg C/ℓ}}{k_f + \text{Food Concentration}}$$
and k_f = Food Concentration at which feeding is half the maximum

$$\text{Temperature Limitation} = \frac{T}{T_{opt}} \exp(1-T/T_{opt})$$

3. $R = r_o \exp(k_r T)$

where: r_o = respiratory rate at 0^{o}C, mg C/mg C/d
k_r = slope of the curve describing respiration as a function of water temperature, per ^{o}C
T = water temperature, ^{o}C

4. $U = F \cdot x$

where: x = the fraction of ingested food which is not assimilated

5. $D = Z \cdot y$

where: D = mortality
y = the fraction of zooplankton biomass consumed by larger predators, per day

IV. DEAD ORGANIC MATTER

1. $$\frac{d(OM)}{dt} = J - X - s + E \pm A$$

where: OM is dissolved and dead particulate organic matter, mg C/ℓ

2. $J = M + U + D/z$

where: J is the input of organic detritus to the water
M = mortality of phytoplankton, mg C/ℓ/d
U = zooplankton feces, mb C/ℓ/d
D = Posidonia detritus, kd(CHNOP), g C/m/d
z = depth, m

3. $X = (X_o\ e^{k_x T}) \cdot (OM)$

where: X = the decomposition of organic detritus
X_o = the detrital decomposition rate at 0°C
k_x = the slope of the detrital decomposition rate as a function of temperature, per °C

4. $$s = \frac{W_s}{z}\ OM$$

where s = the loss by sinking, mg C/d
W_s = sinking rate, m/d
z = depth, m

5. E = inputs from all external sources

6. A = advective exchanges

V. SEDIMENT ORGANIC MATTER

1. $$\frac{dS}{dt} = J' - X'$$

where: S = standing crop of sediment organic matter, g C/m^2
X' = the decomposition of organic detritus on the bottom, g C/m^2/d
J' = input of organic detritus to the bottom, g C/m^2/d

2. and $J' = M + s \cdot z$

where: M = the input of Posidonia leaves on day 270, g C/m^2/d
s = sinking of dead organic matter from the water column, mg C/ℓ/d
z = depth, m

3. $X' = (X'_o\ e^{k_x T})S$

where: $X^{o\prime}$ = normalized decomposition rate of sediment organic matter at 0°C, per day
k_x = slope of the sediment organic matter decomposition rate as a function of temperature, per °C

VI. NUTRIENTS

1. $$\frac{dNH_4}{dt} = 12.6\ (Rz + X + \frac{X'}{z} - dP - \frac{dM}{z}) - N + E \pm A$$

where: NH_4 = concentration of ammonia in water, µmol/ℓ/d
12.6 converts stoichiometrically from mg C/ℓ to µmol NH_4/ℓ
Rz = zooplankton respiration rate mg C/ℓ/d
X = decomposition of OM, mg C/ℓ/d
z = depth, m
X' = decomposition of sediment organic matter, g C/m^2/d
dP = phytoplankton growth mg C/ℓ/d
dM = Posidonia growth, d CHNO/dt, g C/m^2/d

N = oxidation of NH_4 to NO_3, calculated by N = exp (k_{ox}·T)
where N_o = oxidation rate at 0°C, μM/μM/d
k_{ox} = slope of the curve expressing the oxidation rate as a function of temperature, per °C
T = water temperature, °C
E = external inputs, μmol/ℓ/d
A = advective transport, μmol/ℓ/d

2. $$\frac{dNO_3}{dt} = N + E \pm A - 12.6(dP + \frac{dM}{z})^*$$

where: N = oxidation of NH_4, μM/ℓ/d
Note: other terms are defined as in Eq. (VI 1).

3. $$\frac{dPO_4}{dt} = 0.8\ (Rz + X + \frac{X'}{z} - dP - \frac{dM}{z} + E \pm A$$

where: 0.8 converts stoichiometrically from mg C/ℓ to μmol PO_4/ℓ
other terms are defined as in Eq. (VI 1)

4. $$\frac{d\ Si(OH)_4}{dt} = 16.6\ (\frac{X'}{z} - dP_d) + E \pm A$$

where: 16.6 converts stoichiometrically from mg C/ℓ to μmol $Si(OH)_4$/ℓ
dP_d = the growth rate of diatoms, mg C/ℓ/d
other terms are defined as in Eq. (VI 1).

---

*NO_3 uptake only if NH_4 drops below 0.5 μm

Table XV
Preliminary values assigned to the various parameters and coefficients used in the Gulf of Naples ecosystem model equations as listed in Table XIV

I PHYTOPLANKTON

(2) μ_{max} = 0.3/d for diatoms and for other phytoplankton in summer and winter

(3) r = 0.028, so growth = 0 at 1% I
C = baseline value, m^{-1} =

	summer	winter
coastal	0.27	0.13
offshore	0.02	0.03

must be corrected for increase due to phytoplankton Chl a (see text)
I_{opt} = 50% of visible light penetrating the water surface
I light incident on the surface as a forcing function

(4) PK1 = 0.05/°C for diatoms
= 0.06/°C for other phytoplankton
Tmax = 26°C for both
T = water temperature as a forcing function

(5) PKN = 1.0 μM for diatoms
0.5 μM for other phytoplankton
PKP = 0.1 μM for diatoms
= 0.05 μM for other phytoplankton
PKSi = 1.3 μM for diatoms, not considered for other phytoplankton

(6) All terms are simulated

(7) m = unspecified, i.e., no data available

II MACROPHYTES (POSIDONIA)

(1) Pmax = 0.022/d (value quite uncertain)
T_{opt} = 20°C

(2) R_{PI} = 135 Ly/d
C = see eq. I (3)
z = total depth

(3) T_{opt} = 20°C
K_d = 0.016/d (value quite uncertain)

III ZOOPLANKTON

(2) F_{max} = 0.5 mg C/mg C/d (filter feeders)
= 1.0 mg C/mg C/d (ciliates)
= 0.75 mg C/mg C/d (carnivorous zooplankton)

kf = 0.050 mg C/ℓ (filter feeders)
= 0.075 mg C/ℓ (ciliates)
= 0.0002 mg C/ℓ (carnivorous zooplankton)

T_{opt} = 26°C summer, all groups
15°C winter, all groups

(3) r_o = 0.034 mg C/mg C/d (filter feeders)
= 0.040 mg C/mg C/d (ciliates)
= 0.017 mg C/mg C/d (carnivorous zooplankton)

k_r = 0.10/°C (filter feeders)
= 0.110/°C (ciliates)
= 0.069/°C (carnivorous zooplankton)

(4) x = 0.12 (filter feeders)
= 0.20 (ciliates)
= 0.10 (carnivorous zooplankton)

(5) y = unspecified, i.e., no data available

IV DEAD ORGANIC MATTER

(3) X_o = 0.5 mg C/mg C/d
k_x = 0.069/°C

(4) 0 = 0.3 m/d

V SEDIMENT ORGANIC MATTER

(2) M = 0.85 CHNOP on day 270, g C/m^2

(3) X'_o = 0.02 mg C/mg C/d

VI NUTRIENTS

(1) N_o = 0.03 µM/µM/d
k_{ox} = 0.069/°C

Computer Program Listing for Biological Model

```
      PROGRAM NAPOLI
C
C   MAIN PROGRAM FOR TESTING PHYTO COMPARTMENT OF UNESCO MODEL FOR THE
C   GOLFO DE NAPOLI.              J. KREMER   ISCHIA, APRIL 1981
C
C      ALL VARIABLES ARE REAL UNLESS SPECIFIED OTHERWISE:
      IMPLICIT REAL (I,J,K,L,M,N)
      INTEGER G,DAY,HR,DT,OUTINT,UNIT,I,NX,NY,NZ,IX,IY,IZ,PLOT
C
      COMMON DAY,HR,G,DIAT(3,18),OTHERP(3,18),NH4(18),NO3(18),
     1      PO4(18),SIL(18),TEMP(18),THICK(2),CKP,CBL(18),ISFC,
     2      UNIT,DT,OUTINT,FINTIM,NX,NY,NZ,
     3      AVGLT,U(2),UMAX(2),R(2),XTMAX(2),PK1(2),IOPT(2),
     4      PKN(2),PKP(2),PKSI(2)
C
C   CALL A SUBROUTINE TO READ IN COEFFICIENT VALUES AND MAKE
C   INITIAL COVERSIONS, ETC.
C
      CALL INIT
C
C    THE FOLLOWING STEPS ARE PERFORMED FOR EACH GRID, PREPARING
C    INPUT FOR THE ECOLOGICAL SUBROUTINES, CALLING THOSE SUBROUTINES,
C    THEN USING THE NEWLY CALCULATED RATES TO INTEGRATE THE CHANGES
C    IN THE STATE VARIABLES.
C
1     CONTINUE
C     WRITE COLUMN HEADINGS EVERY 4 DAYS:
      IF(MOD(HR,96).EQ.1)WRITE(UNIT,2)
2     FORMAT('DAY HR  G  S:')
      DO 1000 IX=1,NX
          DO 900 IY = 1,NY
          G= (IX-1)*NX+IY
          ITOP=ISFC
              DO 800 IZ=1,NZ
C             G.IS CUMULATIVE INDEX FOR THE GRIDS
              G=G+NX*NY*(IZ-1)
C
C             COMPUTE EXTINCTION COEFFICIENT, AND AVERAGE LT
              C=CBL(G)+CKP*(DIAT(1,G)+OTHERP(1,G))
C                 + CKDM(DM(G)  WHEN DEAD MATTER IS INCLUDED.
C
C             FOR TOP LAYER ITOP=ISFC; BELOW, ITOP IS LIGHT
C             REACHING TOP OF THE LAYER.
              CZ=C*THICK(IZ)
              X = EXP(-CZ)
              AVGLT=ITOP*(1.-X)/CZ
              ITOP=ITOP*X
C
C             SUBROUTINE WILL RETURN ESTIMATED GROWTH RATE
C
              CALL PHYTO
C
C             ... OTHER SUBROUTINES WILL GO HERE...
C             CALL FILTER
C             CALL CILIAT
C             IF(IZ.EQ.2)CALL BENTHS
C             CALL INPUTS
C
C             COMPUTE UPTAKE OF NUTRIENTS, BEFORE ALLOWING GROWTH, TO
C             BE SURE DEMAND DOESN'T EXCEED SUPPLY.
C
              NH4(G)=NH4(G) - (U(1)*DIAT(1,G) + U(2)*OTHERP(1,G))*DT
C                     + OTHER FLUXES WHEN INCLUDED...
              IF(NH4(G).GE.0.)GO TO 100
C             ELSE:
                   NO3(G)=NO3(G) + NH4(G)
                   NH4(G)=0.
                   IF(NO3(G).GE.0.)GO TO 100
C                  ELSE:
                        NO3(G)=0.
```

```
                         WRITE(UNIT,90)
90                       FORMAT('N UPTAKE EXCEEDS SUPPLY; CHANGE DT?')
100            CONTINUE
C              NO3(G)=NO3(G) + OTHER FLUXES WHEN INCLUDED...
C
               PO4(G)=PO4(G) - (U(1)*DIAT(2,G) + U(2)*OTHERP(2,G))*DT
C                       + OTHER FLUXES WHEN INCLUDED ...
               IF(PO4(G).GE.0.)GO TO 150
C              ELSE:
                    PO4(G)=0.
                    WRITE(UNIT,140)
140                 FORMAT('P UPTAKE EXCEEDS SUPPLY; CHANGE DT?')
150            CONTINUE
               SIL(G)=SIL(G) - (U(1)*DIAT(3,G) + U(2)*OTHERP(3,G))*DT
C                       + OTHER FLUXES WHEN INCLUDED ...
               IF(SIL(G).GE.0.)GO TO 200
C              ELSE:
                    SIL(G)=0.
                    WRITE(UNIT,190)
190                 FORMAT('SI UPTAKE EXCEEDS SUPPLY; CHANGE DT?')
200            CONTINUE
C
C              NOW UPDATE PHYTO BIOMASS BY INTEGRATING CHANGES
C
               DDIAT=U(1)
               DOTHER=U(2)
C              WITH OTHER FLUXES, DDIAT =  U(1) - GRAZING - SINKING ...
C
               DO 250 I=1,3
               DIAT(I,G)  =DIAT(I,G)   + DDIAT *  DIAT(I,G)*DT
               OTHERP(I,G)=OTHERP(I,G) + DOTHER*OTHERP(I,G)*DT
250            CONTINUE
C
C              OUTPUT INTERVAL DEFINED BY OUTINT:
               IF(MOD(HR,OUTINT).GE.DT)GO TO 800
C              ELSE:
                    WRITE(UNIT,700)DAY,HR,G,(DIAT(I,G),I=1,3),
     1                   NH4(G),NO3(G),PO4(G),SIL(G),
     2                   (OTHERP(I,G),I=1,3)
700            FORMAT(3I3,' D1',' N',F7.3,' P',F7.3,' SI',F6.3,' A,N',
     1         ',P,SI',3X,4F7.3/9X,' O2',3F9.3)
C
C              NEXT DEPTH LAYER
800            CONTINUE
C
C           NEXT GRID IN Y-DIRECTION
900         CONTINUE
C
C       NEXT GRID IN X-DIRECTION
1000    CONTINUE
C
C       PHYSICAL MIXING WILL GO HERE:
C       CALL ADVECT
C
C       NOW UPDATE TIME AND CHECK FOR END OF RUN...
C
        HR=HR+DT
        IF(HR.LT.24)GO TO 1
C       ELSE:
             DAY=DAY+1
             HR=0
             IF(DAY.LE.FINTIM)GO TO 1
C            ELSE:
                  STOP
         END
             SUBROUTINE INIT
C   SUBROUTINE FOR INITIALIZING COEFFICIENTS IN UNESCO MODEL FOR THE
C   GOLFO DE NAPOLI.             J. KREMER  ISCHIA, APRIL 1981
C
C       ALL VARIABLES ARE REAL UNLESS SPECIFIED OTHERWISE:
       IMPLICIT REAL (I,J,K,L,M,N)
       INTEGER G,DAY,HR,DT,OUTINT,UNIT,I,NX,NY,NZ
```

```
      CHARACTER A,FNAME*15,LINE*80
      DIMENSION TMAX(2)
C
      COMMON DAY,HR,G,DIAT(3,18),OTHERP(3,18),NH4(18),NO3(18),
     1       PO4(18),SIL(18),TEMP(18),THICK(2),CKP,CBL(18),ISFC,
     2       UNIT,DT,OUTINT,FINTIM,NX,NY,NZ,
     3       AVGLT,U(2),UMAX(2),R(2),XTMAX(2),PK1(2),IOPT(2),
     4       PKN(2),PKP(2),PKSI(2)
C
C       DEFAULT VALUES ARE READ FROM FILE.  NOTE THAT SOME
C       INPUT/OUTPUT SYNTAX IS SPECIFIC TO THIS COMPUTER SYSTEM.
C
      WRITE(*,100)
100   FORMAT('ENTER FILENAME FOR COEFFICIENTS:',$)
      READ(*,6)FNAME
      OPEN(2,FILE=FNAME)
C
C     READ IN TIME AND SPACE VARIABLES, AND PROGRAM CONTROL:
      DAY=1
      HR=1
      READ(2,110)DT,OUTINT,NX,NY,NZ
110   FORMAT(10X,BN,I7)
111   FORMAT(10X,BN,10F7.0)
      G=NX*NY*NZ
      READ(2,111)FINTIM,(THICK(I),I=1,2)
      UNIT=1
      WRITE(*,5)
5     FORMAT('OUTPUT TO PRINTER?')
      READ(*,6)A
6     FORMAT(A)
      IF(A.EQ.'Y') OPEN (1,FILE='PRINTER:')
      IF(A.NE.'Y') OPEN(1,FILE='CONSOLE:')
C
C    READ IN ECOLOGICAL COEFFICIENTS:
C
C      PHYTOPLANKTON:
C          STANDING STOCKS (NITROGEN BIOMASS):
           READ(2,111)(DIAT(1,I),I=1,G)
           READ(2,111)(OTHERP(1,I),I=1,G)
C
C          CONVERT BIOMASSES TO P AND SI CONCENTRATIONS (UG-AT/L)
           READ(2,111)DNP,DNSI,ONP,OSIN
           DO 20 I=1,G
              DIAT(2,I)=DIAT(1,I)/DNP
              DIAT(3,I)=DIAT(1,I)/DNSI
              OTHERP(2,I)=OTHERP(1,I)/ONP
              OTHERP(3,I)=OTHERP(1,I)*OSIN
20            CONTINUE
C
C      GROWTH RATES & LIGHT LIMITATION PARAMETER:
           READ(2,111)(UMAX(I),I=1,2)
           READ(2,111)(R(I),I=1,2)
C            R   IS VALUE OF STEELE'S LIGHT-LIMITATION EQUATION AT
C          1 %  OF IOPT;  BELOW THIS WILL GIVE A NEGATIVE RATE,
C          SIMULATING NET LOSS (RESPIRATION > PRODUCTION).  BELOW
C          UMAX IS ADJUSTED FOR THE VALUE OF R, AND SCALED FOR DT.
C
C      TEMPERATURE:
           READ(2,111)(TEMP(I),I=1,G)
           READ(2,111)(TMAX(I),I=1,2)
           READ(2,111)(PK1(I),I=1,2)
C
C      CONVERT GROWTH RATE TO "PER-HOUR, CALC GROWTH AT TMAX:"
       DO 10 I=1,2
          UMAX(I)=UMAX(I)*(1.+R(I))*DT/24.
          XTMAX(I)=EXP(PK1(I)*TMAX(I))
10     CONTINUE
C
C      LIGHT & CHLOROPHYLL PARAMETERS:
          READ(2,111)ISFC
          READ(2,111)(IOPT(I),I=1,2)
          READ(2,111)(CBL(I),I=1,G)
```

```
         READ(2,111)NCHL
         READ(2,111)CKP
C        NCHL = UGAT-N / UG CHL A ,  TO CONVERT CKP TO CORRECT UNITS
         CKP   = CKP * NCHL
C
C     NUTRIENT KINETIC PARAMETER & AMBIENT CONCENTRATIONS:
         READ(2,111)(PKN(I),PKP(I),PKSI(I),I=1,2)
         READ(2,111)(NH4(I),I=1,G)
         READ(2,111)(NO3(I),I=1,G)
         READ(2,111)(PO4(I),I=1,G)
         READ(2,111)(SIL(I),I=1,G)
C
200   CLOSE(2)
      RETURN
      END


C
             SUBROUTINE PHYTO
C  SUBROUTINE FOR PHYTOPLANKTON COMPARTMENT IN UNESCO MODEL FOR THE
C  GOLFO DE NAPOLI.              J. KREMER  ISCHIA, APRIL 1981
C
C       ALL VARIABLES ARE REAL UNLESS SPECIFIED OTHERWISE:
      IMPLICIT REAL (I,J,K,L,M,N)
      INTEGER G,DAY,HR,DT,OUTINT,UNIT,S,NX,NY,NZ
C
      COMMON DAY,HR,G,DIAT(3,18),OTHERP(3,18),NH4(18),NO3(18),
     1      PO4(18),SIL(18),TEMP(18),THICK(2),CKP,CBL(18),ISFC,
     2      UNIT,DT,OUTINT,FINTIM,NX,NY,NZ,
     3      AVGLT,U(2),UMAX(2),R(2),XTMAX(2),PK1(2),IOPT(2),
     4      PKN(2),PKP(2),PKSI(2)
C
C     THE FOLLOWING STEPS ARE EXECUTED FOR THE GRID G EACH TIME THIS
C     SUBROUTINE IS CALLED FROM THE MAIN PROGRAM.
C
C     FOR EACH OF THE 2 PHYTOPLANKTON GROUPS, S:
      DO 100 S=1,2
C
C          LIMITATION ON GROWTH, DUE TO LIGHT -- STEELE'S EQUATION
C          MODIFIED TO INCLUDE LOW-LIGHT RESPIRATION.
C
C          (X IS USED AS A TEMPORARY VARIABLE, CHANGING MEANING..)
           X=AVGLT/IOPT(S)
           LTFACT=X*EXP(1.-X) - R(S)
C
C          TEMPERATURE FACTOR, ASSUMING 1.0 AT SPECIFIED TMAX. FACTOR
C          XTMAX HAS BEEN CALCULATED TO HAVE THIS RESULT.
           X=EXP(PK1(S)*TEMP(G))
           TFACT=X/XTMAX(S)
C
C          NUTRIENT FACTOR, WILL BE THE MOST LIMITING OF 3 TERMS:
           X=NH4(G) + NO3(G)
           NLIM=X/(PKN(S)+X)
           PLIM=PO4(G)/(PKP(S)+PO4(G))
           SILIM=SIL(G)/(PKSI(S)+SIL(G))
C
C          GROWTH RATE ESTIMATE  FOR THESE CONDITIONS IS:
           U(S)=UMAX(S) * LTFACT * TFACT * AMIN1(NLIM,PLIM,SILIM)
C
C          WRITE OUT RESULTS PERIODICALLY BASED ON OUTINT:
           IF(MOD(HR,OUTINT).GE.DT)
     1     WRITE(UNIT,10)DAY,HR,G,S,U(S),LTFACT,TFACT,NLIM,PLIM,SILIM
     1          ,AVGLT
10         FORMAT(4I3,' U',F7.3,' L',F7.3,' T',F7.3,' N,P,SI',3F7.3,
     1            ' AVL',F5.1)
C
100        CONTINUE
       RETURN
       END
```

INTRODUCTION

Participants conducting research in other Mediterranean ecosystems were invited to summarize the modelling efforts in their respective countries. This provided a mechanism to discuss a broad spectrum of problems associated with the application of conventional data sets and their analyses to the development of ecosystem models. It also stimulated specific comparisons to the Gulf of Naples situation as encountered in the modelling exercises.

No uniform criteria were set for the content of the following summaries, and therefore they should not be regarded as complete in each case, nor comparable between cases.

PHYTOPLANKTON ECOLOGY STUDIES IN SARONIKOS GULF AND ELEFSIS BAY

Introduction

Saronikos Gulf is an extension of the Aegean Sea between the Attikis Peninsula and the northwestern Peloponessus. At the north end of the Gulf lies Elefsis Bay, a semi-enclosed shallow embayment connected to the Gulf east and west via narrow and shoal channels. The upper part of Saronikos Gulf and the eastern part of Elefsis Bay are influenced by domestic waste discharges and industrial effluents so that the conditions in these areas (eutrophic system) are so different from those found in the lower Saronikos Gulf (oligotrophic system) that they must be considered separately.

Existing Data

Information on phytoplankton ecology of this area has come from numerous expeditions performed since 1966. Fig. 71 shows the area and the location of stations, and Tables XVI and XVII the period covered, frequency of collections, parameters measured and their annual range.

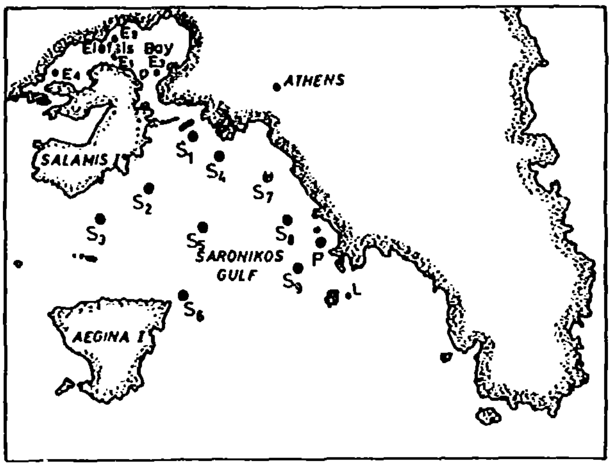


Fig. 71. Saronikos Gulf with sampling stations.

Stages of Modeling

All data were analyzed statistically and provided the following information:

a. annual cycle of phytoplankton and zooplankton

b. species composition, succession and diversity of phytoplankton and zooplankton

c. vertical distribution of phytoplankton

d. phytoplankton-zooplankton relationships

e. phytoplankton spatial distribution

f. annual and spatial distribution of nutrients.

The results showed significant variations of chemical and biological parameters between areas. The upper Saronikos Gulf and the eastern part of Elefsis Bay were influenced by the sewage outfall and had higher concentrations of phosphate, nitrate, ammonia, organic nitrogen and organic phosphorus (STATHOULOPOULOU and IGNATIADES, 1981; IGNATIADES, in prep.), in relation to lower Saronikos Gulf (IGNATIADES and BECACOS-KONTOS, 1969; IGNATIADES et al., 1981). A well-defined annual phytoplankton cycle with maxima in spring and autumn was recorded in lower Saronikos Gulf (IGNATIADES, 1969; IGNATIADES et al., 1980). In the upper Saronikos Gulf and Elefsis Bay the eutrophication conditions affected the periodicity of phytoplankton conditions (irregular pattern of blooms), the species composition, succession and diversity (TETT and IGNATIADES, 1976; IGNATIADES and MIMIKOS, 1976; 1977). Studies on the spatial distribution of phytoplankton along a horizontal nutrient gradient between the upper and lower Saronikos Gulf (IGNATIADES, 1981) showed remarkable heterogeneity of algal populations which gave rise to coefficients of variations up to 120% for observations of cell counts and chlorophyll concentrations between stations 12 km apart. In Elefsis Bay (semi-closed environment), a remarkable heterogeneity in plankton composition between stations was recorded and gave rise to coefficients of variation up to 50% in species diversity and up to 120% in diatom/flagellate ratio (IGNATIADES, 1982).

The study of the vertical distribution of phytoplankton in Elefsis Bay (IGNATIADES, 1979) showed that significant variations in the vertical profile between taxa existed at certain periods. During the mixing period marked depth variations appeared occasionally in the concentrations of coccolithophores and flagellates, whereas diatoms in general were uniformly distributed throughout the water column. These differences in the vertical profile between taxa were mainly attributed to the motility of coccolithophores and flagellates versus the non-motility of diatoms. During the period of strong stratification of the water column, all taxa were accumulated in the upper 10 m, and this behavior was attributed to certain physical parameters (light penetration, water density) which favored the accumulation of all taxa in the upper layers.

Table XVI

Information on physical, chemical and biological parameters measured in Saronikos Gulf and Elefsis Bay, during the period 1965-1930.

Station	L	S_1,S_2	$E_1 - E_4$	E_1,P	$S_1 - S_3$	$S_1 - S_9$
Year	1965[a]	1972[b]	1975-1976[c]	1977-1978[d]	1979[e]	1980[e,f]
Period	Monthly Sampling	Autumn Sampling	Monthly Sampling	Monthly Sampling	Monthly Sampling	Monthly Sampling
Parameters						
T °C	+	+	+	+	+	+
S ppt	+	+	+	+	+	+
O_2			+		+	+
Secchi	+	+	+		+	+
Chlor.					+	+
Phytopl.	+	+	+	+	+	+
Zoopl.				+		
$P-PO_4$	+		+	+	+	+
$N-NO_2$	+		+	+	+	+
$N-NO_3$	+		+	+	+	+
$N-NH_3$					+	+
$Si-SiO_2$	+		+	+	+	+
Org. N					+	+
Org. P					+	+
Petroleum hydrocarbons			+			

References:

[a] IGNTIADES (1969), IGNATIADES and BECACOS-KONTOS (1969)
[b] TETT and IGNATIADES (1976)
[c] IGNATIADES and MIMIKOS (1976 and 1977), IGNATIADES (1979 and 1982)
[d] MORAITOU-APOSTOLOPOULOU (1976) and MORAITOU-APOSTOLOPOULOU and IGNATIADES (1980)
[e] IGNATIADES (1981) and STATHOULOPOULOU and IGNATIADES (1981)
[f] IGNATIADES et al. (1980)

Table XVII

Annual range of hydrographic parameters at surface waters of Saronikos Gulf and Elefsis Bay.

Parameter		Saronikos Gulf		Elefsis Bay
		Upper	Lower	
Temp.	(°C)	13.3-27.2	13.2-26.7	11.0-25.8
Sal.	(S ppt)	37.24-38.60	37.56-38.94	34.12-38.51
Oxyg.	(ml/l)	1.91-6.05	3.02-7.33	1.00-5.88
Ext. coeff.	(m^{-1})	0.48-0.11	0.15-0.05	0.68-0.19
Chlor. a	(mg/m^3)	0.65-12.32	0.11-0.81	-
Phytopl.	(cells/l)	$3x10^5-3x10^7$	$7x10^3-1x10^6$	$6x10^3-4x10^6$
Zoopl.	(ind./l)	$4x10^2-3x10^3$	-	-
$P-PO_4$	(μg-at/l)	0.04-6.00	0.02-0.50	0.50-2.72
$N-NO_3$	(μg-at/l)	0.20-4.50	0.10-1.60	0.58-6.50
$N-NO_2$	(μg-at/l)	0.02-1.80	0.00-0.53	0.05-1.58
$N-NH_3$	(μg-at/l)	0.45-17.40	0.21-2.74	-
$Si-SiO_2$	(μg-at/l)	3.4-12.9	3.1-14.0	3.6-10.9
Org. N	(μg-at/l)	2.84-54.16	7.31-37.30	-
Org. P	(μg-at/l)	0.19-9.13	0.23-3.82	-
Petr. hydr.	(mg/l)	-	-	14.9-21.85

The study of the phytoplankton-zooplankton relationships (MORAITOU-APOSTOLOPOULOU and IGNATIADES, 1980) revealed that quantitative relationships among these populations were influenced by the trophic level of the environment and their stocks were significantly correlated only in non-polluted conditions. The quantitative relationship between the principal grazers in the zooplankton population (Acartia clausi, Oithona nana) and the phytoplankton dominant species Exuviaella baltica, upon which these species were believed to graze, was tested, but the correlation coefficient proved to be non-significant, indicating that these grazers did not feed exclusively on the dominant flagellate.

EVENT-ORIENTED APPROACH TO THE ECOLOGICAL MODELLING OF LAKE KINNERET

Introduction

Lake Kinneret belongs to the group of the best investigated water bodies in the world. The scientific team under aegis of Kinneret Limnological Laboratory has been studying the lake since 1968. The list of publications (1969-1981) related to geological, physical, and ecological conditions in the lake contains about 150 items, including a monography (SERRUYA, 1978). The existing body of data about different aspects of Lake Kinneret ecology and the level of understanding of the main processes of ecological significance makes this lake an ideal object for modelling (BERGSTEIN et al., 1978, BERMAN et al., 1978; BERMAN and GERBER, 1980; CAVARI and HADAS, 1979; DUBINSKY and BERMAN, 1981; GOPHEN, 1981; POLLINGHER, 1981; C. SERRUYA et al., 1978, 1979, 1980; WYNNE, 1981). The efforts of modelling some processes in the lake go back to the year 1975 (VOLOHONSKY and SERRUYA, 1975). The models of hydromechanical processes in the lake (currents and seiches) have been recently developed by Serruya (articles in preparation). We realized rather quickly that conventional physical models of thermal stratification, though valid within the framework of their own, do not fit to be a basis for ecological models because of too small time and space scales used in the former. This was one of the reasons we turned to discrete representation of formation and maintenance of water biotopes. This approach resulted in 'event oriented' model WBIOTOP (VOLOHONSKY et al., 1980). The intensive discussions among the authors concerning the principles of discrete modelling led us to formulation of what we call 'event oriented approach.' The basic principle of such approach is that the time scale (or time scales) should not be granted, but elaborated by the model as functions of its state parameters, just in the same way as its space scales. The 'time' of such a model is a series of discrete events, and the duration of each event in units of natural time appears as one of the parameters of 'event.' This principle, initially used in WBIOTOP, has been expanded on the general ecological model (GEMLK) and led to certain modifications of its state-and-processing framework as compared with conventional models.

Time and Space Scales

Each event is defined as change of parameters of a certain set of ecological entities within time and space and both treated as parameters as well. In this sense event as such physically is 'dimensionless.' The physical dimensions are implied by the form of process equations. The only dimension is a formal one--the consecutive number of the event. The events are hierarchical: the events of higher levels are built up by the events of lower levels; and these, in turn, by elementary events, occurring within the lowest time and space scales. The time and space scales used in GEMLK are represented in Table XVIII. Here elementary events occur within TSTEP3 (those of discrete character e.g. cell division) or within TSTEP4 (of continuous character, e.g. algal nutrition) and within SSCALE2 ('patches'). The biological entities appear in the model as a set of subpopulations, treated as 'pseudo-individuals' meaning that elementary events occur with the subpopulation as total. The 'pseudo-individual' appears in the model as a set of parameters of an individual organism plus the parameter of 'representativity,' a number of organisms represented by this individual in the population.

Physical and Biological Submodels

General conceptual structure of GEMLK is drawn in Fig. 72. The physical submodel is virtually independent on the output of GEMLK. The TSTEP1 is elaborated from observed wind pattern (Figs. 73 and 74). SELWD-program transforms hourly wind speeds into a set of STORM and STILL events. Each event here has three parameters of physical significance: S-time of start, D-duration in hours, W-averaged wind speed. Duration time is equivalent to the basic step TSTEP1. We had a set of hourly measured wind speed values for an 8 to 9 year period. This gave a good basis for elaborating three typical wind regimes for each month: (a) when the number of storms is low; (b) when it is high; (c) when it is about the mean value (Fig. 74). This output is used as a source of data for WBIOTOP model (VOLOHONSKY et al., 1980), which elaborates SSCALE1 (volumes of water biotopes for each STORM or STILL event and volumes of water transferred from and to these biotopes on each step). The rest of the physical submodel divides TSTEP1 into a set of steps of lower level (TSTEP2) according to the sign of heat input resulting in a set of 'events' called DAY STORMS, NIGHT STILLS, etc., and this output is used in the biological submodel.

The further subdivision of the space scale is performed by PATCH subroutine. It uses the wind speed at a certain time step (of the physical submodel) and the numbers of 'individuals' N_B in the list (of the biological submodel) in order to calculate the number of elementary "patches" in each of the water biotopes by means of a function:

Table XVIII

Time and space scales used in GEMLK

Scales	Source	Order of Magnitude
Time:		
YSTEP	granted	1 year
MSTEP	granted	1 month
TSTEP1	SELWD	4 hours - days
TSTEP2	PHYS. SUBMODEL	$\leq$ 1 - 14 hours
TSTEP3	BIOL. SUBMODEL	$\leq$ 1 - TSTEP2
TSTEP4	BIOL. SUBMODEL	$\leq$ TSTEP2
Space:		
VOLUME	granted	volume of the lake (km^3)
SSCALE1	WBIOTOP	volume of water biotopes
SSCALE2	PHYSICAL AND BIOLOGICAL SUBMODELS	$\leq$ SSCALE1

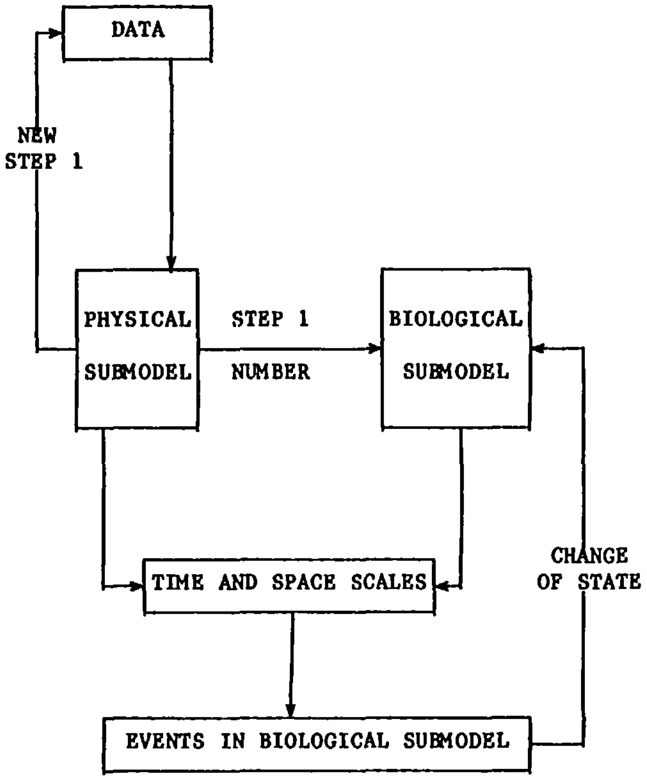


Fig. 72. Conceptual structure of GEMLK

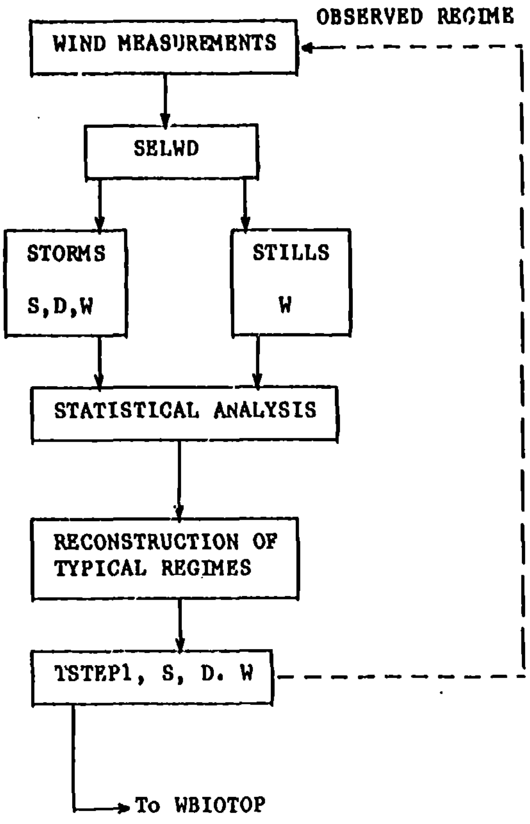


Fig. 74. Formation of TSTEP 1

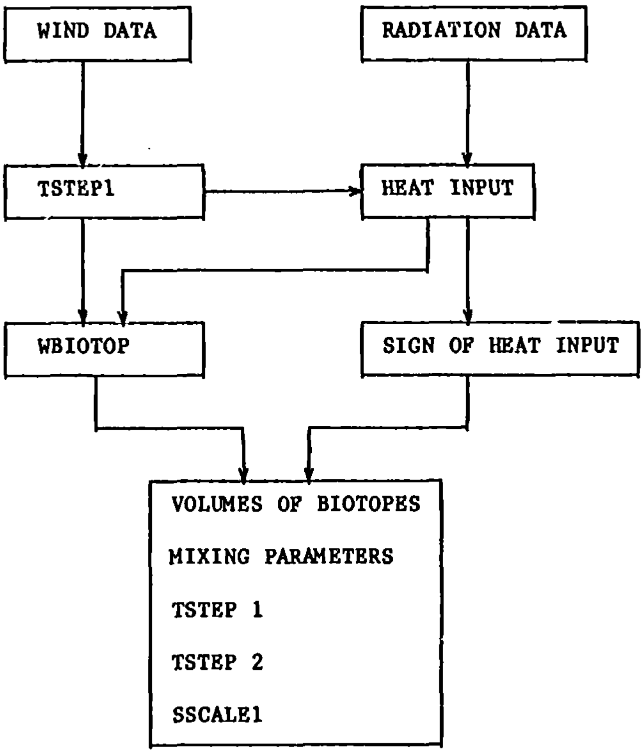


Fig. 73. Physical submodel

$$P\ (W,\ N_B) + S\cdot A\ (N_B)^{E\ (W)} \qquad (1)$$

where

P	is a number of elementary patches,
$A\ (N_B)$	is an integer greater than one (as N_B increases so does A),
$E\ (W)$	is an integer greater than one (as W increase E decreases), and
S	is an arbitrary integer defining the scale of resolution.

The volume of each elementary patch is then

$V_e = V_B/P$ where V_B is the volume of a biotope (2)

Some of these elementary patches are treated as equivalent according to polynomial distribution:

$$P/S = \sum_{i\,=\,1}^{i\,=\,k} M_i, \qquad (3)$$

where

the M_i	are coefficients of a polynomial expansion of A^E;
k	is the number of terms of the polynome; and
M_i	represents number of equivalent patches which are jointed to form a 'working' patch P_W with a volume:

$$V^W = V_e\cdot M_i, \qquad (4)$$

and number of working patches is then

$$M^W = k\cdot S\ . \qquad (5)$$

The individuals of the list are distributed into M_W working patches by a randomizing subroutine, and if the list of individuals is long enough, the distributions of densities of organisms per unit of volume should have approximately normal character. (If the information about conditions of coexistence of different species is available, it should be reflected in the rules of distribution.) Each patch is assumed to exist during TSTEP1. The formation of the patches is shown schematically in Fig. 75.

The next step of biological submodel (Fig. 76) treats the patches after they have been formed and consists of the events within each patch, such as mixing within a biotope, and of the events associated with mixing of water biotopes. The active and passive movements of individuals are considered as well.

Elementary Events

The subroutine describing the events within a patch form the very heart of the biological

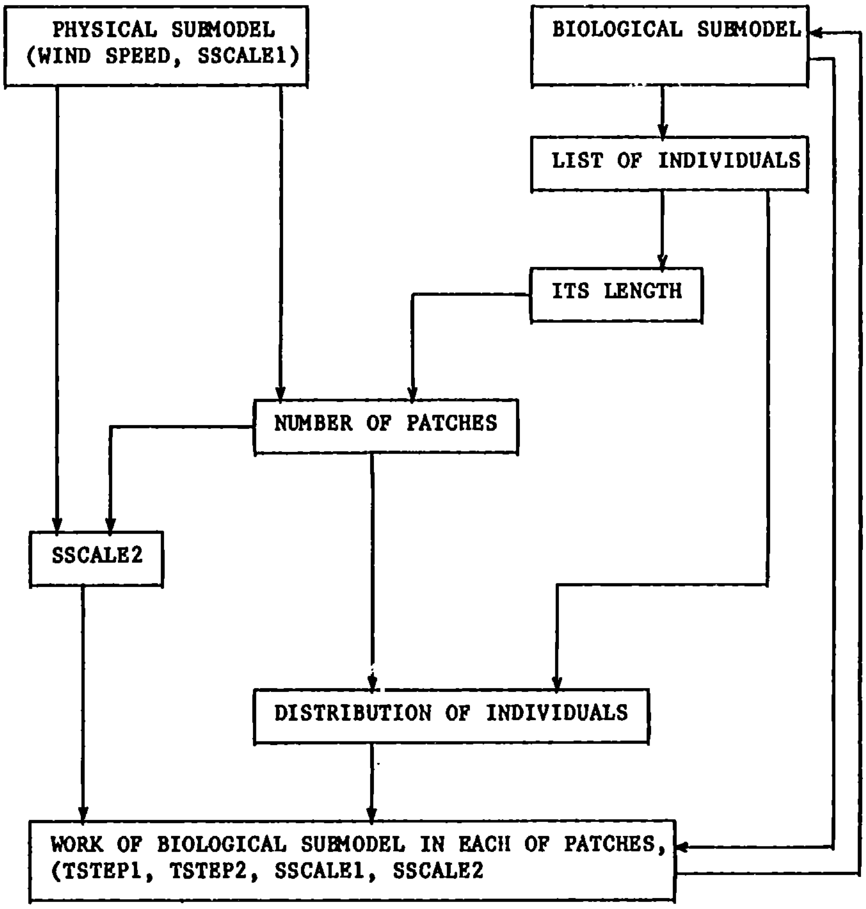


Fig. 75. Formation of SSCALE2 (PATCHES)

submodel. Here the lowest time scales (TSTEP3 and TSTEP4) are elaborated as functions of the state of the system and intrinsic properties of the species (Fig. 77). All available information about the biology of the species should be used in order to describe the behavior of the individual as realistically as possible (Fig. 78). Since the time scales are short enough, the process equations are significantly reduced to nearly verbal level (e.g., the cell has divided or has not divided). The calculations as such are then clear and simple, but the material balance should be strictly held. Then the calibration procedure will consist of the rejecting of sets of conditions resulting in unrealistic parameters of an individual (weight, chemical composition, etc.). The parameters of individuals used in the model and examples of processes associated with the variations of these parameters are in Table XIX.

The Model Output

The model output may be obtained as a set of states on any prescribed level of resolution and/or as sets of dynamic parameters related to the transition from event to event on any hierarchical level as well. An interesting point is that we can model the process of sampling, that is, include the investigator into the very body of the model. Then the results of 'measurements' and the objective model output may be compared.

Problem of Causality

The elementary processes in this model are purely deterministic. Most of them are treated as discrete events, and even those of physically continuous character may be reduced to the same form of output because of their local nature. The stochasticy is introduced, not on the level of process equations, but on a higher level where the patches are formed. Then the display of outputs may be treated as a set of more or less probable scenaria of the behavior of the system with the same set of coefficients of process equations. The 'present' state of the model in such a context may be conceptualized as a superposition of consequent 'scenaria' that occurred in the 'past,' and as such it gives a more realistic insight into the problem of the system's stability and the prognosis for the future.

Stage of Development

The physical submodel of GEMLK is practically finished. The PATCH subroutine in its simplest version is now operating as well (the problem of coexistence has not yet been considered). The PERIDINIUM-DETRITUS submodel has been computerized and jointed with the PATCH submodel. Our next step is to join the full scale physical submodel with the developed part of the biological submodel. The ZOOPLANKTON-DETRITUS submodel has been conceptually developed.

Table XIX

Parameters of pseudoindividual

Parameter	Group	Examples	Associated processes (examples)
1 Water biotope	address	epilimnion	sinking
2 Patch	address	patch 7	
3 Community	identity	phytoplankton, zooplankton, etc.	death
4 Species	identity	*Peridinium cintum*	
5 Stage	identity	egg, nauplius, adult	moulting
6 Sex	identity	♂, ♀, no sex	maturing
7 Generation	identity	1, 2, 3, ...	cell division
8 Birthday	time	1981; 03; 28	excystation
9 Age	time	75 hours	aging
10 Representativity	formal	10^6 organisms	effect of grazing
11 Carbon	chemical composition	7.14×10^{-8} g/cell	nutrition
12 Nitrogen	chemical composition	5.20×10^{-9} g/cell	dissimilation
13 Phosphorus	chemical composition	3.10×10^{-10} g/cell	division etc.
14 Surface	shape	5.01×10^{-4} cm^2/cell	nutrition
15 Weight	shape	1.02×10^{-6} cm^2/cell	dissimilation

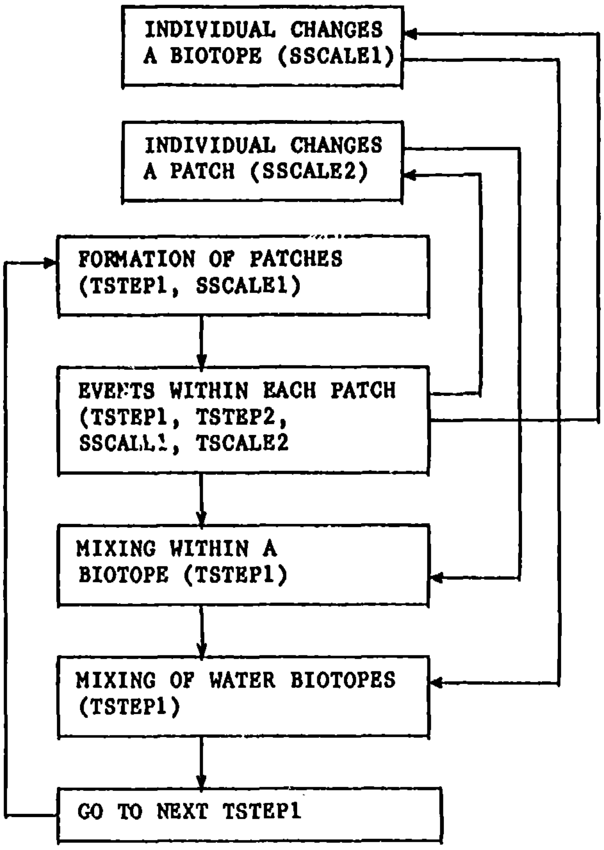


Fig. 76. TSTEP1 of biological submodel

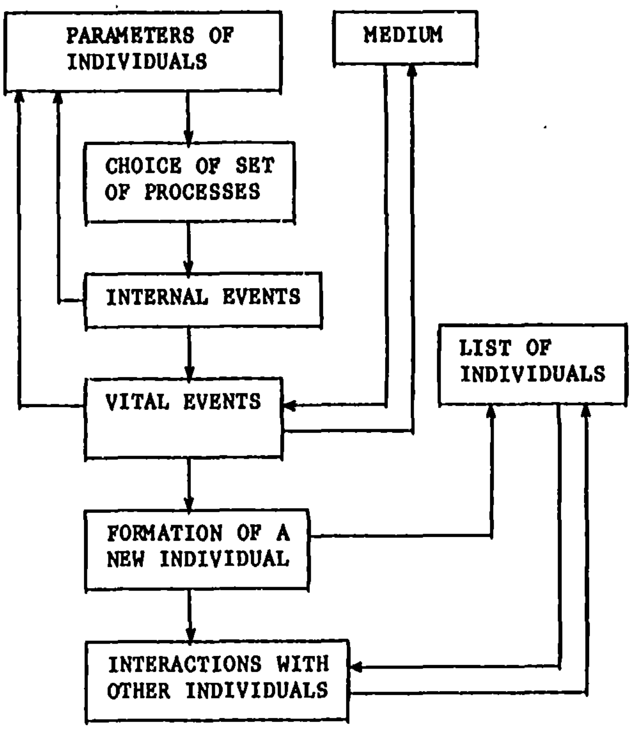


Fig. 78. Events with an individual

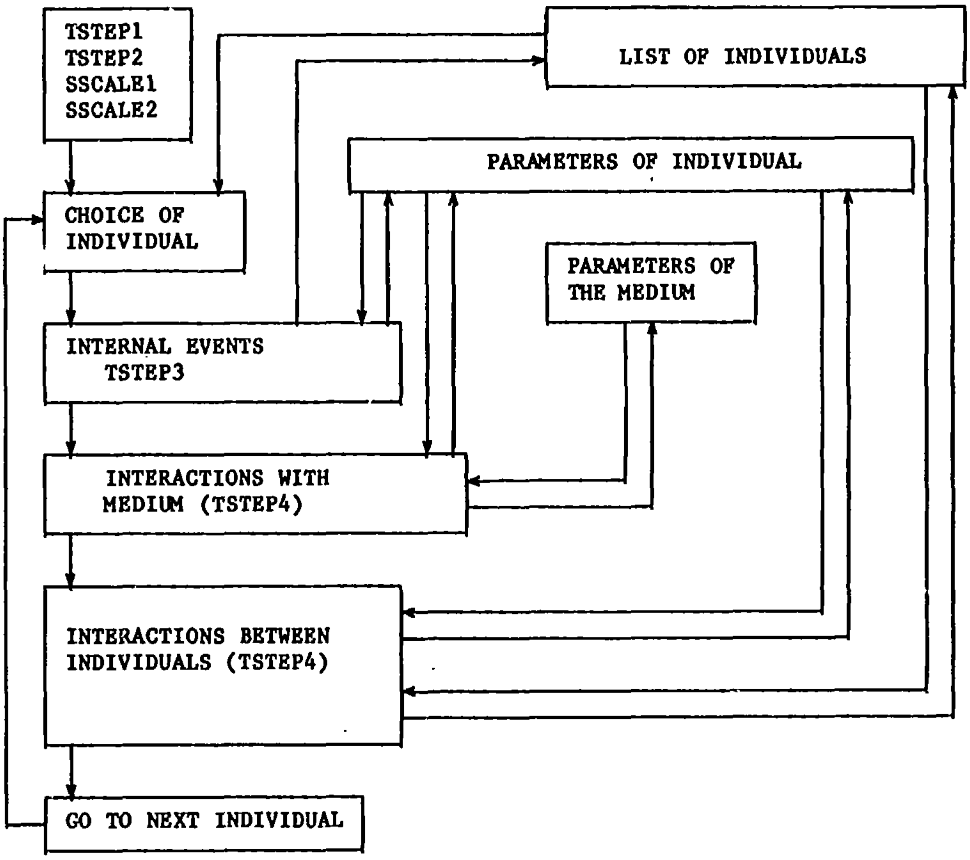


Fig. 77. Events within each patch.

GENERAL REVIEW OF THE ECOLOGICAL CONDITIONS OF ABU QIR BAY, EGYPT

Introduction

Abu Qir Bay is of great scientific and economic importance. Until recently, Abu Qir Bay supported one of the most important marine fisheries in Egypt. For many years, the fish catch obtained from the bay amounted to about 10% of the total marine fish catch in Egypt. This was before the construction of the High Dam at Aswan, when huge amounts of Nile water drained into the sea through the Rosetta Nile branch. This water with the suspended matter of the Nile waters enriched the bay with large amounts of nutrient salts and growth promoting substances. Consequently, the production of phytoplankton and zooplankton was exceedingly high, and the bay was considered among the most fertile regions along the Egyptian Mediterranean coast. Furthermore, the area of the Bay provided a good environment for the breeding of many commercially important fishes as well as for the subsequent development of fish fry.

The bay, because of its physical boundaries, presents an excellent model area for studying various problems, such as: air-sea interaction, water circulation inside a semi-enclosed bay, water exchange with coastal lakes freely connected to the sea, and many other coastal oceanographic problems. Because of present major technological and industrial developments in the Alexandria region, particularly around Abu Qir Bay, and the effects caused by the Aswan High Dam, the bay has been ecologically affected to a great extent. For these reasons, Abu Qir Bay has been the site of relatively intense oceanographic investigations during the last decades. As a result, a fairly good data base is now available on the bay environment, a fact which encourages the selection of Abu Qir Bay as a pilot study area for the simulation of a coastal marine ecosystem and for modelling purposes.

Physiographic Features of the Bay

Location and Dimensions

Abu Qir Bay comprises the area which lies between longitudes 30°3' and 30°22' East and latitudes 31°16' and 31°30' North. The bay is a semi-closed basin bordered from the west by Abu Qir Peninsula and from the east by the Rosetta branch of the Nile river, with a shoreline of about 53 km. The area of the bay is about 500 km^2 and the volume of water is about 6.0 km^3 with an average depth of 12 m (Fig. 79).

Sediment Characteristics

The sedimentological investigations of Abu Qir Bay carried out by MOUSSA (pers. comm.) showed that the recent sediment distribution in the bay is greatly affected by the nature of the bottom.

Five types of sediment units are present, namely: sand, silty sand, sand-silt-clay, clayey silt and silty clay. From the distribution chart, a clear and gradual zonation is revealed. Fine grained sediments of silty clay type cover the bottom around the Rosetta branch of the Nile. This type is deposited as the Nile water loaded with silt and clay particles meet the saline seawater. This fine silty clay gradates outwards into another zone of clayey silt. A sandy patch is marked within this clayey silty zone. Still further outwards the clayey silt merges into the complex type of sand-silt-clay which in turn gradates into silty sand. Finally, sand sediments cover the largest area of the bottom. In the western part of this area some rocky patches exist of which Nelson Island is obvious above seawater. A patch of sand-silt-clay exists in the center of this sandy area. It seems that this patch is formed as a result of the mixing of sand with silt and clay discharged with the lake water through El-Maaddiya opening and removed a little farther northwards, away from the lake sea connection.

Chemical analysis of bottom sediments in the bay indicated that the pH ranges between 7.3 and 8.9 where all values lie on the alkaline side and no acidic sediments were observed. From the distribution of pH values for the bottom sediments in the bay, sediments with lower pH values (ca. 7.5) are found opposite to the Nile mouth. The pH value increases gradually westwards to reach the higher values (pH = 8.0 and greater) in the western part of the bay, except for the area in front of El-Tabia Station

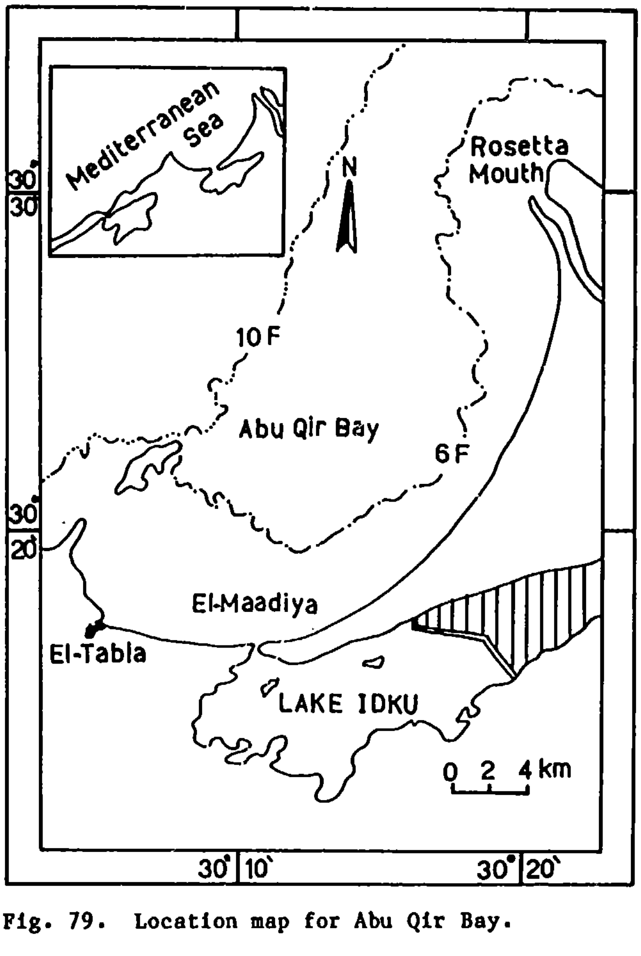


Fig. 79. Location map for Abu Qir Bay.

outfall, where the discharged sludge is slightly acidic. Such distribution is more or less correlated with the sediment distribution units.

The distribution of calcium carbonate in the sediments of the bay indicates a distinct regional distribution. In the eastern side of the bay, affected by silt and clay discharged from the Rosetta branch of the Nile, calcium carbonate is minimum, being less than 1%. Sediments poor in carbonate cover a wide area of the bay gradating to the west into a zone higher in carbonate content (4-12%) and with a coarser texture. The sandy areas are richer in carbonate content being 12-24% and increasing to more than 24% at the southwestern part of the bay. Thus it is clear that the sediments derived from the River Nile contain very little carbonate content due to the solubility of calcium carbonate in fresh water. Accordingly, lower carbonate values are found in the eastern part of the bay where the fine grained sediments are not suitable for benthic life. The increase of carbonate content westwards is due to the fact that the environmental conditions in the western area are more favorable for many faunal assemblages and there is a lesser contribution of the fine Nile sediments. Moreover, the increase in salinity of seawater away from the Nile mouth is also responsible for the increase of carbonate content. It is therefore clear that the calcium carbonate content is influenced by the silt-clay content.

The distribution of organic matter in the bottom sediments of the bay shows that generally, the organic matter increases from west to east. At the western side of the bay, minimum organic matter content is found, being 0.3% increasing gradually to 0.9, 1.5, 2.1 and 2.7% proceeding eastward until it becomes again 1.9% immediately in front of the Rosetta branch of the Nile. The distribution of organic matter is correlated with the distribution of sediment type. The organic matter content is lowest in sands and increases towards the Nile where the grain size of the sediments decreases. The relatively higher values of organic matter eastwards are mainly due to the detritus coming from the River Nile as well as to the deposition of finer material.

Meteorological Conditions

Air temperature. The monthly mean air temperatures fluctuate between a minimum of 13°C in January to a maximum of 28°C in July. It is clear that the monthly variation of air temperature of Abu Qir is typical for the Mediterranean climate with maximum in July and minimum in January. The absolute maximum air temperature may reach 39.4°C in summer, while in winter the observed minimum air temperature may reach as low value as 8°C.

Atmospheric pressure. The mean monthly atmospheric pressure is a maximum at about 1020 mb in January and a minimum at 1007 mb in July. These correspond to the maximum and minimum in the mean air temperatures.

Relative humidity. High values of relative humidity are encountered in summer, and lower values in winter; however, the annual amplitude is relatively small (12.6%). The lowest value (67.2%) is observed in April, when many khamasin dry heat waves affect the coastal area of Egypt. Meanwhile, in the beginning of the summer, when NW winds attain maximum frequency of occurrence (94%), the relative humidity is at its peak (80%). The monthly variation is less regular than the temperature and pressure variations.

Mean scalar wind speed. The daily wind speed at Abu Qir, a representative station, varied between 1.6 and 12.1 knots. The daily records showed higher values in winter and lower values in summer. The mean wind speed during the period of investigation increased from 3.9 knots during January to reach the value of 6.5 knots in March. The higher speeds are encountered in winter due to cyclonic atmospheric activities.

Wind direction. During January 1977, the prevailing wind was generally a westerly wind in both the NW and SW directions, with equal frequencies. Starting from February until May, the NW direction prevailed with less frequencies in the other directions. Meantime, the NW component prevailed only in the months of June, July, August and September, while in the month of October, both the NW and NE components prevailed with the NW having larger magnitude. From November, the SW component appeared beside the NW component, then the SW component prevailed during the months of December 1977 and January 1978. In February 1978, only westerly winds prevailed. It is thus clear that in winter months the winds are more variable, but the predominant wind direction in the area is the SW, resulting from the winds blowing around the SW periphery of a Cyprus low. On the other hand, the winds in summer are more steady, and are mainly from NW.

Cloud cover. During the winter season the cloud cover is greater than that of the summer season. In January and December about 50% of the sky was covered by clouds, while in June 1977 the total cloud cover was about 10% only. Table (XX) gives the number of hours of sunshine in the Abu Qir area.

Rainfall. Rainfalls in Abu Qir are relatively small and subject to relatively large variations from one season to another. The rainfall over the area is confined to the period from October to April, with a maximum usually during the winter months (January and February). From May to September there was no precipitation. Rainfall in January and December was more than 75% of the total rainfall during the year which amounts to 300 mm.

Sources of Land Drainage to the Bay

The area of the bay is subjected to land drainage through three sources: Rosetta branch of the Nile, Boughaz El-Maaddiya, and El-Tabia pumping stations.

Table XX.

Monthly averages of Sunshine (in hours per day) over the Alexandria region (compiled from records of the Meteorological Dept.)

Month	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1960	6.6	6.4	9.4	10.6	11.6	11.8	12.2	11.6	10.6	10.1	8.6	7.1
1961	7.1	6.8	7.2	10.4	11.7	12.2	12.4	11.6	10.4	9.4	8.1	7.1
Mean	6.85	6.6	8.3	10.5	11.65	12.0	12.3	11.6	10.5	9.75	8.35	7.1

Rosetta branch of the Nile. The flow of the Rosetta Nile water into the Mediterranean is controlled by Edfina Barrage erected 35 km south of Boughaz Rashid. Before the construction of the Aswan High Dam, the annual discharge of the fresh Nile water into the Mediterranean Sea through the Rosetta branch was on the average about 40 km^3.

As a result of the erection of the High Dam in 1965, the summer of 1964 witnessed the last normal discharge of flood water into the Mediterranean. From 1965 the discharge remarkably decreased. Information on the yearly discharge of the River Nile, measured at Edfina, indicated that from 1966 to 1977, i.e., for 12 successive years, the average annual discharge ranged between 2-7 km^3. Thus the annual discharge now averages only about 10% of its usual value before the erection of the Aswan High Dam.

Moreover, the annual cycle of the discharge has also changed markedly. The discharge which used to flow through both the Rosetta and Damitta branches is now flowing only through the Rosetta branch. The maximum discharge is now registered in winter. About 70% of the total annual discharge now flows into the sea during the three months of December, January and February. Thus such a change in both the total amount and the pattern of discharge would certainly affect the physical, chemical, as well as biological conditions in the investigated area (GERGES, 1976a).

As far as the solid matter is concerned, it was indicated by (SHUKRY, pers. comm.) that before the regulation of the Nile, about 57x10^6 tons of suspended sediments were discharged yearly into the Mediterranean Sea. A large amount of the sediment was carried during the flood period; one cubic meter of Nile water contained, at the peak of the flood, up to 4 kg of suspended solid material. The subsequent regulation of the freshwater outflow from the Nile River prevented more than 90% of the usual discharge with its suspended sediment load from reaching Abu Qir Bay.

Boughaz El-Maaddiya of Lake Idku. Boughaz El-Maaddiya is a shallow channel with an average depth of about 3 m, and average width of 20 m. It provides free connection between Lake Idku and Abu Qir Bay, through which water exchange between both regions takes place. It also facilitates the migration of organisms from one environment to another.

Lake Idku receives drainage waters from different drains. The annual total amount of drainage water discharged into Lake Idku (e.g., in 1974) was about 2 km^3, about 30% of which reached the lake during summer season. Actually, the net amount of lake water discharged into the sea through El-Maaddiya channel is not precisely known. However, a good amount of lake water reaches the sea, particularly in summer and autumn season, when it spreads to variable distances in the southeastern part of Abu Qir Bay.

The pattern of exchange between Lake Idku and southwestern part of Abu Qir Bay, through El-Maaddiya channel, is a dynamic one, changing seasonally, monthly and even daily. It is mainly controlled by two factors: the amount of drainage water received by the lake, and the velocity and frequency of the prevailing northerly and westerly wind. The large amount of drainage water reaching the lake in summer causes a slight elevation of the lake water above mean sea level, creating a lake-sea current. In winter, on the other hand, when the drainage water entering the lake is at its minimum and strong westerly winds prevail, a sea-lake current is established through Boughaz El-Maaddiya, and the seawater invades the lake.

Tabia pumping station. El-Tabia pumping station lies in the southwestern part of the bay. This station pumps out the industrial wastes of 22 different factories representing four major categories of industry, namely: food processing and canning, paper industry, fertilizer industry, and textile manufacturing. The water pumped to the sea averages a daily amount of 1.5 to 2x10^6 m^3. These wastes are directly discharged to, and eventually mixed with, the water in Abu Qir Bay. The combined effect of both discharges from Lake Idku and El-Tabia pumping station would create a distinct pattern of water type distribution in the bay as illustrated in Fig. 80.

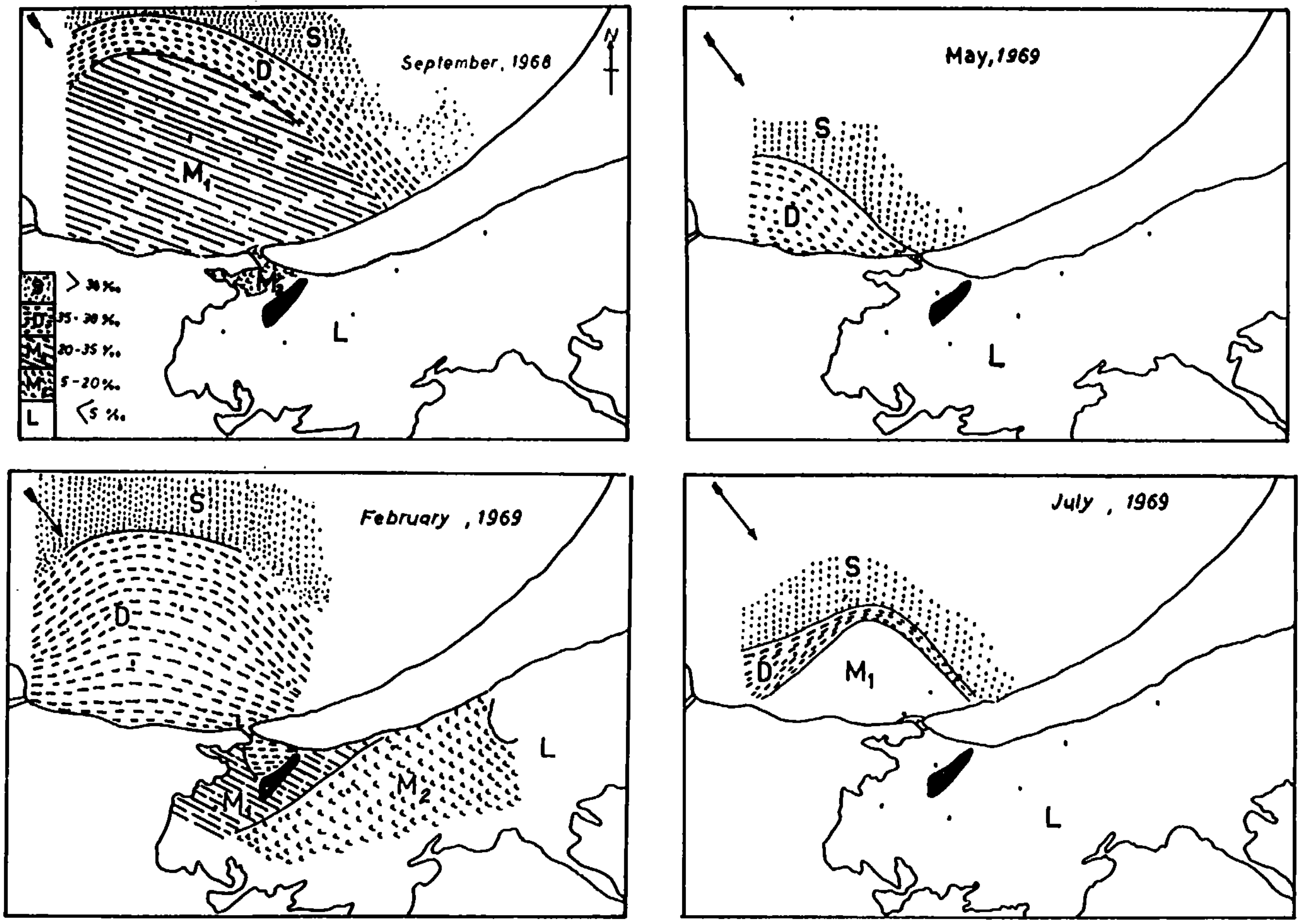


Fig. 80. The seasonal distribution of salinity in Abu Qir Bay and Lake Edku. The letter code and shading intervals for different salinity ranges are given in the upper left panel. The arrow designates the dominant wind direction, and the date of the observations is given at the top of each panel. From DOWIDAR and EL-MAGHRABY (1973).

Physio-Chemical Characteristics of the Bay Waters

The following representation of the physio-chemical characters of the bay waters is based on data collected regularly through monthly surveys of 18 stations covering the bay during the period from February 1974 to January 1975.

Physical Characteristics

Temperature. The annual average surface temperature was 22.6°C with a maximum of 28.8°C in August and a minimum of 16.1°C in February. Generally, surface water of the area off the El-Tabia outfalls was warmer than other regions in the bay during all seasons with an annual average of 23.2°C reflecting the thermal effect of the warm effluents of the outfalls. The subsurface temperature was lower than that of the surface and followed nearly the same trend with a maximum of 28.2°C in summer and a minimum of 16.2°C in winter. Because of the shallowness of the bay, a proper thermocline was not clearly demonstrated. The maximum vertical temperature gradient was 0.4°C per meter recorded at the northern border of the bay in summer, where thermal stratification was clearly marked with decreasing temperature from surface to bottom.

Salinity. Generally, the salinity of the bay water is lower than that of the eastern Mediterranean waters. There are four distinguishable regions in the bay:

a. The eastern area, exposed to the effect of the Rosetta Nile water particularly during the winter season. The salinity of this region is usually high in all seasons, except in winter when the surface values were low (36.4 ppt).

b. The area off El-Maaddiya channel, the outflowing water from Lake Idku lowers the surface salinity of a rather large area in the southern and central parts of the bay in almost all seasons (average 24.4 ppt). This decrease was particularly pronounced during late spring and summer, when waters of salinity of 5-20 ppt cover the area (Fig. 80).

c. The area subjected to the polluted water off the El-Tabia outfalls, which is limited to about 7 km in front of the outfalls. The average surface salinity of this area was 36.5 ppt.

d. The offshore area that is not affected by land drainage, the boundaries of this region are variable and depend on the prevailing wind and magnitudes of the drainage water reaching the bay. The surface salinity of this region was high in almost all seasons with an annual average of 38.86 ppt.

The effect of drainage water discharged into the bay is typically restricted to lowering the salinity of the upper 5 meters. The annual average of subsurface salinity was remarkably high, i.e., 38.39 ppt, varying between 37.69 ppt in winter and 39.1 ppt in summer. Vertical mixing was more pronounced in winter and nearly homohaline conditions prevailed in the whole water column. The maximum vertical difference in salinity observed in summer was on the average ~2.35 ppt. Single values were often much higher and may reach about 30 off El-Maaddiya.

Oxygen content. The annual average of dissolved oxygen is 4.43 ml/ℓ, varying between 5.56 ml/ℓ and 3.45 ml/ℓ in spring and autumn, respectively. The absolute values varied between 0.73 ml/ℓ and 8.51 ml/ℓ. The area off El-Tabia showed the lowest values in almost all seasons (average 3.13 ml/ℓ). The Rosetta region on the other hand showed the highest values (average 4.94 ml/ℓ). Because of the shallowness of the bay, variations in the oxygen content at the surface and subsurface layers were on the average not significant.

The bay water as a whole was undersaturated with oxygen with an annual average of 90%. Supersaturation of the bay water was achieved in spring (average 112%). The lower values were observed in autumn (average 71%). The lowest saturation values were recorded in the area off El-Tabia outfalls (average 85%). The low oxygen water of the El-Tabia region is sometimes advected northward causing local decreases in the oxygen content.

Chemical Characteristics

Hydrogen-ion concentration (pH). The pH values of the bay water were always slightly alkaline. The annual average value was 8.13. Higher values were recorded during winter (average 8.35), while lower values occurred in summer (average 7.68). The area in front of El-Maaddiya channel acquired the least annual average pH 8.00. The area off El-Tabia pumping station showed relatively high values with an annual average of 8.12.

Nutrients. The concentration of ammonia in the bay water was remarkably high. The annual average content of ammonia in the bay was 0.22 µg-at/ℓ reaching a maximum in summer (average 0.44 µg-at/ℓ) and a minimum in autumn (average 0.07 µg-at/ℓ). The absolute values varied between a maximum of 12.92 µg-at/ℓ observed in winter 1974 in the subsurface water off El-Tabia outfalls and 0.00 in the surface and subsurface waters in the different seasons. Generally, ammonia concentrations were higher in the surface layer than in the subsurface layers (averages 0.29 and 0.15 µg-at/ℓ, respectively). This indicates an allochthonous origin of ammonia rather than regeneration from the bottom sediments. Regarding the spatial variations, the area off El-Tabia pumping station showed an annual average 0.20 µg-at/ℓ. The water of El-Tabia discharge was practically free of ammonia during the spring and autumn seasons, while in winter its ammonia content was remarkably high (0.76 µg-at/ℓ). The concentration of ammonia off El-Maaddiya channel (av. 0.22 µg-at/ℓ) was relatively high. The water in the area off the Rosetta mouth was relatively lower in ammonia than other regions (ammonia av. 0.11 µg-at/ℓ).

The nitrite content of the bay water was also very high. The annual average content was 0.34 µg-at/ℓ and varied between a minimum of 0.04 µg-at/ℓ in spring and a maximum of 0.60 µg-at/ℓ in winter. Nitrite was relatively higher in the surface waters than in the subsurface layers of the bay (average 0.4 and 0.28 µg-at/ℓ, respectively). The drainage waters are considered to be the main sources of nitrite. The highest concentrations of nitrite were found in the El-Tabia area with an annual average of 0.54 µg-at/ℓ. The lowest values were found at the offshore stations, with an annual average of 0.24 µg-at/ℓ.

The annual average of nitrate-oxygen in the bay (0.23 µg-at N/ℓ) was considerably lower than that of nitrite. As with ammonia and nitrite, nitrate was also concentrated in the surface water, indicating an allochthonous origin. Seasonal variations showed an increase in the concentration of nitrate during winter and autumn (averages 0.36 and 0.28 µg-at N/ℓ, respectively), and a decrease during spring and summer (0.12 and 0.17 µg-at N/ℓ, respectively). Spatial variations of nitrate were significant. The area off El-Maaddiya channel was the richest in the bay throughout the whole year (average 0.60 µg-at/ℓ), while the area at the vicinity of El-Tabia outfalls had only moderate concentrations (average 0.46 µg-at N/ℓ) and varied between complete depletion in summer and 1.19 µg-at N/ℓ in autumn. The reducing conditions at that area favored the absence of nitrate during summer through the processes of denitrification. The area off the Rosetta mouth contained lower values of nitrate (average 0.28 µg-at/ℓ) and was characterized by high nitrate concentrations during winter. These were mostly derived from the large quantities of Nile water discharged into the sea during this season.

Reactive phosphate. The reactive phosphate content in Abu Qir Bay water was relatively high with an annual average of 0.48 µg-at P/ℓ. The average concentration in the surface water was nearly the same as in subsurface layers (i.e., 0.50 and 0.47 µg-at/ℓ, respectively). Wide regional as well as seasonal variations were recorded in the bay. The budget of reactive phosphate in the bay is mostly allochthonous in origin. Seasonal variations showed an increase in the concentration of reactive phosphate during winter (average 0.73 µg-at P/ℓ) and a decrease during summer and autumn (0.38 and 0.34 µg-at/ℓ, respectively). Spatial variations were more pronounced. The reactive phosphate content off El-Tabia outfalls was remarkably high with an annual average of 0.99 μg-at/ℓ, while the area at the vicinity of El-Maaddiya channel was relatively low (average 0.58 μg-at/ℓ). The offshore water showed the lowest phosphate concentration during the whole period of investigation with an average value of 0.23 μg-at/ℓ.

Reactive silicate. The annual average concentration of soluble silicate in Abu Qir Bay amounted to 14.2 μg-at/ℓ. In all seasons the silicate content of the surface layer was remarkably higher than that of subsurface water (average 16.3 and 12.1 μg-at/ℓ, respectively). This implies that the principal source of silica enrichment is the drainage water. The concentration of silicate in the area off El-Maaddiya was always high (average 24.3 μg-at/ℓ); the annual average off El-Tabia was 17.0 μg-at/ℓ while that off the Rosetta and of the oceanic water was much lower, being on the average of 13.4 and 11.5 μg-at/ℓ, respectively. On the whole, silicate content was high in summer (average 20.5 μg-at/ℓ) as a result of the great quantities of lake water rich in silicate (ca. 56.5 μg-at/ℓ) discharged into the bay. Lower values were recorded during autumn (average 10.6 μg-at/ℓ).

Water Circulation in the Bay

Current Measurements Available

Direct current measurements in the southeastern Mediterranean are generally fragmentary, limited in number and scattered in coverage. However, several attempts have been made to obtain some measurements of the current in Abu Qir Bay. Four different types of current observations are now available, namely:

a. surface and subsurface current measurements using Ekman current meters,

b. measurements of surface current using drifters,

c. measurements of surface and subsurface currents using drogues, and

d. measurements of bottom currents using self-recording current meters.

In the following, a description is made of the available data to present a plausible pattern for the surface and bottom water circulations in the bay.

Surface Circulation

The information on surface currents in Abu Qir Bay, as obtained from a series of monthly release experiments of surface drifters (GERGES, 1976b, 1978), revealed some important features of the surface circulation pattern in the bay and its seasonal variability.

The water circulation in the bay can be characterized by the existence of two large gyres. The speed and areal extent of each of these gyres differ markedly from one season to another. However, during some transitional periods (e.g., in May), the existence of these two gyres fades and instead, one large gyre covering the whole bay appears to dominate the surface circulation. In the western one third of the bay, a cyclonic (counterclockwise) gyre exists during the major part of the year. The eastern two thirds of the bay is occupied by an anticyclonic (clockwise) gyre.

Although the velocity values obtained from the movement of the surface drifters represent only rough estimates of the current velocity, of water transport under certain wind conditions. Excluding the dubious returns, the experiments gave the following ranges of current speed: in March from 3 to 6 cm/sec; in May from 3 to 7 cm/sec at the outer boundaries of the bay, and from 22 to 27 cm/sec inside the bay; in September from 6 to 22 cm/sec; and in November from 6 to 19 cm/sec.

The results obtained from the few concurrent drogue experiments in later summer indicated the existence of a southerly current at Abu Qir Head and southeasterly current near the outlet of El-Tabia pumping station, both at 1 m level below the surface. This clearly supports the conclusion drawn from the results of the drifters experiments regarding the cyclonic gyre existing in the western part of the bay. The velocities obtained from the drogues movement range from 7 to 12 cm/sec.

Obviously, the effluents from the outlets of El-Tabia pumping station, Lake Idku, and from the Rosetta mouth play an important role in setting up the pattern of surface circulation described above. Particularly important is the fresh water influx of the lake which on exit divides the bay into two parts, creating the two gyres mentioned earlier. Depending upon the amount of fresh water discharged from Lake Idku on one hand and from the Rosetta mouth on the other, the areal extent of each gyre is determined. Fig. 81 illustrates the patterns of surface drift current as revealed from the drifters experiments in the various months representing the four seasons of 1977.

Phytoplankton

Phytoplankton cell counts and species determinations were made on monthly surface samples collected from 14 stations in Abu Qir Bay during 1974.

Species composition. The number of phytoplankton species recorded in the bay is fairly low; the diatoms were represented by 73 species and the dinoflagellates by 38 species. In addition to the diatoms and dinoflagellates, several fresh and brackish water forms belonging to the Cyanophyta and Chlorophyta were recorded, of which representative of the genera Oscillatoria, Lyngbya, Spirulina, Merismopedia, Scenedesmus and Pediastrum were at times rather frequent in the areas directly affected by the discharge of Nile water through the Rosetta outlet and Lake Idku channel. However, their contribution to the total production did not exceed 1.0% of the annual phytoplankton crop. On the other hand, the diatoms dominated the phytoplankton community of the bay in all seasons constituting on the average 94% (25,240 c/l) of the total cell counts. The genera: Chaetoceros, Skeletonema, Thalassionema, Asterionella, Lithodesmium, Rhizosolenia, Leptocylindrus, Nitzschia, Melosira, Bacteriastrum, Lauderia, Hemiaulus, Thalassosira, Coscinodiscus, Pleurosigma, and Navicula were quantitatively the most important. The dinoflagellates constituted about 5% of the average annual crop, quantitatively the leading genera were: Peridinium, Prorocentrum, Exuviaella, Gonyaulax and Ceratium.

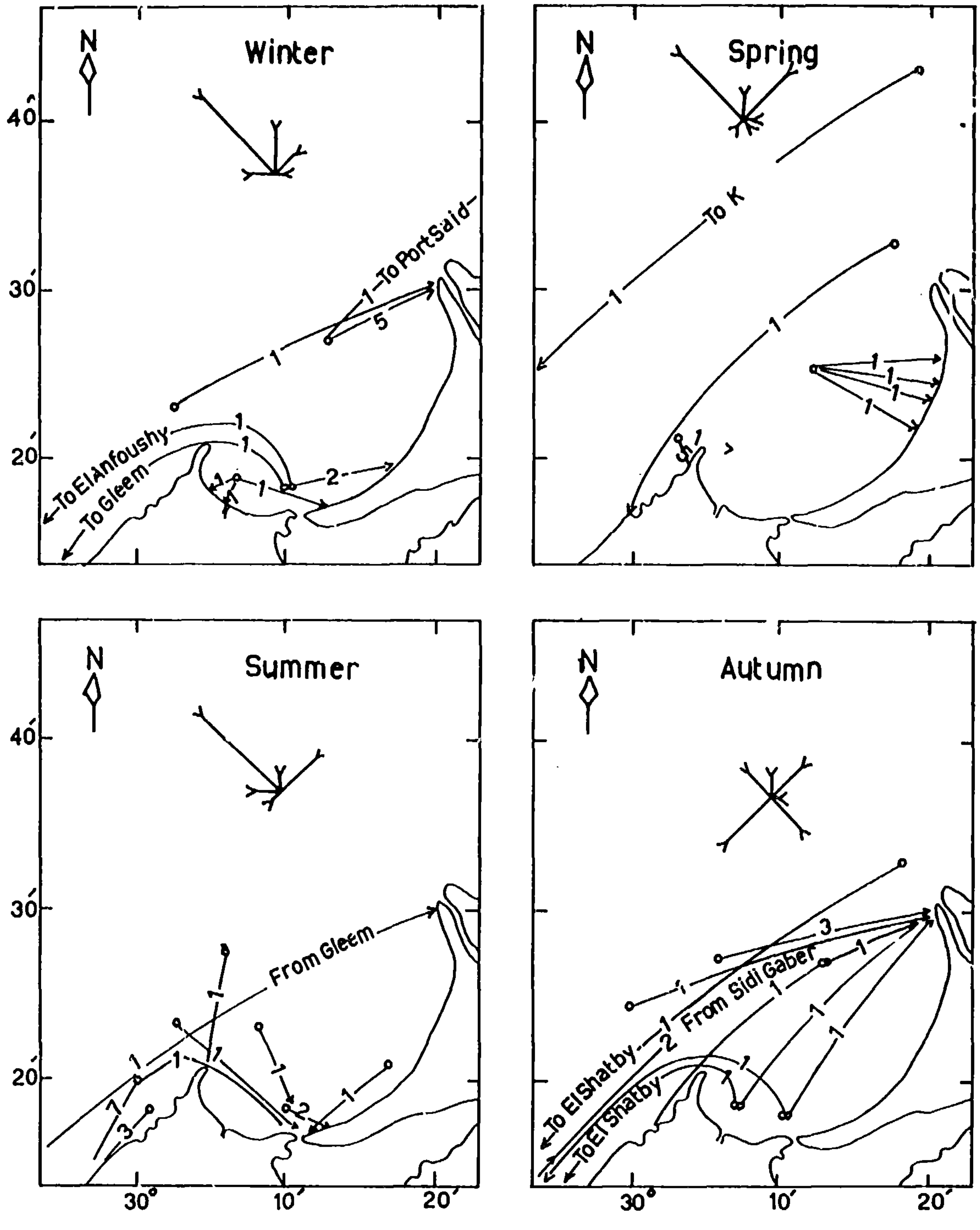


Fig. 81. The trajectories of surface drifters indicating the current patterns in the four seasons.

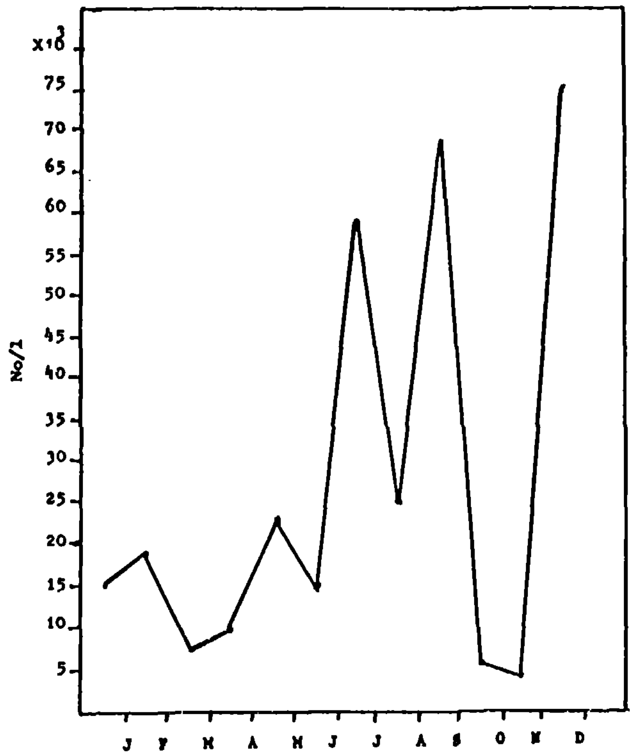
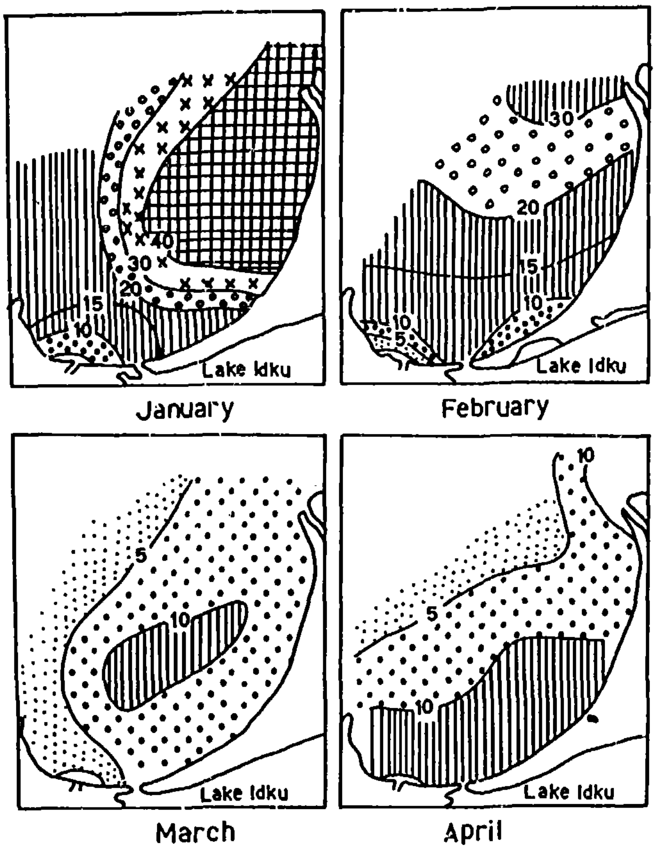


Fig. 82. Observed monthly variation of phytoplankton (cells/ℓ) in Abu Qir Bay.



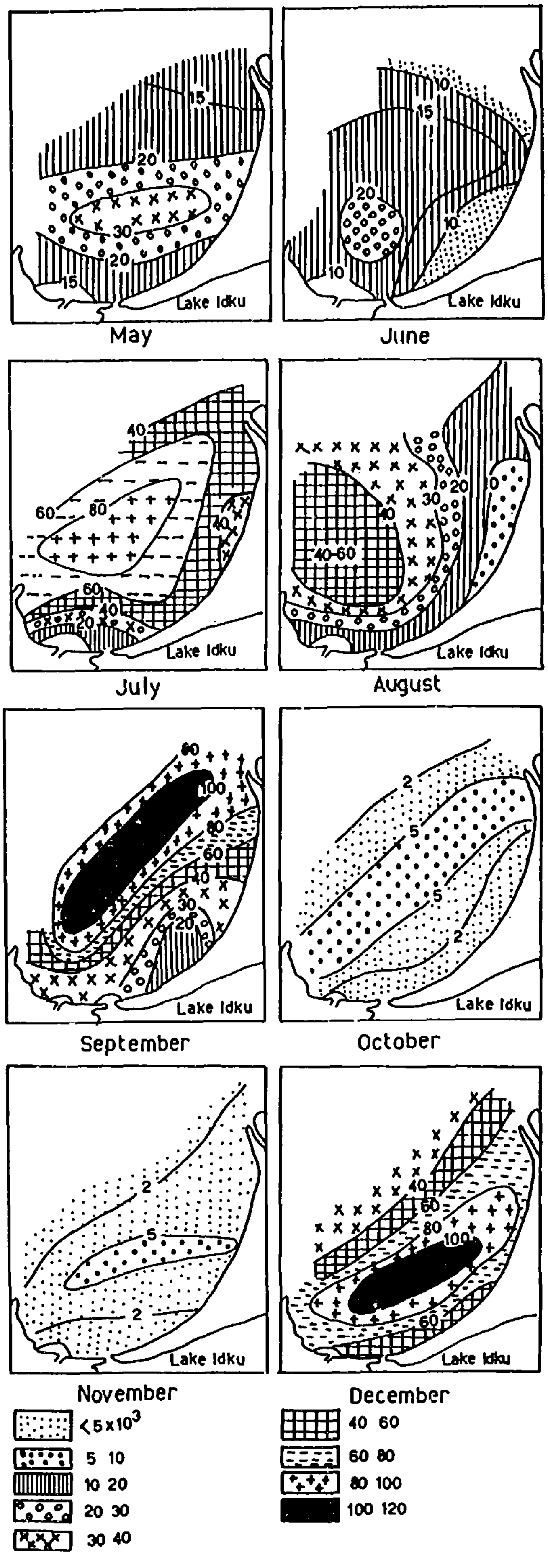


Fig. 83. The distribution of phytoplankton (total number of cells/ℓ) from the surface waters of Abu Qir Bay. Distributions for each of the twelve months are shown in three panels. The key for the contours is given at lower right.

The standing crop. On the whole the standing crop of phytoplankton in the bay was relatively low compared to other neritic areas in the vicinity of Alexandria. In terms of cell numbers, the monthly mean was about 26,850 c/ℓ. The absolute values varied between 120,000 c/ℓ and 1500 c/ℓ. Based on mean values (Fig. 82) peaks of abundance were recorded during July, September and December. It seems that high phytoplankton production in the bay is more or less correlated with periods of maximum discharge of fresh and brackish water. As stated before, the maximum outflow of Lake Idku water occurs during summer while the corresponding maximum of the Rosetta Nile water occurs during winter. The winter peak, which was also the most pronounced (average 74,630 c/ℓ), was dominated by Thalassionema nitzschioides, Skeletonema costatum, Chaetoceros curvesitum, Chaetoceros affinis, Chaetoceros sociale, Bacteriastrium hyalinum, Asterionella japonica, and Coscinodiscus spp. The autumn peak was exclusively dominated by Thalassionema nitzschioides (70%) together with Chaetoceros curvisetum, C. affinis, Asterionella japonica, Coscinodiscus spp, Prorocentrum micans and Ceratium furca. The summer peak (July) was exclusively dominated by Skeletonema costatum (70%), together with Chaetoceros spp (7%), Asterionella japonica (5%), Bacteriastrum spp (3%), Nitzschia spp (3%) and Rhizosolenia spp (2%). The small size observed in May (22,400 c/ℓ) was mostly due to Chaetoceras curvisetum, C. affinis, C. decipiens, Skeletonema costatum, Thalassionema nitzschioides, Nitzschia spp, Peridinium spp, Prorocentrum spp, Exuviaella spp and Ceratium spp.

The spatial and temporal distribution of phytoplankton in the bay is shown in Fig. (83). It is important to mention that phytoplankton production in the area directly affected by the industrial wastes of El-Tabia outfalls is almost negligible. In all seasons the standing crop in that area (about 2 km^2) did not exceed 250 c/ℓ. In nearly all seasons maximum production in the bay occurs at the central area of the bay probably away from the harmful effect of pollution and/or dilution caused by discharged water around the outlets.

Zooplankton

Quantitative zooplankton samples (No/m^3) were collected seasonally during January, April, July and September 1974 from 14 stations in Abu Qir Bay. As shown in Table XXI the standing crop in terms of number of organisms/m^3 was high during summer and autumn with a pronounced peak in July. The annual average was 13,690 organism/m^3.

The spatial and temporal distribution of the zooplankton biomass in terms of total numbers/m^3 is shown in Fig. 84. In winter, the area adjoining the Rosetta estuary was more productive, away from which the standing crop decreased and the lowest crop occurred in the southwestern portion of the bay that is affected by the Tabia outfalls effluents. Production was rather localized in other seasons, probably through dilution by the brackish water of Lake Idku entering the bay through El-Maaddiya channel. As shown in Table XXI, copepods dominated the community by an annual mean of 71.4%, followed by Tintinnids (9.4%) and Appendicularians (5.4%); Cladocerans mostly Evadne tergestina constituted on the average 4.1% of the total community but was particularly common during summer and autumn. In both seasons, E. tergestina was mostly confined to the southwestern area of the bay, i.e., the area affected by the brackish water of Lake Idku. The salinity in that region was usually below 38 ppt, while that of the eastern part was higher. Cirriped nauplii were particularly common in winter in the western region of the bay, its annual contribution being 2.8%. The copepod population is limited to several small-sized species, typical of the neritic waters off Alexandria. The following indigenous and perennial species

Table XXI

Seasonal variations of the zooplankton standing crop in Abu Qir Bay (mean number/m^3) and the percentage composition of the community

Season	Winter	Spring	Summer	Autumn
mean No/m^3	6130	10330	21050	17250
Copepods	60.0	78.0	71.0	72.0
Tintinnids	15.0	7.0	10.0	8.0
Appendicularians	4.0	8.0	9.0	4.0
Cladocerans	-	-	5.0	7.0
Coelenterates	4.0	2.5	1.0	2.5
Chaetognaths	0.2	0.2	0.4	0.6
Radiolarians	0.2	0.1	0.2	0.1
Cirripede nauplii	15.0	2.8	1.4	3.0
Veliger larvae	1.4	1.0	1.4	0.5
Polychaete larvae	0.2	0.3	0.5	0.5

formed the greater bulk of the population: *Oithona nana*, *Euterpina acutifrons* and *Paracalanus parvus*. Other species such as *Centropages kroyeri*, *Isias clavipes*, *Acartia latisetosa*, *Acartia negligens*, *Oithona linearis*, *Oithona helgolandica*, *Paracalanus pygmeaus*, *P. aculeatus* and *Clausocalanus arcuicornis*, inhabit the bay and are able to build up relatively large populations in certain seasons.

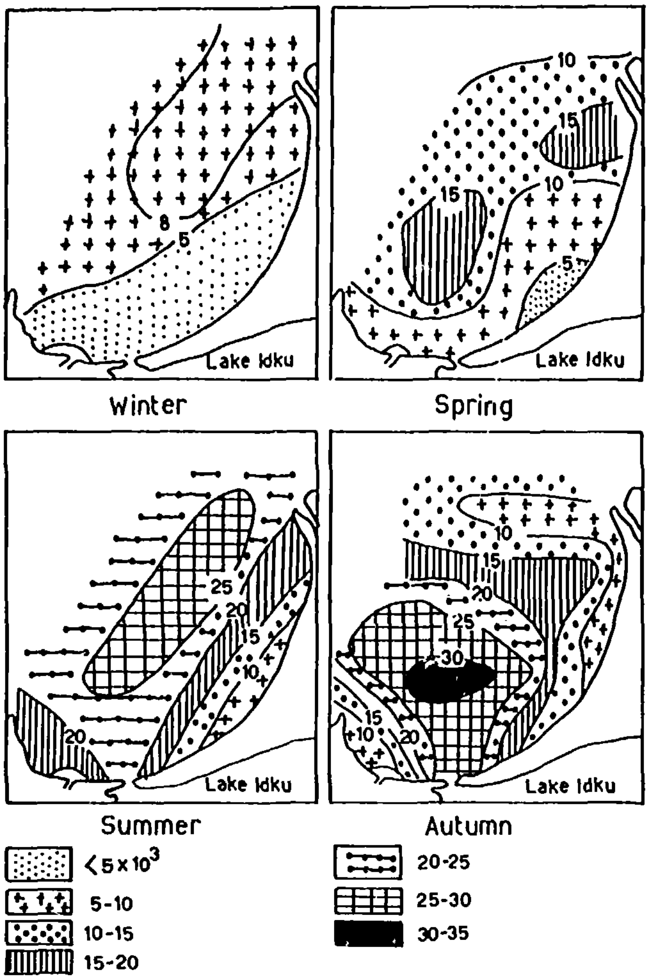


Fig. 84. The seasonal distribution of zooplankton (thousands/m³) from the surface waters of Abu Qir Bay.

LAKE OF TUNIS, SOME CHARACTERISTICS OF THE EUTROPHICATION OCCURRING IN THE NORTHERN PART OF THE LAKE

Introduction

The northern part of Lake Tunis is a shallow lagoon (1 m depth) showing extreme eutrophication, due in part to untreated and treated waste discharge, and to poor flushing. This is manifested by a variety of biological conditions that are symptomatic of nutrient excess, i.e., dense populations of fishes, phytoplankton, macroalgae, and reefs of the tube dwelling worm *Ficopomatus*. This study shows the effect of sewage waste discharge on the distribution and variability in space and time of nutrients and on the supported biomass. Nitrite, nitrate, phosphorus and biomass of phytoplankton and macroalgae are studied within three different organic polluted zones (1,2,3) shown in Fig. 85. For further information on some physicochemical and biological aspects of the Lake of Tunis see also: BAIER et al., 1977; BJORK, 1972; BRUNN, 1940; CROUZET, 1971, 1972; HARBRIDGE, 1974; HARBRIDGE et al., 1976; HELDT, 1929; KTARI, 1972; PIMIENTA, 1959; STIRN, 1966, 1968, 1971; ZAOUALI, 1971.

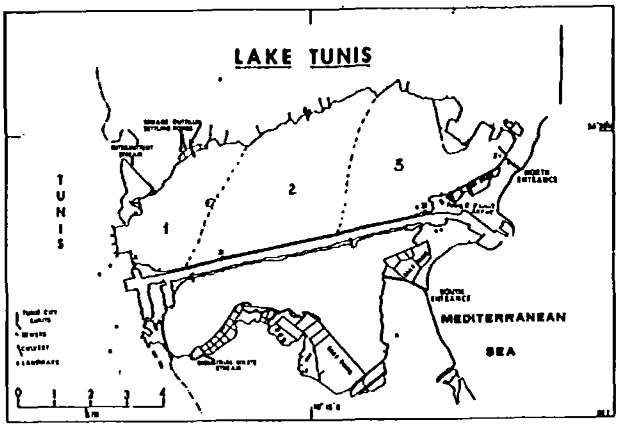


Fig. 85. Location map for Lake Tunis. The northern part of the lake is divided into three zones for reference in the text.

Methods

Water samples were obtained using a specially designed sampling device. Oxygen was determined using the Azide modification of the Winkler method; NO_2, NO_3, and PO_4 with the method of STRICKLAND and PARSONS (1965); and Chl-a by filtration through Whatman GF/C glass filter, maceration in 90% acetone, and spectrophotometric analysis with the method of STRICKLAND and PARSONS (1965).

Algal biomass was estimated by placing a cage, with a 1 m^2 opening at the top and bottom, on the substrate and collecting all of the algae using a dip net. Excess water was removed by gentle squeezing and the sample transported to the laboratory in a plastic bag. After 24 hours the sample was washed with tap water over screens to remove sediments and associated animals. The species were sorted, gently pressed between blotting papers, and weighed to a precision of 1 gr to give net weight.

Results and Discussions

Nutrients. In the most polluted zone (1), phosphate values (10-25 µg-at/ℓ) are always two to 25 times greater than in zones (2) and (3). This was usually so for nitrate as well. Nitrate was present in appreciable quantities (6 to 18 µg-at/ℓ), except during a few months. In the polluted zone (2) ammonia was observed to be rapidly liberated from Ficopomatus reefs and rapidly converted to nitrate (KEEN, 1978). Large nutrient fluctuations occurred from month to month, sometimes synchronized at all stations, sometimes only at particular stations. Nitrate and nitrite show a striking decrease at the time of the spring bloom (0 to 4 µg-at/ℓ), while phosphate peaks (4 to 6 µg-at/ℓ) during the spring and summer (Fig. 86). It appears that nitrate was the limiting nutrient. Macroalgae are perhaps most important in removing nutrients during the summer, but phytoplankton must play the more important role when macroalgae are less abundant from October to June. Peaks in nutrient concentration occur at the times of maximum rainfall, possibly because of surface runoff and changing chemical conditions.

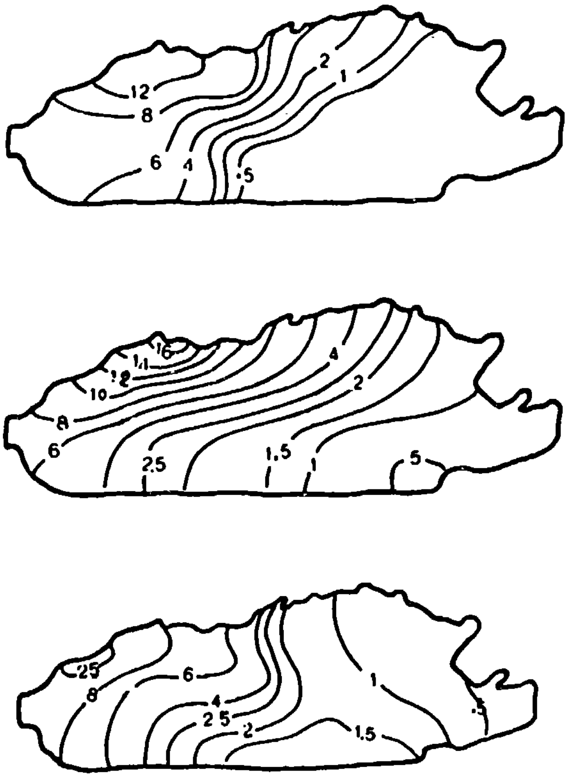


Fig. 86. Nutrient distributions. Upper panel: Nitrate µg-at/ℓ from November 1976; middle panel: Nitrate in µg-at/ℓ from November 1976; and lower panel: Phosphate in µg-at/ℓ from June 1976.

Dissolved oxygen. Dissolved oxygen was present at all times of sampling except in August 1975, after a red tide, although diurnal studies suggest strongly that the water becomes anaerobic at night.

Phytoplankton. Three distinct phases of phytoplankton biomass were noted at all stations. Low biomass was found from November through February, with a spring increase from February through April (Fig. 87). A rapid decrease, nearly to zero, occurred from July through September. Obviously considerable light, nitrate, and phosphate are present during the autumn and spring months leading to appreciable blooms during those periods. The later summer decrease is difficult to explain, but may be due to heavy grazing by Mercierella, some shading by Ulva, and possibly competition with macrophytes for an unidentified nutrient. Mercierella grazing is thought to be a probable cause of these reductions because the dry weight of Mercierella increased by about 100 g/m^2/day. This was accompanied by very clear (presumably well filtered) water between September and November. The lack of decrease in zone 3 may be due to a combination of vicinity to the sea, to a lack of Mercierella, and to a lack of macroalgae in that zone.

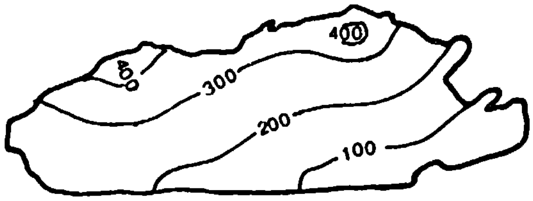


Fig. 87. Maximum phytoplankton biomass distribution in mg Chl a/m^3 from March 1976.

Macroalgae. Five important separable types of macroalgae are found in the Lake: Ulva lactuca, Cladophora spp, Enteromorpha spp, Chaetomorpha spp, Gracillaria spp. and unidentified brown algae. For all except Ulva, the biomass remained fairly constant, but obviously Ulva dominated at all times, particularly in the late summer, and formed the huge deposits of decomposing organic material.

As shown in Fig. 88, the major biomass of Ulva is in the middle zone of the Lake. This is also the region of greatest development of Mercierella reefs, which apparently serve as points of attachment in shallow, well lighted water as well as active sources of nutrients. It seems likely that Mercierella grazes phytoplankton, and liberates nutrients that favor the Ulva, thus favoring Ulva growth relative to phytoplankton.

There is a relative absence of Ulva in zones 1 and 3, and an absence of all other macroalgae in zone 2. The macroalgae in these areas are nearly all associated with Mercierella reefs. Ulva thrives best in calm water, and its absence from zone 1 may be explained by fewer nutrients, calmer water, deeper bottom (and hence less light), and perhaps less active Mercierella reefs. The absence of Ulva from zone 3 is unexplained, but the growth experiments show that it cannot survive, and it is possible that there may be toxic levels of nutrients or organic compounds present. Petroleum degradation products are present in zone 3 and may be the cause, since there is also oil discharge from a power plant.

The filamentous greens (Enteromorpha and Cladophora) were of some importance during October 1975, but were not as significant as Ulva at most other times. The brown algae are most important near Mercierella reefs, but the biomass was difficult to estimate because of their attachment to the reefs (Fig. 89). Gracilaria is perhaps the most important form in zone 1 being adapted for varying its pigment concentrations and thus to lower light intensities in deeper water; pigmentation varies with depth.

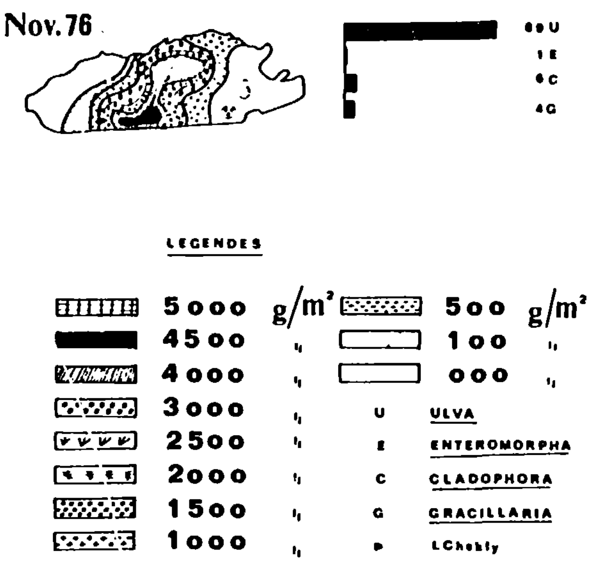


Fig. 88. Maximum macroalgae biomass distribution in g/m^2 from November 1976.

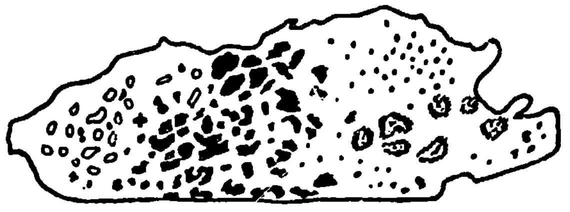


Fig. 89. Distribution of Ficopomatus reefs within the northern part of the lake.

ECOLOGICAL STUDIES OF RIJEKA BAY

Introduction

The geographical location of Rijeka Bay and its favorable climate have been the main reasons for its fast urban, industrial, and touristic development. Being aware that without careful planning these activities could irreversibly alter in an unacceptable way the bay's ecological system, scientists were asked to describe the bay's ecological characteristics and to predict its ecological waste receiving capacity. A multidisciplinary program was implemented for this purpose, and investigations were performed in the period from summer 1976 to summer 1978.

Background Information

Rijeka Bay is located in the Northern Adriatic (Fig. 90) between the Istrian Peninsula, the mainland, Krk Island, and Cres Island (SEHULIC, 1977, 1980). It is connected to adjacent waters through three channels: Vela Vrata, Srednja Vrata, and Tihi Kanal (Fig. 91). Vela Vrata is situated between the Istrian Peninsula and Cres Island. It is 6,400 m wide and has a cross-sectional area of 250,000 m^2. Srednja Vrata lies between Cres and Krk Islands, it is 7,600 m wide and has a cross-sectional area of 264,000 m^2. Tihi Kanal is located between the mainland and Krk Island, it is 3,800 m wide and has a cross-sectional area of 20,000 m^2. The surface area of Rijeka Bay is about 500 km^2, with a volume of 27 km^3. The average depth of the bay is about 60 m.

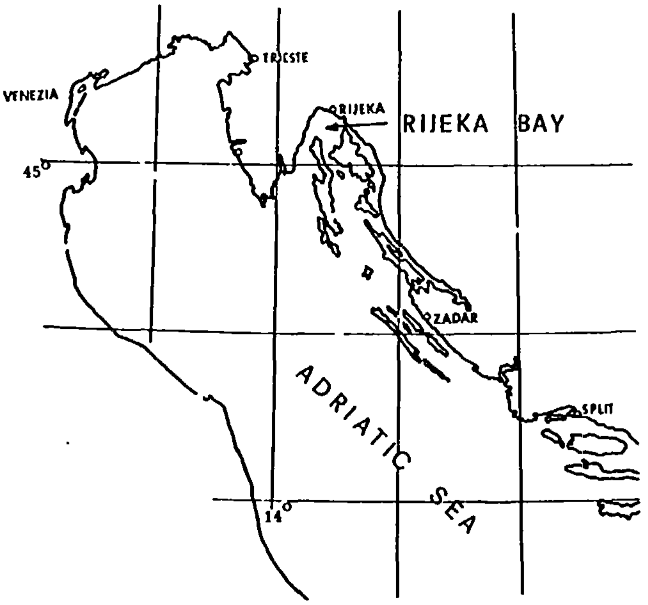


Fig. 90. The location of Rijeka Bay within the Adriatic Sea.

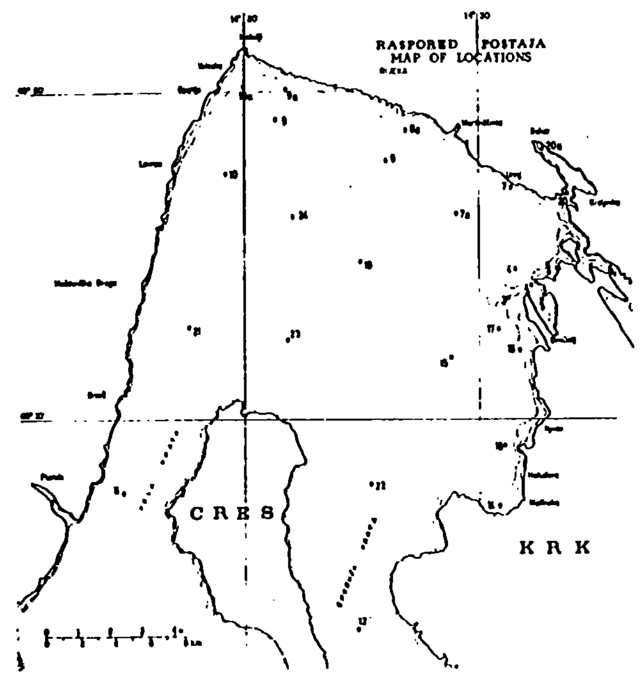


Fig. 91. Rijeka Bay with place names and station locations.

Rijeka Bay is mesozoic, formed mainly of karstic limestone with some dolomites mostly in the northern part. The only river worth mentioning is Rijecina (length 17 km, width at the river-mouth 15 m). Rijecina has a very variable flow of water averaging 10-50 m^3 sec. Along the northern shore of Rijeka Bay there are a number of sea-bottom fresh water springs. Their activity is quite variable with the most active periods in the late spring and late autumn.

Prevailing winds for the 21 year period are from the northeast (41%). The next most frequent wind is from the southwest (11%). Yearly mean air temperature for a 21 year period is 13°C, with absolute maximim of 36°C and absolute mimimum of -12°C. Yearly total precipitation for the area is about 1400 mm with a maximum in autumn and another one in winter. Yearly mean insolation is about 47% of the total possible sunshine.

Along the shores of Rijeka Bay live more than 250,000 inhabitants, and the largest agglomeration is the city of Rijeka with a population of 150,000. The touristic load is mainly concentrated in summer and consists of about 4 million nights per year in that area.

Along the shores of Rijeka Bay a number of industial enterprises like refineries, powerplants, cokeries, shipyards, petrochemical factories, oil-terminals, paper-mills, an industrial harbor, etc., are in operation or under construction. The estimated BOD load for the area is 56,975 t/y (50,402 by industry), COD load is 170,956 t/y (157,709 by industry), suspended matter is 113,588 t/y (72,497 by industry), total N is 11,355 t/y (10,609 by industry), total P is 1,194 t/y (971 by industry), and oil is 4,480 t/y (2,210 by industry and 1,972 by precipitation). For additional information see SEKULIC (1977 and 1980).

Parameters Measured

The following parameters were measured:

(a) Basic parameters for meteorology and air-sea interaction: wind, air temperature, relative air humidity, atmospheric pressure, visibility, cloudiness, incident radiation, precipitation, sea state;

(b) Hydrological parameters in sea water: depth, pressure, sea temperature, salinity, density, water transparency, sea color, sea currents (current meters, drifters, driftcards), sea level, dissolved oxygen, pH, alkalinity, nitrates, nitrites, ammonia, phosphates, silica, chlorophyll a, primary production (^{14}C), qualitative and quantitative analysis of phytoplankton, qualitative and quantitative analysis of zooplankton;

(c) Basic parameters in sediments: granulometric analysis, density, water content, specific surface, mineralogical analysis, carbonates, biomass and abundance of benthic and pelagic fish and benthic biocenosis;

(d) Specific parameters of pollution in sea water: polyaromatic hydrocarbons, saturated hydrocarbons, chlorinated hydrocarbons, total surface active substances, anionic detergents, benzopyren monooxygenaze induction, complexation capacity, trace elements (lead, cadmium, mercury, zinc and copper); and in sediments: polyaromatic hydrocarbons, saturated hydrocarbons, chlorinated hydrocarbons, trace elements (lead, cadmium, zinc, copper and mercury), benzopyren monooxygenaze induction; microbiological contaminants: total coliforms, fecal coliforms, fecal streptococci.

Frequency and Distribution of Sampling

A total of ten cruises were performed: June, August, September, and December, 1976, February, August, September, and December, 1977, March and June 1978. The grid of stations shown in Fig. 91 was used to collect data. For scientific, financial and organizational reasons not all parameters were measured at every cruise and each station. The same applies also for the number of depths at which measurements were done. Basic meteorological and hydrographical parameters were measured at all cruises and stations, at least at standard depths.

Complementary Activities

In order to understand better the influence of man on the ecological system of Rijeka Bay, toxic effects of soluble fractions of oil, diesel oil D-2 and Aroclor 1242 on certain organisms have been studied in the laboratory. (LUCU et al., 1979)

A survey of all industrial, touristic and urban developments has been performed in order to get as clear a picture as possible about the sources and amounts of pollution from human activites. (SEKULIC, personal communication)

Summary of Physical, Chemical and Biological Characteristics

Only a summary of physical, chemical and biological characteristics which are relevant to this workshop are presented.

Hydrography

Rijeka Bay is characterized by changeable hydrographic features (DEGOBBIS, 1977, 1979; DEGOBBIS et al., 1978). They are caused by the interaction with the atmosphere, influence of freshwaters from sea-bottom springs, Rijecina River, waste water effluents and exchange of waters with adjacent parts of the Adriatic Sea. These changes are more pronounced in the northernmost part of the bay, especially in the upper part of the water column where the strongest influence of fresh water occurs (Fig. 92).

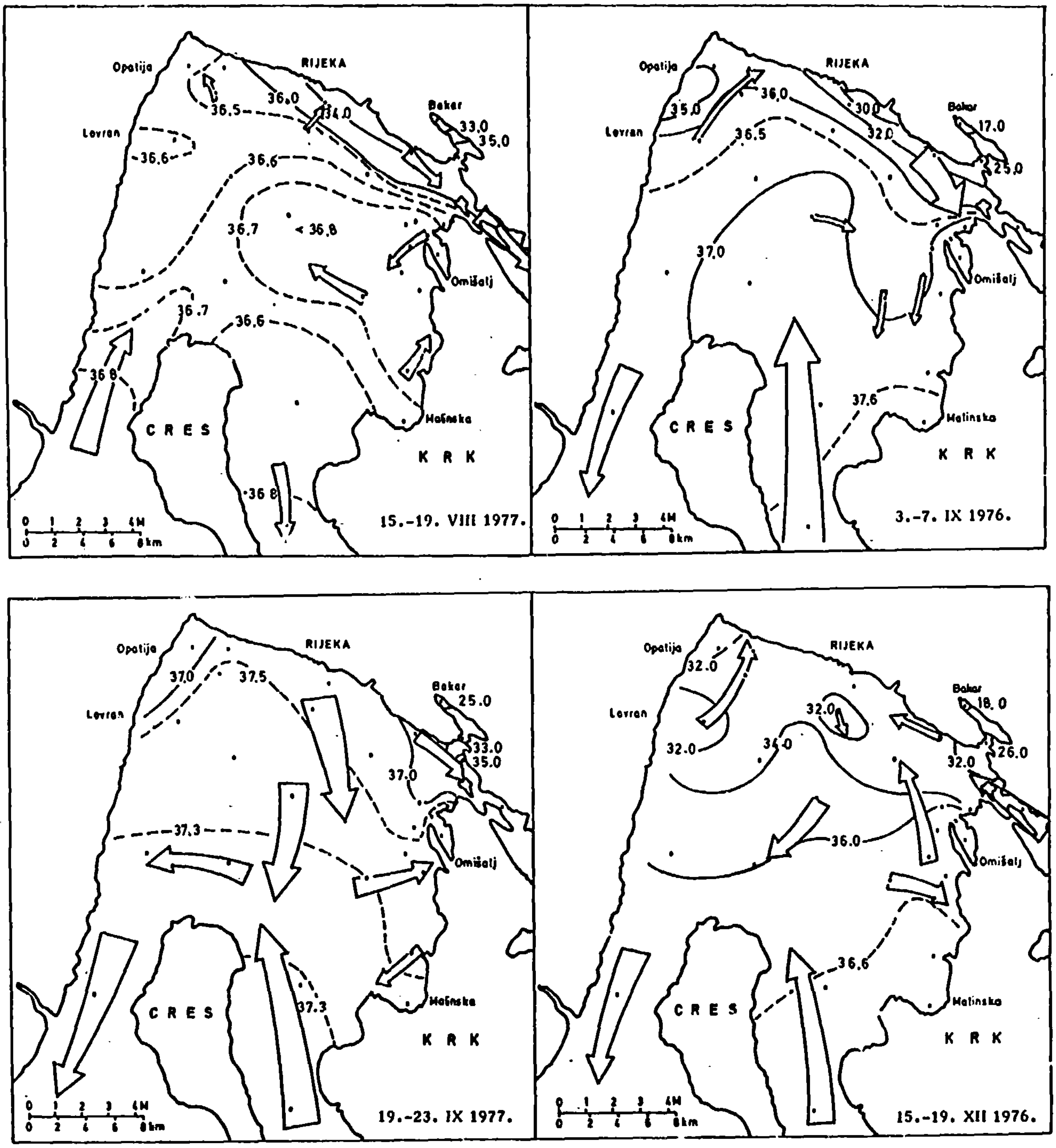


Fig. 92. Observed surface salinity distributions and surface currents. The sampling dates for each panel are written in the lower right hand corner.

In the winter, water of high salinity enters the bay through Srednja Vrata. The summer layer of lower salinity enters the bay through the Vela Vrata.

Stratification of the water column is pronounced in the summer period when the density of the surface layer is decreasing because of the increase of temperature and the decrease of the salinity. The degree of stratification is mostly due to temperature.

Dynamics of the Water Masses

Conclusions on the dynamics of water masses are based on measurements of sea currents by current meters, drifters, and driftcards (ILIC and NOZINA, 1979; ILIC et al., 1978, 1979).

In Rijeka Bay, pronounced differences in the direction and intensity of currents exist during two periods of the year. During winter the direction is counterclockwise, and during summer clockwise. The intensity of currents decreases by the factor of 5 from the surface to the bottom and from all three channels to the center of the bay. Maximal values of instantaneous currents in the surface layer were recorded as 28 cm/sec during both summer and winter periods. General flow patterns are indicated on Fig. 92.

Nutrients and Chemical Hydrography

Studies on nutrients and chemical hydrography were done by DEGOBBIS (1977, 1979). The percent saturation of dissolved oxygen for the surface layer ranges from 95% in the winter to 100% in summer. For the bottom layer it is somewhat lower, ranging from 80 to 100% (occasionally around 70%).

Total alkalinity, pH and total CO_2 are in the usual ranges for coastal waters and values are rather evenly distributed throughout the bay.

Nutrients are generally lower in the surface layer during summer than winter. During the summer period with its greater insolation, primary production is higher, and inflow of fresh water lower. During winter the low photosynthetic rates and high runoff cause the accumulation of nutrients. Phosphates are rather low, values being typical for the Adriatic Sea. Only in the surface layer, low-salinity plume higher values were recorded occasionally. The surface layer in the northern part of the bay is heavily loaded with nitrates and silicates (Fig. 93). There exists an inverse linear correlation between the nitrates (silicates) and salinity. The origin of nitrates and silicates is fresh water runoff, and its dispersion is the main factor for their distribution in the surface layer. Nitrates and silicates are evenly distributed in deeper layers.

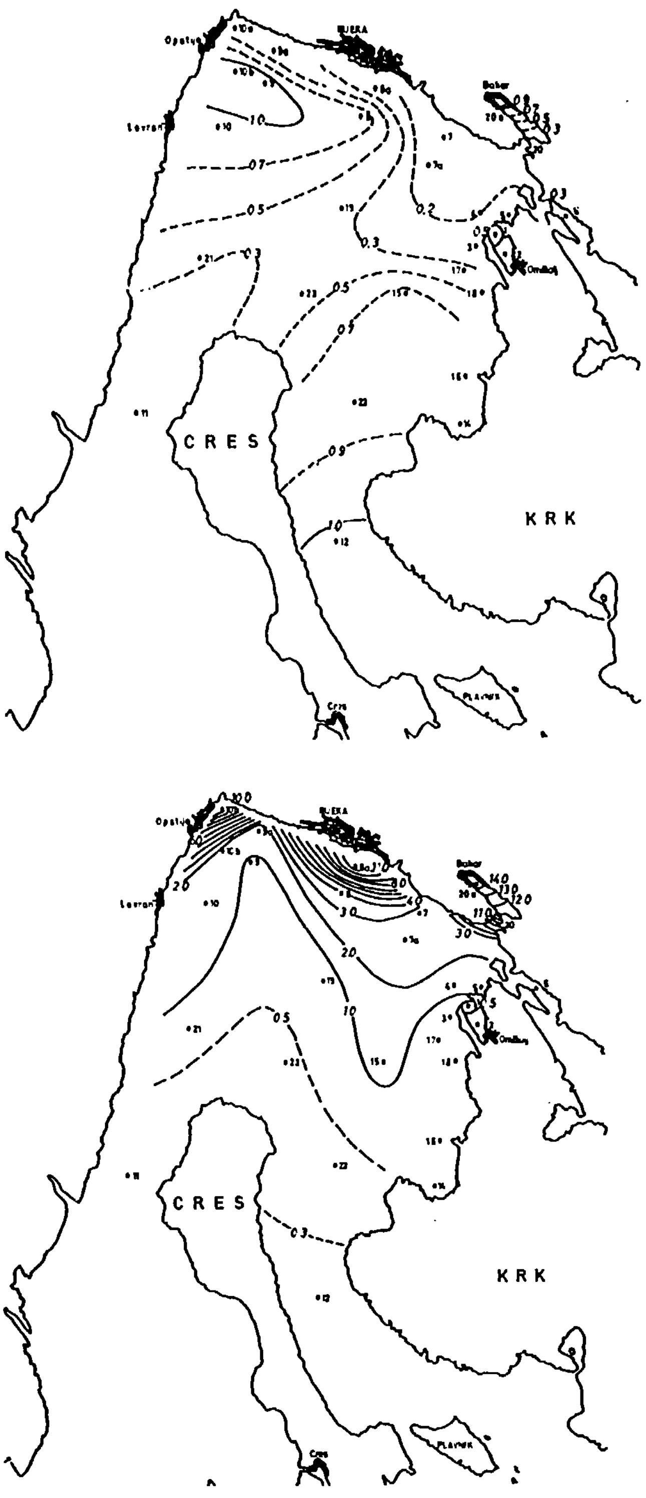


Fig. 93. The surface distribution of nitrates (upper panel) and of silicates (lower panel) expressed in μg-at/ℓ from September 5-7, 1976.

Primary Production

The density of phytoplankton in Rijeka Bay is rather evenly distributed (PUCHER-PETKOVIC et al., 1977; POJED and SMODLAKA, 1979). Somewhat higher values were found in the coastal region. The biomass of phytoplankton is not very high; it is typical for the 'channel areas' of the Adriatic. On the other hand photosynthetic activity of phytoplankton in the coastal region compares with the most productive areas in the

Adriatic. Some signs of eutrophication are visible in the northern part of the bay.

Zooplankton

Microzooplankton of Rijeka Bay consists mainly of developing stadia of crustaceans (copepods) and several species of protozoans (VUCETIC et al., 1977; BENOVIC and KRSINIC, 1979).

Zooplankton is primarily comprised of copepodes that may in winter constitute 90% of the net plankton. For other groups, only cladocerans are present in significant amounts during summer. The amount of all other groups is negligible.

The biomass of the zooplankton has higher values in the center of the bay, in the vicinity of Krk Island and in the northernmost part of the bay. A higher content of the inorganic matter in the biomass was found, especially in the vicinity of Rijeka Bay.

Benthic Biocenosis

Benthic biocenosis are richest in the vicinity of the western coast of Krk Island and in the southwestern part of the bay (ZAVODNIK and SPAN, 1977; ZAVODNIK, 1979). The coastal region of the northern and northwestern part of the bay, between Urinj and Krk, is under constant influence of polluted waters from the coast. This is demonstrated by degraded communities in deeper waters.

Modelling Efforts

Using all necessary data, a thermal-plume was constructed for the power station site near Rijeka and the petrochemical complex at Krk Island (KUZMIC, 1977; KUZMIC and JEFTIC, 1977, and KUZMIC et al., 1980).

A conceptual ecological model also was constructed to serve as a basis for development of a comprehensive mathematical model of Rijeka Bay (LEGOVIC et al., 1977; LEGOVIC and JEFTIC, 1979).

A mathematical model of a pelagic ecosystem has been constructed for Rijeka Bay and calibrated with data collected during a two year ecological study of the bay. The model is sufficiently general and can be calibrated to almost any pelagic ecosystem. Furthermore it has been coded in such a way that it can be run on any minicomputer with 8K words in memory. The model gives semiquantitative predictions of the change in dynamics of three functional groups of phytoplankton, four functional groups of zooplankton and a pelagic fish as induced by the change in temperature, solar radiation or limiting nutrients (nitrogen, phosphorus, and silicon) (LEGOVIC and JEFTIC, 1979; LEGOVIC, 1980).

LIST OF ACRONYMS

CIESM	Commission Internationale pour L'Exploration Scientific de la Mer Méditerranée
CNR	Consiglio Nazionale delle Richerche National Research Council, Italy
CNRS	Centre National de la Recherche Scientifique, France
COEC	Comite Central d'Océanographie et d'étude des Côtes
DRIFTEX	Drifter Experiment
FAO	Food and Agriculture Organization of the United Nations
GFCM	General Fisheries Council for the Mediterranean (FAO)
GONEG	Gulf of Naples Ecological Group
GONEP	Gulf of Naples Ecological Program
ICSEM	International Commission for the Scientific Exploration of the Mediterranean Sea (CIESM)
IIASA	International Institute for Applied Systems Analysis
INSTOP	Institut National Scientifique et Technique d'océanographie et de Pêches (Tunisia)
IOC	Intergovernmental Oceanographic Commission
IRPTC	International Register of Potentially Toxic Chemicals (UNEP)
MARE	Model of the Adriatic Regional Ecosystem
MEDIPROD	Mediterranean Productivity (Program)
MEDOC	Mediterranean Occidental Survey
MEDPOL	Coordinated Mediterranean Pollution Monitoring and Research Programme (UNEP)
MIT	Massachusetts Institute of Technology
NSF	National Science Foundation
ONR	Office of Naval Research (U.S.A.)
OTAN	Organization du Traite de l'Atlantique Nord
SCOR	Scientific Committee on Oceanic Research (ICSU, International Council of Scientific Unions)
UNEP	United Nations Environmental Programme
UNESCO	United Natious Educational, Scientific and Cultural Organization

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APPENDIX

SUGGESTED RESEARCH PROGRAMS

In the Mediterranean there are many ongoing research activities which have developed along different lines and with different goals, mostly framed within small scale ecosystems. All aspects of marine research are, of course, necessary in order to gather the badly needed baseline information for such complex and diversified ecosystems as occur in the Mediterranean. All coastal countries have become increasingly aware of the disruptive effects of pollution and, consequently, are initiating programs designed to understand the functioning of their marine environment. International agencies have prompted and coordinated many of the ongoing activities in this field.

It is felt, however, that all possible effort must be made in order to:

a. further promote research activities, particularly in those areas where basic knowledge is still missing or inadequate;
b. implement present and future research by integrating the necessary descriptive phase with studies on processes and fluxes;
c. coordinate the activity of research teams in adjacent areas;
d. promote cooperative programs covering large areas of the Mediterranean;
e. standardize and intercalibrate field and laboratory activities.

The achievement of any of the above requires the application of the best possible research strategies. Ecosystem modelling has proven to be an efficient resource-saving tool. The present report is intended to serve also the purpose of providing a guideline for researchers active in the Mediterranean by offering an illustration of the dynamics of model building through the analysis of a small-scale ecosystem. The importance of the availability of adequate data including both the qualitative and quantitative aspects of the environment, particularly including for example, those key processes governing growth rates and recycling mechanisms, is self evident.

It is hoped that the contents of this report (together with the suggestions and the considerations included in its different sections) might provide a practical representation of the dynamics, problems, and benefits of modelling techniques and thereby facilitate the use of this important research tool among the Mediterranean scientific community.

In this respect, an important role can be played by national and international agencies by providing the appropriate scientific framework, coordination, and facilities suggested in the following section, entitled Recommendations.

RECOMMENDATIONS

The Workshop,

Considering that the numerical modelling of ecosystems as a whole, or of their parts, can provide a powerful tool for assisting in the decision making processes leading to environmental management policy;

Considering the requirement for predictive models dealing with the dispersion of certain pollutants in marine environments;

Considering Unesco's important role in propagating the idea of ecosystem modelling among marine scientists in the Mediterranean and the necessity to continue with such action;

Considering the enthusiastic response from marine scientists participating in this and former Unesco workshops, and the substantial progress achieved by this workshop compared to the former ones;

Considering that a major lack of knowledge exists concerning the fluxes, rates, and processes in the Mediterranean ecosystems;

Recognizing that the acquisition of sufficient baseline data is a necessary prerequisite for any successful modelling effort;

Considering the need to update marine scientists in the methodology of modelling;

Recognizing the importance of maintaining continuous interaction between regional research groups and the need for standardization of methods used in marine ecosystem studies;

Being aware that most Mediterranean Institutions have yet to acquire a sufficient level of competence and experience in this field and that the relevant documentation is still unavailable to many Mediterranean Institutions;

Recommends to Unesco and the member states of Unesco:

- that national efforts to model small- and meso-scale ecosystems of particular interest be supported through training and consultation;

- that multidisciplinary modelling teams with long term, detailed programs be organized at a regional level;

- that workshops be convened on larger scale modelling of the eastern Mediterranean, Adriatic Sea, Ionian Sea, Aegean Sea, Levantine Sea, Red Sea, Black Sea;

- that periodic workshops be continued at intervals of 2 to 3 years for the purpose of evaluation, comparison, and improvement of models generated within the Mediterranean areas. These workshops should be of such a caliber and scope that they provide the essential forum for exchange, evaluation, and confrontation of modelling methodology, concepts, and related baseline research requirements. These should provide a progressive modelling sequence towards the realization of an eastern Mediterranean model;

- that a Mediterranean Regional Modelling Center be established in cooperation with UNEP, FAO(GFCM), IOC, and Mediterranean countries, to promote and help modelling efforts in the Mediterranean by collecting and disseminating data and literature, by publishing a newsletter, by organizing individual training, seminars, meetings, and workshops;

- that a mechanism for reviewing current literature and data sources in the Mediterranean relevant to numerical modelling be organized. This could be done by the active participation in one of the existing journals of a small editorial board consisting of Mediterranean scientists;

- that concept of modelling be considered whenever appropriate to be included in agenda of workshops, seminars, meetings, working groups, etc., which are sponsored by Unesco;

- that Mediterranean field and laboratory research on ecological patterns, fluxes, rates, and processes be strengthened and incorporated in research programs whenever appropriate;

- that the necessary steps be continued to standardize techniques, measurements and data analysis for various fields of ecological research; in particular, for phytoplankton biomass and productivity, zooplankton biomass and fluxes, benthic biomass and functional processes, chemistry of nutrients and kinetics, physical processes, organic pollutants and trace elements;

- that conceptual modelling be used as a complementary tool for establishing research and field programs in order to upgrade base line data;

- that support be given to the acquisition of data sources relevant to numerical modelling, which are not accessible through normal procedures;

- that Mediterranean institutions of developing countries be provided with adequate modelling literature.

Recommends to UNEP:

- that because of the importance of modelling for the understanding and the solving of pollution problems, the modelling component of the Mediterranean Action Plan - Phase II be revised and supplemented by recommendations from this workshop.

WORKSHOP CONCLUSIONS

The Workshop:

Considering that to produce a numerical model of a particular ecosystem is at least a several man-year effort;

Considering that the objectives of the workshop were both educational (to provide an integrated exposure to the methodology of marine ecosystem modelling) and operational (to construct a numerical model of the Gulf of Naples ecosystem);

Being aware of the fact that the available data base for the Gulf of Naples was not adequate for a comprehensive numerical model;

Being aware that participants of the workshop were experts from various fields and of pronounced differences in modelling experience;

is of the opinion:

- that the workshop was extremely successful in fulfilling both objectives;

- that this didactic exercise was a concrete step toward providing the participating scientists with the essential exposure to the mechanisms involved in generating an ecosystem model;

- that the role and enthusiasm of Unesco and Strazione Zoologica was one of the main factors for the success of this workshop;

- that the workshop provided a cost efficient means to achieve the anticipated objectives;

- that the choice of faculty and their intensive work during the workshop, in addition to the enthusiastic response of the attendees, contributed substantially to the success of this exercise;

- that the informal atmosphere was conducive to effective interaction and provided a forum for vigorous exchange and discussion of common research problems.

- that the participants, by being exposed to the numerical modelling methodology through this step-by-step procedure, became aware of the major aspects and problems connected with modelling allowing them to assess the application of modelling to their own Mediterranean region.

OPENING ADDRESS

Ladies and Gentlemen,

It is indeed a great pleasure for me to welcome you on behalf of Unesco at the opening session of this workshop. I also take this opportunity to thank the Zoological Station in Naples for hosting this meeting, for the excellent facilities they are putting at its disposal, and for their generous financial support.

As some of you will remember, the present meeting is the third in a sequence of workshops, sponsored by Unesco on the request of Mediterranean scientists, aimed at enhancing the modelling and simulation approach in marine ecosystem studies. For those of you, however, who did not attend the preceding workshops, and also as an introduction to the present workshop, I would like to review briefly the history and the outcome of the preceding two workshops.

The importance and the desirabilty of the modelling approach to marine ecosystem studies in the Mediterranean were emphasized during the IBP/PM-Unesco Symposium on the Eastern Mediterranean held in Malta in September 1973. The scientists participating in this symposium formulated an action plan and strongly recommended that an interdisciplinary study of this basin with its unique characteristics be carried out in the modelling perspective. In response to this recommendation, Unesco agreed to support a regional workshop on the subject of modelling.

The first workshop was hosted by the University of Alexandria in December 1974 with the particpation of scientists from several countries in the region: Egypt, Lebanon, Lybia, Malta, Syria, and Tunisia. Modelling specialists and scientists were also invited in their personal capacity. The activities of the workshop served two major objectives:

a. to review the state of marine sciences in the region and formulate priorities and requirements for a general Eastern Mediterranean model. Though attention was focused on the Egyptian coastal zone as an example, summaries of the current marine research activities in other countries were given by the participants.

b. to familiarize the participants with the concepts and mechanisms of model development. Conceptual submodels were elaborated by the participants with guidance from the Unesco consultants and later they were discussed and interrelated by the workshop as a whole.

The Alexandria workshop endorsed several recommendations. Besides the usefulness of the modelling methodology as a tool in marine research, the participants also recognized the absence of sufficient expertise in the Eastern Mediterranean. They specifically recommended that the Alexandria Workshop be followed by a second workshop, focusing on some other Eastern Mediterranean region.

This second workshop was held in Dubrovnik in October 1976. Prior to this Dubrovnik meeting, an important development had taken place in Mediterranean marine science, namely the adoption of the Action Plan sponsored by UNEP (Barcelona, February 1975), and particularly the Coordinated Monitoring and Research Program consisting of seven pilot projects.

In consequence, the membership and scope of the Dubrovnik workshop were widened to encompass not only the East Mediterranean, as earlier planned, but the whole basin.

The participants in this workshop agreed that the Monitoring and Research Program would benefit greatly from the development of modelling concepts and methodology in the Mediterranean. With this objective in mind, they separated into three working groups, undertaking the task of modelling a) the ecosystems and communities, b) the heavy metals in the marine ecosystems, and c) the physical processes.

The workshop participants stressed the essential importance of the modelling methodology for assessing the impact of pollution on ecosystems and for providing the information needed for the management of the environment. They also recognized that, at this stage, many Mediterranean institutions were still lacking in competence in this field. An educational effort to promote modelling was recommended and requested from Unesco. It was also recommended that multidisciplinary working groups of scientists meet to produce some specific models at different levels of complexity.

As a follow up, and in response to this request, two consultation meetings were held (Antalya, November 1978; and Napoli, March 1979) to decide on which lines to proceed, particularly as there were two separate proposals: a workshop on the marine ecosystem of the Levantine basin, or a training course on marine ecosystem analysis. After careful deliberation, it was decided to organize a workshop on the Quantitative Analysis and Simulation of Mediterranean Coastal Systems.

The consultation meeting also reviewed the possible Mediterranean coastal subregions which would meet with the criteria defined at the Dubrovnik workshop, to serve as a case study for the modelling exercise, and selected the Gulf of Naples for this purpose. This brings us to our present meeting.

One of the major objectives of this workshop is that it should contribute substantially to developing capabilities in the Mediterranean countries in the methodology of ecosystem modelling. It is strongly hoped that with the experience that you have in your respective fields of specialization and your active participation in the workshop activities, this objective will be attained.

As you know, the modelling concepts are still regarded with much skepticism in many scientific and managerial circles. The modelling methodology as a tool for the assessment of pollution impact and for the management of the ecosystem was stressed by the Dubrovnik workshop.

It is hoped that this and other similar activities will promote a consensus on the importance of ecosystem modelling among the decision-makers around the Mediterranean.

In this perspective, and in the light of past activities and recommendations, it is hoped that during your formal and informal discussions, you will give some thought to the future. The question is: How do you visualize the activities needed on both the individual and institutional levels? In other words, what do you propose to do in your own personal capacity as scientists, and what do you expect from your national programs and from Unesco and other international bodies. We wish to be enlightened about the activities you recommend that are relevant to the objectives of this workshop.

Before closing, ladies and gentlemen, you may wish to join me in expressing our sincere gratitude to Professor A. Monroy, the former Director, to Professor S. Genovese, the present Director of the Stazione Zoologica and to Dr. Gian Carlo Carrada, the convener of this workshop. I would like to acknowledge Dr. D. Fazio, the Director General of the Ministry of Education for the generous financial contribution in support of this workshop. Also our special thanks go to Dr. E. Fresi the Head of Benthic Ecology Department of Ischia, who serves as host for this meeting; and to Mr. G. DeVivo, the Secretary of the Stazione Zoological; and to the staff for their unfailing efforts in the preparation of this workshop. Our thanks are also due to the Consultation Committee for their positive and active contribution to the organization of this workshop.

I wish you a pleasant stay and an enjoyable and successful meeting.

Selim Morcos

CLOSING ADDRESS

Ladies and Gentlemen,

At the close of this workshop, following two weeks of exciting and factual collaboration, it is time again for an official speech. I will nevertheless refrain from following the abused tradition of officialism and keep to the informal mood that has characterized the atmosphere of our meeting.

Should I have the presumption of considering myself an expert on something, I could hardly claim it to be in the field of ecological modelling. Therefore I will not attempt to make an evaluation of our work on the specific basis of modelling theories and strategies. This would be a rather superficial exercise. Rather, I leave the judgment to each of you as the best judge of the cultural and scientific value of your participation in this meeting. I therefore take this occasion to pose a few considerations of a more general character.

First of all, I have been glad to welcome here many old and new friends, most of whom are active members of the Mediterranean scientific community. Occasions for discussion are always useful, and so much more so when they involve, as in our case, people operating on common problems within such diversified scientific and economic structures as the Mediterranean countries. All of us know too well the everyday difficulties arising from the shortage of research funds and personnel while facing, at the same time, a mounting concern about the environment. A rational use of the limited resources available for research is therefore more than ever imperative. Under this perspective, if, as I believe, this workshop has contributed to the rationalization of our future activities, this contribution must be considered more than a secondary outcome of our meeting.

I am sure that the role played by the UNESCO Division of Marine Sciences in fostering marine research is a guarantee that the series of workshops on Mediterranean ecosystem modelling will successfully continue for the benefit of the scientific community. However, I do not wish to leave the impression that this meeting has been permeated by a slight taste of Mediterranean chauvinism: the fact that we have left a large part of the workshop's daily activities on the shoulders of our non-Mediterranean colleagues is, I believe, the best proof that we have kept an open minded attitude.

Finally, I am sure that the rapport acquired during these days of close collaboration will shelter me from the accusation of ingratitude if I do not mention explicitly the contribution given by each of you to the success of this workshop.

Gian Carlo Carrada

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