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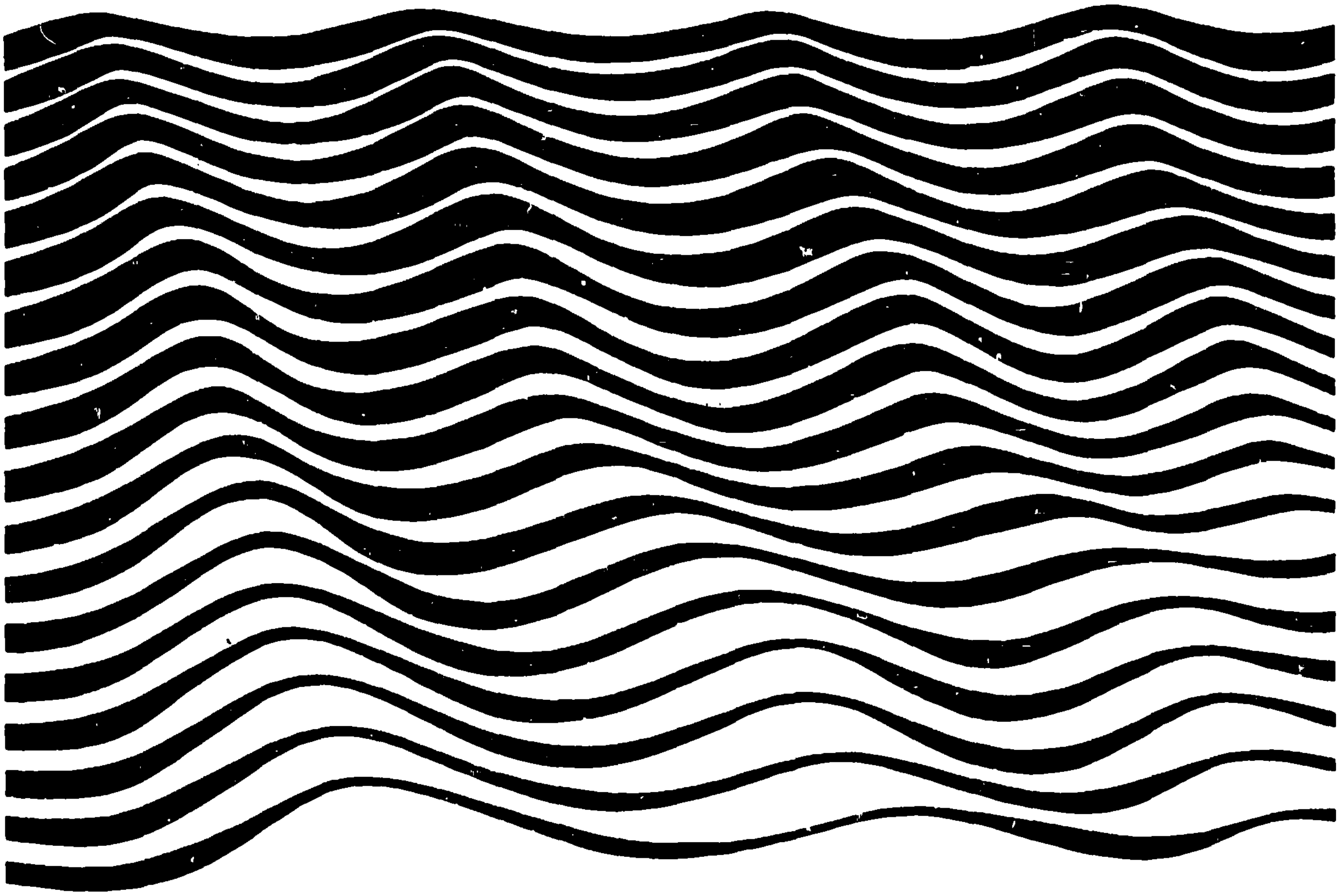
Coastal lagoon research, present and future

Proceedings of an Unesco/IABO
Seminar



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PREFACE

This series, the *Unesco Technical Papers in Marine Sciences*, is produced by the Unesco Division of Marine Sciences as a means of informing the scientific community of recent developments in oceanographic research and marine science affairs.

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INTRODUCTION

The present volume constitutes the compilation of the papers presented at the Seminar on Coastal Lagoon research, Present and Future held at the Duke University Marine Laboratory, Beaufort, N.C., U.S.A. from 29 August to 2 September 1978 under the section of the Seminar entitled "Present Coastal Lagoon Research". It goes in sequence with No. 32 of the Unesco Technical Papers in Marine Science which contains the Report and Guidelines of the Seminar.

A description of the objectives of the seminar and the list of participants will be found respectively in the Introduction and in Annex II of No. 32.

A review of some general features of coastal lagoons

by

Fred B. Phleger

At the symposium on coastal lagoons in Mexico City in 1967 I presented what seemed to be appropriate comments on some general features of coastal lagoons (Phleger, 1967a). Considerable research by numerous investigators during the intervening years makes it desirable to review these generalizations and to make modifications and additions. I shall not refer to others by name, although it is obvious that my comments are based on the work of many people. My remarks, however, express my own opinions and they are based mostly on my own experience studying lagoons.

The type of coastal lagoon which I am discussing is a body of brackish, marine or hypersaline water impounded by a sandy barrier and having an inlet connecting with the open ocean. Each coastal lagoon differs from all others. These differences fundamentally involve size, shape, tidal range, runoff of tributary streams, climate of the area, number and size of inlets and kind and amount of sediment available. Differences in water movement, chemistry, geology and ecology result from these basic factors. Differences may be great or small, but nevertheless it is possible to formulate generalizations which apply to many or perhaps most lagoons. I have found these useful in guiding lagoonal studies and as an aid to interpretations. The following are some of my present generalizations in abbreviated or note form. I am sure that additions and/or modifications can be made to these.

1. Many or most modern lagoons have developed during the rising sea level of the last 6,000-8,000 years. There is a well-established pause in the rise of sea level about 7,000 years ago when the level was about 10 m lower than at present. A sand beach was formed at this level at this time. As sea level rose later, this sand deposit grew upward and prograded seaward to form a lagoon barrier, as shown, for example, at Ojo de Liebre Lagoon (Phleger and Ewing, 1962) in Mexico and at Galveston Bay, Texas (Bernard, Le Blanc, Major, 1962).

2. Lagoons develop on aggrading or formerly aggraded coastal plains which are gently sloping seaward and where there is abun-

cant sediment. They are always associated with modern or formerly active rivers which are tributary to them or flow into the ocean nearby. The rivers supply sediment to the nearshore turbulent zone which is accumulated on the sand barriers by wave and longshore tranport. The river valleys may also constitute a part of the lagoonal basins.

3. The basic shape of a lagoon which is formed by a wave-built barrier on a gently sloping shoreline is an elongate basin parallel to the coast. This may be modified by a tributary basin at right angles to the coast which resulted from a river valley incised at lower sea level. Many of the bays in South Texas are examples of this - San Antonio Bay is the best known (Shepard and Moore, 1960).

4. The principal and usually the deepest channel in a lagoon is adjacent to the lagoon barrier. A bifurcating system of channels occurs in a lagoon where they are preserved, but in many areas the channel system has been obscured by deposition of sediment (Phleger, 1967a). Channels are most shallow in the innermost locations in the basins.

A river with a high volume flow may have a deep channel cutting across a lagoon.

5. The coarsest sediment is in the inlet where current velocities are maximum, and the finest sediment is in the innermost reaches where current velocities approach zero. A high volume of river flow into a lagoon usually results in fine sediment throughout the basin except at and near the barrier and in the river channel. Abundant shell such as oyster reefs form hard bottoms characterized by hard bottom fauna and flora.

6. Current velocities and the rate of water exchange are functions of size of the lagoon, its shape, number and length of inlets, tidal range and amount of river flow. Maximum current velocities are at the inlet and minimum velocities are in the innermost reaches of the lagoon. Within a lagoon, there is a delay in time of maximum current velocities and water level from that of the inlet; in some lagoons this delay is about 1 hour per 10 km distance. The higher the current velocities, the deeper the channels and the more suitable the lagoon for ship navigation.

7. The depth of the channel over the entrance bar (outer "inlet delta") which is the shoalest part of the entrance area is a function of tidal range, tidal wedge, amount of river flow and the

size and direction of approach of ocean waves which reach the shore. Waves are the critical modifying factor in causing this channel to be the shoalest part of the entrance area (Phleger, 1965).

8. The size or cross-section of an inlet is a function of the amount of water which flows through it due to tidal wedge and amount of river flow.

The spacing of inlets in some places appears to be a function of tidal range. In the Ojo de Liebre area of Mexico (Phleger and Ewing, 1962) which has a maximum tidal range of almost 3 m inlets are relatively close together. In the Laguna Madre area of south Texas and northeast Mexico where tidal range is very low, inlets are as much as 150 km apart (Rusnak, 1960). Rivers also influence the spacing of inlets.

Very long inlets are in areas where very large amounts of sediment have been deposited. One example is Huizache-Caimanero Lagoon in southern Sinoloa, Mexico, where two rivers which bracket a lagoon have deposited sediment over large deltaic areas (Phleger and Ayala-Castañares, 1972). The inlets here are approximately 8 km long. In St. Lucia Lagoon, South Africa, the inlet is 20 km long (Phleger, 1976).

9. Barrier beaches are kept "healthy" with no erosion by a resupply of sand which is transported by rivers to the nearshore turbulent zone. Where adequate resupply does not occur, there is erosion of the beach and loss of sand seaward. This occurs where rivers have been dammed for water use or flood control. In other areas the supply of sand on the continental shelf after rise of sea level has become exhausted. California and northwest Mexico have many sand-starved lagoon barriers. Parts of the Laguna Madre Texas barrier, formerly supplied with sediment brought in by the Rio Brava (Rio Grande), have almost disappeared (Rusnak, 1960). Part of the barrier for San Diego Bay (California) is in critical condition.

10. Very small or "pocket" lagoons frequently occur at the seaward end of a stream which has a small drainage basin and thus limited amount of runoff. Where the rainfall is seasonal, the inlet of such a lagoon is open only during the rainy season and is closed by wave action and longshore drift during the dry season (Stewart, 1958). Some or perhaps most of these lagoons have a significant amount of water exchange with the open ocean by seepage through the porous sandy-barrier.

Inlets of two of these lagoons have been observed to open by a process known as thixotropy. As the lagoon is filled with water, the sand of the barrier becomes saturated with water. If there is a heavy surf, the pounding of the saturated sand of the barrier by waves causes the sand to become fluid and flow seaward at the position of the previous inlet. Then water flow from the lagoon, where the water level is higher than in the adjacent ocean, takes over and finishes the opening.

11. After its formation a lagoon may be divided into two or more separated but connecting basins. This may be a result of different processes.

Shell reefs may grow across the lagoon at right angles to the tidal currents, eventually separating one or more basins. This has occurred in Alvarado Lagoon, Mexico, and is still occurring (Phleger and Lankford, 1978).

Where there are two or more inlets the tidal currents meet approximately midway between inlets and cancel each other. Sediment being transported is deposited where the tides meet. This has been observed occurring at Santo Domingo Lagoon in Baja California, Mexico. The next stage is seen in the Ojo de Liebre area of Baja California, where a single lagoon has been fragmented into 3 lagoons connected by shallow channels (Phleger and Ewing, 1962).

In Patos Lagoon in southern Brazil the cuspate spits may be due to eddies. Some lagoons with these features eventually may be segmented (Closs 1962).

12. Most lagoons are almost filled with sediment. This is shown by the shallow depths, 1.5-2 m, and the absence of a channel system in many lagoons, except near the inlet. Bypassing of sediment onto the adjacent continental shelf occurs during times of large river flow (Phleger, 1967b). Deposition within the lagoon is mostly in deltaic areas and in fringing marshes.

13. Inner and lower water masses occur in lagoons which are sufficiently large to develop them. These have distinctive assemblages of some benthic organisms, of which the foraminifera are perhaps the best known.

14. A very long inlet (several km) filters out tidal effects and is a barrier to some open-ocean benthic organisms. St. Lucia Lagoon in South Africa is a good example of this, based on distribution of foraminifera and on hydrographic observations (Phleger, 1976). Very high runoff into a lagoon also may be a barrier to

open-ocean organisms. This is shown in Alvarado Lagoon, Mexico, by the distribution of benthic foraminifera.

15. Organic production is high in most lagoons compared to most areas of the continental shelf. One of the most productive areas is near river effluents, probably due to soil extracts from river water. Marshes have high production, which may be due to frequent resupply of nutrient-rich sediment and abundant plants and blue-green algae. Lagoons also obtain trace materials from sea water, including nutrients, from tidal activity. Hypersaline lagoons are very productive, probably due to constant resupply of nutrients from seawater.

If there is little river flow into a lagoon and poor water exchange with the open-ocean, productivity may be low. Superior Lagoon on the Pacific coast of the Isthmus of Tehuantepec, Mexico, is an example of this (Cromwell, 1975). Most of the stream water is used for irrigation and the complex lagoonal system filters out most of the tidal action. Water exchange thus is very slow.

16. Lagoons are ephemeral. They may be considered as events or processes on generally prograding shoreline.

17. Extensive marshes characteristically occur within lagoons where their borders are being aggraded. Abundant sediment usually is in suspension in lagoon waters and this is mostly deposited around the margins at the end of the tidal excursion where current velocities approach zero. The finest sediment in the area is deposited in such marshes. Marshes also occur on deltas which may be tributary to lagoons and these are built primarily from sediment transported by river flow and deposited as the river debouches into relatively open water which contains electrolytes.

The lower boundary of the marsh is at the local tide level of mean lower high water where observations of tide levels have been made in areas of a semidiurnal tide. The bare intertidal flats are between mean lower high water and mean lower low water. The actual relief of the marsh depends upon the tidal range, and extends to highest high water. Characteristically low and high marsh are present and they contain different assemblages of plants and animals; the boundary between the low and high marsh zones is at the level of mean higher high water. The elevation of the marsh boundaries can be used, therefore, to estimate the mean tidal ranges in the area (Phleger, 1970).

Marshes have high organic production, usually the highest in the lagoonal environment, and they are important nursery areas for juvenile fish, shrimp, etc.

18. The principal non-living resources of lagoonal areas are salt deposits and sand and shell used for construction materials.

Production of salt (NaCl) requires the presence of low dikes between the salt evaporation pans and the main part of the lagoon. Such dikes may be artificial or natural, and there must be delivery of lagoon water to the salt pans by flooding or pumping or both (Phleger, 1969).

The dredging of shell from lagoons may damage or destroy the only hard bottom habitat where oysters, for example, can attach and develop. This has happened in some of the south Texas lagoons. Dredging of sand should be carefully controlled.

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THE FLUSHING OF WELL-MIXED TIDAL LAGOONS AND ITS SEASONAL FLUCTUATION

by

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INTRODUCTION

The flushing of a coastal lagoon with water from the adjacent shelf sea is an important abiotic factor in its ecology. For the purposes of the discussion, we consider coastal lagoons to be inland sea areas, stretched along the coast, protected from direct contact with the open sea by a barrier in which only relatively small inlets provide a means of communication between the lagoon and the sea (Phleger, 1969). Any tide in the lagoon is forced by co-oscillation with the tide of the open sea, penetrating through the inlet(s). Lagoons may or may not be influenced by fresh water runoff from the land. If they are, such a runoff produces, apart from other significant chemico-biological effects, a decrease of the salinity in the lagoon as compared with the open sea. This differential thus provides a means by which to calculate a relevant flushing time scale. If fresh water supply is absent or insignificant, the reverse may occur; i.e., evaporation in the lagoon may cause the salinity in the lagoon to be greater than the value at the seaward entrance (Phleger and Ewing, 1962). A flushing time scale is much less easily calculated in this case because of indeterminacy in the magnitude of evaporation.

As will be shown in the next chapters, the flushing time scale of a particular lagoon may differ appreciably according to its definition. However, whatever the definition may be, it can be stated that the flushing time scale depends on the character and strength of the physical transport processes in the lagoon and also, to some extent, in the adjacent sea. There is a rather limited amount of literature on specific physical transport mechanisms acting in such areas, specially as compared with the extensive literature on this subject in the more familiar estuaries. Although it may be supposed that estuarine transport processes are also of importance for coastal lagoons, it should be kept in mind that due to their different morphology and to the often lesser importance of fresh water runoff, the significance of tidal and wind-induced transport processes, as compared with the (thermo) haline circulation, may be more important. An elementary account of these processes in coastal lagoons has been given by Groen

(1963). For more extensive surveys one is forced to consult the relevant reviews on estuaries (cf. Bowden 1967; Fischer, 1976). From hereon we shall only deal with lagoons in which density currents play a negligible role in the gross transport pattern. Such lagoons will be well-mixed vertically due to the combined effect of tide and wind-induced turbulence.

We now turn to the central topic, that is, the presence of any seasonal fluctuation in the flushing of coastal lagoons. Seasonal fluctuations in the strength of physical transport processes are not dealt with in either of the reviews mentioned. After all, this is not surprising. The present author knows of no extensive study reported in the literature concerning the seasonal fluctuation of flushing intensity in any coastal lagoon or inland sea. For this reason alone such a study should be strongly encouraged as a topic of future research. In the meantime we shall deal with the subject in an indirect way by reasoning from what is known about seasonal fluctuations in quantities of interest to flushing processes. It will be evident that the tide cannot be regarded as such; the only effect of (limited) significance being a seasonal modulation of the solar tides according to distance and declination of the sun. On the other hand, any seasonal effect will be strongly coupled to atmospheric processes. The influence of the latter on the lagoon can be roughly subdivided to direct and indirect effects. Included in the former is the locally induced wind-drift currents in the lagoon as well as any set-up of the water level connected with these currents; in the latter the variable (non-tidal) transport of water through the inlet(s) forced by the variable action of the atmosphere on the adjacent sea. These transports too can be connected with sea level variations in the lagoon. After reviewing in the next chapter the general aspects of the flushing of coastal lagoons, we shall deal in a rather tentative way with its seasonal cycle.

PHYSICAL TRANSPORT PROCESSES IN COASTAL LAGOONS

Advection - diffusion

It is common practice to classify physical transport processes as being either advection or diffusion. Although the division itself is not free of ambiguity we shall follow that division. Loosely speaking, processes that carry a given water mass form one point to another without changing its spread are called advective; those processes that concurrently change their spread are called diffusive. It should be noted that the division depends on the time and space scales under consideration. Now, given any two points (A, B) in a lagoon separated by a distance (L), we may form two time scales related respectively to the advective and the diffusive processes acting along the transport path from A to B. If U is a characteristic velocity of advection and K a characteristic diffusion coefficient, the time scale to move any water mass by advection from A to B is L/U, whereas the time scale for a complete mixing of the water mass between A and B is of order L^2/K. A dimensionless (Peclet, Pe) number may now be formed:

$$Pe = \frac{K}{LU} \tag{1}$$

According to the value of Pe, transport processes may be classified as either advective (Pe << 1) or diffusive (Pe >> 1). Associating the length scale L with the overall dimension of the lagoon, the Pe-number is a measure of the relative strenth of advective and diffusive processes in producing a complete flushing of the lagoon. Realistic values for the scaling parameters in a lagoon are:

$$U \ (0 \text{ to } 10^{-1} \text{ m sec}^{-1}), \ K \ (10 \text{ to } 10^{3} \text{ m}^{2} \text{ sec}^{-1}),$$
$$L \ (10^{3} \text{ to } 10^{5} \text{m})$$

Thus the Pe-number may show a large range of values, from << 1 to >> 1. However, in the absence of any significent, more or less time independent flow through the lagoon, its flushing will always have to be classified as diffusive. Such a situation is certainly met with in a tidal lagoon which has only one inlet at its seaward end and no runoff entering from the land.

Diffusive processes

As we do not consider the effects of density currents here, we shall say that any diffusion in the lagoon must arise either from tidal or wind action. The former is normally the most important process, although the way in which the tide generates mixing in coastal embayments is nearly always complicated. First, there is a direct production of small scale turbulence by tidal currents. However, small scale turbulence becomes an important diffusive agency only by its interaction with large scale spatial irregularities in the current velocity field. These irregularities themselves are produced by the geometry of the basin which is often very complicated. Three processes, producing large scale diffusion due to the basin geometry may be mentioned here:

(1) longitudinal diffusion due to lateral shear of the tidal current caused by friction along the sides of the channel or over a varying bottom topography. The effect is only of importance if the time scale of cross-channel mixing by small scale turbulence is of the order of the tidal period. See Fischer (1976) for further discussion.

(ii) longitudinal diffusion due to temporal storage of water in stagnant areas, over tidal flats, etc. Such a storage may cause a shift of parts of a water mass and thereby promote its spreading. The process has been discussed qualitatively by Postma (1954). A quantitative theory has been given by Okubo (1973) and, more recently, by Dronkers (1978). The latter author has shown that the effect of tidal storage basins may lead to realistic values of the longitudinal diffusion coefficient in the order of 10^2 m^2 sec^{-1}.

(iii) longitudinal diffusion by tide-induced residual currents. In shallow tidal areas of complicated geometry the tide itself generates, by nonlinear interaction, a residual current velocity field (see Zimmerman, 1981 for a review). Superposition of irregularly distributed residual currents upon the tide gives rise to a diffusion process, as has been described by Zimmerman (1976b, 1978). Residual currents may account for very large diffusion coefficients, in the order of 10^3 m^2 sec^{-1}.

In all three cases the diffusion coefficients may be expressed in the tidal parameters l (horizontal displacement amplitude) and U (velocity amplitude) by

$$K = cUl \tag{2}$$

The "constant" c, however, represents different physics, according to which of the processes mentioned is described by (2).

As to the effect of the wind field over the lagoon in producing enhanced mixing, the effect of an irregular bottom topography may also give rise to circulation cells as in the case of residual circulation induced by the tide. A simple picture is given in Groen (1969). Although we suppose that its effect is quantitatively of minor importance as compared with that of the tide, it might provide a mechanism which gives a slight seasonal fluctuation in the strength of the internal mixing processes in the lagoon.

Flushing time scales

A representative time scale for the flushing of a lagoon is the average transit time through the basin of water parcels entering at a particular place. If, in a stationary state, the flux of parcels into (and out of) the lagoon is given by F and the total mass of the parcels present in the basin, having entered at that particular place, is M, it has been shown by Bolin and Rodhe (1973) that, no matter what the spread in the transit times may be, the average transit time, τ_0 , is given by:

$$\tau_0 = \frac{M}{F} \qquad (3)$$

It should be noted that values of τ_0 may vary considerably for sea water entering and leaving through the inlet and, for instance, fresh water entering the lagoon at its landward side and also leaving through the coastal inlet (Zimmerman, 1976a).

Another time scale, related to the average transit time, is the average age, τ_a, of water parcels that entered at a particular place; the age being the time interval that has passed after the parcel has entered the basin. Bjorkstrom (1978), in a discussion of Bolin and Rodhe (1973) and Zimmerman (1976a) has shown that the average age is related to the average transit time and the m.s. spread, σ_t^2, of the transit times around that average by

$$\tau_a = \frac{\tau_0}{2} + \frac{\sigma_t^2}{2\tau_0} \qquad (4)$$

Hence, any spread in the transit time increases the average age. As such a spread is completely due to diffusive processes, it is suggested that there may exist a definite relationship between the basin Peclet-number (1) and the average age.

Now, if speaking about the flushing time scale of a lagoon in the rest of this paper we mean the average transit time defined by (3), applied to parcels entering the basin through the coastal inlet ("sea water parcels").

Tidal and non-tidal flushing

If we ignore, for the time being, any influence on the ecosystem of a coastal lagoon exercised by runoff from the continent, then we see that its internal development, including a possible seasonal cycle, is strongly dependent on the flushing of the lagoon with water from the adjacent sea. Normally the boundary between open sea and lagoon, located near the inlets, forms a discontinuity for a lot of ecological factors. The extent to which the lagoon can maintain an equilibrium determined only by local processes depends on the flushing time scale of the lagoon as compared with the time scale of the processes considered. As to the flushing time scales(s) connected with the intrusion of sea water, it is the processes nearest to the inlet which determine to a large extent the rapidity of the flushing. Also physical transport processes may show a pronounced discontinuity in character at the boundary between lagoon and sea. As for tidal lagoons, the flushing with sea water both by tidal and non-tidal processes can be understood by a reappraisal of the classical "tidal prism" concept (see Bowden, 1967 for a discussion).

Let us suppose that the boundary between "sea water" and "lagoon water" is situated in the inlet at low water slack. During the next flood a volume V , called the tidal prism, is introduced into the lagoon. V can be written as the product of the amplitude of horizontal tidal displacement, l, and an effective area A as $V = 2lA$. In its simplest form the concept of flushing by means of the tidal prism method now assumes:

(i) that the volume introduced during the flood is completely mixed with the low tide volume of the lagoon, and

(ii) that the volume subsequently leaving the lagoon during the ebb is completely mixed with the adjacent sea, supposed to be of infinite volume.

Both assumptions, of course, can be criticized. First, the mixing of the volume introduced during the flood with the low tide volume of the lagoon can be more realistically thought of as a piston pushing a volume into the lagoon, thereby only shifting the boundary between "sea" and "lagoon" water inwards. At the same time the inflow is producing an intense turbulent mixing process, thereby "diffusing" the boundary between both water masses. If the diffusion process is characterized by a diffusion coefficient K, then the volumes effectively exchanged across the boundary of both water masses during a tidal period, T, will be of the order $A(2KT)$. Thus a fraction α of the introduced volume (tidal prism) is exchanged with the sea during each tide, being given by

$$\alpha = \frac{(2KT)^{\frac{1}{2}}}{2l} \qquad (5)$$

Substituting (2) for K in (5), we have

$$\alpha = (\pi c)^{\frac{1}{2}} \qquad (6)$$

As c may vary between 10^{-2} to 10^{-1} (orders of magnitude), α will show a range of values from about 10^{-1} to 0.5. It now remains to be seen whether the exchanged volumes are, at the same time, completely mixed either with the "sea water" volume or with the volume of "lagoon water". For the latter, this will be the case if the "internal mixing time scale" is of the order of the tidal period. If L is the effective length of the lagoon, this time scale is of the order $l^2/2K$. Hence, only if $L = 2\alpha l$ is the exchanged volume almost completely mixed with the low tide volume of the lagoon. However, such a situation will only be met with in cases of very small lagoons. On the other hand complete removal rather then complete mixing of the exchanged volume of lagoon water with water from the adjacent sea often takes place due to the hydrographic situation near the inlet at its seaward side. Longshore currents and asymmetry in the tidal outflow and inflow pattern give rise to a rapid displacement of the water leaving the lagoon during the ebb, so that during the next flood almost completely "new" sea water enters the lagoon. In this case, it will be evident that, following the above reasoning, the fraction of lagoon water replaced each tidal cycle by sea water is given by $\alpha V_t/V$ (V being the low tide volume of the lagoon). Its reciprocal value can be regarded as the average transit time of sea water parcels (the tidal period acting as the time unit), bearing in mind that αV_t represents a flux of sea water parcels, if divided by T, and V in the "mass" of sea water present in the basin (see (3)).

We have seen that, roughly speaking, the volume exchanged between sea and lagoon during each tidal cycle is proportional, but not necessarily equal to the "tidal prism". The factor of proportionality (6) depends on the way along which the tide generates a diffusive velocity field. It should be noted that the proportionality is a result of coupling the diffusion coefficient K to the tidal parmeters U and l in (2), as can be seen by following the derivation of (5) and (6); i.e., the flushing of the lagoon increases with V_t not because of an increase in tidal prism volume proper, but because such an increase does give rise to an enhanced diffusion coefficient, due to larger tidal velocities. In some way the energy of the diffusive part of the velocity field is dependent upon the amount of tidal energy dissipated in the lagoon per unit mass and time. The latter is roughly proportional to U_t^3/H (H being a representative depth).

Apart from the periodic tidal intrusion of sea water in the lagoon there often exists a considerable non-tidal flux of sea water through the entrance, forced by non-tidal long waves on the adjacent shelf. These non-tidal fluxes do not show the strict periodicity of the tidal discharge, but may be thought of as a random superposition of oscillating discharges of different periods and amplitudes. As for a given velocity amplitude, the displacement of a water mass is inversely proportional to the frequency, subtidal frequencies may play an important role in the displacement spectrum (Smith 1977, 1978), sometimes even having greater influence than the tides, although they may be of minor importance in the velocity spectrum. Since the internal diffusion processes are related to the energy dissipation forced by the velocity spectrum, it may be supposed that the internal mixing processes, represented by a longitudinal diffusion coefficient K, are less influenced by the subtidal frequencies in the discharge through the inlet of the lagoon. On the other hand, the "non-tidal prism" may be of the same importance as the tidal prism. It now remains to be seen in which way the non-tidal prism may add to the flushing of the lagoon.

Keeping the random character of the non-tidal fluxes in mind, we may form a representative non-tidal prism, V , from the mean-square non-tidal velocity, $U^* = \langle U_0^2 \rangle^{\frac{1}{2}}$, and an integral correlation time scale of the non-tidal velocities, T^* :

$$V_0 = AU^*T^* .$$

Analogously to the above reasoning concerning the water exchange by the tidal prism, we now suppose that over a time interval T^* a volume V is introduced into the lagoon. By the concurrent action of the diffusive processes, mainly induced by the tide, a volume of order $A(2KT^*)^{\frac{1}{2}}$ is exchanged with the lagoon water volume. This exchanged volume is subsequently transferred to the sea and completely removed when the non-tidal prism has again left the lagoon, as in the case of the tidal prism. However, due to the concurrent existence of flushing by the tidal prism over the time interval T^*, part of the volume $A(2KT^*)^{\frac{1}{2}}$ may have been transferred to the sea by tidal exchange. Hence the effective exchange by the non-tidal prism is that part which has not yet been removed from the lagoon by tidal exchange. An estimate of the latter can be derived as follows. Whereas a volume $A(2KT^*)^{\frac{1}{2}}$ of the non-tidal prism is exchanged with the lagoon at its landward side, the same volume is exchanged with the sea at its seaward side by the tidal prism. If these volumes overlap each other it is the non-overlapping part of the volume exchanged with the lagoon at the landward side of the non-tidal prism that is effectively removed by non-tidal processes. Hence there is an optimum in the non-tidal exchange if the volumes exchanged at the seaward and landward side of the non-tidal prism are precisely equal, so that they just do not overlap each other. In that case the exchanged volumes $A(2KT^*)^{\frac{1}{2}}$ each occupy half the non-tidal prism:

$$\tfrac{1}{2}U^*T^* = (2Kt)^{\frac{1}{2}} \qquad (8)$$

or

$$\tfrac{1}{8}\langle U_0^2 \rangle T^* = K. \qquad (9)$$

For a given T^*, (9) gives an optimum value for water-exchange by the non-tidal prism. If the equality (9) is not satisfied, exchange by the non-tidal prism is less effective: either, in the case of small U^*, by the fact that part of the exchange is effected by the tide as it would be in the absence of the non-tidal prism; or, in the case of large U^*, by the fact that for given τ^* there is not enough time to fill half the non-tidal prism with water from the lagoon by turbulent tide-induced diffusion. Hence, whereas the volume exchanged by the tidal prism is proportional to the tidal prism itself, according to (5) and (6) the fraction β of the non-tidal prism, which consists of lagoon water effectively exchanged by the in- and outflow due to non-tidal currents, is a function of the ratio $\langle U_0^2\rangle\tau^*/K$. As β depends on the statistical parameters $\langle U_0^2\rangle$ and τ^* of the non-tidal long wave spectrum, it may be thought that any seasonal effect in the flushing of a lagoon will be produced by a seasonal fluctuation of these parameters. Evidence for such a fluctuation will be discussed in the next section.

SEASONAL FLUCTUATIONS

Fluctuations in sea level

The non-tidal prism discussed in the previous section is connected with non-tidal sea level fluctuations. These are forced by the atmosphere, mainly in a random way. As was shown, it is the variance of the current velocity spectrum at the lagoon inlet (or the variance of the sea level spectrum) and its correlated time scale which are of importance in the process of non-tidal flushing. We summarize here some of the literature on this subject.

Non-tidal sea level fluctuations in coastal areas are reported by Smith (1977, 1978), Wang and Elliott (1978) and Elliott and Wang (1978). The first author reported dominant sea level fluctuations at periods of 4-6 days in Corpus Christi Bay, Texas. That period was also observed to be of importance in the Chesapeake Bay by the latter authors. In both cases it was the fluctuation in the cross shelf component of the wind stress which was thought to be responsible for sea level fluctuations in the bays at the frequency considered. It is well known from meteorological data that in mid-latitudes at a period of 3-5 days, spectra of several variables show a peak associated with the time scale of depressions formed in and advected by the mid-latitude zonal westerly flow. Hence the observed peak in the sea level spectrum at 3-5 days may be a direct consequence of this effect. However, it should be noted that also a completely white atmospheric noise spectrum might induce a peaked sea level fluctuation spectrum at these periods if the adjacent shelf should have a normal mode in that frequency band, as has been reported by Brooks (1978). Wang and Elliott (1978) also found a peak in the sea level spectrum at periods of about 20 days. This peak was thought to be produced by the alongshore component of the wind stress producing an Ekman transport perpendicular to the coast. Without observing such a peak, Smith (1978) also thought Ekman transport to be responsible for the very low frequency part of the sea level spectrum. As to the existence of a peak at 20 days for Chesapeake Bay, it is not clear whether this peak is a direct consequence of atmospheric forcing at that frequency or that another mechanism having a preference for that period plays a role. Finally, it should be noted that the observed large variance of the sea level at sub-tidal frequencies with one or more pronounced peaks probably requires: first a location at mid latitudes, and secondly, the existence of a pronounced continental shelf in front of the coast. The latter is necessary for the curl of the wind stress to produce appreciable set up or set down along the coast. The former provides large variance in the wind stress with a dominance of fluctuations having a time scale of the order of 3-5 days. If a shelf is almost absent, as near islands in the open ocean, the response of sea level to variable weather is merely of the inverted barometric effect, with wind stress playing a minor role. The spectra show monotonously increasing variance with decreasing frequency ("red" spectra) without the existence of pronounced peaks, except at the annual frequency (Groves and Hannan, 1968; Wunsch, 1972).

Fluctuations in flushing intensity

Returning now to the question of seasonal variability in the flushing intensity of a coastal lagoon, we may speculate, in view of the literature reviewed above, that such a variability might arise from a seasonal effect in the intensity of non-tidal discharges through the lagoon inlet, assuming its integral time scale to be a constant of the order of 3 to 5 days. As the effectivity of non-tidal flushing has an optimum for fixed τ^*, given by (9), it is not *a priori* clear whether an increasing $\langle U_0^2\rangle$ may increase or decrease the effect of non-tidal flushing. However, a rough estimation shows that in general an increase in $\langle U_0^2\rangle$ increases the flushing effectivity. A reasonable range for K in (9) is 10^2 to 10^3 $m^2 sec^{-1}$. Using τ^* as given above, it may be shown that $\langle U_0^2\rangle^{\frac{1}{2}}$ should have a value between 5 and 20 cm sec^{-1}.

An estimation of $\langle U_0^2\rangle^{\frac{1}{2}}$ from non-tidal sea level variance can be made as follows. If L is the length of the lagoon ($L = 10^3 - 10^5 m$), h, a measure of the mean-square sea level variance ($h \simeq 10^{-1} m$) and H the depth of the lagoon ($H \simeq 10m$), then $\langle U_0^2\rangle^{\frac{1}{2}}\tau^* \approx Lh/H$. Using the above given values, $\langle U_0^2\rangle^{\frac{1}{2}}$ will at most be of the order 10^{-2} m sec^{-1} which is below the estimated optimum value. Hence any increase in $\langle U_0^2\rangle$ will give an increase in the non-tidal flushing effectivity. As $\langle U_0^2\rangle$ must be expected to be large in autumn and winter and small in late spring and summer, the flushing of a coastal lagoon will correspondingly be large in winter and smaller during the summer.

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SEDIMENTARY PROCESSES IN COASTAL LAGOONS

by

Maynard Nichols (1) and George Allen (2)

INTRODUCTION

A coastal lagoon is a distinct dynamic environment where different energy forces act to supply and distribute sediment from land and sea. The interplay of energy and sediment operates in a shallow body of water which is partly enclosed by a barrier and which has restricted or ephemeral communication with the sea through one or more inlets (Phleger, 1960). The presence of an enclosing barrier distinguishes a lagoon from an estuary. Sedimentary processes active in lagoons, like erosion, transportation and deposition create distinctive morphologic and sedimentary features. By recognizing these features, or by observing the processes directly, one can gain an understanding of sedimentary processes. Such an understanding is an essential link in any multidisciplinary effort to solve practical problems in an environment which is threatened by population expansion, accelerated residential and commercial development, engineering works and by pollution.

The purpose of this paper is to review the present understanding of sedimentary processes controlling the influx, transport and deposition of sediment in coastal lagoons. Important questions addressed are: What are the important sediment sources and dynamic factors active in a coastal lagoon? How is the amount and type of lagoonal sedimentation affected by different sedimentary processes? What is the effect of climatic stress? What salient processes common to many lagoons provide a rational means for categorizing lagoon types? The search for an understanding of lagoon processes reveals many unsolved problems. This paper not only provides students and interdisciplinary workers a review of lagoon processes, but also encourages study in an area where much work remains to be done.

HISTORICAL PERSPECTIVE

Knowledge of sedimentary processes in lagoons over the past 80 years has grown along different lines of inquiry. Early interest centered on morphological features that relate to geological evolution of lagoons, adjacent marshes, inlets and barrier islands (e.g., Davis, 1898; Johnson, 1919; Lucke, 1934). The problem of recognizing ancient lagoon and barrier deposits as a guide for petroleum exploration stimulated much inquiry during the 1950's. Sedimentary patterns were delineated from textural, compositional and structural features of modern deposits in the Wadden Sea (Van Stratten, 1954, 1959), in tidal flat lagoons bordering the North Sea, and in lagoons of the USA Gulf coast (Shepard and Moore, 1960; Rusnak, 1960). Some of the patterns and features were related to hydraulic conditions and depositional processes in a general way.

The first notable study directed specifically to sedimentary processes was that of Krumbein (1939) in Barataria Bay of the USA Gulf coast, in which he showed that distributions of particle size were sensitive to hydraulic conditions. Inman and Chamberlain (1955) demonstrated that particle size distributions in Texas Bays, USA Gulf coast, result from different transport processes, mainly bottom wave agitation, and from different amounts and types of sediment supply. The detailed results of Stewart (1958) in San Miguel Lagoon, Mexico, showed how textual and compositional properties are closely linked to environmental processes.

The problem of fine sediment accumulation in the Wadden Sea and the cause of landward transport from the North Sea led Dutch workers (Van Stratten and Kuenen, 1957; Postma, 1954, 1961, 1967) to study the dynamics of sediment transport by direct observation of suspended sediment and water movement. This approach, and related flow measurements and lag effects, has been applied to problems in estuaries, (Nichols, 1974; Allen and Castaing, 1973), a tidal creek (Boon, 1975) and in lagoon inlets (Byrne, 1975; Oertel, 1972). Only a few studies report the effects of wave processes on shoals and flats (Anderson, 1972; Postma, 1957). A pratical need to stabilize inlets resulted in studies by Bruun and Gerritsen (1960) that defined a ratio of tidal prism to longshore drift for maximum stability. O'Brien (1969) found that the flow area of an inlet is a function of tidal prism. Because hydraulic conditions are often complex, hydraulic models have been employed to predict sediment transport effected by engineering works (Simmons, 1966). Increasingly, predictions have been facilitated by numerical models, e.g., Odd and Owen (1972), Leendertse *et al.* (1973) and April and Brett (1975).

After it was learned that organisms exert a profound effect upon sediments in which they live (Sanders, 1958), numerous studies of animal-sediment relationships emerged. Burrowing in sediment results in particle displacement (Schafer, 1962) and in turn, affects mass properties (Rhoads, 1974). Some deposit-feeders fractionate and sort particles of different sizes (Myers, 1977); others deposit sediment as fecal pellets and pseudofeces (Warme, 1967; Haven and Morales-Alamo, 1972) and thus enhance sediment accumulation. A detailed review of the growing volume of literature on effects of animals and plants on sediments is beyond the scope of this paper. The reader is referred to papers by Pryor (1975); Howard and Frey (1975) and Frey and Basan (1978).

An understanding of chemical processes in lagoon sediments stems from studies of evaporite deposition from models (Scruton, 1953) and field observations (Evans and Bush, 1973). Chemical conditions for flocculation of clay minerals were treated by Whitehouse, *et al.* (1960), Einstein and Krone (1961) and Gibbs (1977). Postma (1969) showed the effect of hydrography on the concentration of chemical compounds associated with suspended matter. Diagenetic changes of sediment chemistry are presented by Friedman and Gavish, 1970 and Oppenheimer, 1960.

During the past decade, a concern with effects of pollution, dredging and filling, and the need for coastal zone management, has provided an impetus for process oriented studies like the case histories by Orme (1975), Harbridge, *et al.* (1976) and Nichols and Towle (1977).

Commonly, lagoons have been studied individually and by different methods, or for the special features they may hold. Few workers have studied more than a single lagoon (Emery and Uchupi, 1972). Consequently, the present state of knowledge consists of a random distribution of data. There are few general reviews of lagoonal sedimentary processes but summaries of sediment characteristics are presented by Emery and Stevenson (1957) and Folger (1972). Many useful sediment papers are found in symposia volumes by Trask (1955), Lauff (1967), Castañares and Phleger (1969), Nelson (1972), Institut de Géologie du Bassin d'Aquitaine (1974), Cronin (1975) and Wiley (1976).

LAGOON-FORMING PROCESSES

Lagoons form where coastal embayments or depressions become partly enclosed by a barrier separating them from the adjacent sea. A barrier will form on a low lying coast where there is an abundant supply of sediment. This usually consists of sand or gravel supplied by longshore drift, or sand which reaches the coast from a river, glacier or eroding headland. Ocean waves must be active, either alongshore or on a gentle sloping offshore bed, to transport sand alongshore or onshore and build the barrier. In some areas, vegetation, coral reefs or tectonic structures create a barrier (Lankford, 1976).

Lagoons develop best on coasts with a history of submergence associated with the Holocene rise of sea level during the last 22,000 years. Emery (1967) showed that lagoons were common where the continental shelf and coastal plain is wide and flat, especially when level rose at a relatively slow pace (Fig. 1).

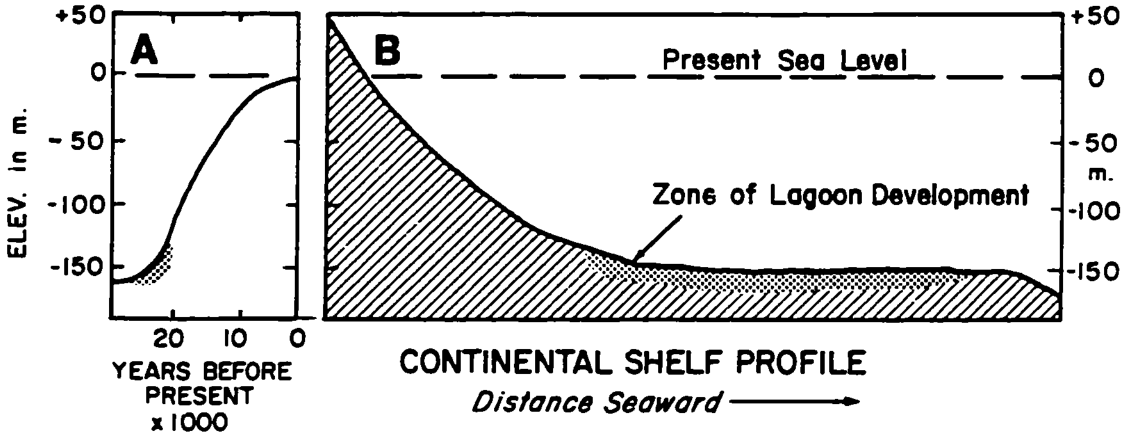

Fig. 1 Relationship of lagoon development to (A) post-glacial rise of sea level and to (B) profile of the continental shelf, dotted zones. Modified after Emery (1967; AAAS Pub. No. 83, p. 11, copyright 1967 by the American Association for Advancement of Science.

Protective barriers can originate in different ways. First, lagoons that form in a submerged coastal depression at a river mouth are enclosed by growth of spits across open water. The barrier spit is often supplied with sediment from local eroding headlands (Gilbert, 1885) (Fig. 2 A) or regional longshore drift. However, where deltaic sedimentation is active, lagoons may form in marginal depressions or in troughs behind cuspate barriers built by reworked deltaic sediment (Fig. 2 B). Second, many lagoons form by submergence and flooding of coastal lowlands behind a former dune ridge or beach (Zeigler, 1959; Hoyt, 1967) (Fig. 3). With a slow rise of sea level, e.g., in the last 5,000 years (Fig. 3-2), the dune ridge becomes a barrier ridge. Inlets occupy low parts and allow passage of river water or tidal currents. Another theory of barrier formation concerns the build up of an offshore bar to form a lagoon barrier (Lankford, 1976). However, this process is controversial and does not appear to be presently widespread. According to Hoyt (1967), depth of the lagoon depends on the amount of submergence and the original altitude of the area (Fig. 4). Width of the lagoon depends not only on the amount of submergence but on the slope of the original land suface. Once formed, a lagoon barrier system may be reworked many times with sediment from the nearshore bed during its landward retreat.

When sediment supply from longshore or offshore exceeds the transport capacity of tidal or fluvial currents to maintain inlet channels between barriers, a lagoon is sealed off from the sea. Such closed or impounded lagoons, often called ponds or "blind estrueries" (Day, 1951), are periodically connected to the sea

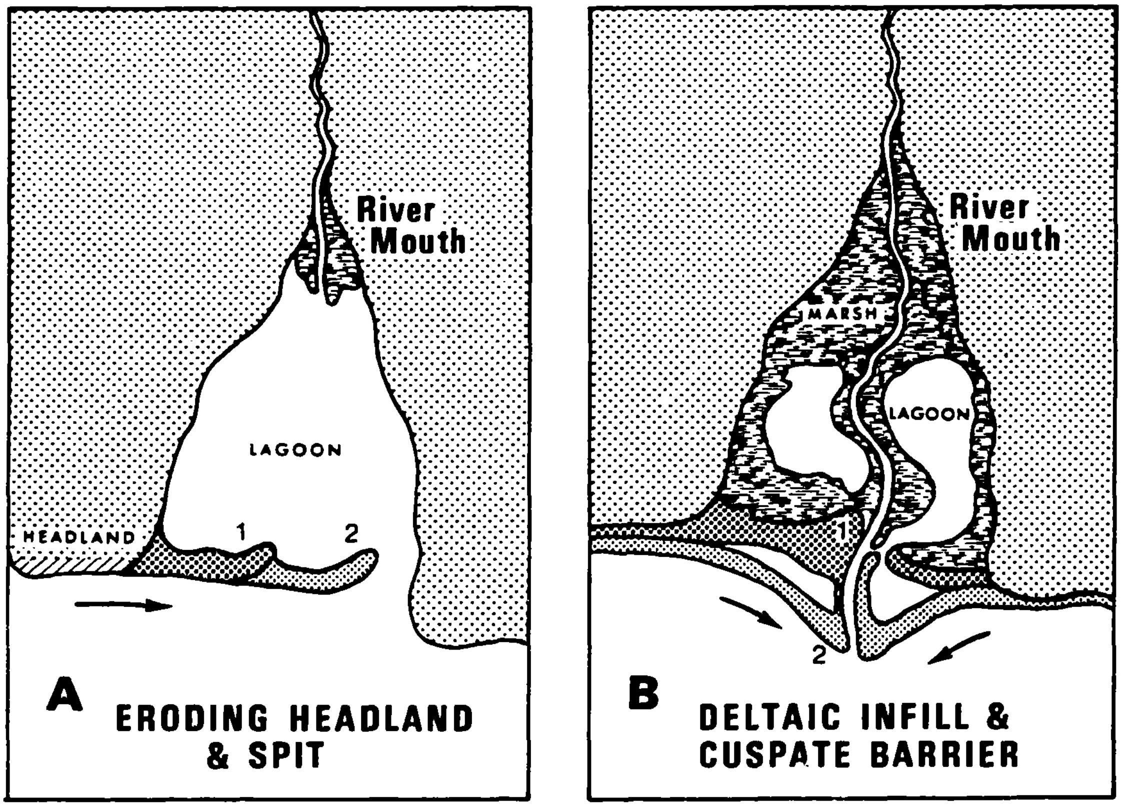

Fig. 2 Types of lagoon formation associated with river mouths: (A) eroding headland and prolongation of a spit; (B) deltaic infill with marshes, marginal depressions containing lagoons and cuspate barriers with lagoonal troughs.

when storm waves breach the barrier. Where barrier sediments are porous, a "closed" lagoon may experience subsurface exchange with the sea.

A lagoon may evolve from partial isolation behind a barrier or spit toward complete closure and thence into a marsh or swamp. Eventually, a lagoon is filled by sedimentation and replaced by a coastal plain with rivers and streams passing seaward through the former tidal entrance. Alternately, if the barrier is eroded, a lagoon may evolve from partial isolation behind the barrier to an open coastal bay. Such changes depend on the rate of coastal submergence, the rate of sediment infilling and supply of sediment to the barrier. Dominant physical processes are discussed in a subsequent section. These factors, in addition to long-term changes of sea level, encroachment of marshes and storms, produce a variety of lagoon configurations with complex histories, e.g., those reported by Lankford (1976) along coasts of Mexico. The geologic

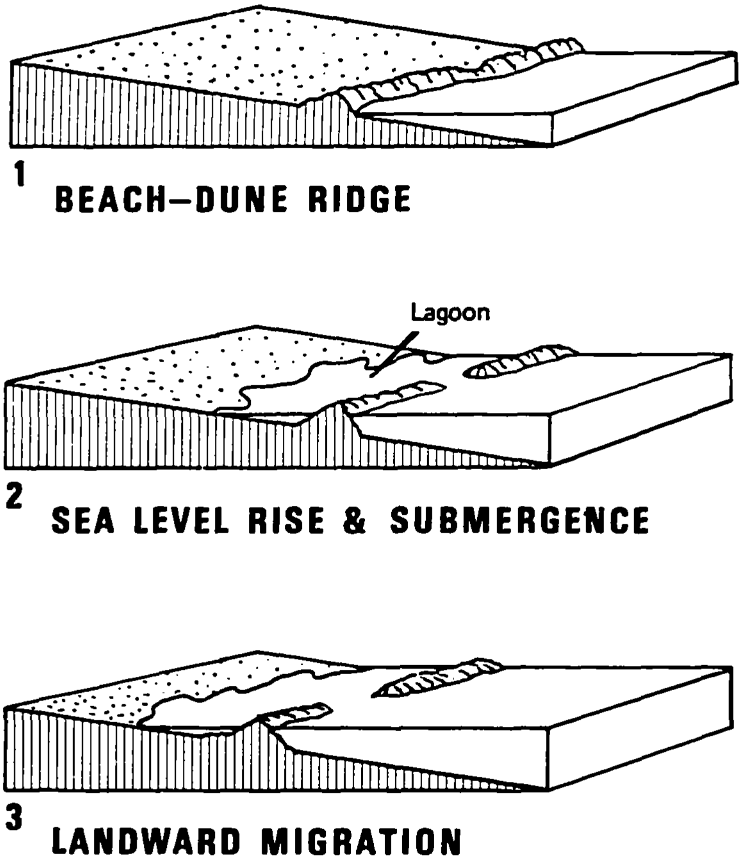

Fig. 3 Stages in the formation of a lagoon-barrier system by flooding of coastal lowlands behind a beach or dune ridge. Modified from Godfrey (1976) and Hoyt (1967).

origin provides a valuable vantage point for describing modern processes and for recognizing different types of lagoons around world coasts.

SOURCES OF LAGOON SEDIMENT

Lagoon sediment is supplied from many sources. In some lagoons the sediment is derived locally from the shores, the barrier, or from production within the lagoon. However, in other lagoons the sediment may have come from great distances either from the sea or the land. On the other hand, sediment may "escape" a lagoon by flushing into the sea, by wind erosion of flats, or by oxidation of organic matter. The proportions of sediment supplied from different sources varies greatly from season to season and from place to place.

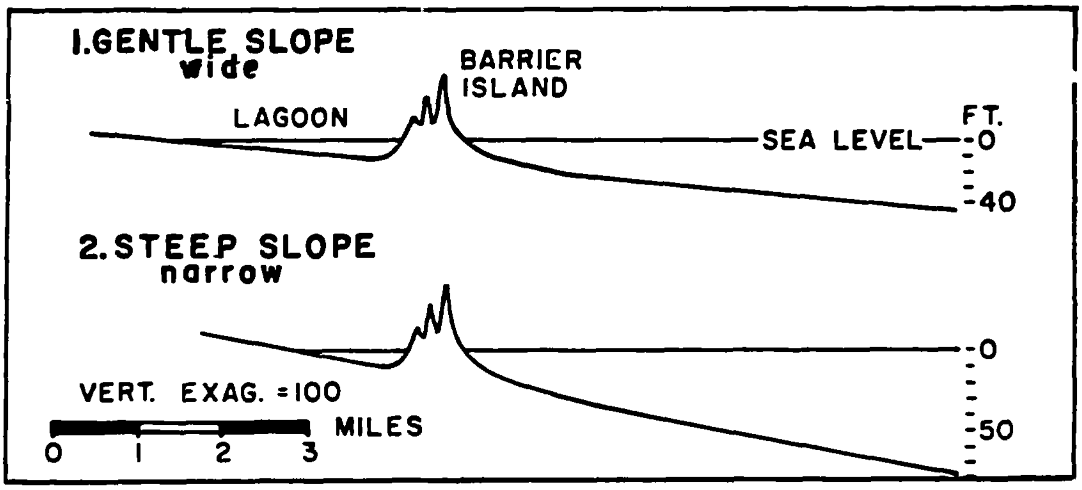

Fig. 4 Relationship of depth and width of a lagoon formed by submergence behind a beech or dune ridge; from Hoyt (1967).

Erosion of a watershed can provide a large amount of fluvial sediment which to a lagoon. Input is relatively high where chemical weathering is active, where precipitation is high and exceeds evaporation and where watersheds have a high gradient for runoff. These factors, added to sediment characteristics, determine the magnitude of erosion. This can be determined by an erosion index of Wishmeir and Smith (1958). In turn, the erosion rates correlate with suspended sediment loads of streams or rivers draining into bays, estuaries or lagoons (Biggs, 1978). During transport by streams, sediments are often fractionated according to particle size or composition. On low terrain only relatively fine-grained sediment or low density material as mica or organic matter is carried into a lagoon, except during floods. Strength of the terrestrial source is controlled by the sediment yield and the magnitude of river inflow.

Erosion of lagoon shores is often a major source of sediment which provides sediment directly to a lagoon. Erodable materials may include glacial drift, organic debris from marshes, or sand from old coastal plain formations. Inputs are commonly estimated by tracing shoreline changes from charts and determining the volume of sediment lost. The lagoon barrier is an important source of sediment for most lagoons. By washovers (Godfrey, 1976) and wind transport (Phleger, 1965) much sediment, mainly sand, is introduced and trapped within a lagoon.

The sea can supply fine-grained sediment in suspension which is transported through inlets. Concentrations are usually quite low, but tidal transport mechanisms can be effective (Postma, 1967). Coarse-grained sediment may be carried from the nearshore bed or from eroding sea cliffs via longshore currents and residual bottom currents directed through the lagoon inlets. By knowing the composition of heavy minerals or nearshore biogenic components of the sand, it is possible to trace these sources.

Sediment can also come from sources inside the lagoon, i.e. (1) from production of organisms in the form of skeletal matter, either calcium carbonate shells, tests and reef debris, or siliceous diatom frustules, or carbonaceous matter like grass and algae; or (2) from lagoon water by chemical reactions like precipitation of evaporites. When supply of inorganic sediment from rivers, shores or the barrier is low, biologically produced sediment is often the predominant source.

A study by Bartberger (1976) provides an excellent example of the varied proportions of sediment supplied to a lagoon from different sources (Fig. 5).

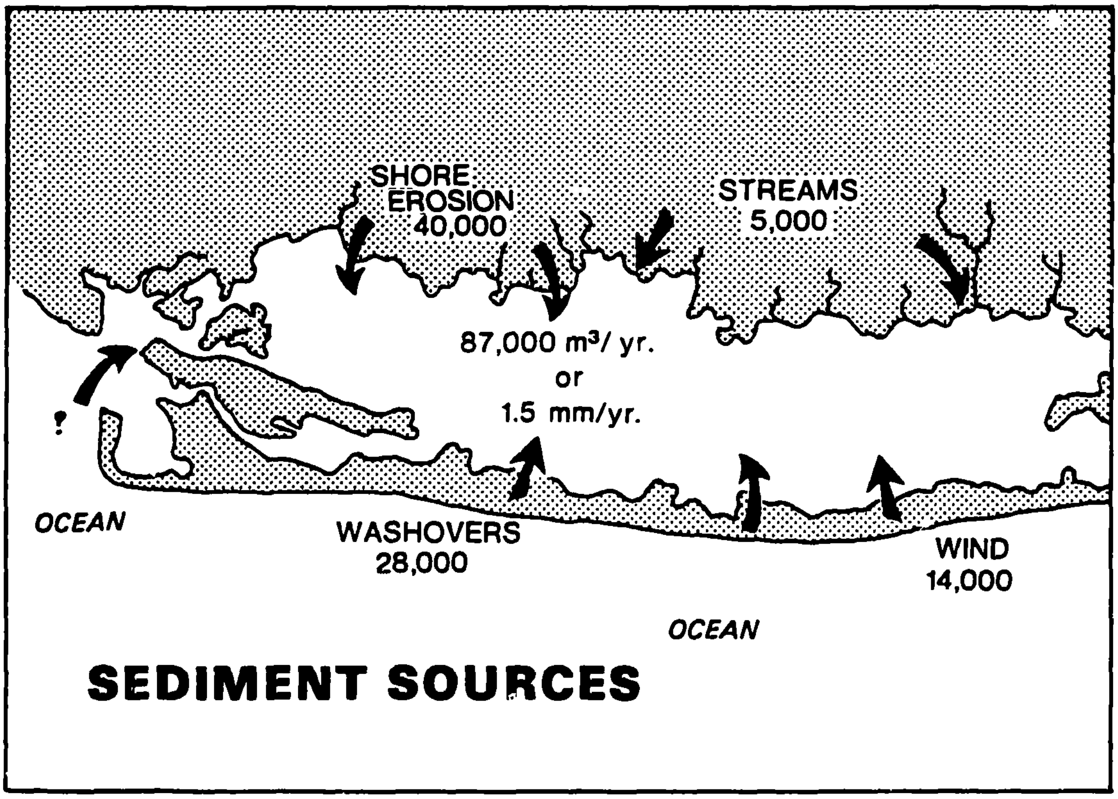

Fig. 5 Supply of sediment to Chincoteague Bay, Virginia, USA from different sources, in cubic meter year^{-1}. Total annual supply is 87,000 m^3 per year over 310 km^2, or average sedimentation rate of 0.3 mm year^{-1}. Data from Bartberger (1976).

SEDIMENTARY PROCESSES

Lagoons are sites where energy input from the land, sea and atmosphere are absorbed. The rate and scale of energy dissipation is especially important in determining the character of the sedimentary processes. In fact, sedimentary processes of lagoons are basically similar in kind the world over. Only their scale and intensity differ.

Sediment characteristics are directly related to the processes controlling erosion, transport and deposition. These processes can be physical, chemical or biological; they can act singly or together. Of the physical processes, i.e., those powered directly or indirectly by solar and gravity energy, the most important are those which produce water movement and turbulence. Tides, waves, wind and river inflow are the essential energy forces that move water and sediment. As energy is dissipated through a lagoon, sediment is transported and morphology is changed.

Biological activity acts mainly to produce sediment or modify its textural or chemical state. Organisms have a capacity to remove enormous amounts of sediment from suspension by ingestion and excretion. Through such processes organisms play a key role in promoting sedimentation.

In lagoons where physical energy is low and sporadic, transport is limited and sediment characteristics are strongly biological or chemical. In quiescent lagoons, where precipitation exceeds evaporation, mud deposition dominates in the lagoon basin and deposits consist of thick bedded sequences of silts and clays. By contrast, in lagoons with a high energy state, transport is active, morphological changes are rapid and sand dominates the bottom sediments. To understand the response of lagoon sediments to different types of processes, the contribution of different energy inputs and their controlling function must be examined.

River Inflow

Freshwater inflow acts both as a source of sediment and a sediment dispersion mechanism. Where the flow of water from rivers and streams is high and dominates over tidal action, suspended sediment loads are high and the river water is mixed with sea water creating a marked salinity gradient. The difference in salinity between river water and sea water, about 35 parts per thousand, is sufficient to generate a two-layered estuarine density circulation (Dyer, 1977). Such a circulation exhibits nodes of converging bottom flows at the inner limit of salty water. When suspended sediment is brought into the convergence from either the river or the sea, it is trapped. Suspended sediment concentrations become higher than those either in the source river or lagoon water. Such a feature, called a turbidity maximum, is characteristic of many world estuaries. Unfortunately, very little is known at present about these maxima, or about density circulation, in lagoons. However, the high inflow and strong salinity gradients reported in some lagoons like Abidjan, West Africa, and the current measurements in Ebrie Lagoon, Ivory Coast (Gallardo, 1978), render this mechanism most probable, expecially in deep lagoons.

Where rivers debouch into lagoons, deltaic deposits accumulate locally near river entrances. When a stream discharges into a lagoon, momentum is dissipated by spreading and mixing with ambient lagoon water. Consequently, the effluent decelerates, looses its transporting ability and deposition ensues. The bed load of sand-size sediment is dropped immediately at the river mouth, forming a delta front shoal. Whereas fine-grained sediment in suspension, which constitutes most of the river-borne load, is carried farther into the lagoon and deposited over a broad area of the basin. In lagoons with sustained river inflow, sediment concentrations and grain size commonly decrease with distance away from the river mouth. The most rapid sedimentation in a lagoon may be found on or near the delta, as documented by Kanes (1970)

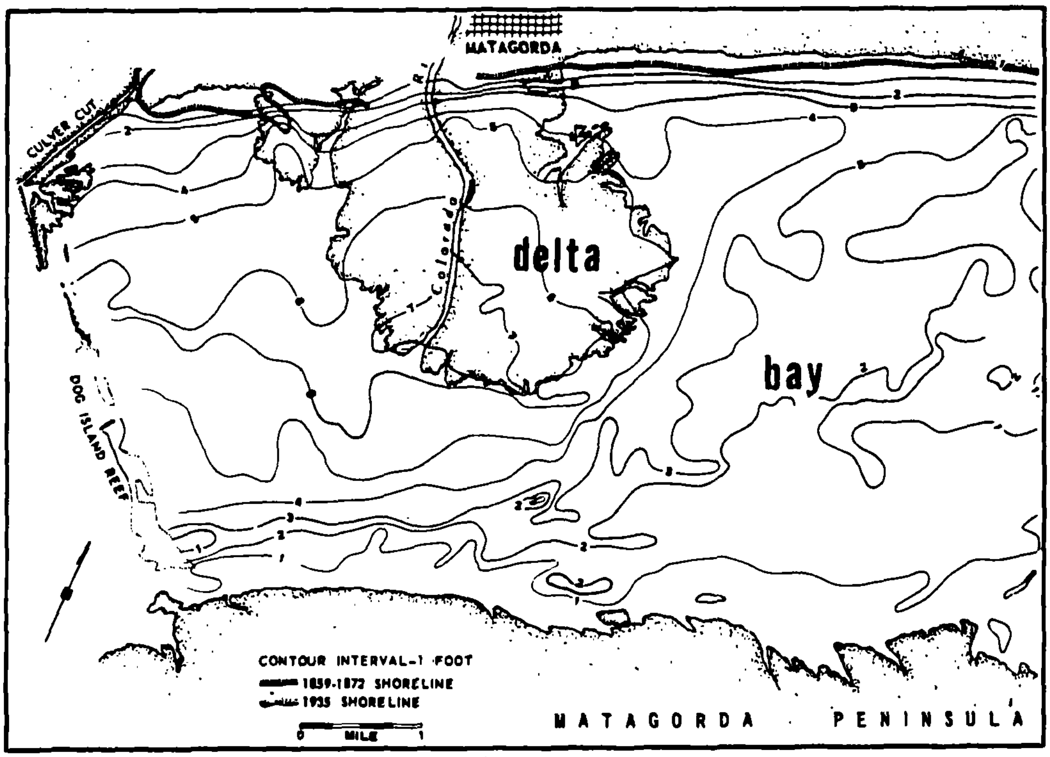

Fig. 6 Colorado River delta in Matagorda Bay, Texas, USA showing shoreline changes between 1859-1872 and 1935 and the thickness of sediment fill between 1891 and 1935. Based on water depth changes; from Kanes (1970).

in Matagorda Bay, Texas (Fig. 6). Long-continued deposition at the river mouth results not only in up-building of the deltaic surface but mainly in out-building of the delta into the lagoon. This process can rapidly extinguish a lagoon. River-borne sediment is then discharged directly into the sea. Infilling proceeds rapidly in lagoons of low latitude tropical coasts (e.g., the Gulf of Guinea coast).

Seasonal variations of river inflow can profoundly modify the rate of sediment influx, the lagoon hydrology and its exchange with the ocean. In mid-latitude humid and temperate areas, spring rains erode uplands and cause river flooding which delivers high sediment loads to lagoons. More sediment can be supplied in a few days of flood than in many months of average inflow. During floods, sediment can be moved outward and deposited seaward of the barrier. If high runoff is sustained, the fresh water will tend to form a dynamic barrier to the invasion of sea water (Phleger, 1960). Separation of lagoon and ocean water masses is pronounced when the dynamic barrier lies close to the geographic barrier. In a closed or restricted lagoon, sustained river inflow may raise water levels high enough to breach the barrier and open a channel for short periods. Because of the lack of continuous flushing action to keep channels free of sediment, they tend to close.

When river inflow is low, tidal movement becomes strong relative to inflow if other factors are equal. As ocean water invades the lagoon, salinity of landward reaches tends to increase and exchange between the lagoon and ocean also increases. Proportionately more suspended sediment may be carried inward by tidal transport mechanisms (Postma, 1967). In long dry seasons between floods, inner lagoon water may become hypersaline due to excess evaporation over precipitation. Therefore, the seasonality of sediment influx into lagoons is not only a function of variable runoff but depends on the seasonal balance between marine and fluvial exchange.

In lagoons where there is no freshwater runoff and the climate is arid, lagoon water becomes hypersaline. Salinities may attain 45 to 80 parts per thousand in landward zones such as Lasguna Madre, Texas (Pusnak, 1960) and Laguna Ojo de Liebre, Mexico (Phleger, 1965). In such cases lagoon sedimentation is dominated by evaporite deposition.

When clay sediment is transported in suspension from fresh water into brackish lagoon water, it may become cohesive and flocculate. This process, studied by Einstein and Krone (1961) and Migniot (1968), promotes deposition by increasing the settling velocity of suspended clay particles. Floccules settle faster than dispersed clay particles because the particle size is increased, despite the lower density of flocs. Growth of flocs is promoted by conditions that bring particles together and make colliding particles stick. Small particles are brought together by an imbalance of ionic charges between particles. While in fresh water the charges act to keep particles dispersed, in the presence of salts above 2 parts per thousand particles of dissimilar charge are attracted. Attractive forces are supplemented by moderate turbulence which promotes numerous collisions. The probability of a particle colliding is a function of the particle concentration. The higher the concentration of sediment, above about 300 ppm, the more rapid flocculation can proceed. An excellent discussion of conditions required for aggregation and how they alter transport properties of sediment is given by Krone (1978). Biological processes may play a very important role in agglomeration of suspended sediment through such processes as organic binding and secretion, and pelletization (Meade, 1972). These processes may amplify lagoon sedimentation but their relative importance to, or action with, salt flocculation remains to be studied.

Although physicochemical flocculation is easily observed in the laboratory, we do not know if this process makes a significant contribution to lagoon sedimentation. Flocculation may be a transient affair that takes place when sediments are in chemical disequilibrium with lagoon water. Dynamic conditions that develop during floods or storms, i.e., sharp fresh-salt water gradients and high sediment loads, favor flocculation. Such conditions occur in polar lagoons of Alaska during spring thaws and in tropical lagoons influenced by high runoff. Einstein and Krone (1961) showed that in San Francisco Bay, California, floccules are derived from wind wave stirring of tidal flats. Field studies are needed to answer critical questions: Is suspended material of lagoons generally aggregated or dispersed? If aggregated what is the state of aggregation and what conditions determine that state? What is the relative importance of salt flocculation and agglomeration by organisms or similar processes, in lagoon sedimentation? Unfortunately, both clay particles and organics are very fragile and reactive; they are easily altered during field collection or laboratory analyses.

Tides

The dynamic character of many lagoons is strongly influenced by the tide. Tides create regular fluctuations of water level, ebb and flood currents, and mixing of lagoon water. Most tidal energy is dissipated in inlets and channels by changing the morphology or by transport of sediment. Because of the wide range of world tides, there is a considerable variation in their effects in lagoons.

Rise and fall of the tide causes a significant change in the area and volume of lagoon water. Where the tide range is high, the area of flats and shoals exposed at low water may be quite large. As a result a large zone of the lagoon floor and marginal zones may alternately experience subaerial exposure, waves and currents. In a macrotidal lagoon (> 4 m range) tidal energy as well as wave energy is intermittently expended on a broad depth zone. By contrast, in a microtidal lagoon, wave energy is concentrated at a more consistent level, a condition that facilitates shore erosion and impedes progradation of marshes and tidal flats.

The principal effect of the tides is to maintain a channel between the lagoon and the sea, thus amplifying lagoon-ocean exchange. The amount of water which flows through the entrance in and out of a lagoon during one flood or ebb period is called the "tidal prism". The tidal prism, which is related to water level fluctuations, is measured by the difference between mean high and mean low tide within the lagoon multiplied by the area. The resulting volume of flow through the entrance is a unique function of the entrance cross-section (O'Brien, 1969), Fig. 7. On coasts of low tide range, runoff and wind-driven tides may have the same effect of maintaining channels as the tidal flow in areas of moderate to high tide range. However, where the total outflow for long periods is low, only narrow, or few entrances can be maintained.

Tidal currents reach greatest speeds in the lagoon entrance. The entrance acts like a nozzle through which the greatest amount of water flows into and out of the lagoon per unit time. Velocity depends on entrance depth and width, channel friction and the hydrostatic pressure created by the difference in water level between the ocean and the lagoon.

Inside a lagoon, both the tide range and the current speed decrease away from the entrance as tidal energy is damped by friction. Damping is reflected by asymmetry of ebb and flood time-velocity curves. When the tide wave travels into a lagoon it is commonly deformed in such a way that the flood wave is shorter than the ebb wave. This effect produces higher current velocities during the flood than during the ebb. Ebb and flood flow move on the average the same amount of water, but the tidal asymmetry has a significant effect on the landward transport of fine sediment. A complete description of the phenomenon, based on observations in the Dutch Wadden Sea, is given by Postma (1961, 1967). Other factors that promote landward transport in a tidal flat lagoon are: (1) the erosion or scour velocity for fine-grained sediment is greater than the critical deposition velocity, i.e., the minimum current velocity needed to pick up the sediment exceeds the minimum velocity necessary to keep it in suspension (Postma, 1967); (2) the landward reduction of average and maximum current speed, a feature that allows fine-grained sediment to settle out on landward shoals at the end of flood; (3) the fact that the average depth of water, which is spread horizontally over a large area at high tide, and confined to channels at low tide, is greater at low tide than at high tide. Thus, more suspended sediment will reach

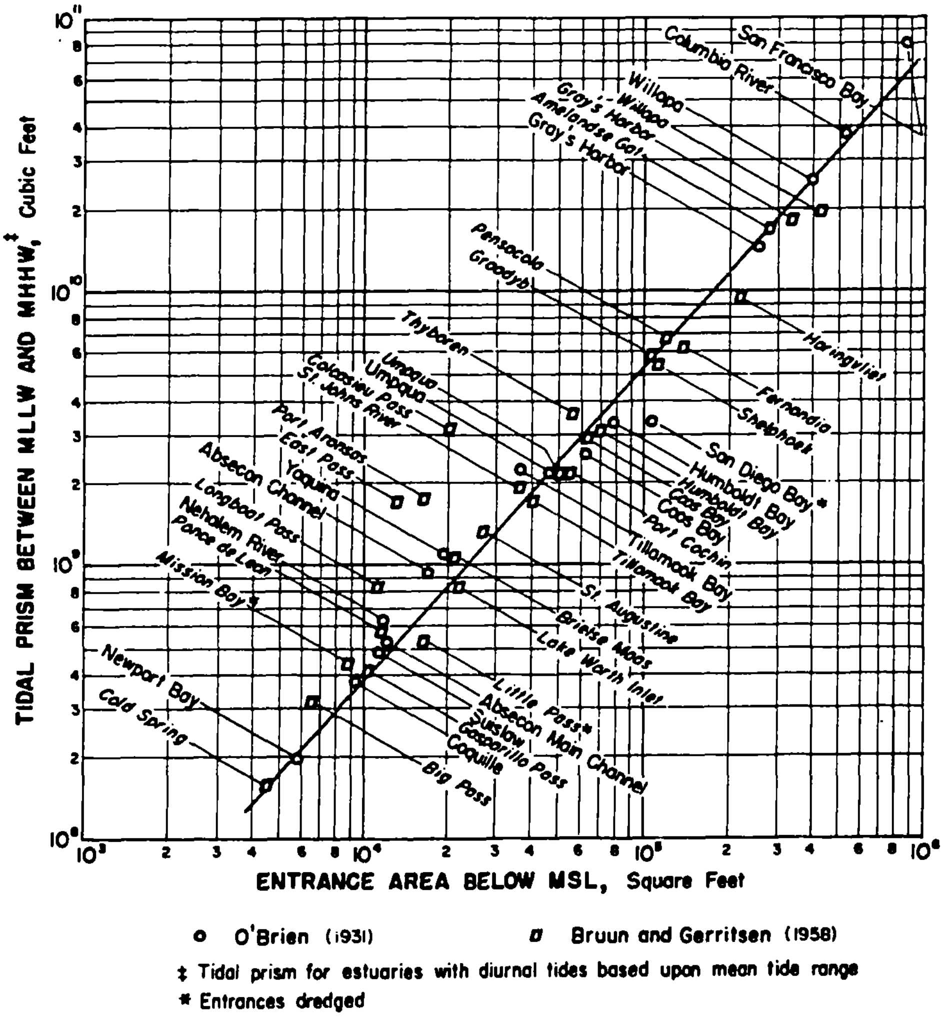

Fig. 7 Relationship between tidal prism and entrance area of different lagoonal bay and harbors. Reproduced from Wiegel (p. 380, 1964) with permission from Prentice-Hall, Inc., publishers.

the bottom at high tide (Postma, 1967). Flood predominance observed by Warme (1971) in Mugu Lagoon, California is produced by (1) onshore waves through the inlet that reinforce flood currents but retard ebb currents; (2) the effect of decreasing bottom friction as the tide rises; i.e., ebb currents are more affected by friction from the bottom and from marsh vegetation as the tide recedes.

Much sediment carried by tidal currents is clay or silt and transported in suspension. A lesser amount, the coarse sandy sediment, is mainly transported as bed load. Ideally, the sediments in transport tend to be graded vertically. The dense and coarse components are carried near the bed by bed load, whereas the fine material is distributed in suspension throughout the water column. Part of the suspended fraction remains in the water column over long periods as a natural "background" at relatively low concentrations, possibly 5 to 25 mg $litre^{-1}$. These sediments consist of fine clay particles, organic detritus, or agglomerates with low settling velocities. They are maintained in suspension by turbulence and vertical diffusion. This fraction follows transport routes of the residual circulation in the lagoon.

Another part of the suspended fraction is intermittently suspended from the bed. Concentrations go up and down with strength of the current. This fraction consists of clay or silt with particle size increasing with increasing velocity (Fig. 8). Net transport of this fraction presumably follows the settling-scour lag model or time-velocity asymmetry (Postma, 1967). A distinction is made (Postma, 1965) between the influence of tidal current velocity, which determines the total amount of sediment brought into suspension, and turbulence which regulates the distribution along the vertical. As in rivers, sediment concentrations carried in a tidal current tend to increase toward the bed, whereas velocity tends to decrease near the bed. Therefore, rates of sediment transport, derived by the product of instantaneous speed and concentration, are greatest just above the channel floor.

Strong tidal currents and marked tide level fluctuations interact with lagoon sediments to produce a distinctive morphology. Shoals and flats of macrotidal lagoons are often incised by intricate networks of channels. Currents in the channels, which can exceed one meter sec^{-1}, create bidirectional bedload transport and a meander action that segregates currents along ebb and flood paths. This reaction results in sigmoidal shaped channel courses. In tropical areas abundant vegetation as mangroves tends to stabilize the shoals and maintain a reticulate channel network (Allen, 1965), (Fig. 9 A). This pattern contrasts to the dendritic forms seen on bare flats of mid-latitude lagoons (Fig. 9 B). Inward transport and accumulation of fine sediment can cause rapid sedimentation along the landward end of tidal channels and also build extensive mud flats or shoals. However, the lagoon floor can only build up to a level consistent with the lower depth of wave scouring.

Large, fan-shaped sand deposits often form along seaward and landward extremities of a lagoon entrance. These deposits, called tidal deltas, form as tidal currents loose strength when they escape a confining entrance (Phleger, 1969). The inner or flood delta, is often built during storms when wave action and the water level is high. With subsidence of storm conditions, the flood delta may become emergent. Some flood deltas are built up into

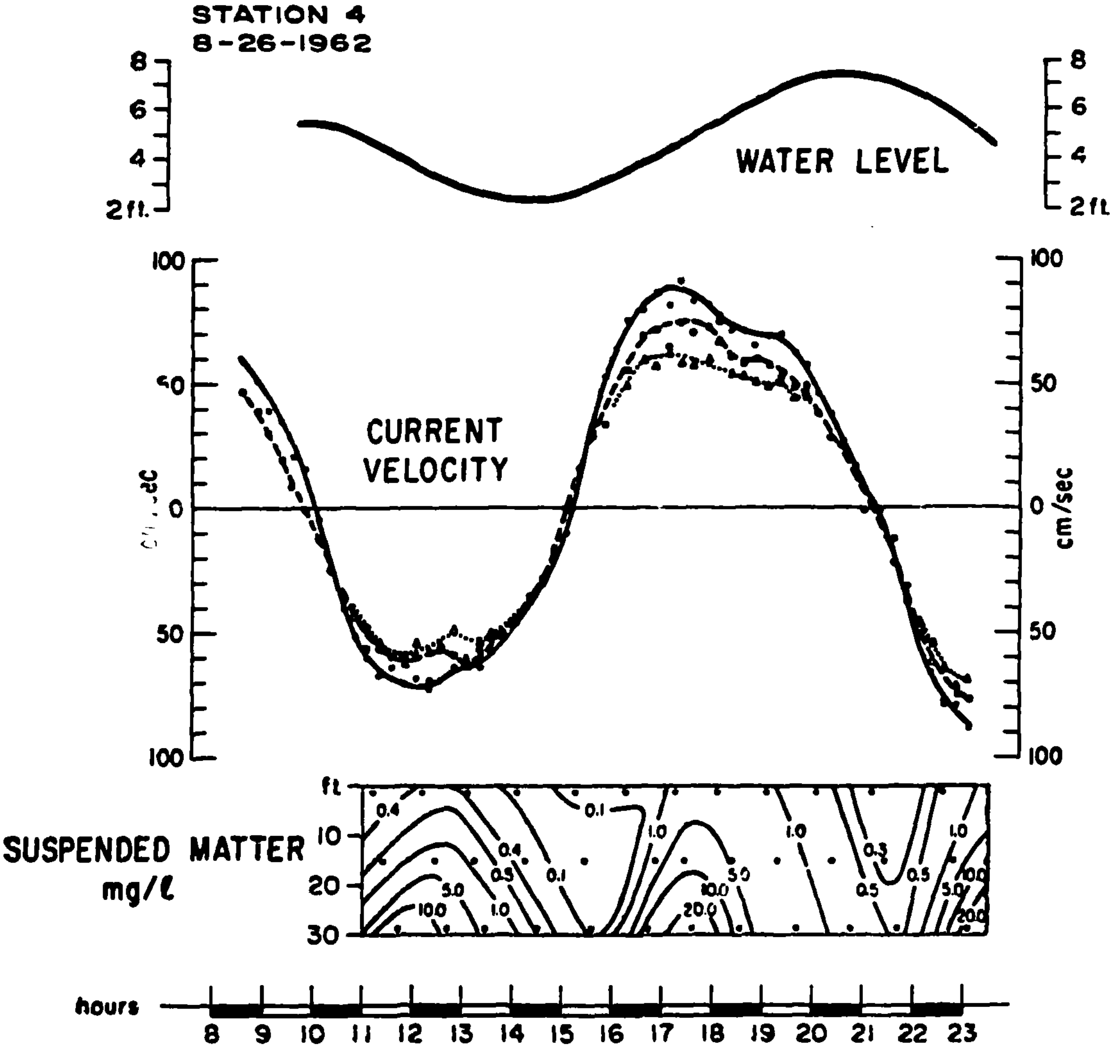

Fig. 8 Measurements of current velocity versus time and concentrations of suspended sediment in Guerrero Negro Lagoon, Mexico. From Postma (1965).

dunes; others are stabilized by vegetation. Flood tidal deltas develop best on coasts of moderate to high tidal range (> 2 m). Ebb tidal deltas, which lie seaward of the inlet in the face of longshore currents and wave action are poorly developed in areas of low tides (Hayes and Kana, 1976).

Lagoons which experience a moderate to high tide range may undergo periodic changes in sediment transport and morphology according to the lunar neap and spring tide cycle. As demonstrated in estuaries (Allen *et al.*, 1976), during decreasing tide

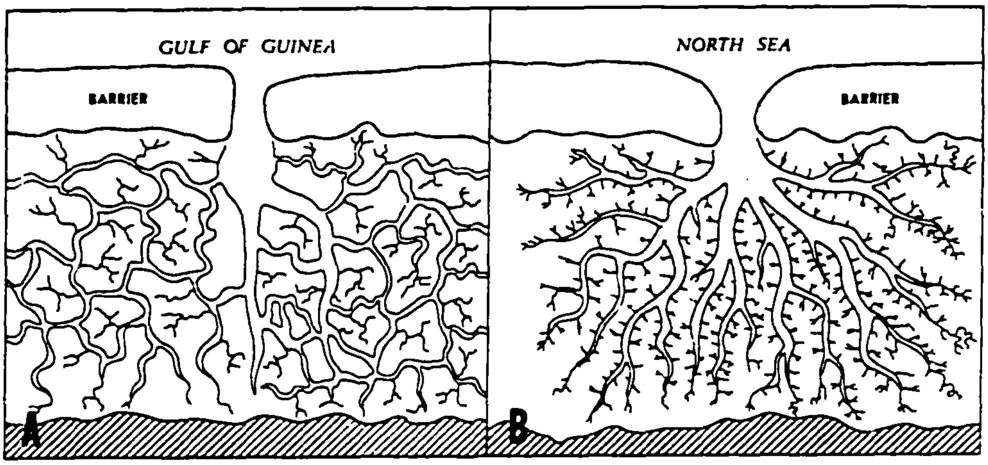

Fig. 9 Channel patterns in lagoonal tidal flats of (A) Niger delta area with reticulate pattern stabilized by mangroves and (B) Dutch Wadden Sea with a dendritic pattern incised in bare flats. Reproduced from Davies (1973) with permission from Longman Group, LTD publishers; based on Allen (1965b).

range, approaching neap range, tidal currents weaken and fine suspended sediment tends to settle toward the bed and deposit. By contrast during increasing tide range, i.e. toward spring range, currents become stronger; the bed is eroded and much sediment is resuspended. Such fortnightly variations also probably modulate mixing and exchange with the sea.

Water level changes affect flooding and drainage of marginal flats and ponds (Warme, 1971). They may set up a cycle of "storage" and release of water from the lagoon and in turn, regulate exchange of fine sediment with the sea. Both these tidal effects are poorly known and deserve attention. Unlike fluctuations of waves and river inflow, tidal processes are regular and predictable.

Waves

Waves play an essential role in lagoon processes. They sort and transport sediments and build shoreline features like spits, beaches and barriers. The intensity of wave action depends not only on the wind duration and velocity, but on the length of fetch and resulting degree of exposure. Therefore, the dimensions of a lagoon and its orientation to the wind direction are important factors for wave intensity. Waves affect three elements of a lagoon system: (1) the lagoon barrier, (2) lagoon margins, and (3) the lagoon floor.

The main effect of ocean waves on the barrier shore is to generate a longshore current which transports sediment alongshore. As waves move shoreward at an angle in shallow water, they provide a vector of wave energy parallel to the shore and in turn, generate a longshore current. On coasts with high wave energy, where great quantities of sediment are in suspension, longshore currents can move several hundred thousand cubic meters annually. Since ocean waves are damped by friction inside lagoon entrances, longshore transport is mainly active on the seaward side of barriers. However, at lagoon entrances where wave action is weak (Bird, 1964), there is a virtual contest between tidal transport through the entrance and longshore transport of sand which tends to seal them off.

Lagoon shores are affected most by waves where they are exposed to the greatest fetch. Long narrow lagoons parallel to the significant wind direction have the strongest wave action along the maximum fetch. Waves create beaches and beach ridges; they erode embayments or promontories and build spits, cusps and cuspate spits. As the spits grow lagoonward, they break up a smooth shore into bays. Eventually they segment the lagoon into separate subcircular basins (Bird, 1964). In turn, the wave regime in the lagoon may change. Segmentation may evolve in stages, (Fig. 10), following trends in lagoons of the Chukchi peninsula (Zenkovitch, 1959). By segmentation, a lagoon adjusts its form to patterns of waves and wind-generated circulation cells. In a study of lagoons on the Texas coast, USA Price (1947) showed that segmentation was part of a dynamic equilibrium between forces shaping the basin according to the fetch, and the depth of effective wave scour. By fill and scour or segmentation, lagoons can maintain a characteristic ratio of average width to maximum depth.

Besides growth of cuspate spits, lagoons can be segmented or reduced in area by encroachment of reed swamps (Bird, 1964) and by growth of deltas. In lagoons with multiple inlets, tidal currents enter simultaneously through lagoon channels, meet in inner parts and cancel each other (Phleger and Ewing, 1962). As sediment accumulates in the current null zone, the lagoon eventually divides.

Although waves are damped inside lagoons, water depths are so shoal that waves resuspend much fine sediment from the bed. Anderson (1972) observed suspended sediments which followed variations of wave intensity. Once stirred up, fine sediment is redistributed in the net current. It tends to settle out in low energy embayments of a lagoon or in basins below wave base. As a result of the winnowing process, coarse sediment, sand, shell or, gravel often reside on shoals within the lagoon.

Wave processes are greatly accelerated during short periods of extreme storm or hurricanes. Studies of storm deposits on the

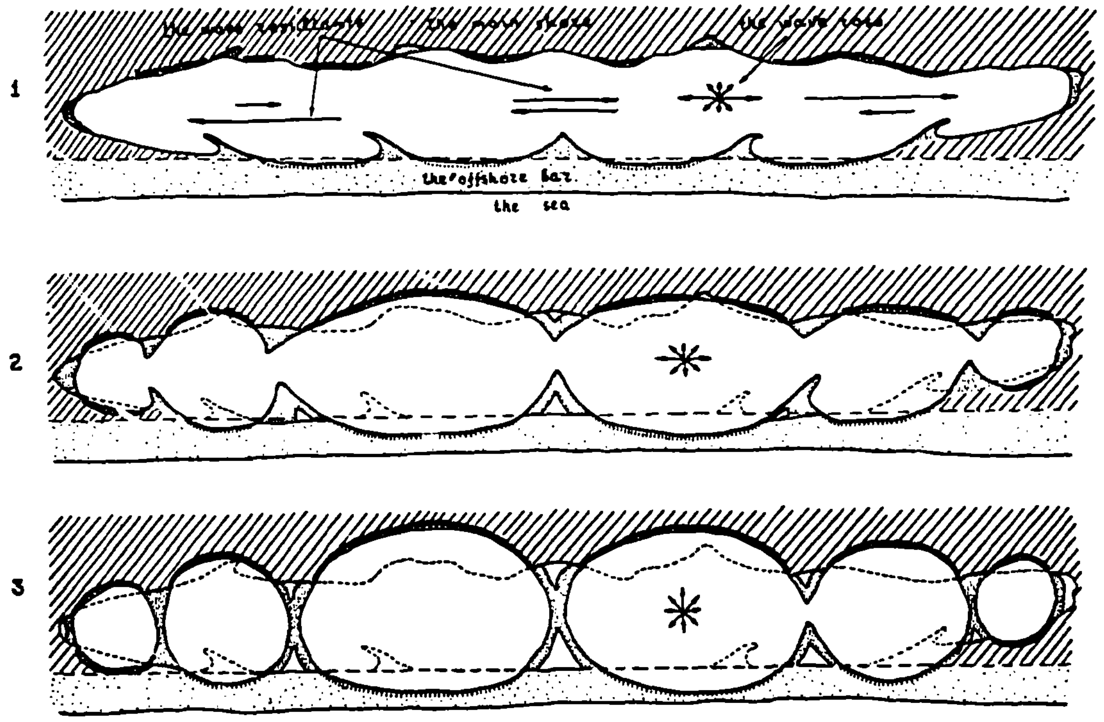

Fig. 10 Schematic diagram of the evolution of a lagoon shoreline leading to segmentation into subcircular bays. Reproduced with permission from Zenkovitch (1959), copyright 1959 by the University of Chicago Press.

Texas coast (Hayes, 1967) indicate more sediment is eroded, transported and deposited during a few days of hurricane activity than during many months or years of normal activity. Water piled against the coast by wind tides, superimposed on barometric tides and resulting storm surge, may raise lagoon water levels 3 to 6 meters above normal levels (Fisher, et al., 1972). Storm tides are generally higher in narrow funnel-shaped lagoons of river mouths then in coast parallel lagoons.

On a barrier island, storm waves drive shelf sand onto the shoreface or beach while high storm waters erode dunes and breach low parts of the barrier island (Fig. 11 A). Storm-generated currents can erode channels through the barrier and transport a large volume of shelf and barrier sand into the lagoon. This sediment is deposited as a washover fan radiating from the barrier breaches.

As the hurricane passes and the winds change from onshore to offshore, storm water piled in the lagoon, in addition to local runoff or river flood water of the passing storm, is suddenly flushed through lagoon entrances or fomer barrier breaches (Fig. 11 B). Such a mechanism can cause a significant transport of lagoon sediment onto the shelf. The occurence of graded sand and mud layers on the inner Texas shelf after Hurricane Carla (Fig. 12) implies sediment was deposited from seaward flowing density currents (Hayes and Kana, 1977). Nonetheless, bulk of the storm deposition seems to be in the washover fans. By washover processes a lagoon serves as a trap for coarse sediment.

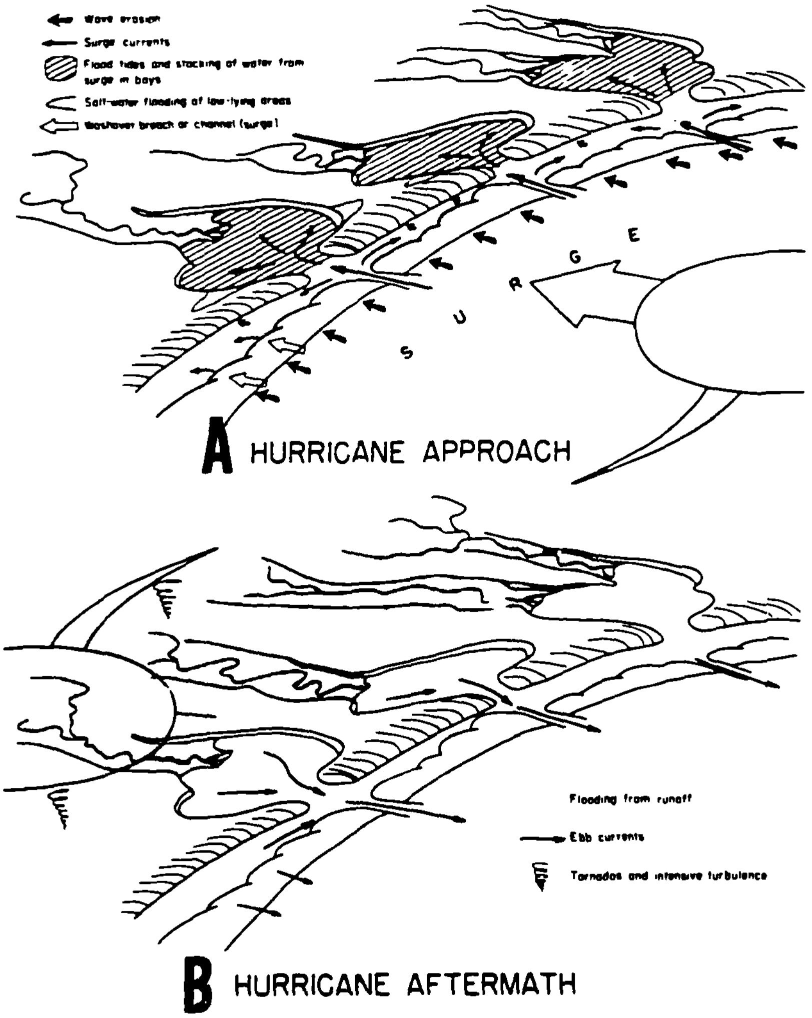

Fig. 11 Schematic diagram of hurricane transport routes in the Texas Beys, USA during (A) approaching hurricane with breaching of barrier and formation of washovers; (B) aftermath of hurricane with flushing lagoons. From Fisher. *et al*. (1972).

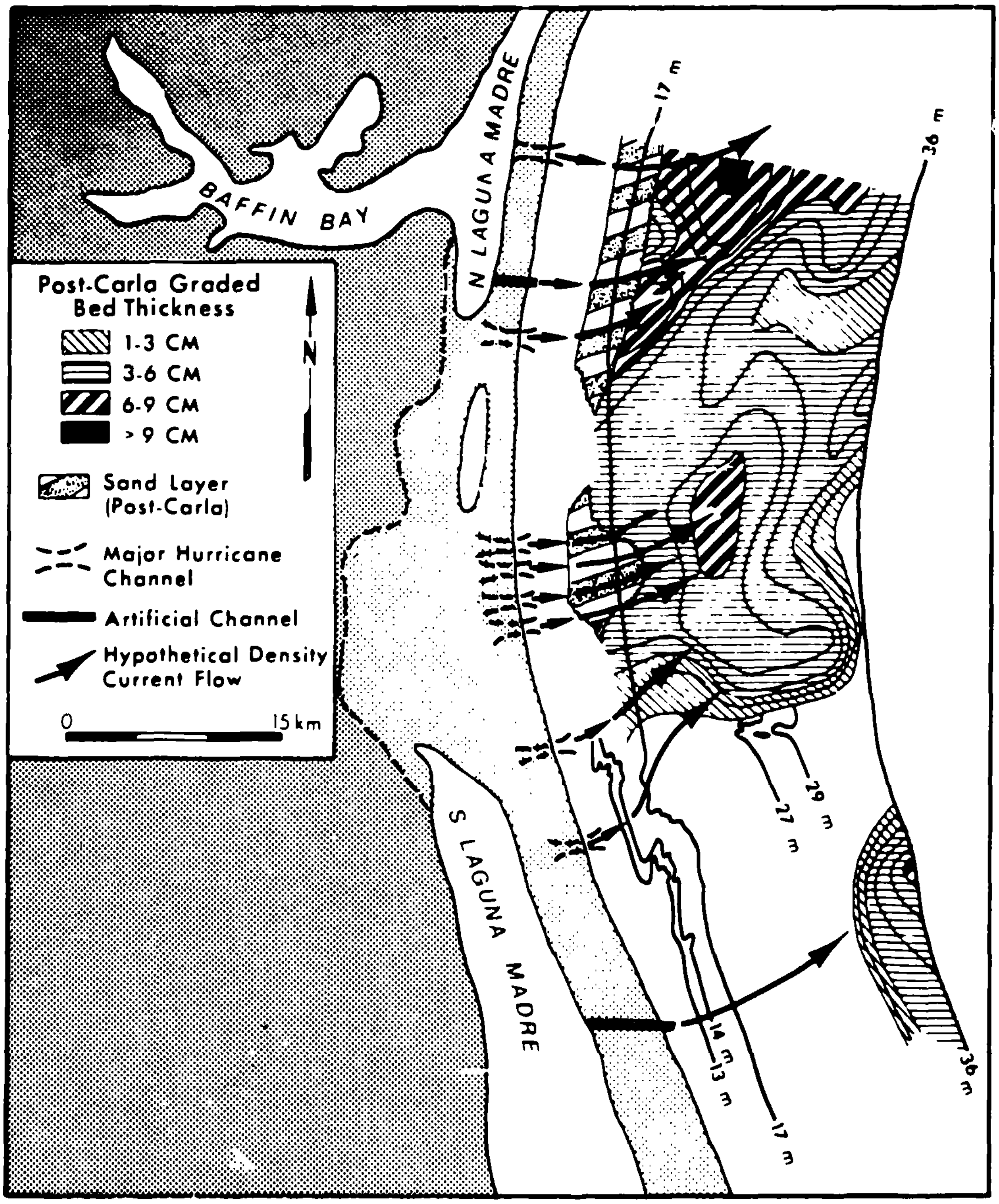

Fig. 12 Thickness of sand and mud layers deposited off Padre Island, Texas, USA after Hurricane Carla, 1961. Arrows represent supposed transport routes. From Hayes and Kana (1976).

Washover deposits are common on microtidal coasts where tidal inlets are few. A continuous barrier reduces or eliminates intrusion of storm water through inlets, and thus increases high water levels conducive to overtopping the barrier. On a geologic time scale washover deposits are associated with barrier island retreat. They have the effect of maintaining shallow water on seaward margins of the lagoon even as sea level keeps rising. In the absence of submergence, they contribute to segmenting and filling a lagoon.

Wind

Wind acts on sediment either directly as a transport agent, or indirectly by creating water level changes and waves or drift currents that transport sediment. The most obvious effects of the wind are sand dunes created on lagoon barriers. These range to 30 m high but some reach 100 m, e.g., along the Aquitaine coast, France; the Patos Lagoon barrier, Brazil; and the Zululand Coast, South Africa (Crme, 1973). Most barrier dunes are formed by the landward transport of beach sediments. In Guerrero Negro Lagoon, Mexico, an arid coastal lagoon, dunes migrate into the lagoon with a sand discharge rate of about 400,000 m $year^{-1}$ (Phleger, 1969). Around some arid coastal lagoons, like Estero Tastiota, Mexico (Nichols, 1960) and Laguna Madre (Fisk, 1959), wind deflates high tidal flats that are exposed for long periods. As clay and algal crusts dry, exposed granules of clay are easily removed by the wind. These are blown to the inner flats where they accumulate as mounds, or to the mainland margin where they form clay dunes 2 to 6 m high. The dunes develop slopes similar to sand dunes but they do not migrate.

Strong wind stress often causes a significant water level change called a "wind tide" (Paris, 1978). Such a change lowers the water level along lee shores and raises the level on windward shores. In Laguna Madre, Texas, USA, water is driven across high tidal flats and marshes penetrating mainland margins and islands as a thin sheet about 30 to 60 cm deep. When the wind shifts direction, a back and forth motion, or seiche, may develop in the lagoon (Rusnak, 1960). When the wind subsides or reverses direction water drains back into the lagoon leaving a portion ponded in troughs and basins. These ponds are local sites for growth of algae and precipitation of evaporite crusts.

Biological Processes

In lagoons where ecological conditions support abundant benthic fauna, biological processes determine the character of lagoon sedimentation. They modify its physical and chemical characteristics and they even produce sediment. Although organisms normally do not directly transport sediment, their effect on local water turbulence, as well as in trapping, binding and precipitating sediment, are such that they play a key, but highly varied role, in sedimentation.

Organisms create sediment by producing organic and skeletal material. Much of this, including shells, tests and frustules, is incorporated into lagoon sediments. In Florida Bay, virtually all the lime mud sediment is skeletal detritus from algae and organisms (Stockman, et al., 1967).

One of the most prominent results of biologic activity is formation of oyster reefs. In some USA Gulf Coast lagoons oyster reefs cover about 5% of the floor. They form bathymetric highs and change the local current regime for sediment transport. The reefs themselves are resistant to erosion. In lagoons with a low influx of terrigenous sediment as on arid coasts, biogenic material is the principal source of sediment.

Suspension feeders, like oysters, clams and mussels, filter large volumes of fine sedimentary material from the water and deposit it on the bed as feces or pseudofeces. Experiments with oysters (Haven and Morales-Alamo, 1966) revealed that oysters biodeposition exceeded gravity settling by seven times. At such rates, oysters covering a 0.4 hectare area of lagoon floor could deposit about 7.6 metric tons of fecal material in 11 days. Deposit feeders like worms and gastropods swallow and ingest much bed sediment to obtain food. Most sediment is expelled, but during digestion the particles acquire organic coatings that bind particles together. Detailed studies on volumetric capacity, rates of biodeposition, etc. are reviewed by Carricker (1967) and Darnell (1967). In a study of Cape Cod bays, Johnson (1974) found that nearly all the silt and clay particles were aggregated. Like floccules, the size and settling rate of fecal pellets or organic aggregates is greater than individual particles, thus facilitating deposition. Consequently, the transport of fine sediment in a lagoon, its vertical distribution and its deposition, can only be better understood if one recognizes that much fine sediment is aggregated.

Benthic endofauna commonly mix much sediment by burrowing, churning and grazing. Most activity is in the upper 5 to 10 cm of sediment; however, some organisms burrow to 30 cm or more. This activity disrupts the initial sediment deposits and destroys laminae or layering. It reduces sediment compaction and increases bottom roughness by creating irregularities like mounds and depressions. These effects make the sediment more susceptible to erosion and resuspension during storms or periods of strong tidal currents.

Most lagoons in non-arid climates have luxuriant growths of vegetation. This vegetation can totally modify the shore configuration, water circulation and alter the sediment transport and depositional regime. Numerous subtidal grasses, salt marshes, mangroves and algae play a significant role in either reducing waves and currents or trapping suspended sediment and binding it to the bed. As plants colonize the shore or bed, they tend to stabilize the sediment and build up new land causing lagoons to fill in. These processes have received considerable attention (e.g.,Frey and Basan, 1978; Wayne, 1976; Pestrong, 1972). Less is known about the activities of micro-organisms like bacteria in sedimentary processes. Many biological processes active in the sediments are very slow and inconspicuous and thus easily overlooked.

WORLD DISTRIBUTION

Lagoons and their protective barriers are found worldwide. They border 56% of the North American coastline and 13 %of the total world coastline, ranging from tropical to polar zones (Berryhill

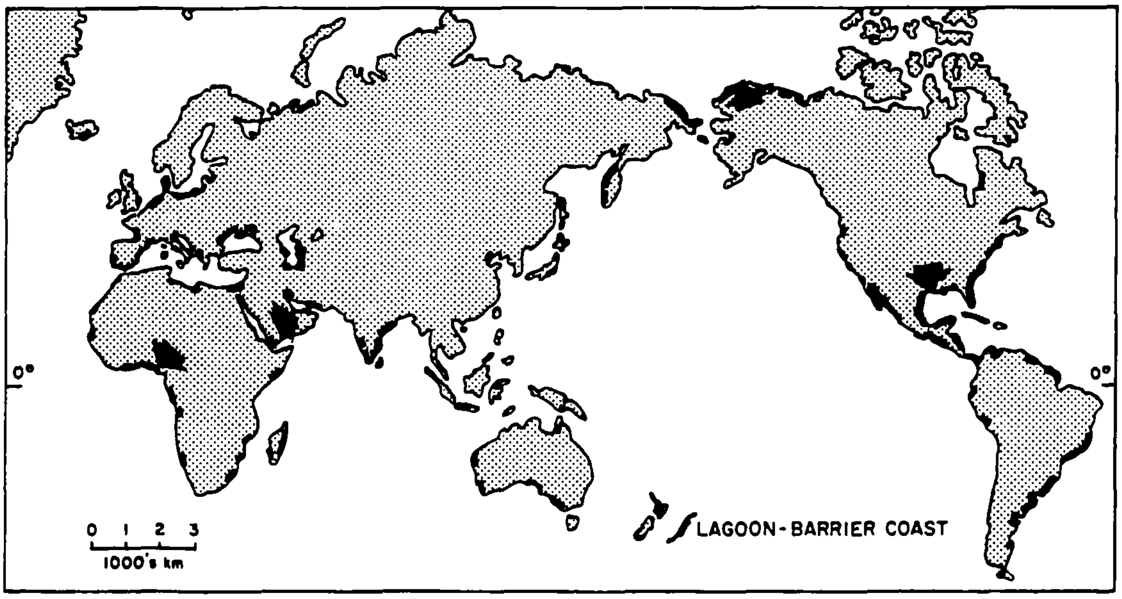

Fig. 13 World map showing distribution of lagoon-barrier coasts. Location of case studies referenced in this paper, arrows. Reproduced from King (1972) with permission from Edward Arnold, LTD publishers, based on data of Gierloff-Emden (1961).

et al., 1969; Gierloff-Emden, 1961), (Fig. 13). Although lagoons are found on some high latitude coasts like northern Alaska and southern Iceland where the tide range is small, they are scarce in areas of coastal emergence created by isostatic glacier rebound such as the Baltic Sea and Hudson Bay. Emergence tends to produce a steep coast; a supply of sediment for barrier construction is scarce. By contrast, on low latitude tropical coasts, high sediment loads supplied by rivers tend to fill in lagoons.

Many lagoons are well-developed on coasts of mid-latitudes, like the Gulf of Mexico, USA and in areas of low to moderate tide range. It is not surprising therefore, that many lagoons face enclosed seas like the Black Sea and Caspian Sea. In such microtidal zones (< 2 m tide range), wave processes dominate in building long, linear barrier islands and narrow tidal entrances. In mesotidal zones (range 2 to 4 m), wave and tidal transport interact. Barriers are shorter and tidal entrances are wider and more abundant than in microtidal zones. In macrotidal zones (> 4 m range) where tidal energy is great, tidal currents tend to breach barrier islands and maintain open mouthed lagoons. The North Sea coast of West Germany and Denmark clearly demonstrates the changing barrier island morphology with variation of tide range (Fig. 14), (Hayes, 1975). As the tide range increases, barrier islands become progressively shorter. In brief, tide range and wave action can determine the extent to which a barrier encloses a lagoon.

Latitudinal Variations

Climatic variations account for differences in the rate of sediment supply to lagoons and the intensity of sedimentary processes. Such differences result from the varying character of energy input and energy dissipation which basically varies with latitudinal changes in solar radiation (Fig. 15 A). In turn, radiation determines the amount of light and primary production in lagoons. It controls temperature, evaporation and precipitation which are the basic determinates of climate. Climate determines the production and type of watershed sediment through weathering and soil formation. In general, intense chemical weathering in low latitudes produces much fine-grained (Fig. 15 C). Most important for lagoons is the magnitude of runoff and its seasonality which depends on the difference between actual precipitation and the potential evapo-transpiration or the amount of moisture required by vegetative cover (Fig. 15 B). In turn, vegetation affects erosion and deposition in lagoon watersheds and around shores. Additionally, wind generated waves and the occurence of storms are keyed to climatic trends. Some specific examples of lagoons from different climatic zones show how latitudinal position can affect source supply and sediment processes.

High-Latitude Lagoons

An example of processes at work in a high-latitude polar lagoon is the one on the north coast of Alaska, described by Faas (1969) and Naidu and Mowatt (1975). Elson lagoon near Point Barrow forms behind a low gravel spit and embraces a basin 2 to 3.5 m deep. Simpson lagoon, near the Colville River delta, forms behind a low barrier island and partly encloses a lagoon 1 to 3 m deep. Both lagoons have tidal communication with the sea through wide inlets. Marginal tidal flats and salt marshes are absent owing to the low tide range and prolonged ice cover (Fig. 16).

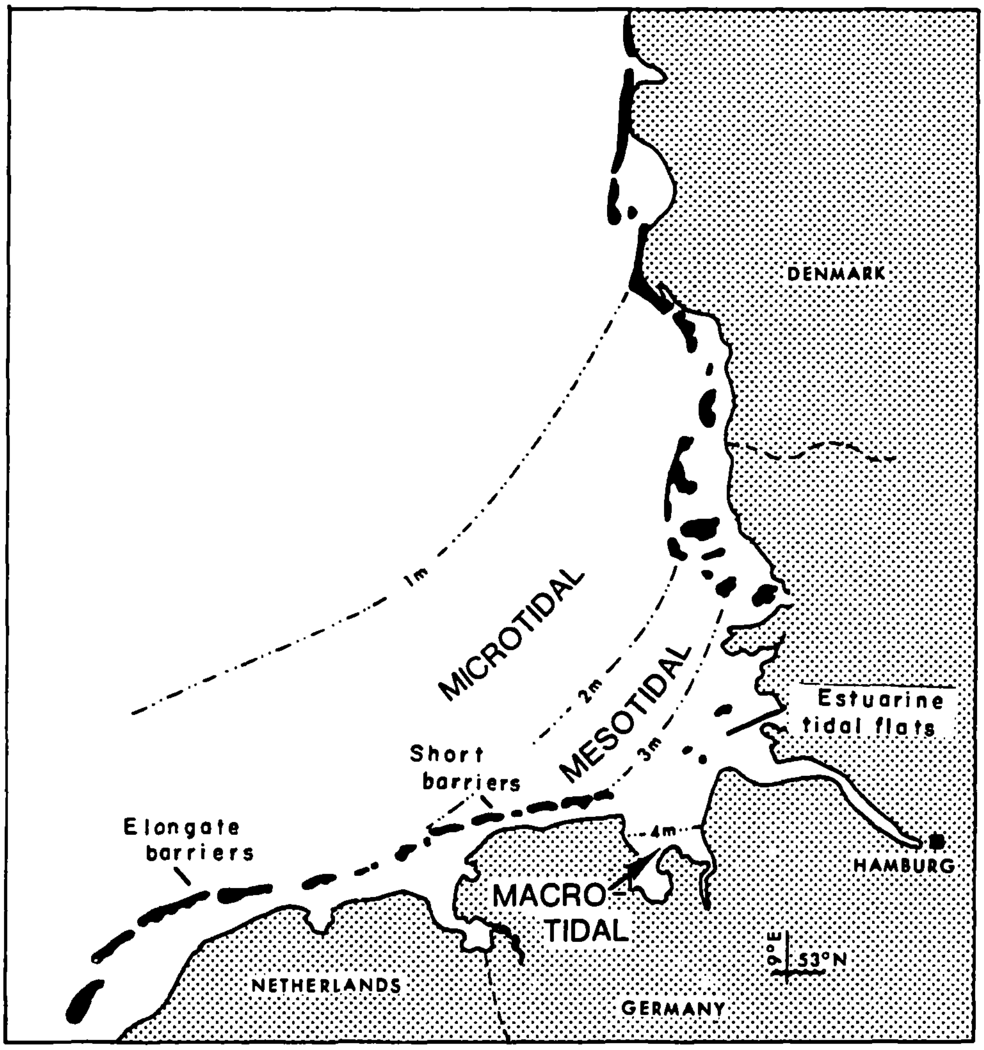

Fig. 14 Relationship of barrier island and entrance size to variation of tidal range along the shoreline of North Sea near Germany and Denmark. Modified from Hayes (1975).

Lagoon processes are greatly influenced by the protracted duration of solid ice cover followed by spring thaw, breakup, flooding, and freezeup. Ice, which covers the lagoons to a depth of 2 m for 8 months, immobilizes many processes active in lagoons of other latitudes. Frozen shores and tundra streams resist normal erosion and ice cover eliminates wind-wave mixing. However, the push of ice or movement by freezing, may produce hummocks or mass movements along shores.

Lagoonal areas less than 2 m deep are frozen to the bed and thus are gouged by grounded or moving ice. Consequently, the

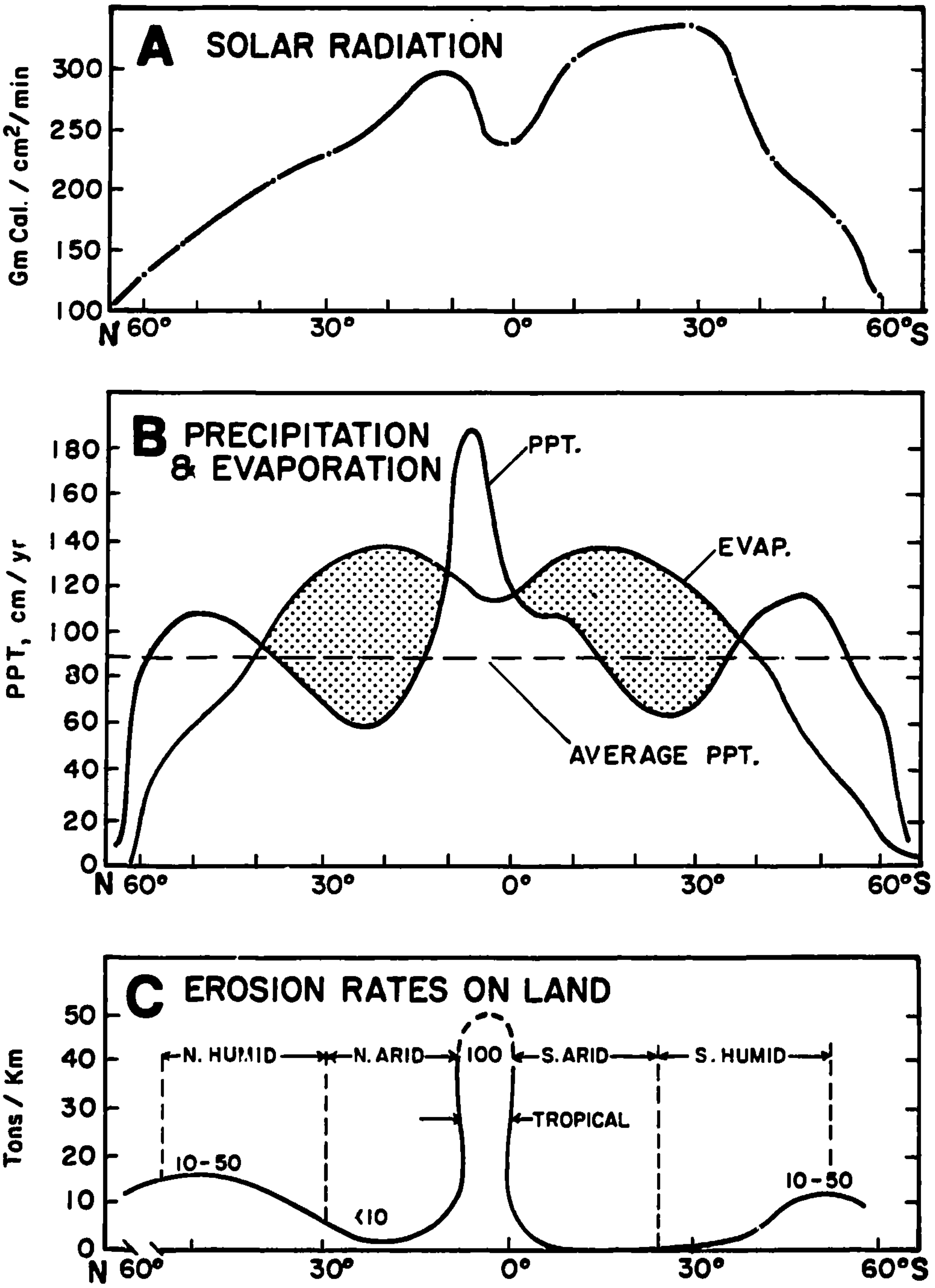

Fig. 15 Latitudinal variations of energy supply and related climatic factors: (A) solar radiation, from Holmes (1957); (B) precipitation and evaporation, from Fleming (1957); (C) erosion rates on land, from Lisitzin (1972).

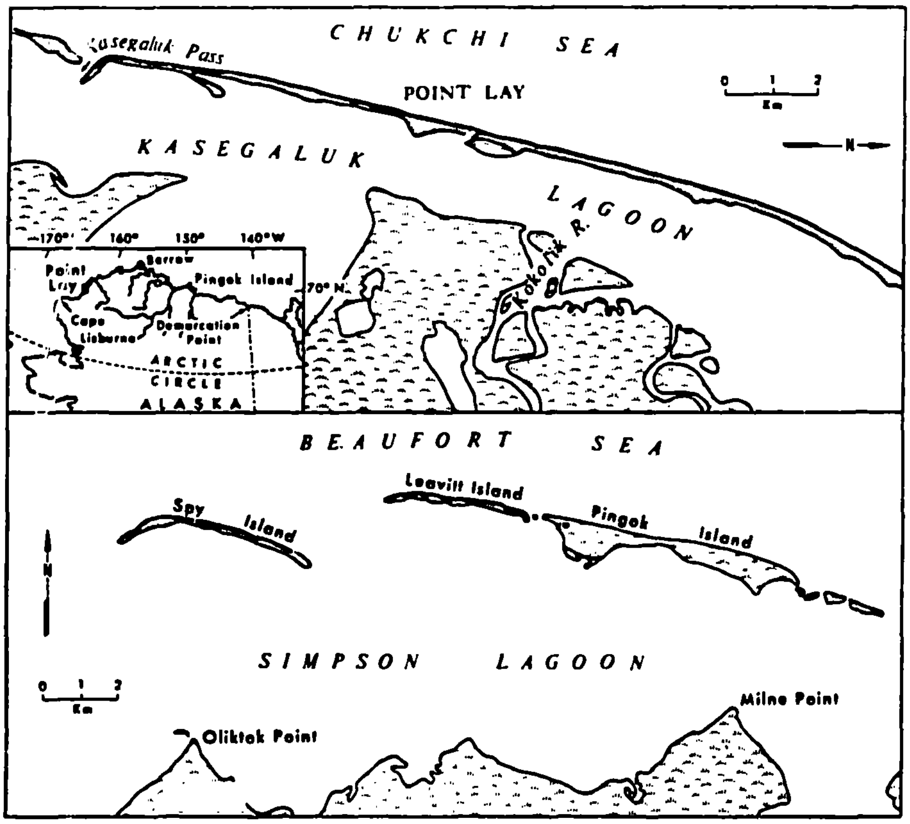

Fig. 16 Location of high-latitude coastal lagoons along the northern coast of Alaska, USA From Short and Wiseman (1974).

upper one meter of sediment may be mixed and the fauna devastated. As lagoon waters freeze downward, salt is expelled producing hypersaline water with salinity values reaching 66% or higher, underneath the ice cover. Photosynthesis ceases and oxygen content is depleted.

The seasonal spring thaw, snowmelt and ice breakup, activate many sedimentary processes. Large amounts of runoff released from tundra pools and streams, flow over and under lagoon ice. Sediment-laden discharge with abundant fine sand, fans out over the ice seaward to the barrier islands or farther, through breaches in the barriers. Some sediment escapes the lagoons during breakup and flooding as peat and terrigenous sediment are reported 40 km offshore. Lagoonal deltas do not develop near the river entrance because sediment by-passes the entrance. Sediment either discharges over the shore fast-ice or is transported seaward of the overflow zone by ice rafting. As melting proceeds lagoon water beneath the floating ice is quickly freshened and stratified. A salt wedge develops near river mouths.

When the ice cover melts, lagoon waters are strongly mixed by the wind. Waters become freshened (23-29 per thousand salinity) and oxygenated for 2 to 3 months. Winds, waves and streams undercut tundra banks and erode ice-cemented sediment, a process called "thermal niching". Sediment released by this process is redistributed in the lagoons by currents, or by high energy wind-wave resuspension. Ice rafting is not a major process and gravel is scarce in bed sediments. Although the astronomic tide range is small and tidal currents are weak, winds produce water level variations up to 1.3 m. This results in currents up to 2 m sec^{-1} through the main inlets that maintain sand transport along the bed. Clay is maintained in suspension for long periods after flooding. At the onset of freezing, transport competence of lagoon water suddenly decreases; both clay and sand settle to the bed producing an admixture of poorly sorted sediment.

Sediment types deposited in the basin of Elson Lagoon follow depth zones. Yellowish-brown silt and clay are deposited in deep central parts, black organic silt and clay in shoal parts and coarse material close to shore. Central lagoon silts and clay, which are deposited below the zone of ice gouging, are interbedded with thin peaty layers. Aided by favorable conditions for preservation, the overall organic content varies between 7.3 to 9.5%. Primary production is low, 1.8 mg per m $hour^{-1}$ in Simpson Lagoon, owing to limited light and nutrients. Animal populations are also low, owing to ice scour of the bed and oxygen deficiencies in winter. Despite the ice stress and low light intensity, grass beds of *Zostera marina* are found in lagoons on the Seaward Peninsula (McRoy *et al.*, (1969).

Most sediment is supplied to high latitude lagoons by rivers and streams while lessar amounts are suplied by shore erosion and barrier washovers. Except for lagoons fed by active glacial meltwater such as on the south coast of Iceland (King, 1972), annual influx of sediment from lagoon watersheds is relatively low, less than 30 tons km^{-1} (Davies, 1973).

Mid-Latitude Humid Lagoons

Processes active in lagoons of a humid or temperate climate can be demonstrated by those in lagoons of the Texas Coast, USA described by Shepard and Moore (1960), Fisher, *et al.* (1972) and McGowen, *et al.* (1976), (Fig. 17). These lagoons form behind a nearly continuous chain of barrier islands broken infrequenly by narrow entrances. The number and size of entrances increases along the Gulf coast as one proceeds from the semi-arid coast of southern Texas to the humid coast of Mississippi. Since the ocean tide range throughout the region is small, river flow is probably responsible for the increased number and size of entrances (Phleger, 1960).

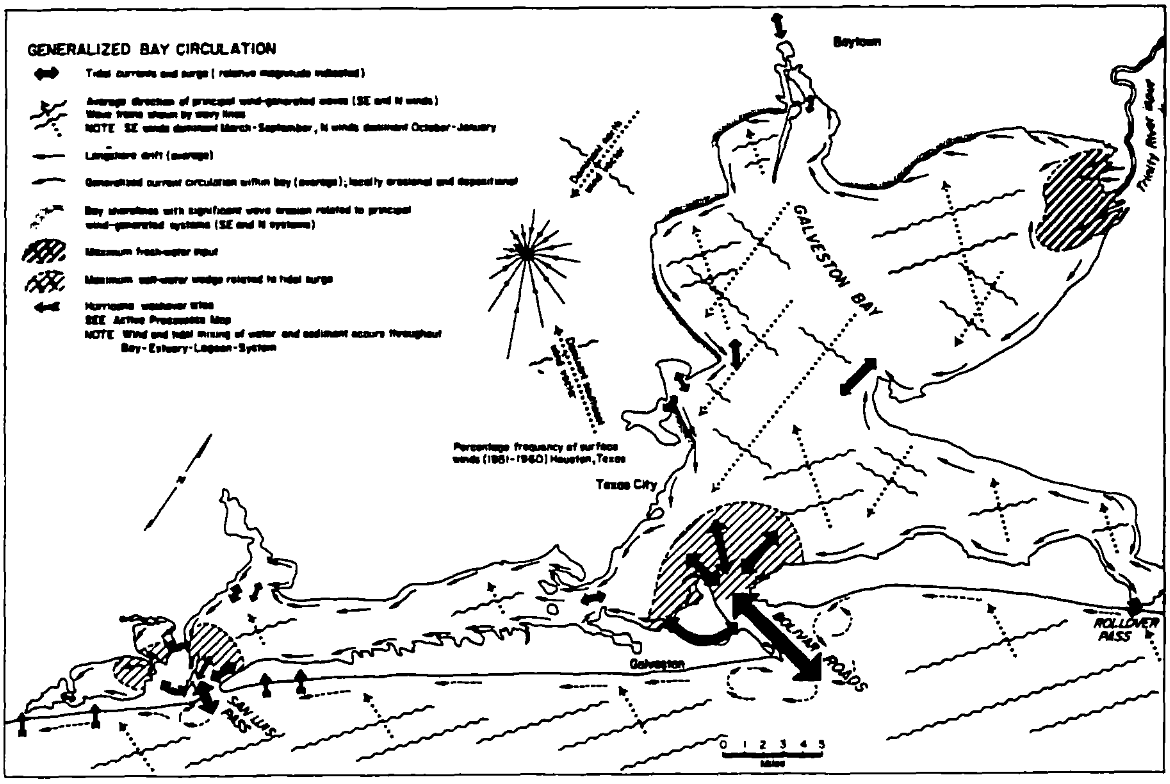

Fig. 17 Schematic representation of processes at work in a mid-latitude humid lagoon, Galveston Bay, Texas, USA From Fisher, et al. (1972).

Of the several sources of sediment, rivers probably supply the bulk of the sediment infill in central Texas bays. Some rivers like the Rio Grande and Brazos have completely eliminated their former lagoons (Shapard and Moore, 1960). Elsewhere prominate deltas fill heads of lagoons like San Antonio and Matagorda Bay (Fig. 6). Annual supply of sediment from a representative watershed in the region is moderate, 139 tons km^{-1} for the Brazos River (Curtis, et al., 1973). The rivers not only produce a horizontal seaward gradient of salinity (< 1 to 30 per thousand salinity) but introduce fine suspended sediment which is transported seaward along western reaches. Some fines are trapped in bordering marshes and flats. Wind and waves are the dominant source of energy that not only maintain vertical mixing of lagoon water, but distribute fine suspended sediment over a broad area of the central floor. Rates of sedimentation range from relatively high on the river and tidal deltas to low (about 32 cm century^{-1}) on the bay floor.

Although tidal currents are slight in the lagoon proper, where the tide range is only 10 cm they are sufficiently strong in the entrance channel (up to 0.7 m per sec) to scour and carry sediment into the lagoon. Some sand moves a short distance in and out. It accumulates at the channel termini in the form of fan-shaped flood or ebb tidal deltas. Some of the outer inlet channels are unstable and tend to migrate in the direction of longshore drift along the barrier islands.

Another zone of relatively high energy is the shoreface, extending from the lagoon beach to about two meters deep. In this zone, breaking waves erode shores of Pleistocene mud and sand and build littoral spits, shell beaches and berms. Winnowed sediment is coarser and better sorted than in deep central zones. Several areas of the bay margin are stabilized by growth of marine grasses and in turn, promote deposition by trapping of sediment.

Dredging and disposal of lagoon sediments by man are major processes in Texas lagoons. They lead to reworking and redistribution of lagoon sediments. Resulting bathymetric changes tend to fragment the natural routes of transport and the patterns of deposition.

Substantial light energy and input of land-derived nutrients and sewage wastes support much benthic grass and phytoplankton. Gross production ranges 3 to 14 g m^{-2} day^{-1} while oyster reef metabolism exceeds these values by about 4 times. Through filtering of suspended sediment, oysters deposit vast amounts of sediment from lagoon water. Organisms burrow and rework central lagoon sediment as evidenced by broken layers, mottled or structureless deposits.

Low-Latitude Arid Lagoons

The lagoons along the Trucial Coast of the Persian Gulf, Arabia, described by Evans and Bush (1969) and Purser and Evans (1973), provide an example of processes active in an arid climate (Fig. 18). The barrier islands were initiated by cemented dunes which were submerged and subsequently enlarged by accretion of reefs, beaches and dunes (Fig. 19). The barriers not only grew laterally through accretion of sand transported by longshore currents, but they grew landward toward the lagoons by intense eolian transport onshore. Gaps between barriers form long tidal channels (7 m deep) and inlets which allow sea water and sediment into the lagoons. The lagoons have depths of 2 to 5 m and the tide range varies from a maximum of 3.5 m in the Gulf to 1 m in the lagoons. Salinity ranges 42 to 45 per thousand in nearshore Gulf water and from 54 to 67 per thousand in the lagoons. Since the area is arid, there is no runoff and no detrital sediment supply. Most sediment is produced locally by extraction of calcium carbonate through biological and chemical processes.

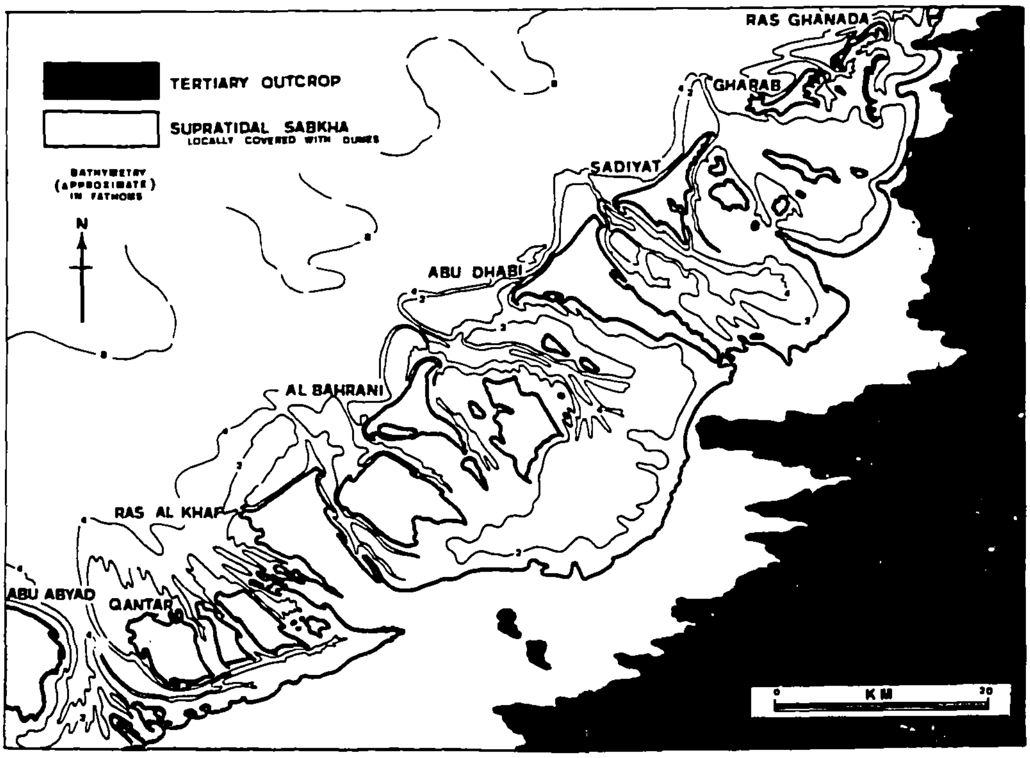

Fig. 18 Morphology of barrier islands and lagoons on the central region of the arid Trucial Coast, Arabia. Reproduced from Purser and Evans (1973) with permission from Springer-Verlag publishers.

The dominant source of energy on the Trucial Coast is the wind. As a result of strong and persistent onshore winds, called "shamal" winds, skeletal, pelletal and oolitic sands are piled into frontal dune ridges reaching 12 m high. Onshore transport moves the sand from the beach and frontal dunes onto back-barrier zones. Here barchans and parabolic dunes migrate more than 4 km landward as a "tail" of sediment. By contrast, offshore desert winds add some fine material to intertidal deposits.

Where wave energy impinges on shoals of the tidal deltas, large amounts of oolitic sand are produced on the deltas. This sand is moved landward through tidal channels or shoreward to form dunes on the barriers. In the lagoon, waves prevent skeletal and pelletal carbonate produced on shoals of the lagoon floor from accumulating. Instead it is resuspended, transported landward and deposited on prograding intertidal flats or algal mats. In some places waves accumulate sand and shell debris forming beach ridges around the lagoon. Tidal currents flowing through entrance channels reach speeds up to 0.65 m sec^{-1} and act with waves to move

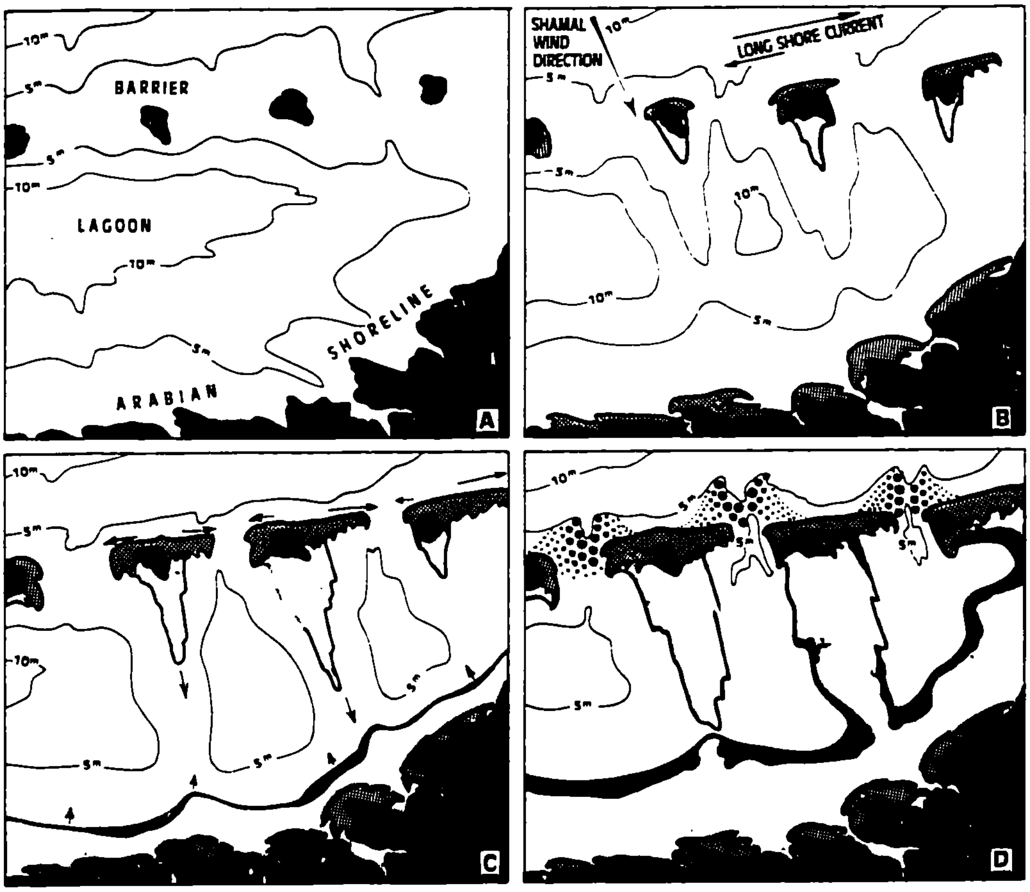

Fig. 19 Chartlets showing evolution of the lagoon-barrier system on the arid Trucial Coast, Arabia. Reproduced from Purser and Evans (1973) with permission from Springer-Verlag publishers.

nearshore sand landward, either along the bed in large megaripples or in suspension. Interaction of waves and currents also produces levees and bars along edges of banks and shoals.

Biological processes contribute significantly to production of carbonate sediment through formation of mollusk shells and pellets, ostracod, polyzoan and foraminiferal tests; and echinoid, coral and algal debris. Relatively high production takes place on the outer lagoon shoals and on the nearshore Gulf floor. Sediment produced by organisms is broken down into sand and fine sediment by mollusks, as well as by worms and crabs. In the process, sediments are heavily burrowed and great amounts of faecal pellets are produced. Algal mats which cover intertidal and supratidal zones act as sinks for much of the fine, pellet-rich sediment. Substantial organic matter is produced in these zones despite relatively low nutrient content of lagoon water. Thick masses of seaweed grow on channel sides and sometimes on lagoon shoals where, together with algae, they act to trap and bind sediment.

A prominent process in Trucial lagoons is chemical precipitation. Oolite production appears to be active on tidal deltas where waves and currents impinge on shoals. Calcium carbonate forms extensive crusts in intertidal and supratidal flats and locally cements dune sands and beach sands forming beach rock. Additionally, subaqueous cementation takes place on the surface of tidal deltas and beneath the lagoon floor. Because of high salinity, high temperature and intense evaporation, calcium sulphate is precipitated as gypsum on the innermost tidal flats. Additionally, anhydrite and dolomite are formed by diagenetic alteration. Evaporite development is determined by the level and frequency of tidal flooding.

Although abundant carbonate sand is produced in arid Trucial lagoons, waves and currents prevent it from accumulating on the lagoon floor. Instead, material transported by curents accumulates landward on intertidal or supratidal flats, or seaward on inner parts of the tidal channels. Elsewhere, sediment accumulates at moderate rates forming tidal deltas, beach ridges and barrier dunes.

Low-Latitude Tropical Lagoons

Lagoons along the Guinea Coast of Nigeria and Dahomey (Benin) described by Webb (1958), Guilcher (1959) and Allen (1965 a, b), illustrate the significant processes active in lagoons affected by high river inflow. These lagoons are long and narrow with many elongate arms extending between multiple beach-dune ridges

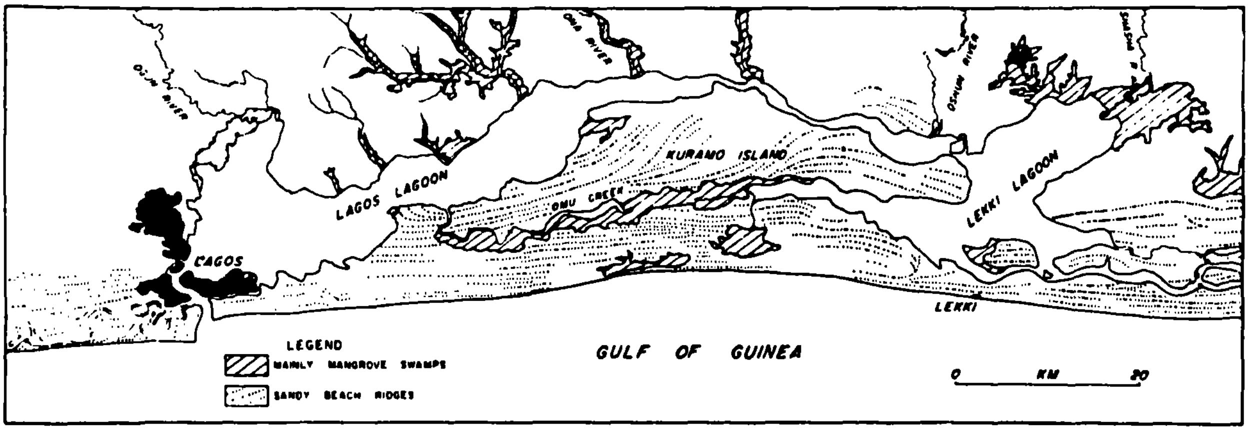

Fig. 20 Lagos-Lekki lagoon barrier complex along the Guinea coast, West Africa. From Allen (1965a); reproduced with permission by Am. Assoc. Petrol. Geol.

(Fig. 20). The barrier islands are nearly continuous and inlets infrequent. The islands are supplied with sand by strong longshore drift directed eastward. By building successive beach-dune ridges, interspersed with lagoons, the coast is gradually prograding seaward.

The lagoons are fed throughout the year by freshwater from rivers and swamps. Massive freshwater influxes occasionally raise lagoon water levels high enough to breach the barriers and discharge suspended sediment loads into the sea. By contrast, when inflow diminishes during the dry season, seawater intrudes more than 32 km landward through inlets. Consequently, lagoon salinity increases from nearly 0 to about 23 per thousand and channel water becomes partly stratified. Depending on the seasonal salinity structure and wind variations, the estuarine circulation changes from bi-directional in upper and lower layers, to seaward at all depths or seaward at mid-depth (Gallardo, 1978). Much suspended sediment is supplied by high gradient rivers but transport patterns are complicated by complex bathymetry.

Tidal currents play a major role in transport and sorting in inlets but their effect diminishes landward as speed diminishes (Webb, 1958). Time-velocity asymmetry causes a greater amount of scour during flood than during ebb and moves bedload landward through inlets.

Deposition occurs in small river deltas along landward margins by entrapment in algal growths and mangroves, or by settling of fines in deep parts. Flocculation is favored by the high floodborne loads of suspended sediment rich in organic matter and by the marked salinity gradients occurring during the rainy season. Although rates of sedimentation are unknown, they are probably higher than in lagoons of other climatic regimes owing to relatively sediment influx of long duration and relatively good conditions for entrapment. In general, mud content increases with water depth and with inward decreasing tidal current strength (Adegoke, *et al.*, 1978).

SIGNIFICANCE OF ENTRANCES

The entrance or inlet is a critical element affecting sedimentary processes in a coastal lagoon. The position of an entrance controls current patterns and therefore determines the pathways of sediment transport. The size and number of entrances determine the amount of water exchange with the ocean and in turn, the exchange of fine suspended sediment. An entrance is normally maintained open by tidal flow augmented by river inflow. When tidal flow fluctuates however, or when longshore transport of sand along the barrier varies, an entrance may exhibit two extreme conditions: open or closed. In many lagoons such changes follow a seasonal cycle. As clearly demonstrated by case studies at Mugu

Lagoon, California (Warme, 1971; Warme, *et al.*, 1976) and at San Miguel Lagoon, Mexico (Stewart, 1958), a change in the entrance can produce large effects.

When the entrance is closed a major source of sediment from longshore drift, the nearshore bed or the ocean, is eliminated. Supply by washovers and wind transport then become the main seaward inputs. Without tidal mixing, lagoon waters are quiet and favorable for settling of fine-grained sediment from suspension. Anoxic conditions may develop and lead to accumulation of organic matter in bed sediments. Depending on river inflow and evaporation rates, salinity may vary from nearly fresh to hypersaline. Such extreme conditions may lead to unusual production of certain organisms or to biochemical precipitation of evaporites. Sediment supplied by river inflow and shore erosion are more effectively trapped within the lagoon than when the entrance is open.

When the entrance is open, sediment input from the ocean becomes significant. Longshore drift feeds sand to the entrance and tidal currents move it into proximal tidal deltas or flats. Tidal mixing produces a stable salinity gradient between the river and entrance. Waters are well-oxygenated and support a diversity of abundant life. With an active tidal exchange, marginal tidal flats and marshes become linked to the lagoon system. Fine-grained sediment in suspension tends to accumulate in the inner reaches rather than in deep channels. In short, a change in the entrance condition can dramatically change the supply of sediment and shift the depositional regime.

CLASSIFICATION OF LAGOON PROCESSES

Because of the great variety of processes, range of sediment types and morphology observed, it is useful to organize lagoons into a systematic framework. Different types of lagoon systems result when the dominant energy forces differ in intensity and character. These differences are reflected in the lagoon morphology and sediment types. By comparing lagoons with a range of dynamic attributes and by generalizing, we can conclude that there are essentially two dominant processes: (1) tides plus river inflow and (2) waves. Tides and river inflow act to maintain a lagoon open to the sea whereas waves and associated longshore drift impound a lagoon. Therefore, two extremes, or end members, are represented by a fully open lagoon (Fig. 21), e.g., a drowned river mouth or estuary, or by a fully closed lagoon. Between these extremes there is a spectrum of types according to the varying intensity of dominant processes. Four types are recognized, each type reflects dominant processes.

An estuarine lagoon is characterised by strong tidal flow augmented by river inflow (Fig. 22 A). Wave energy and drift is low relative to the tide. Tidal currents maintain large and abundant

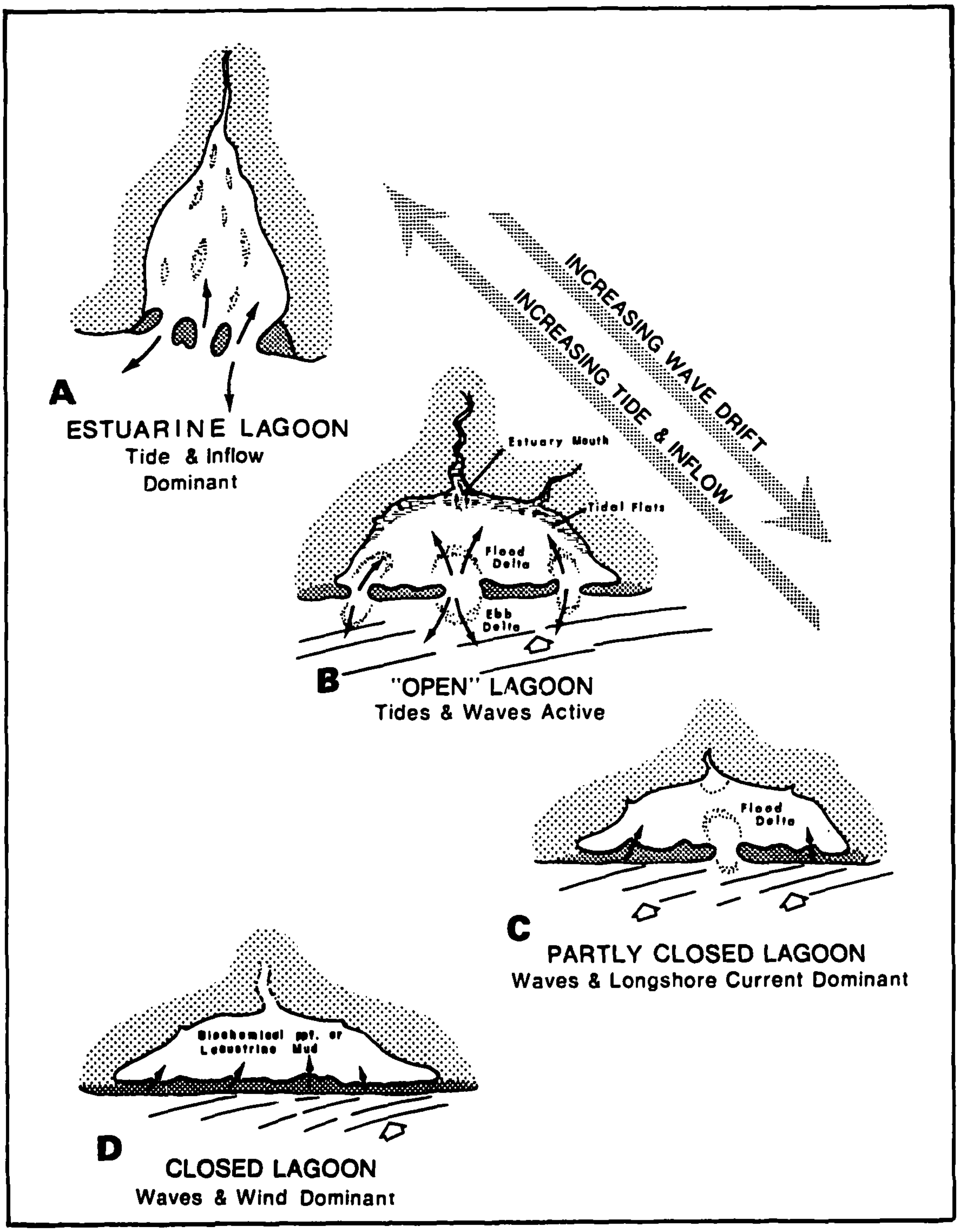

Fig. 21 Schematic classification of lagoon types according to dominate processes: (A) Drowned river mouth or estuary type, (B) "Open" lagoon, (C) Partly-closed lagoon, (D) Closed lagoon, impounded.

inlets and promote strong exchange. As a result, sediment transport is high and morphologic change is great. The floor is fashioned into deep channels and elongate shoals. The river supplies either mud or sand, though entrapment of fine sediment is restricted to the river entrances. Unfortunately, there are few systematic studies of this type of lagoon. The tidal areas of

Table 1. Comparison of lagoon features and processes in different climatic zones.

FEATURE		HIGH LATITUDE, POLAR ALASKA[1] ppt 25 cm/yr TEMP. -35 C to 15 C WIND NE, onshore to 100 km/hr VEG'T tundra	MID-LATITUDE, HUMID TEXAS[2] ppt 115 cm/yr TEMP. 6 C to 35 C WIND SE, onshore VEG'T dense	LOW-LATITUDE, ARID PERSIAN GULF[3] ppt 5 cm/yr TEMP. 12 C to 46 C WIND NW, onshore VEG'T. sparse, strong xerophytic	LOW LATITUDE, TROPICAL GUINEA COAST[4] ppt 250 cm/yr TEMP. 20°C to 33°C WIND SW, oblique to coast VEG'T. dense rainforest
MORPHOLOGY AND DEVELOPMENT	LAGOON	Shallow broad basin *Coast parallel* Depth 3 m max	Shallow broad basin *Coast parallel & transverse* Depth 3 m max.	Shallow small basin *Coast parallel, dissected by barrier accretion lobes* Depth 2-5 m	Shallow narrow basin with elongate arms *Coast parallel* Depth 1.3-3.0 m
	BARRIER	Narrow gravel spit or low sandy islands Moderate longshore migration	Sandy islands with ridges 2-3 m high Stable, washovers locally	Wide sandy islands with ridges 12 m high Landward accretion with spillovers	Wide sandy islands with multiple beach ridges Seaward progradation and longshore migration
	MAIN MARGINS	Ice and tundra	Marsh, wind-tidal flats, beach, deltaic flats	Tidal flats numerous algal flats, wind-tidal flats, beach ridges, mangroves locally	Mangroves, swamps, marshes; tidal flats locally
	INLET	Wide, numerous Open in summer, closed by ice in winter	Narrow, intermittent Open throughout year, mainly stable	Wide, numerous Open throughout year, stable prominent tidal channels	Narrow, few Ephemeral barrier breaches
WATER	CHARACTER	Salinity, 23-66 ‰ *Stratified to well-mixed* Anoxic under ice	Salinity < 1 to 34 ‰ *Well-mixed*	Salinity 42-67 ‰ *Well-mixed*	Salinity: < 1 to 30 ‰ *Partly-stratified to well-mixed*
	EXCHANGE LAGOON-SEA	Moderate in spring and summer	Low tidal exchange except high during hurricanes	High tidal exchange	Moderate tidal exchange, high during river floods
SEDIMENT SOURCES	PRIMARY	Rivers and streams	Rivers and streams	Biological Co_3 production	Rivers and streams
	SECONDARY	Shore erosion & barrier washover	Barrier washovers, shore erosion, oyster growth	Lagoon water via ppt Barrier via onshore wind	Barrier and shoreface via inlet & washovers
TRANSPORT PROCESSES	RIVER DISCHARGE	Low, except in spring Overflow by-passes shore	Moderate river flooding	Very low inflow	High river inflow and flooding
	TIDE	Low astronomic range, 0.3 m High wind tide, 1.3 m strong drift currents	Low range, 0.1 m High wind tide, 1.0 m tidal deltas	Intermediate range, 1.0-3.5 m Moderate wind tides, strong tidal currents, 0.65 m/s	Low range, 0.3-1.0 m Moderate tides
	WAVE ENERGY	High in summer	Moderate on shoreface, bed resuspension, longshore currents	Moderate onshore to barrier & shores Bed resuspension and beach ridge formation	Low activity Bed resuspension on shoals
	WIND ENERGY	Strong, but effective only in summer	Moderate, eolian transport along barrier & shores	Strong eolian transport from barrier and shores	Weak, limited influence
	UNIQUE PROCESSES	*Ice shove, gouging local rafting* Thermal niching River overflow on ice	*Dredging* Hurricane tide & surge	*Chemical ppt of evaporites*	*Rainwash on barrier & flats* Barrier breaching, seaward
	SEASONALITY	Strong, spring thaw with flooding	Moderate, northerly wind winter, southeast, summer	Seasonally stable	Seasonal low to high rainfall Lagoon flooding, flushing thru inlets
DEPOSITIONAL PROCESSES		Settling of river-borne suspended load Strudel infilling Flocculation probable	Settling of river-borne suspended load Rapid accretion at river delt Entrapment in marshes washovers & inlet deltas Oyster reef deposition Bio-deposition & bioturbation	Biologic extraction of Co_3 Entrapment by algal mats Chemical ppt on flats Settling of resuspended sediment Biodeposition & bioturbation	Settling of river-borne suspended load Entrapment by algae and mangroves Flocculation Accretion at river delta
BED SEDIMENTS	CENTRAL LAGOON	Silt, clay & organic layers	Silty clay with oyster reefs	Pelletal and foram mud	Organic rich silt and clay or sandy mud
	MARGINAL ZONES	*Sand & silt*	*Silt & clay in marsh* Sand & shell on beaches	*Shell beach ridges* Evaporite flats, gypsum, anhydrite Pelletal & foram sand shoals Oolite on tidal deltas	*Shelly sands*

[1] Elson Lagoon (Faas, 1969) and Simpson Lagoon, Alaska (Naidu and Mowatt, 1975).

[2] Aransas and San Antonio Bay (Shepard and Moore, 1960) and Galveston Bay, Texas, U.S.A. (Fisher, et al., 1972)

[3] Trucial Coast, Arabia (Evans and Bush, 1969, Purser and Evans, 1973)

[4] Lagos-Lekki Lagoon Complex, Nigeria (Webb, 1957; Allen, 1965a and b) and Dahomey Coast Lagoons (Guilcher, 1959)

northwest Germany may be representative. (Refer to Table 1).

An "open" lagoon is a product of waves acting in combination with moderate tides and river inflow (Fig. 22 B). High waves and longshore drift build short barriers islands whereas bi-directional tidal currents maintain several moderate size entrance channels with well developed flood and ebb tidal deltas. Generally, mud tends to accumulate on flats along inner parts whereas sand is common to the channel floor and entrance shoals. This type can display a large variety of sediment patterns depending on the relative strength of waves and tides. If the lagoon basin is relatively deep, mud covers the basin floor. Ocean-lagoon exchange is intermediate and entrapment of fine sediment is good. The Dutch Wadden Sea and the Mississippi sound provide examples of this type.

In a partly closed lagoon high wave energy acting on the nearshore bed or headlands and strong longshore currents build an extensive barrier island (Fig. 22 C). Tides are subdued and tidal sediment transport is limited to entrance reaches. It produces a prominent flood delta but only an insignificant ebb delta. Over long periods tidal currents and wave power may reach a dynamic balance. Low energy in central and deep parts of the lagoon favors mud accumulation whereas wave action on shoals and shores results in sand. In shallow lagoons experiencing high wind waves, sand accumulates on the central floor and in washovers whereas mud accumulates in protected embayments. Ocean-lagoon exchange is poor and entrapment of both sand and mud is good. The Rockport Bays on the USA Gulf coast are representative of this type.

A closed lagoon is produced by intermediate to high waves, and strong longshore drift (Fig. 22 D). In the absence of tides and continuous river inflow, the lagoon is impounded. Washovers or winds across the barrier are the chief processes of sediment influx. Sediment transport within the lagoon is limited to local wind waves. Without ocean-lagoon exchange entrapment is significant. Organic production or chemical precipitation are often the chief sediment producing processes.

STUDY APPROACHES

From the descriptive review of processes and comparison of world lagoons, it is evident that a complete understanding of sedimentary processes in lagoons has not yet been reached. Most results have been descriptive; a number of significant ideas have been put forth but not confirmed. A moderate amount is known about the bed sediments and a little about the hydrodynamic processes. Almost nothing is known, however, about how the sediments interact with dynamic parameters to create mechanisms for sediment dispersion or entrapment.

As a guide for future lagoon research, study of sedimentary processes should be organized to focus on: (1) sedimentary deposits; (2) specific processes or mechanisms; (3) the lagoon as a sedimentary system.

The first approach views the bed sediments or deposits, as end products of the processes. They are integrated products of many

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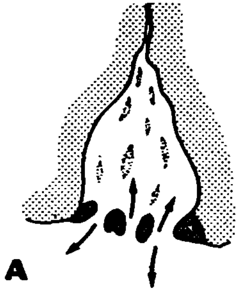
<td>
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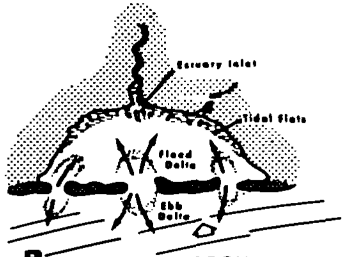
<td>
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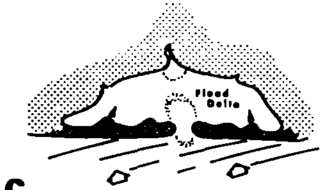
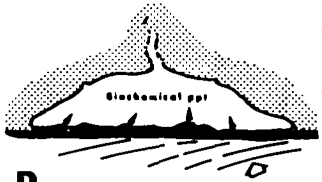
"OPEN" LAGOON
Tides & Waves Active</td>
<td>
C
PARTLY CLOSED LAGOON
Waves & Longshore Current Dominant</td>
<td>
D
CLOSED LAGOON
Waves & Wind Dominant</td>
</tr>
<tr>
<td>Features</td>
<td colspan="4">HIGH ← TIDES AND RIVER INFLOW ← LOW
LOW — WAVE DRIFT → HIGH
OPEN ← ENTRANCE CONDITION → CLOSED</td>
</tr>
<tr>
<td>Morphology</td>
<td>Short barrier
Deep channels & tidal flats</td>
<td>Elongate barrier wide entrances
Fld. & ebb deltas well developed</td>
<td>Elongate barrier narrow entrances
Reduced ebb delta</td>
<td>Continuous barrier</td>
</tr>
<tr>
<td>Dominant Processes</td>
<td>Tidal transport and river influx</td>
<td>Tidal transport</td>
<td>Waves, washovers & longshore current</td>
<td>Washovers, wind
Organic production
Chemical ppt.</td>
</tr>
<tr>
<td>Sediment</td>
<td></td>
<td>Sand seaward
Mud landward or in basins</td>
<td>Sand shoals seaward
Mud in basins</td>
<td>Organic-rich lacustrine mud
Evaporites</td>
</tr>
<tr>
<td>Ocean-Lagoon Exchange</td>
<td>High</td>
<td>Intermediate</td>
<td>Low</td>
<td>No surface exchange; sub-surface percolation thru barrier</td>
</tr>
<tr>
<td>Example</td>
<td>NW Germany; Mobile Bay</td>
<td>Dutch Wadden Sea; Mississippi Sd.</td>
<td>Rockport Bays; Texas</td>
<td>Solar Pond, Israel; LacTogo, Guinea Coast</td>
</tr>
</table>

Figure 22. Processes dominant in different lagoon types.

and varied processes deposited by long-term average conditions, or short-term catastrophic conditions. In this approach sediments are characterized by their textural, compositional or structural properties. An attempt is made to relate the resulting distributions of properties to the morphology, or to whatever can be inferred about the processes. For example, in a study of San Miguel Lagoon, Mexico, Stewart (1958) used a size-distribution diagram (Fig. 23) to delineate sediments deposited in different process regimes. Allen (1971) differentiated zones dominated by bed load from zones of suspended load transport using the C-M textural system of Passega (1957). The approach assumes that the sediment is not relic but formed by processes active in over-lying water or the environment of deposition. Besides textural and compositional characteristics of the sediment, the physical or geotechnical properties need to be examined, i.e., bulk density, shear strength, as well as acoustical properties. Such properties relate to rates of sediment accumulation and to aging processes of the sediment. Study of sedimentary deposits is useful for identifying the important processes at work in different parts of a lagoon and thus a good subject for starting a lagoon study. It is a useful approach for examining processes with long-time scales or, for short-term processes that result in high accumulation.

The second approach deals with measurements of specific physical parameters, waves, tides and currents and the corresponding sediment behavior; e.g., velocities required to initiate particle movement, lag effects due to unsteady flow, role of bedforms in transport and in sorting of sediment, effects of flocculation and processing of sediment by organisms. One can learn about the processes by: (1) direct field observations in the environment and (2) observations of sediment behavior in a laboratory flume or a hydraulic model. Whereas field observations often include effects of many variables active simultaneously, laboratory experiments permit some degree of control and isolation of different variables. Hydraulic models are particularly useful for predicting effects of changing lagoon geometry, (i.e., channels and dikes, on the circulation regime) on the tides or salinity under average steady state conditions. Because of scale effects in models and the two dimensional limit of flumes, there is a question of how well natural processes are reproduced. Field observations can be made by either limnological or oceanographic methods and adapted according to characteristics of the lagoon under study. The study of Oyster Pond, Massachusetts, Emery (1969) provides a model for well-balanced multidisciplinary observations which applies simple and low-cost techniques to a coastal lagoon. For most lagoon studies, a bathymetric chart must be obtained or constructed. When bathymetric surveys are repeated at time intervals of years or decades, the resulting depth changes can indicate rates of sediment scour or fill in response to currents or waves. Water level variations provide useful basic information on the hydrographic regime of a lagoon. Most physical aspects usually require that

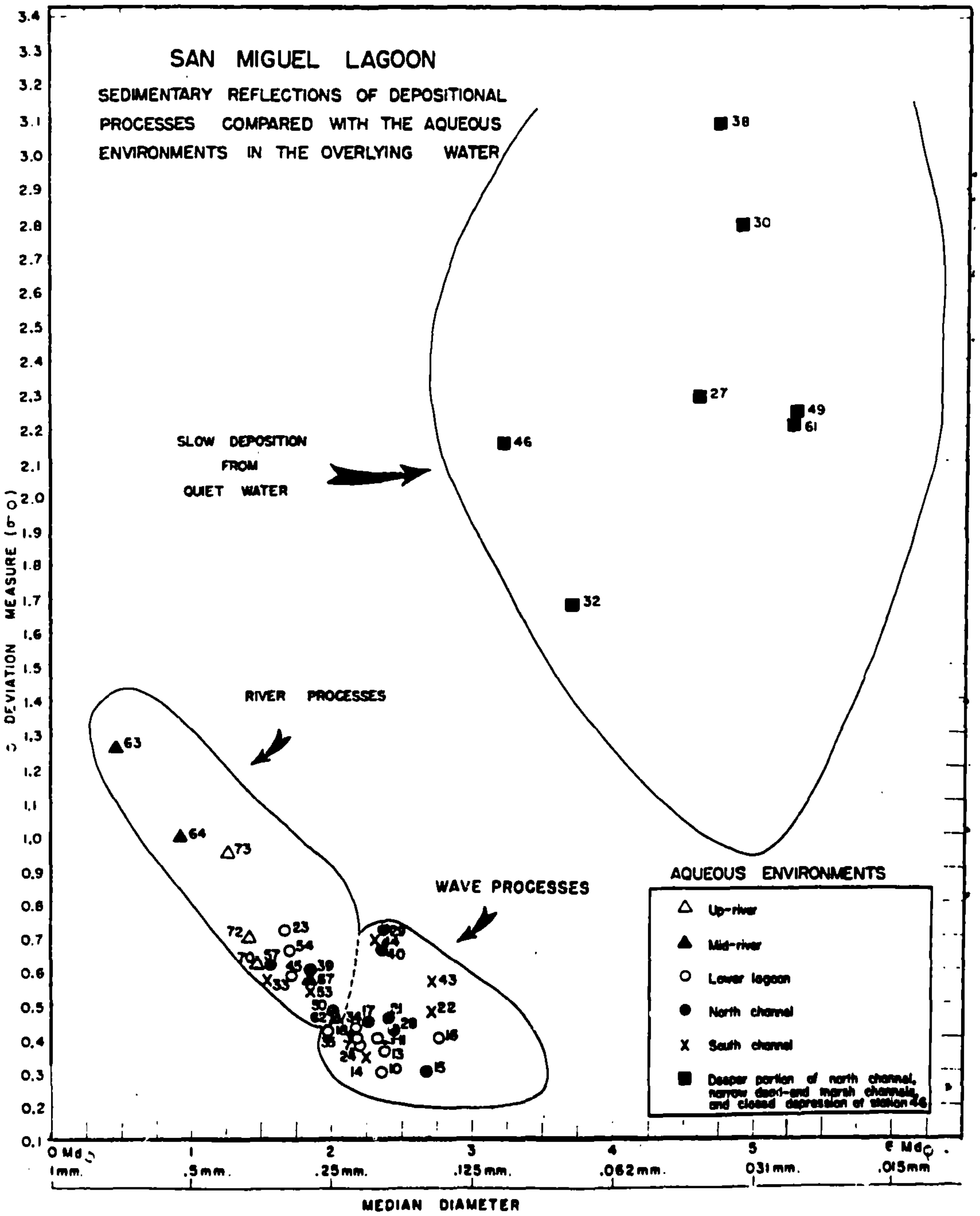


Fig. 23 Size-distribution diagram of bed sediments from San Miguel Lagoon, Mexico with comparison to different lagoon processes. Numbers are station numbers. From Stewart (1958).

unsteady and bi-directional flow properties be measured over a period of time. Pertinent sediment measurements include: mass concentration of particles, particle size distributions, state of aggregation, organic and inorganic content and sediment composition. Such direct observations are also essential input for a systems study of processes.

The third study approach may take different directions. It is useful to consider the lagoon as a sink for sediments from different sources and then to draw up a material budget for all contributions. It is assumed that sediment in the sink is carried from its source by some energy agent. The location of sediment sources must be accounted for and the rates of input to the lagoon must be determined. Budgets can be refined by differentiating sink sediments into zones that relate to sediment sources. In some areas sources are contaminated with pollutants. These materials are often more distinctive than the sediments they are associated with and thus serve as tracers to identify sediment sources and routes of transport.

To balance a budget it is necessary to determine the total rate of deposition and ideally the proportions of sediment from different sources. Studies by Biggs (1970) and Bartberger (1976) show how this approach can be used successfully despite limitations of available data. As demonstrated by Ryan and Goodell (1972) in Mobile Bay, USA Gulf coast, not all sediment supplied to a lagoon is deposited therein. A fraction may by-pass the lagoon and escape through the entrance. Results of a sediment budget are useful to show the relative importance of different sources in a single lagoon; to compare lagoon systems under different hydrologic and climatic regimes, and to assess large scale man-made changes like dredging.

When field data are incomplete, assumptions must be made, the dimensions reduced and solutions sought, in a mathematical model. Mathematical models have been used with reasonable success for hydrodynamics of lagoons and for sediment in estuaries (Odd and Owen, 1972) and in nearshore systems (Fox, 1978). Modeling usually starts with governing hydrodynamic equations and involves some sort of spatial averaging to simplify the problem to one or two dimensions. Exchange ratios, source and sink terms, are either assumed constant or considered a simple variable that fits the available prototype data. An array of techniques and approaches are given by Fox (1978) and Ariathurai and Krone (1976).

Another system approach treats characteristics of the sediments as a response to certain dynamic processes. This concept is usually structured into a process-response model showing relations between attributes of the environment and corresponding attributes of the sediments being e.g., Table 2 (Krumbein and Sloss, 1963).

Table 2. Generalized structure of a process-response model.

```
Process Elements                       Response Elements

Tidal height        '       '   Suspended sediment concentrations
Tidal currents      '       '   Sediment transport
Wind velocity       ' -----> '  Dispersal patterns of sediment
River inflow        '       '   properties
Longshore current   '       '   Morphological change velocity

          '                            '
          '                            '
          '                            '
          --------- Feedback <----------
```

As sediments respond they may exert an influence or "feedback" on the process elements. For example, a shoal may be built up which may affect currents or wave refraction. An excellent example of a process-response study is that of Davis and Fox (1972) for nearshore sand bars. Krumbein and Sloss (1963, p. 240) show how the approach is used in a coastal lagoon, Barataria Bay, USA Gulf Coast. Fox (1978) reviews statistical and computer techniques. In many problems the objective of using a process-response approach is to predict the response of sediment attributes under different process conditions. This paper is contribution number 998 of the Virginia Institute of Marine Science.

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ON THE HYDROGRAPHY AND CHEMISTRY OF SOME COASTAL LAGOONS OF THE PACIFIC COAST OF MEXICO

by

Enrique F. Mandelli

INTRODUCTION

Along the coast of the State of Guerrero, Mexico, there are several coastal lagoons with areas varying from 2 to 60 km^2. A general study of these lagoons was undertaken by the Centro de Ciencias del Mar y Limnologia of the UNAM from 1973 to 1976, with the purpose of formulating recommendations for their proper use and management.

Information regarding the geological, hydrographic and chemical characteristics of the lagoons are recorded in several technical reports, as well as in a doctoral dissertation (Mee, 1977).

The rather unstable conditions affecting some of these lagoons leads to many unsolved problems with regard to the various processes which take place in these water bodies. The lagoons selected for this analysis showed differences in their hydrographic regime, mainly due to climatic stresses. The purpose of this work was to analyze the information gathered from 1975 to 1976 in order to gain some understanding of the complex nature of these systems. The main objective of this study was the identification of those critical processes which affect the lagoons under varying hydrographic conditions.

DESCRIPTION OF THE AREA

The coast of the State of Guerrero is an almost continuous low sandy beach, broken only where outcrops of the Sierras reach the sea. Various small rivers cross the coastal plain and seasonally discharge their waters into the sea or into the various coastal lagoons. These lagoons, with their associated channels, occupy almost half of the Guerrero coast. Lankford (1977) described the lagoons of Guerrero as "barred inner shelves", originally long narrow lagoons that since the time of their formation, 5,000 years ago, became divided and isolated. Some of these lagoon segments have now been completely infilled or survive as marshes. The coastal lagoons of the State of Guerrero, Mexico, are presented in Figs. 1 and 2.

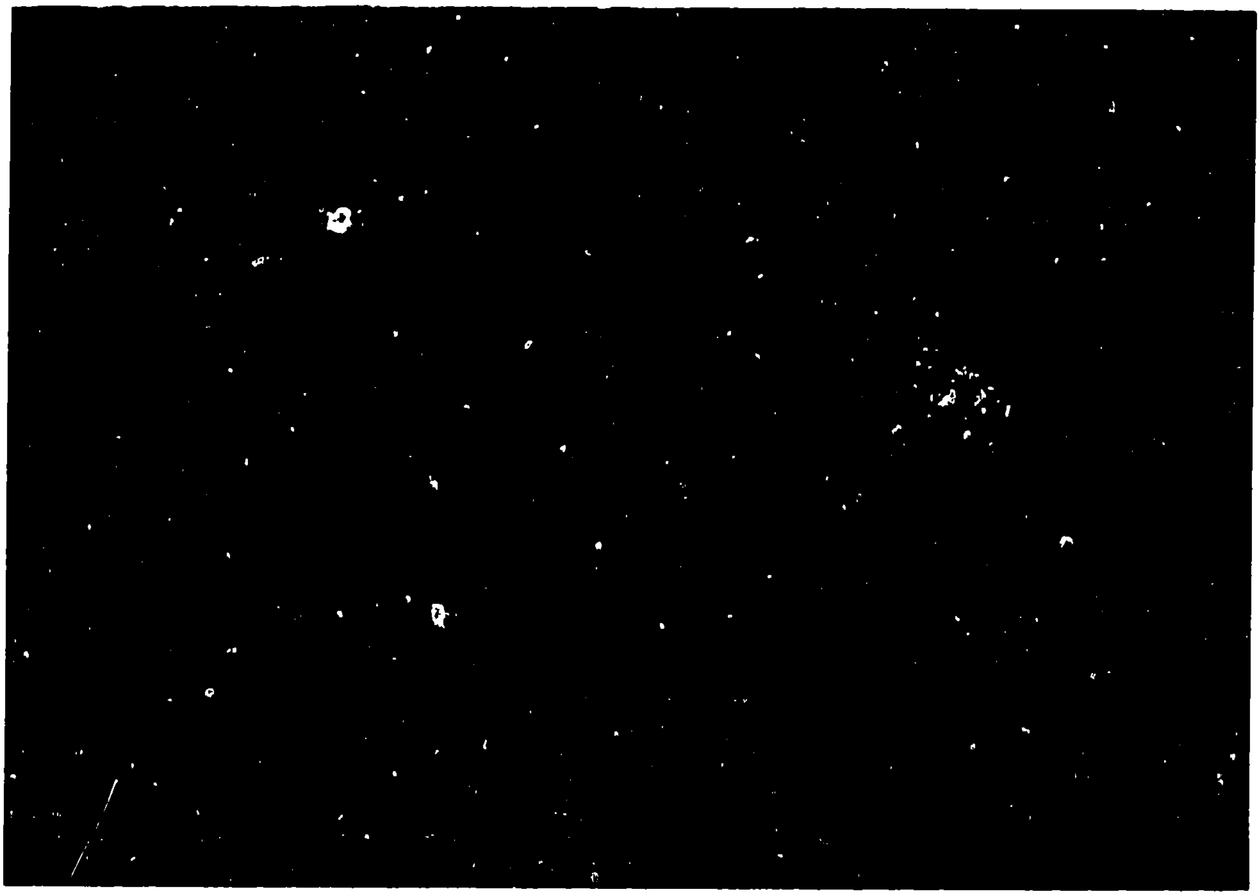

Fig. 1 Satellite photograph of the State of Guerrero coast NW of Acapulco, Mexico.

HYDROGRAPHIC REGIMES

Perhaps the most important factors determining the hydrography, and hence the ecology of coastal lagoons, are the freshwater inputs (runoff), the rate of evaporation, and the mixing and circulation processes with coastal waters. With few exceptions, the hydrographic regimes of the lagoons of Guerrero are characterized by their annual variability.

One of these exceptions is Chautengo Lagoon which has a fairly stable hydrographic regime. This regime was first observed by Mandelli and Botello (1976) who described it as having an annual cycle of four stages (Table 1).

The duration of the different stages of the cycle for Chautengo Lagoon varies from year to year. Surveys conducted in 1975 and

Fig. 2 Satellite photograph of the State of Guerrero coast SE of Acapulco, Mexico.

1976 indicated that Stage I lasted four months, State II one month and Stages III and IV for a seven month period. For some of the other lagoons included in this study, particularly San Marcos and Mitla, the hydrographic cycle was reduced to only two stages during the same period.

I A period in which evaporation exceeds runoff inputs (dry season).
II A period in which rainfall causes the lagoons to be refilled (rainy season).

Net evaporation values were estimated for Chautengo, San Marcos, Mitla and Nuxco during the 1975 survey, based on mean depth and salinity changes. The resulting figures were compared to evaporation values calculated from climatological data. In Table 2 are shown monthly evaporation rates calculated for each of the

Table 1. Hydrographic regime of Chautengo Lagoon

Stage	Characteristics
I	Bar closure and a period where evaporation exceeds runoff inputs.
II	A period where heavy rainfall causes the lagoon to be refilled.
III	The bar opens and the Lagoon partially discharges into the sea.
IV	A period of tidal exchange together with river discharge into the Lagoon

Table 2. Estimated and calculated monthly evaporation loss in the lagoons for the March - May 1975 period

Lagoon	Area (km^2)	Evaporation loss (x$10^6 m^3$) Estimated (1)	Calculated (2)
Chautengo	36	2.65	5.40
San Marcos	21	2.60	3.15
Mitla	36	6.10	6.70
Nuxco	6.5	1.43	1.62

(1) Volume changes based on mean depth and salinity changes
(2) Water loss calculated from climatological data

lagoons during the March-May, 1975 period. For the overall period Chautengo Lagoon received considerable freshwater inputs of river origin during the first stage of the cycle.

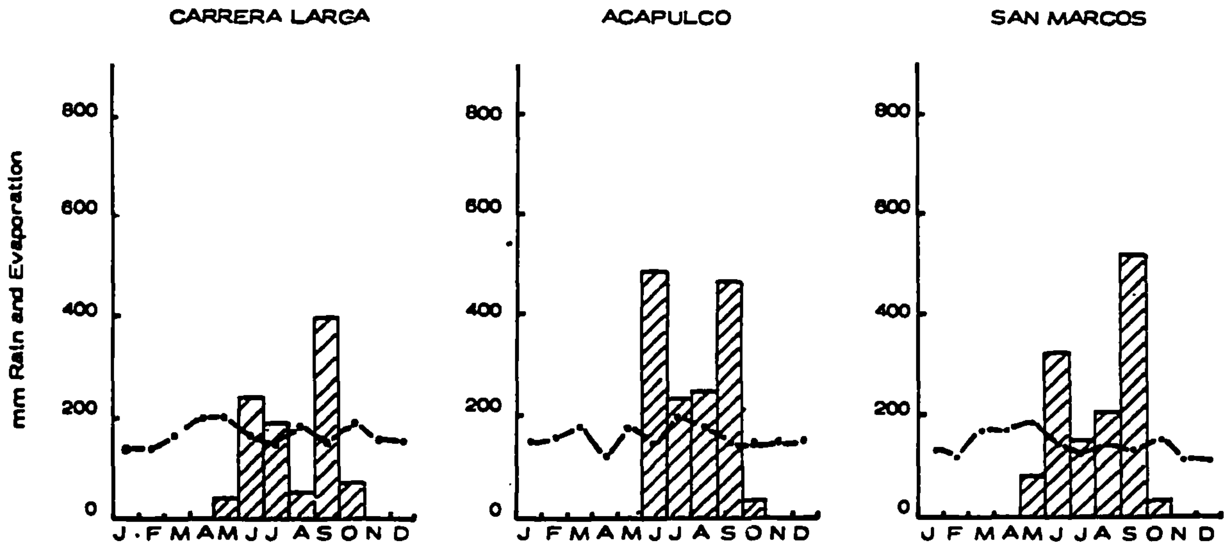

Fig. 3 Monthly rain and evaporation recorded during 1974 at three climatological stations located on the coast of the State of Guerrero.

Table 3. Total annual discharge of the Nexpa River into Chautengo Lagoon

YEAR	DISCHARGE ($x10^6$ m^3)
1969	1192
1970	971
1971	308
1972	252
1973	611
1974	1045
1975	890

With the onset of the rainy season the lagoon volumes increased due to direct precipitation and runoff. The general distribution of rainfall affecting the lagoons is typical of tropical areas, with large initial rainfall in June, followed by a sharp decrease then later a gradual build-up which reaches a second maximum in September or October (Fig. 3).

It is interesting to note that in many instances most of the rainfall takes place in a few days. The wide annual variation in total rainfall is also indicated by a similar variation in the total annual discharge of the rivers. This is illustrated for the Nexpa River in Table 3.

Table 4. Changes in the volumes of the Lagoons from May 1975 to July 1975

Lagoon	Estimated Volume (x10 m^3) May 1975	 July 1975
Chautengo	28.4	76.8
San Marcos	9.1	14.9
Mitla	69.0	73.3
Nuxco	11.7	13.6

In Table 4 are shown the changes in the lagoon volumes calculated from mean depth and salinity changes for May-July, 1975. It can be seen that during the initial period of the rainy season of 1975 the lagoons receiving only direct precipitation and immediate runoff inputs refilled less dramatically than Chautengo which received in addition inputs from two rivers (Nexpa and Copala).

Before discussing the third stage of the hydrographic cycle of the lagoons, it is necessary to consider the nature and morphology of the lagoonal inlets to the sea. In Table 5 are given the general characteristics of the coastal lagoons considered in this work.

The mechanisms for the opening and closing of the sand bar of coastal lagoons were discussed by Lankford (1977), who indicated that the opening of these sand bars was the result of internal hydrostatic pressure and external wave erosion. For lagoons with long meandering channels and lack of direct river inputs, such as the case of San Marcos Lagoon, the opening of the sand bar takes place only during years of exceptionally high rainfall. In the particular case of Mitla, a lagoon with a sand bar inlet, two factors have contributed to its isolation from the sea during the past fifteen years. One factor has been the restriction imposed on the flow of Coyuca River toward the lagoon which has considerably reduced the input of freshwater to build up the necessary hyd-

Table 5. General Characteristics of the studied Lagoons

Lagoon	Type of runoff received	Type of sea Connection	Salinity range parts per thous.
Chautengo	River + direct runoff	Sand bar	5-30
San Marcos	Direct runoff	Long channel (7 km)	8-55
Mitla	Direct runoff	Sand bar	2-4
Nuxco	Seasonal river + direct runoff	Short channel (< 1 km)	15-23

rostatic pressure. The second factor has been the reinforcement of the sand inlet mediated by man.

The third stage of the cycle starts with the "bar opening" when there is a large discharge of lagoon water (together with dissolved and particulate materials) to the littoral zone. In the particular case of Chautengo Lagoon, the volume of water discharged into the sea was calculated from changes in the mean water depth. These discharges were estimated at 38.4 x 10^6 m^3 and 25 x 10^6 m^3 for July, 1975 and June, 1976 respectively.

Following the opening of the bar, the lagoon water levels are quickly equilibrated with that of the sea. The water level of Chautengo is shown to vary during the "bar opening" period, according to the annual cycle of offshore mean tide levels (Fig. 4). These variations have the effect of reducing the volume of the lagoon considerably when compared to volumes recorded prior to the opening of the bar.

The nature of the physical processes of mixing and circulation for Chautengo during these periods was described by Mee (1977). This author established an estuarine circulation pattern influenced by wind action in studies conducted in 1976.

The sealing off of the bar caused by littoral transport takes place after the end of the rainy season at a time of very low freshwater input, mainly from rivers, and low offshore mean tide levels. (Fig. 4).

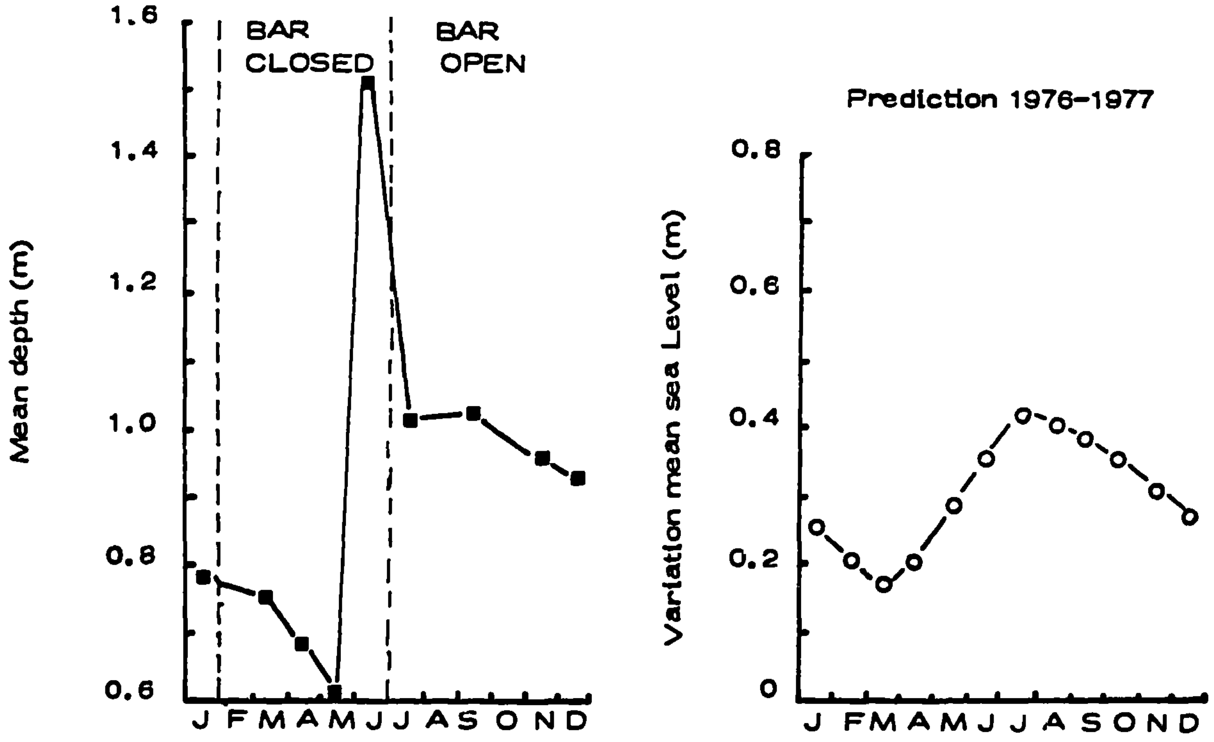

Fig. 4 Mean depth changes recorded in Chautengo Lagoon and variation of the mean sea level during 1976.

Stages III and IV of the hydrographic regime were not observed for San Marcos and Mitla Lagoons which consequently behaved as lagoons with cycles of two stages. With regard to the Nuxco Lagoon, Stages III and IV were observed for a brief period of two weeks during September, 1975.

CHEMICAL PROCESSES

A coastal lagoon provides the site for a large variety of chemical interactions to take place. These include interactions within and between the three reservoirs of material present: dissolved substances, suspended particulates and lagoon sediments.

For the present consideration, a coastal lagoon will be regarded as a basin having overall chemical inputs and losses, and in which a variety of internal processes are acting. The supply of dissolved and particulate materials to a coastal lagoon depends on the external reservoir of the materials and the transport mechanism which carry them into the lagoon.

Tropical lagoons in areas which have highly seasonal rainfall therefore have seasonal supplies of dissolved and particulate materials of continental origin. When considering the runoff into the lagoon, it is often necessary to take into account the effect of direct rainfall as well. While the effect of inputs is generally to dilute the lagoon waters, rain may carry an appreciable quantity of nutrients (Reinhold and Daiker, 1967).

An increasingly important source of material into the lagoon environment is from domestic, agricultural or industrial sources. The most generally observed source of introduced materials is that arising from sewage discharges and agricultural runoff. The fate of the dissolved and particulate materials brought by natural runoff or introduced by man within the lagoon environment is largely dependant on biological, chemical and physical factors. (Okuda, 1960; Oppenheimer and Ward, 1965; Pomeroy _et al._, 1965; Nichols, 1966 and Postma, 1969).

Preliminary studies on the water chemistry of Chautengo, San Marcos, Mitla and Nuxco Lagoons, conducted in 1975, indicated that the pattern of seasonal variation in the chemistry of these lagoons is closely associated to their annual hydrographic cycles.

Seasonal variations in the concentration of the dissolved nutrients and particulate chlorophylls in the waters of Chautengo Lagoon were followed throughout the hydrographic cycle in 1976.

Stage I. _Dry Season, lagoon isolated from the sea_

During this stage, river runoff into the lagoon is very low and evaporation exceeds input. Under these conditions the reservoir of dissolved nutrients and the particulate chlorophylls remained fairly stable, with nutrients declining slightly and particulate chlorophylls increasing toward the end of this stage. The concentration of total dissolved phosphorous in the water ranged from 2.4 to 3.0 ug-atom P $litre^{-1}$ with an average value of 2.5 ug-atom P $litre^{-1}$ while the total dissolved silicates ranged from 75 to 100 ug-atom S $litre^{-1}$ (Fig. 5). Data on total inorganic nitrogen was only available for May with $N - NH_4^+ + NH_3$ as the major source. The average concentration of total inorganic nitrogen was 1.5 ug-atom N $litre^{-1}$. The N:P ratio in the water column was 0.6 for May, apparently indicating a nitrogen deficient system. Particulate chlorophylls during Stage I ranged from 10 to 18 mg m^{-3} and primary organic production was estimated at 0.6 g C m^{-2} day^{-1} for May, 1976. Thus, it is reasonable to assume that during this stage, there is continuous utilization of dissolved nutrients by phytoplankton that is compensated for by regeneration processes within the water column and the water/sediment interface. In a shallow water environment, such as in the case of Chautengo Lagoon, regeneration and mobilization of nutrients can be favored by biological, physical and chemical processes. (Okuda, 1960; Pomeroy _et al._, 1965 and Nichols, 1966).

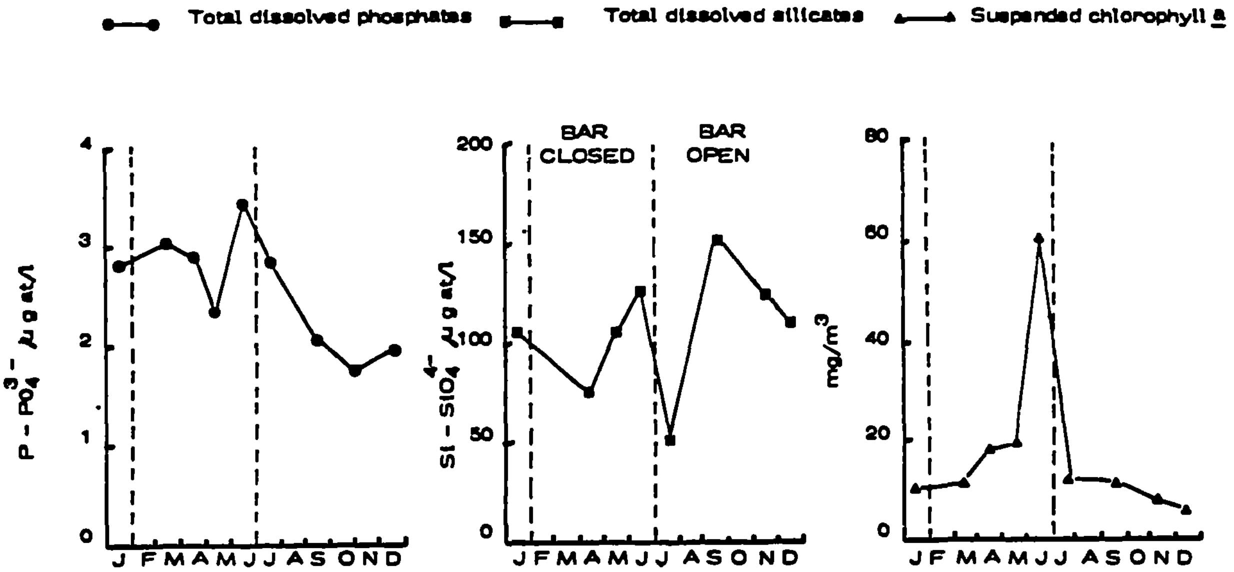

Fig. 5 Monthly variations in dissolved phosphates, silicates and suspended chlorophyll a in Chautengo Lagoon, during 1976.

Stage II Beginning of the rainy season, filling of the lagoon

The large increase in the volume of the lagoon, following the first rainfall, was also marked by an increase in the total quantities of all the dissolved nutrients and the particulate chlorophylls. During this short lived stage (one month), the mean concentration of total dissolved phsphorous in the water averaged 3.2 ug-atom P $litre^{-1}$, while total dissolved silicates averaged 120 ug-atom S $litre^{-1}$. The average concentration of total nitrogen, on the other hand, remained low with a value of 2.41 ug-atom N $litre^{-1}$ with $N - NH_4^+$ plus NH_3 as the major source, following in order of importance $N - NO_3^-$. The N:P ratio in the water column remained low with a value of 0.7.

The first rains of the season cause considerable flash flooding and runoff from low-lying lands bordering the lagoon. Such runoff provides a temporally more important source of nutrients than the river discharge and regeneration processes within the lagoon. In Fig. 6 are shown the variations of the total dissolved phosphorous and silicates contained in the lagoon waters. During Stage II the phosphorous reservoir increased from 1.5 to 5.0 metric tons, while the dissolved silicate increased from 60 to 170 metric tons. Particulate chlorophylls increased from 18 mg m^{-3} to 60 mg m^{-3} and primary organic production from 0.6 to 1.4 g C m^{-2} day^{-1}.

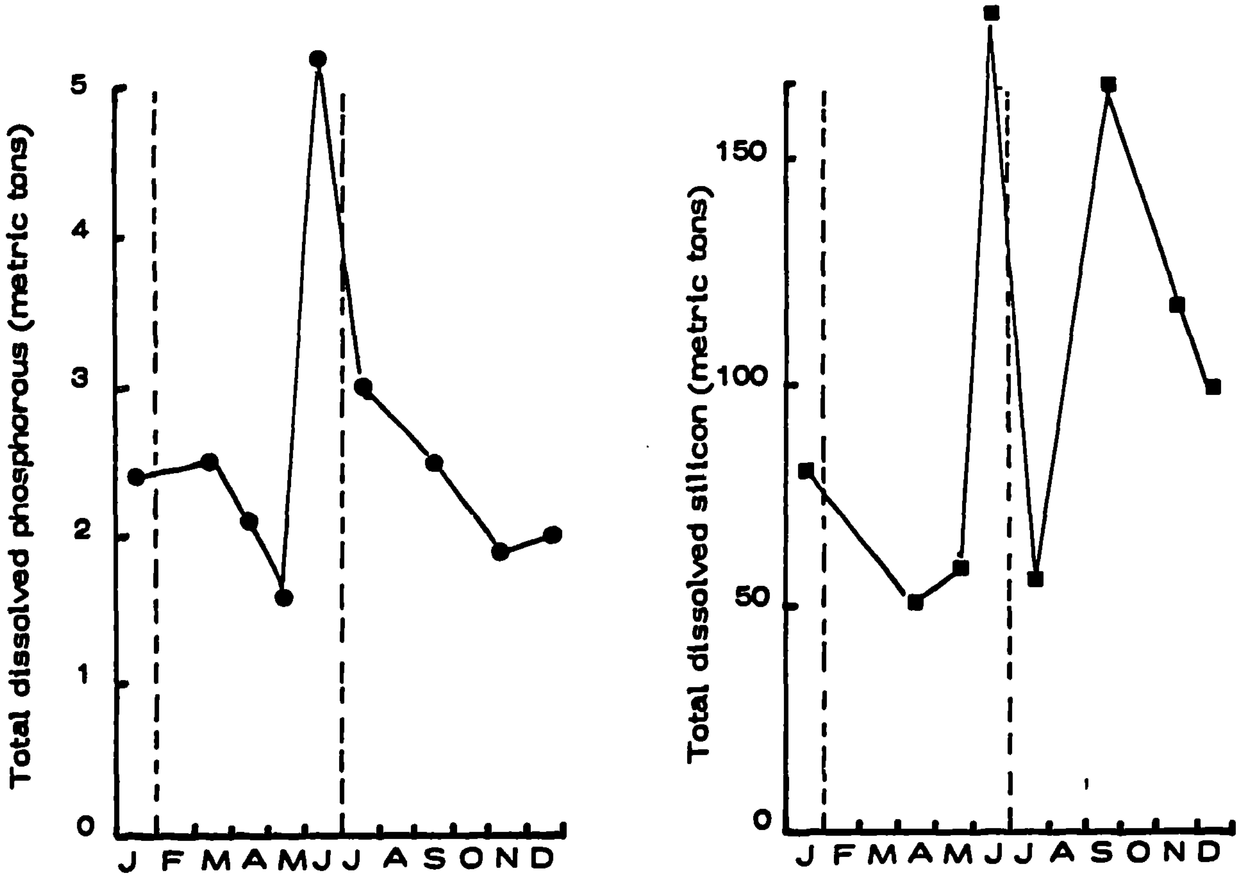

Fig. 6 Changes in the reservoir of the total dissolved phosphorous and silicon in the water of Chautengo Lagoon, during 1976.

Stage III <u>Opening of the bar and discharge of lagoon water to the sea</u>

Following the opening of the bar, there is an initial period of discharge of lagoon waters to the coastal zone until the lagoon reaches a stable level that varies with the mean sea level. During this short period there is a considerable amount of dissolved and suspended material exported to the littoral zone.

The total dissolved phosphorous and silicates lost to the sea were estimated at 2 and 120 metric tons, respectively. Presumably a considerable amount of particulate organic matter was also exported to the sea if we consider the changes recorded in the concentration of the particulate chlorophylls from 60 mg m^{-3} to 10 mg m^{-3}. However, it is necessary to point out that at the time of the July, 1976 sampling the mean salinity of the lagoon had changed from 10.3 per thousand, recorded in June, to 18.5 per thousand, recorded in July, thus indicating that tidal exchange with the sea had already started.

The average concentration of total dissolved phosphorous in the water remained within the ranges previously recorded which was 2.8 ug-atom P litre^{-1}, while total dissolved silicates declined from 110 ug-atom Si litre^{-1} to 50 ug-atom Si litre^{-1}. The average concentration of the total inorganic nitrogen increased slightly over previous values: 5.2 ug-atom N litre^{-1}, mainly from $N - NH_4^+ + NH_3$ and $N - NO_3^-$ sources. The concentration of $N - NO_3^-$ increased particularly where the Nexpa River discharges into the lagoon. The N:P ratio during this stage increased to a value of 1.9. Primary organic production declined considerably to a value of 0.32 g C m^{-3} day^{-1} during this stage.

Stage IV Tidal exchange with the littoral zone

During this period, which lasted approximately seven months, there was a gradual decrease in the concentration of total dissolved phosphorous, total inorganic nitrogen and suspended chlorophylls in the lagoon waters. The dissolved silicate concentration rose to a maximum in September and then steadily decreased toward the end of the stage (Fig. 5). In this period of more steady conditions following the initial rains, the river assumes an important role as a nutrient source. Consequently, the concentration of dissolved nutrients in the water is the result of a mixture between the river and seawater sources of these materials. In Table 6 are shown the input of dissolved nutrients by the Nexpa River into Chautengo Lagoon, with figures taken from July through December, 1976 (Mee, 1977). Processes of uptake and regeneration of dissolved nutrients are also important in maintaining a continuous supply of particulate and dissolved materials to the littoral zone.

The ecological implications of the initial discharge of dissolved and particulate materials followed by their less dramatic but coninuous flow to the littoral zone during Stage IV were not established. For lagoons, such as Mitla and San Marcos, where Stages III and IV are not existent, there is a gradual accumulation of runoff materials into their basins. In the particular case of Mitla Lagoon this gradual accumulation of nutrients has led to a high standing crop of phytoplankton (with chlorophylls ranging from 0.2 to 0.7 g m^{-2}). This standing crop appears to be almost entirely maintained by nutrient regeneration. The large oxygen demand of such a biomass leads to a water column in which the water adjacent to the sediments may become diurnally anoxic or, following seasonal stratification of the lagoon, completely anoxic.

Table 6. Variations in the input of dissolved nutrients into Chautengo Lagoon by the River Nexpa during July-December, 1976 (After Mee, 1977)

Date	River flow m sec^{-1}	Si - SiO$_4^{4-}$ ug-atom Si litre^{-1}	Total dissolved P ug-atom P litre $^{-1}$	Total inorganic N ug-atom N litre^{-1}
18/6	4.6	212	4.18	1.81
11/9	8.5	245	2.60	-
2/11	14.2	260	2.93	2.20
9/12	-	300	2.54	2.00

Apparently Mitla Lagoon is at a steady state, with a high concentration of carbon, phosphorous and nitrogen found in the sediments, which seems to indicate that the annual supply of nutrients to the lagoon is accompanied by similar loss to the sediments. The effects of isolation on San Marcos Lagoon, which is more saline and shallower than Mitla, is to produce initially hypersaline conditions and following that to dry completely, with the exception of the narrow meandering channel that occasionally communicates the lagoon with the sea.

CONCLUSIONS

The previous discussion illustrates to what extent the climatic conditions influence the hydrography and, as a consequence, the chemistry of the tropical coastal lagoons considered in this study. It was also observed that the morphology of the lagoons and the amount of the runoff which they receive determines whether or not they will communicate with the sea during the rainy season. On the other hand, the loss of particulate and dissolved materials to the sea, following the opening of the sand bar, effectively prevents the eutrophication of the lagoons.

A general outline of the most important factors that will insure the viability of the studied lagoons are the following:

1. Steady input of river water

2. Seasonal communication with the sea

3. A period of time (as yet undetermined) of mixing and exchange with the littoral zone.

The climatic stresses on these lagoons are the most important factors to be considered in any management planning. Nevertheless, it is also necessary to gain a better understanding of the ecological impact caused by the opening of the sand-bar on the adjacent coastal areas as well as to assess the period of time necessary to insure the proper biological exchange. This information is essential before decisions concerning the management of these lagoons can be reached.

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BIOGEOCHEMISTRY AND GEOMICROBIOLOGY OF LAGOONS AND LAGOONARY ENVIRONMENTS

by

W. E. Krumbein

I. The definition of lagoons given by F. B. Phleger (1978) for this meeting or by the "AGI Glossary of Geology" corresponds very well with annotations given for comparable but slightly different environments such as the "Wattenmeer" described in numerous publications by H. E. Reineck and collaborators. One feature in addition to the geological and geomorphological descriptions given above is the approach to lagoons as ecosystems (Reineck, 1978). Another dimension of terms then has to be added. The classical definition talks about "a shallow stretch of sea water or a salt water lake separated from the sea by a low, narrow, elongated strip of land such as a reef, a sandbank, a spit or chain of small islands and sand banks". As far as ecological and biological approaches to lagoons are concerned, some dimensions have to be added (Lasserre 1977). In biological approaches terms such as "mangrove", "protected environments", "unbalanced" or "stable ecosystems" are encountered. In ecological terms lagoonary environments are regarded as "immature" or "progressing ecosystems". Large differences in opinion may occur. The lagoon systems are called "robust ecosystems" or "fragile" ecosystems by different authors.

In terms of exploitation for human demand certainly the "mangals", the French "etangs" and the broad strips of "Wattenmeer" on the Dutch, German, and Danish coasts have been most important for and also most degraded, if not devastated, by human needs. Common features among these three systems that are described in the literature (e.g., Lasserre 1977 for a summary) are: extremely high productivity, sometimes coupled with sudden catastrophies and perturbances of the system; and difficulties in defining the degree of maturity which arises from the fact that most lagoonary systems are extremely young. The geological energy which may have important impacts on chemical and biogeochemical energy (i.e., biogeochemical cycling of materials) is high, which is expressed by progression of morphological features as well as by fast successions of ecosystems and biochemical balances. The interface between land and sea with the various input mechanisms for terrestrial and marine materials, which have the tendency to get trapped in the lagoon, leads to the high variability and also different ecological interpretations given above. Lasserre's (1977) comparison, derived from my own observations and the literature (Morowitz, 1968) can be applied as well to our biogeochemical approach to the system:

"Lagoons are regarded as machines of biological nature, kibernetic systems", which process, transfer, and upheave enormous amounts of energy and chemicals. No wonder that the controversial discussions about energy and material levels in the trophic foodweb, which took place mainly between Odum and Rigler during the First International Congress of Ecology, focussed themselves very soon on reef and other lagoonary ecosystems. The II INTECOL Conference will also deal with these environments, especially mangals. Whatever is used as units of transfer of mass or energy in these systems, be it biomass, expressed in protein or number of organisms; Joules; calories; or concentration of nutrients such as C, N, P, S, one of the most astonishing features will not be considered if one omits speed and acceleration as terms and units. Energy alone is not the most outstanding feature of lagoons but rather the speed of transfer of energy will be the ultimate key to understanding these environments and ecosystems, their development and their potential for expoitation by man.

Going by bicycle or walking, "biking" or "hiking", is neither difficult nor dangerous. Using a car needs a special permit, going by jet is restricted to very few persons. However, though "driving" and "jetting" are subject to special conditions and permits in human societies, no one has to get a "permit" to take advantage of the enormous "drive" of such unbalanced and rapidly developing and "cycling" systems. The damage done to very productive and rapidly cycling systems can by far exceed the damage and degree of destruction excerted by human exploitation of stabilized "mature" ecosystems.

We often regard the interrelation between the inorganic geochemical cycles and the driving and speeding biogeochemical impact exerted by the entire life system as an enormous spaceship containing a dynamic system and moving with progressive speed. The scientific approach to Earth evolution and to the evolution of ecosystems since the Precambrian is usually to look at it metaphorically as a huge spiral, piling up energy in biosystems at constantly accelerating speed against the apparent laws of thermodynamics. This contradiction can easily be explained and solved by applying the approach of Prigogine and Glansdorff (1971) which has been determined as "steady state thermodynamics" or "non-equilibrium-thermodynamics" meaning that more and more energy has to be provided to protect fast and productive ecosystems from the consequences of the 2nd law of thermodynamics. The consequences of this principle and approach for ecosystems are demonstrated very nicely in lagoons while the consequences for the evolution of ecosystems have been elaborated by Riedl (1975) in his book "Die Ordnung des Lebendigen".

With the background of the above thoughts on lagoons, lagoonary ecosystems, and their dynamics, we may now try to find a definition in microbiological or biogeochemical terms for these systems. The interrelation of the biochemical with the geochemical cycles will be consequently stressed to some extent.

II. In biogeochemical terms lagoonary systems can be regarded as the "gearing system" of a semimodern "butter cask" or "churn" where very slow but later accelerated turning of a handle makes it easier and easier to bring the cask itself to enormous speed and subject the cream to increasing centrifugal forces. In some laboratories one still finds the same system operating in the small centrifuges screwed to the rim of the desk. Another and maybe better image of the system may be derived from the "humming-top" or "magic knob" games we used to play as children, where forces, i.e., energy, are piled up in a semistatic system. When one stabilizes energy input at a certain level, the system will remain static. By increasing or decreasing the energy input one will decrease or increase its cycling speed. As soon as we increase energy input beyond a certain point, the "magic knob" or "humming top" will fly away, break or at least change its colour, its music or shape according to its making. The biogeochemical balance will break and "export" of energy will be a consequence. Export may mean heat flow, sedimentation, or transport and transfer into the open sea. Also sedimentation at a certain speed will ultimately destroy our "toy" because it will fill up the lagoon at increased speed, as we shall see.

If, on the other hand, we decrease energy input, the "humming top" will turn more slowly, again change its colour or sound or temperature (or population dynamics) until, finally, it falls and drops dead. Sabkhas of tropical environments are lagoonary "humming tops" almost completely dead through decreasing energy input, as we shall see later.

In geochemical terms the lagoon is the centerpoint of two constantly changing and developing energy flows, one from the continent and one from the open sea. Energy comes directly (physically) by wave movement, water flow and sediment transport and chemically by import of nutrients and chemicals (also pollutants). It comes furthermore by sun irradiation and evaporation. In tropical areas seasonal fluctuations are less marked and intensive and very often energy input and nutrient input becomes unidirectional, when e.g., desert conditions are prevailing on the land side and no major streams are entering the lagoonary system. In these cases single events like "desert sheet floods" may, however, drastically change the direction and speed of events in the biogeochemical cycling. In biogeochemical terms the lagoon can be regarded as the centerpoint of four large reservoirs from which material and energy are transferred into it. The biological mill-wheel will pick up some of the energy and some of the materials to incorporate it into its own steady state system which as a result turns faster and faster, speeding up the reactions and storing the products, until a maximum productivity is reached and energy uptake gets limited again.

The four reservoirs are as follows. (1) Endogenic forces which create the system and keep it dynamic, in some cases (e.g., the Graben system of the Red Sea and Gulf of Aqaba, with its constantly changing coastline). These forces include those which effect the dynamics of the sea-floor regulating the Indonesian coastal lagoons and the consequences of plate tectonics regulating ice-times and hence the coastline all over the world during the past 10 000 years. These forces take care as well of the constant supply of nutrients because without relief energy no weathering and liberation of nutrients from rocks would take place. (2) Sun energy which drives most of the productive processes within the lagoon ecosystem and speeds up the cycle of reduction of carbon to reduced carbon compounds. Theoretically, however, chemosynthetic energy transfer and carbon reduction is possible to some extent and does take place in these systems. (3) Import of energy and nutrients from the sea and export of chemicals and/or biomass not needed or fixed physically to the system. (4) Import of nutrients and sediments from the terrestrial side, including nutrients in the form of chemoorganotrophic energy (organic matter). The confined system of coastal lagoons will usually respond to these major forces by turning at a faster speed rather then by expansion, since no space is available for the latter. Principally greater speed will result in faster export, mainly by sedimentation. Since the coastal energy usually counteracts the export tendency while rivers ultimately create certain outlets, the chances are high of annihilation of the system within geologically extremely short time periods, expecially in arid regions. For these reasons fossil lagoonary systems are relatively rare and difficult to map in geological formations. They are, as Phleger (pers. comm.) says, ephemeral.

By describing examples of lagoonary biogeochemical systems from a tropical arid system and comparing them to the north-German marshes of the Wadden Sea, some of the functional principles and also some of the descriptive characteristics in Phleger's papers (this volume) will be explained. Also, I will try to explain to some extent the definition given below of biogeochemical principles in lagoons.

Biogeochemistry of lagoons can be described as the ephemeral upheaval of reduced organic compounds and speeding up of biochemical reactions as a consequence of constant exchange of lagoons with the open sea in cases of hypersaline systems and with the sea and the continent in the case of brackish and freshwater lagoons.

III. A common feature of almost all lagoonary systems is high organic production by photosynthetic activities. Many authors so far have stressed the densities of phytoplankton in lagoons and the contribution of this part of the ecosystem to overall productivity data. Odum (1975) gives productivity data for lagoons and reef lagoons which exceed almost any natural system and reach productivities of artificially fertilized and managed (and highly unstable) man-made agricultural ecosystems. Recently several papers have been published (e.g., Krumbein *et al*, 1977; Krumbein *et al.*, 1979; Por *et al.*, 1977) which clearly demonstrate that in coastal tropic lagoonary environments benthic production by far exceeds the phytoplankton production. The same is true for mangals and their populations. If we ask how and why these high productivities can be maintained we will find some explanations which are redundant. Analyses of nutrients in waters of the sea of terrestrial sources, and of the lagoonary system itself, will show that the ratios of phosphorus and nitrogen (to name only the major limiting nutrients) under normal conditions are exactly the same in the waters as needed in the organisms living in them. The explanation is relatively easy to understand in terms of B. Loveluck's hypothesis of "life" being an "entity" (Gaea) taking care of itself on our spaceship (Loveluck, 1979). Availabilities of phosphorus according to these theories should limit the whole system, while nitrogen is constantly fixed by microorganisms and mainly by prokarkyotic bacteria (chemoorganotrophic bacteria and photosynthetic cyanobacteria) at a rate controlled by P availability.

This does not hold true for temperate regions with import of nutrients from the mainland. In these regions it is obvious that nitrogen is limiting, that phosphorus is available in excess and that still no major nitrogen fixation occurs to balance the P excess. The explanation is simple for two reasons: (1) P is cycled more readily and faster than N and (2) less energy is needed to fix and release P from the biological phase to the mineral phase and vice versa. Energy in the form of light energy is less available in these regions and very often a limiting factor for the whole system. It was suggested by some authors a few years ago that eutrophication in coastal lagoons could be much faster if P in detergents was replaced by N-containing compounds since N is the real limiting factor of such systems. I do not believe in this. I would guess that N would get fixed in the sediments which might be anoxic and eutrophic at a faster speed in the deeper parts. But in temperate regions the real limitation of productivities in shallow lagoons would be light limitation on a total basis. For moderately non-polluted regions with high irradiation P must limit the system, while in temperate regions heavily polluted, N may become limiting and in addition at high concentrations of both elements other limiting factors such as light penetration, toxins and cycling speed will be the real limiting factors. In some cases also carbon dioxide deficiencies may be responsible. Lately carbon dioxide has become more and more available, however, as a result of drastic increase of carbon dioxide production by fossil fuel burning and deforestation. No doubt, all considerations on nutrient cycles and global productivities as well as on productivity of restricted areas will end at the conclusion that it is difficult to estimate man's influence on ecosystems at present since the whole world is emerging from an ice-age and therefore these natural changes are very difficult to separate from man-made changes of the system. During the "Dahlem conference on fossil fuel burning and its impact on global chemical cycles" (Stumm, 1977) it was stressed that lagoons and other coastal environments in fact are "key-ecosystems" for study of global biogeochemical cycles of elements. The continental photosynthetic area is more or less decreasing, though the productivity of some areas has been intensively increased by agricultural use. The large ocean reservoirs have probably been changed very little by human influence. But the crucial points of investigation of biogeochemical cycles are coastal lagoons for several reasons:

(1) The biogeochemical cycles of C, N, O, and P are interlocked in the biosphere. The release of man-made products of various kinds may largely alter the biological equilibrium of these cycles. It is important to state that the present equilibrium of N and O in the atmosphere is thermodynamically instable. This means that the composition of the atmosphere is ruled by Prigogine thermodynamics rather than by classical thermodynamics. In consequence, biogenic energy constantly is moved into the atmosphere to keep this equilibrium necessary for life. We have calculated the amounts of N and P necessary to balance carbon dioxide produced by the two above mentioned mechanisms in case this in turn could be fixed by biological productivity increases. It was found that fertilizer production as well as phosphorus mining and use in detergents are not sufficient to balance this. Two main other explanations may be envisaged, one of which is intimately related to the topic of lagoonary research.

(a) Changes and uncoupling of the biologically controlled interactions in the biogenic "steady state system" of the atmosphere may alter the critical relationships between O and N in the atmosphere thus producing acid rains which, in turn, will release large amounts of nitrogen and phosphorus and sulfur from rocks by increase in the speed of weathering which again is subject to biological control by many means (Krumbein, 1972). Hereby increasing amounts of P, N, and trace elements would be washed into the rivers and channelled to the sea.

(b) This together with other factors would increase productivities, mainly in estuaries and coastal lagoonary environments.

(2) Since terrestrial production decreases at least the storage capacity of soils for organic materials, we have to look for large reservoirs taking up these enormous amounts of reduced organic substances, nutrients, and trace metals which are transferred at increasing speed into coastal environments. Again coastal areas are the natural systems which have to be examined and where we might be able to detect changes first.

(3) With the background of global imbalances and speeding up of certain biologically linked biogeochemical cycles, we have to look for the crucial points of the globe where carbon and nutrient fluxes and changes of these would be detectable and where possible sinks are available. The crucial points in my opinion are the margins betwen the terrestrial and oceanic ecosystems, i.e., lagoons, estuaries, and coastal waters of any kind. Mainly it will be semi-closed systems which might get or already be the "kitchen-middens" of our modern system driving cars with fossil fuels, agriculture with artificial fertilizers under decrease of humic matter enrichment in soils and deforesting for agricultural and other purposes again combined with transfer of organic compounds to the sea. The establishment of a net-work of monitoring stations in temperate (fully human-influenced) areas and in tropical and arid (less man-stressed) parts of the world's coastlines is therefore urgently needed.

IV. It is the aim of the planned establishment of a governmental "Institute of Coastal Biology" in Wilhelmshaven, Germany on the North Sea coast to solve some of the problems discussed above by careful analysis of biogeochemical cycles in natural ecosystems (for example, heavily polluted and disturbed lagoons of industrial zones such as the Jadebusen or Wadden Sea or tropical lagoons on arid coasts with no influx from terrestrial sources as reference systems. The institution shall also study possibilities of taking advantage for human society of the productivity of these areas and the potentials in them by intensifying research on the development of agricultural methods in mangals, lagoons, and other coastal ecosystems. This could be achieved by fertilizing or taking advantage of fertilized salt-water and irrigating salt-water adapted plants selected for man's purposes.

If one looks at the tremendous effort of 3 000 years of selection and almost 200 years of scientific research on barely 20 plant species from the savanne-tropical rainforest border which maintain the present day protein, fat and carbohydrate production; if one considers in turn the tremendous potential of hundreds of plant species never explored for their potential use for man, it is evident that the increasing efforts on salt-water plant cultivation, which has barely begun, must be doubled and tripled.

In addition to this, the surface area of the world which is readily available for agriculture approximates only 30 % of the terrestrial area. Out of these almost 80 % is already in use. The main limiting factors for agricultural surface use are relief and water availability. Low relief and high water availability throughout the year are necessary for agriculture. Coastal areas, namely in tropical regions adjacent to deserts, are the best areas in terms of relief and accessability. If one found enough salt-water resistant plants useful for men, or if one bred plants more useful for men than in their wild-type form, one would open tremendous potential areas of intensive agriculture in the lagoons (comparison between rice-fields and mangrove) and on the coastal strips adjacent to lagoons (comparable to the Roman Erythrea area or the Dutch and German marshes with their tremendous food production potential). Let us go one step further and regard the ancestors of our present day culture plants in terms of usefulness for a technical civilization. Rice, corn, wheat, soy-beans, apples, whatever we take we will arrive at the picture of an ancestor comparable to modern grass, useless brushes, and poor trees with bitter and hard fruits.

This opens perspectives to many lines of research in coastal biology, which we intend to investigate, during the coming decade. Studies of coastal biology will certainly also include polluting influences of industrial society by analysing metal absorption capacity of lagoons and estuaries and the potential danger of rapidly increasing eutrophication, both topics for geomicrobiological research. From the above mentioned allusions to the double-mill-wheel with its influence from terrestrial and men-influenced energy sources, and its oceanic and natural energy sources, it becomes evident that such studies cannot be restricted to temperate regions adjacent to industrial countries. The coastlines of developing countries, e.g., the Persian Gulf, the coasts of the Red Sea etc., have to be included in these studies for many reasons:

(1) These are the coasts and regions where famine and starvation have to be counter-acted.

(2) These are the natural undisturbed and simpler systems.

(3) Seasonal fluctuations of water supply, climate, precipitation, and productivity are less accentuated in these areas, thus enabling faster and more efficient inventories of coastal ecosystems.

(4) The variety of organisms is smaller in these systems though the productivity per species is higher.

(5) The energy input is unidirectional in lagoons with no freshwater supply which again facilitates research on the food-web of the ecosystem and the biogeochemical cycles.

(6) Many of these environments are hypersaline which rules out many eukaryotic organisms including both plants and animals to some extent. Biogeochemical cycles and balances therefore can be studied much more easily in these areas.

(7) The evaporative pumping system with brine reflux clearly demonstrated for some of these systems (e.g., Cohen et al., 1977; Por, 1972; Poretal, 1977; Krumbein *et al.*, 1979) is an excellent model for biogeochemical and geomicrobiological studies because gradually all eukaryotes are excluded and ecosystems develop which have only small numbers of participating species, e.g., stromatolitic microbial mats.

(8) These systems in many places of the world are changing more rapidly than any other lagoonary environment. As a matter of fact, we have studied small lagoons and near-shore pools which have run through a whole cycle of the mill-wheel within less than 3 000 years.

The suggested and planned "Institute of Coastal Biology" therefore will have to focus:

(1) on plant adaptation to salt-water,
(2) on biogeochemical cycles,
(3) on polluting influences from the main-land such as trace metals and organic pollutants such as oil spills and insecticides or other man-made organic substances
(4) on comparative studies in tropical arid areas.

It is the aim of this contribution to stress these points. It seems that the governmental authorities in the Federal Republic of Germany are in fact inclined to initiate such an institution as soon as possible in the city of Wilhelmshaven adjacent to the largest lagoonary environment the German coast has to offer.

V. In conclusion we may summarize here some of the findings we collected in our studies on coastal lagoons along the Gulf of Aqaba in the years between 1971 and 1977.

Approximately 3 500 years ago global sea-level rises as well as local rift tectonics created many new embayments of small scale along the coast of the Gulf of Aqaba on the Sinai side. Those have been rapidly filling and producing small closed off strips by two major morphogenic forces:

(a) reef growth and

(b) fast and the erosive action of desert sheet floods deposition of sediments by the high relief energy. These have competed in closing off back-reef lagoons of classical sand bar and gravel bar character.

Evaporation is extremely high reaching almost 5 000 mm per annum compared to annual precipitation of less than 30 mm. Therefore sea water inflow, evaporation, and reflux of brine through the porous material of reef and gravel have been established. Gradually macroorganisms were excluded from these environments. Some of the lagoons, however, have developed ephemeral mangals (Por *et al.*, 1977) which are the youngest and simplest mangals of the world for mainly two reasons: (1) no detrital organic matter is imported, and (2) the climate regime is the limiting borderline for reef and mangal development further north. The exclusion of macroorganisms continues until a lagoonary stage is reached where only mytilids, *Pirenella*, *Cassiopeia* and a few flat fish survive. Finally, these are excluded at salinities of approximately 49 to 53 %.

At this point the development of extant stromatolitic microbial ecosystems is initiated. Phosphorus supply is extremely low in the beginning. But any atom of P which is imported by evaporative pumping and inflow through the inlet is fixed and stored in the system since no fish or macroorganisms are exporting the organic material produced. On the contrary, benthic productivity which exceeds planktic productivity in these environments by factors of 10 to 100 upheaves in extensive cyanobacterial mats. These compete for space with the evaporative minerals deposited in the same lagoons by mainly two principles: (1) growth of mats is replacing evaporative minerals physically by emerging from the water into the air, (2) sulfate reduction running at high speed by *Desulfovibrio* and possibly many other sulfate reducing microorganisms are decreasing tremendously the amounts of gypsum precipitated from these waters. Thus, the lagoons become filled with organic matter, calcium carbonate of biogenic, or rather biogeochemical origin, and some gypsum. Most of the halite is refluxing to the open sea through capillary action in the underground as soon as the brine becomes heavy enough to sink through. Occasionally sheet floods and sand-storms enhance the process as well as partially biogenic and partially physical heliothermal heating and stagnation (e.g., Solar Lake). Finally, the productivity of the lagoon becomes gradually "faster and faster" in terms of productivity because more and more phosphorus and nitrogen get trapped in the system. The water gets shallower and also evaporation rates increase by increase of surface: volume ratios.

Later the lagoon is filled, and a Sabkha develops. The last remainders of productivity are embedded in halite crusts which the Bedouins of Sinai use for the classical biologically influenced salt mining. Finally sand and organogenic stromatolites are upheaved to a degree that water already evaporates completely far below the sediment surface and light penetration zone. Therefore in the humid layers no productivity takes place, nutrient cycles become abiogenic, gypsum is precipitating at fast rates within the sand and cementing the layers at depths between 50 and 80 cm below the surface. At the surface itself bitter salts are precipitating, thus killing any trace of life. Ultimately the evaporative pump stops because the sand below gets too strongly cemented. The whole Sabkha will be buried below desert dune sand or gravels from sheet floods, until new endogenic forces create new embayments and the cycle starts all over.

This very brief summary of (1) trapping of nutrients, (2) increase and speeding up of biogeochemical cycles in a stromatolitic microbial mat system with high storage capacity of the produced organic matter leading often to petroleum source rocks, (3) peaking of production in the shallow water lagoon and Sabkha, (4) decrease after complete filling, and (5) sealing off by evaporative forces underneath the surface has been described in part in published papers. The data for other parts of the investigations are still being processed.

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Processes in the sediments and at the water-sediment interface

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THE SEDIMENT BUDGET

Generally, lagoons contain a complete range of sediment assemblages from coarse sands or even gravel and shell banks to very fine grained muds. This variation reflects the wide range of prevailing hydrodynamic forces. It follows that there is a certain "equilibrium" between the areal distribution of these forces and types of sediment.

This statement is somewhat provocative. Accurate measurements are needed to verify how far it is true and how large existing deviations are from the state of equilibrium.

One important deviation is that, considered over a longer period, most lagoons are depositional, i.e., more sediment is coming in than going out, but undisturbed particle by particle deposition which would allow a time series study is extremely rare. In fact, lagoon deposits are mostly reworked in a season or less to depths of a few decimeters whereas net deposition is at best only a few centimeters. An important agent is bioturbation.

Another deviation is that deposition will exceed erosion in one period, but that erosion will dominate in another. Furthermore, the closer equilibrium is attained, the more it is of a dynamic character: the upper sediment layer being moved contantly from one place to the other, and back.

These considerations are of great importance in the study of the properties of and the processes in the sediments, especially from the point of view of seasonal variation. Such variations are not necessarily restricted to temperate and cold latitudes, but take place in the tropics as well. An extreme example is the occurrence of tropical storms; the changes of dry and rainy seasons are less extreme, with corresponding fluctuations in river flow. In the following, a number of general characteristics which could profitably be studied are discussed.

Coarse and fine grained materials can enter a lagoon from the land, mainly by rivers, and from the sea. In the case of fine grained material, which is distributed fairly uniformly in the water column, amounts and sources can be traced with relative ease by measurements in strategic localities such as tidal inlets and the lower reaches of rivers. Such measurements, however, should be continued over long periods to evaluate periodic and aperiodic changes. Transport measurements of coarse grained material such as sand are much more difficult, since the amounts in suspension vary greatly with wave and current strength, whereas at the same time large amounts are carried close to the bottom (bed load). Generally the best approach is to measure bathymetric changes in a lagoon over a number of years.

A good estimate of the sediment budget is of importance to understand the properties of the lagoon deposits. As already stated, particle by particle deposition is very rare, but also irregular net deposition leads to a certain preservation of past characteristics. This is important, for example, in connection with the studies of pollution in lagoons: in cases of over-all sediment accretion there is a greater possibility of accumulation of pollutants than in cases of overall erosion.

THE ORGANIC MATTER BUDGET

A simple closed cycle of organic matter is one of net production in the water column and net decomposition in the bottom after which the products of mineralisation return to the overlying water. Such a cycle occurs, however, only in basins without appreciable horizontal water movements. In lagoons lateral water movements dominate. Import of organic matter to and export from adjacent areas is the normal state of affairs. In most lagoons the import is greater than the export. This characteristic is an indication of their relatively large fertility. A reliable estimate of the difference between import and export is of great value from the point of view of the basic productivity. Obviously such a study is closely related to the study of sediment transport, since most of the particulate organic material in transit behaves like fine grained inorganic matter. It should be stressed, however, that net import of organic matter occurs even if there is no net import of inorganic matter.

In lagoons with a net import, most of the organic matter is stored on and in the bottom. Very high percentages of organic matter may then occur, especially in fine grained muds. More organic matter is added to this store by primary production *in situ*, either by algae or sessile plants. The fauna living in and on the bottom profits from the presence of this large amount of organic matter. Another part is consumed and modified by bacteria. The free oxygen in the sediment is easily consumed, so that most lagoon deposits are anaerobic.

Recently, the load of organic matter in many lagoons has increased dramatically. Although this might in principle lead to higher productivity, this seems rarely to be the case. Organic waste is seldom suitable food for estuarine benthos and density of valuable species is not often regulated by food, but rather by other limiting factors. Most extra organic matter is, therefore, decomposed by bacteria. In extreme cases decomposition activity in the overlying water becomes so large that anoxic water masses spread over large parts of a lagoon. Such conditions may be detrimental for the economic and recreational uses of lagoons. The limits of permissible organic loads are defined by rates of decomposition of organic matter (oxygen demand), rates of water renewal in the lagoon and rates of exchange between the water and the deposit.

Obviously these processes are interrelated. A rapid water exchange between a lagoon and the adjacent sea promotes relatively pure marine conditions inside the lagoon and assures a fast removal of decomposition products such as plant nutrients. It will also further the leakage of such products out of the sediments. Inversely, an isolated lagoon with little exchange with the sea will build up a greater reservoir in the sediments and the overlying water. Comparative studies and modelling of different types of lagoons will greatly increase our insight into these processes.

CONDITIONS IN THE SEDIMENT DEPOSITS

The two main processes determining the chemical conditions in a deposit are the rate of deposition of organic matter and the rate of renewal of the interstitial water. Since there is only a small amount of dissolved oxygen in sea water and a much larger quantity available as sulfate, anoxic conditions prevail. However, the rate of decomposition of organic matter proceeds very rapidly also under these conditions.

Modern methods of oxygen utilization measurement show that the "new" organic matter added to the sediment in the growing season is easily decomposed within the same period. If, nevertheless, total organic matter per m^2 of sediment in the upper decimeters is often much higher than the supply per m^2 of one season, this is due to "old" organic matter which does not or only very slowly participate in the cycle. Total organic matter percentages in lagoon sediment range mainly from 1-10 %; however, perhaps only 0.1 % is "active".

The composition and the fate of the organic matter resisting decomposition is only poorly known. Part of it will be terrestrial or derived from marsh plants. Another part may be imported from the ocean. In both cases the less resistant components may have been mineralized before the material settled in the lagoon. In addition the metabolic pathways of organic matter decomposition do not necessarily lead straight to complete mineralisation. A considerable amount is first degraded to dissolved organic matter.

This follows from the fact that the concentration of dissolved organic matter in interstitial water is greater than in the overlying water. Of this dissolved material, part will escape to the main water body of the lagoon and from there to the open sea. Another part, however, undergoes chemical condensation reactions in the sediment, leading to compounds with a higher molecular weight, among which so-called "humic matter". The condensation process may lead to redeposition of organic matter which will form a third organic component in the sediment resistant to decomposition.

The inorganic decomposition products of organic matter (phosphate, ammonia, silica and other trace elements) also dissolve into the interstitial water and concentrations of these substances are built up, possibly in orders of magnitude higher than in the overlying water of the lagoon.

These concentrations of the dissolved substances depend on the rate of mineralisation and the rate of renewal of the pore water. In quiet water bodies the rate of renewal is determined by relatively slow vertical diffusion processes which are caused by molecular diffusion assisted by moderate bioturbation and compression. The fairly regular fluxes of water and nutrients out of the sediments can be measured, for example by placing bell jars on the bottom, or by measuring vertical concentration gradients in the sediments. A typical replacement rate is perhaps once per season.

Interstitial water renewal in lagoons, however, generally proceeds with a much greater velocity aided by several mechanisms other than diffusion. As already mentioned, there are displacements of whole deposits. Benthic faunistic elements may plow the bottom several times per year to depths of decimeters. In areas with significant relief, such as lagoons with tidal channels and intertidal flats, there may be considerable percolation of interstitial water through the sediment. During periods of emersion, interstitial water evaporates, causing upward migration of pore water. In deepwater exchange, may be promoted by wave action (subtidal pump).

Which of these mechanisms or combination of mechanisms is actually important obviously depends on locations and structure of the deposits and the time of the year. It is also obvious that determination of the rate of interstitial water renewal will not be easy. Profiles of dissolved chemical species are mostly more vertically homogeneous than those in sediments with simple diffusion characteristics and are often quite irregular, so that they provide no information on exchange rates.

In lagoons with changing salinities, the salinity of the interstitial water responds with a certain time lag to the changes in the main water body. This provides a means of estimating rates of exchange. In a case recently studied by this writer, water renewal in the upper 30 cm appeared to be a matter of only a few weeks. Another study showed sudden release of nutrients from the sediment during strong winds after a period of quiet weather. Obviously, renewal does not proceed at a constant rate. It is the writer's impression that sediments in shallow lagoons are thoroughly "cleaned" in the winter season, at least in temperate and cold regions, so that an almost new start is made every spring. In severe winters also the benthic population is decimated.

An important question is whether the release of benthic nutrients influences primary production in lagoons. The following calculation may provide some guidelines. Let us assume a concentration of "active" organic matter of 0.1 %, an "active" sediment depth of 25 cm, a water column of 2.5 m and an interstitial water volume of 20 % (sandy deposit). Let us further assume that the organic matter is mineralized in 6 months and that it contains 1 % of P and 8 % of N.

Per m^2 about 500 g of "active" organic matter is present and 50 litres of interstitial water. Complete mineralisation would yield 100 mg of P per litre and 800 mg of N (chiefly ammonia). In the case of storage during 6 months the concentration of P and N in the interstitial water would increase to 3000 ug-atom $litre^{-1}$ of P and 48000 ug-atom $litre^{-1}$ of N.

Actual measurement of nutrient concentrations in interstitial water of lagoons seldom yields values of more than one tenth of these concentrations, whereas much smaller concentrations are usually due to the fact that pore water renewal is much more rapid than once in six months.

A gradual release over six months would add 0.2 ug-atom $litre^{-1}$ of P and 3.2 ug-atom $litre^{-1}$ of N per tide. Although low, such concentrations could promote primary productivity, especially in lagoons with a low nutrient content. It should immediately be added that, of course, a net benefit to estuarine productivity is only possible in cases of a net input of organic matter into a lagoon and releases from the sediment during the vegetative season.

A sudden release at the end of six months would raise the nutrient content in the overlying water column to 65 ug-atom $litre^{-1}$ of P and 1000 ug-atom $litre^{-1}$ of N, perhaps a hundred-fold increase. Such a "shock effect" would be extremely rare, but it happens on a more moderate scale in temperate regions at the end of summer and it may happen elsewhere under extreme meteorological conditions.

The two nutrients discussed above are just taken as examples. Several other chemical substances are enriched in lagoon sediments. A third nutrient is silica, which is liberated from buried diatom frustules. Release of dissolved silica from lagoon deposits may be an important erichment factor even for adjacent coastal waters since dissolution of silica is often a phenomenon located in lagoons.

Several trace metals are also enriched in lagoon sediments. The pore chemistry of trace metals is a complicated process. The factors involved are different speciation and solubility under oxic and anoxic conditions, including precipitation as sulfides or dissolution via chelation by "humic matter", and absorption and desorption processes. The behaviour of metals such as iron, manganese, mercury, copper, zinc, lead have been studied intensively in recent years by geochemists who have turned to lagoons and estuaries to explain part of their behaviour in the open ocean. For obvious reasons their studies tend to select areas of quiet and continuous deposition. It is stressed here, however, that most lagoon deposits are structures with only a short lifespan, certainly on a geological timescale, so that trace element storage is nearly always temporary.

Nevertheless, since many metals are bound to suspended matter in the water column, they become accumulated in lagoons and concentrations of dissolved metals in interstitial water may subsequently reach orders of magnitude higher than in the overlying water. In polluted lagoons the deleterious effect of a sudden release of heavy metals either by strong winds and currents or by human activity (dredging, fishing) should be reckoned with.

Also, a number of major inorganic components of sea water undergo significant concentration changes in sediments. Under anoxic conditions sulfate may vanish completely by reduction to sulfides. Potassium may be enriched by breakdown of feldspars. Calcium may precipitate as calcium carbonate, which can become highly supersaturated in interstitial water by the increase of CO_3^{--} through breakdown of organic matter. This only holds for marine muds in which a relatively high pH (>7.5) is maintained; in muds where pH is lower, enrichment of HCO_3^{--} far dominates over CO_3^{--} and calcium may go into solution.

A deficit or an enrichment of ions may also result from simple migration through the sediment. It seems, for example that neutral moleucles of $CaSO_4$ and $MgSO_4$, constituting 10 % of the assembly, migrate more freely than positively charged K, of which the movement is retarded by the clay minerals with a negative charge. Interesting changes in element ratios occur especially on high tidal flats in arid regions with long periods of emergence. The moving force is in such cases the capillary rise of interstitial water by evaporation in the upper layer.

It must, finally, be taken into account that in lagoons the main water bodies themselves may already have chemical element ratios deviating from the "normal" oceanic relations, for example, since such ratios are different in river water. A number of combined factors can be responsible for "abnormal" ratios in sediments, which may not easily be disentangled. For example, decrease of sulfate in a deposit may be due not only to bacterial reduction, but also to losses by migration. A comparative study of lagoon deposits in different environments will assist in unraveling such relationships.

SUMMARY

1. Lagoon sediments are moved and reworked more frequently than most other marine deposits. This leads to a dynamic equilibrium between sediment size distributions and hydrodynamic forces. The consequences of seasonal shifts in this equilibrium and of exceptional (meteorological) disturbances need further study.

2. As a result of these frequent disturbances, residence times of pore waters in the upper layers of the deposits are relatively short, but they show great variability. Several additional processes such as wave action, emergence at low tide, evaporation on tidal flats and bioturbation also influence these residence times. A comparative study of lagoons may shed light on the relative importance of the different processes involved.

3. Biological, chemical and physical processes in lagoon deposits cause drastic concentration changes for a large number of chemical species and the ratios in which elements are present in pore waters differ greatly from those in normal sea water. Most of the concentration changes result in the build-up of reserves of dissolved compounds in the interstitial water; some lead to depletion. Release of stored substances to the overlying water of a lagoon may be gradual, or follow a sasonal pattern, but it can also take place in an abrupt manner. The mechanisms of build-up and release and their influence or the productivity of lagoons need further study.

4. Organic and inorganic pollutants follow, as long as amounts are moderate, the same transport paths as their natural counterparts. The information obtained about storage in sediments of unpolluted lagoons can, therefore, be used as a basis for studies of the fate of pollutants as a first estimate of deleterious effects.

INORGANIC AND ORGANIC NITROGEN CONTENTS IN SOME COASTAL LAGOONS IN VENEZUELA

by

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INTRODUCTION

Several coastal lagoons and small bays have formed along the central- eastern coast of Venezuela. These areas offer favourable conditions for fisheries and recreation.

From the point of view of social and economic importance, special attention has been paid to these areas in order to preserve proper environmental conditions for aquatic organisms.

The purpose of the present study is to illustrate some features of the different forms of inorganic and organic nitrogen found in the Laguna Unare, Laguna Tacarigua and Laguna Las Maritas which are different types of coastal lagoons from a geomorphological view-point.

Laguna Unare has no continuous connection with the open sea. There is occasional exchange of lagoon water with the open sea through the mouth of Unare River during the rainy season, depending upon the tidal range and the water level of river and lagoon. During the dry season, (from early February to early June) the mouth of the river is closed because of a decrease in river flow. During this period the lagoon water is isolated not only from the open sea but also from the Unare River (Okuda et al., 1965a; Okuda, 1965; Okuda 1969). Laguna Tacarigua is connected with the open sea throughout the year through a small canal. The Guapo River and several streams around the lagoon supply a continuous flow of fresh water to in the lagoon (Gamboa et al., 1971; Okuda, 1969). Laguna Las Maritas is not associated with a river. Its source of water supply is from the rainfall and the open sea with which it is connected through a narrow inlet (Bonilla and Okuda, 1971; Bonilla and Benitez, 1972). Thus, these three lagoons have different topographical features.

For a better understanding of the relation between nitrogen content and topography, the overall observations of these three coastal lagoons were compared with those of Bahía de Mochima and Laguna Grande. These are not really coastal lagoons, but rather small bays with narrow mouths that allow a free flow of water from the open sea (Okuda et al., 1968).

DESCRIPTION OF THE AREAS

Three lagoons (Laguna Grande, Laguna Tacarigua and Laguna Las Maritas) generally have high temperatures above 30°C during the daytime, due to their shallowness. The general geographical features and hydrographical conditions of these coastal lagoons are summarized in Table 1 along with two small bays (Bahía de Mochima and Laguna Grande) in the same area (Fig. 1).

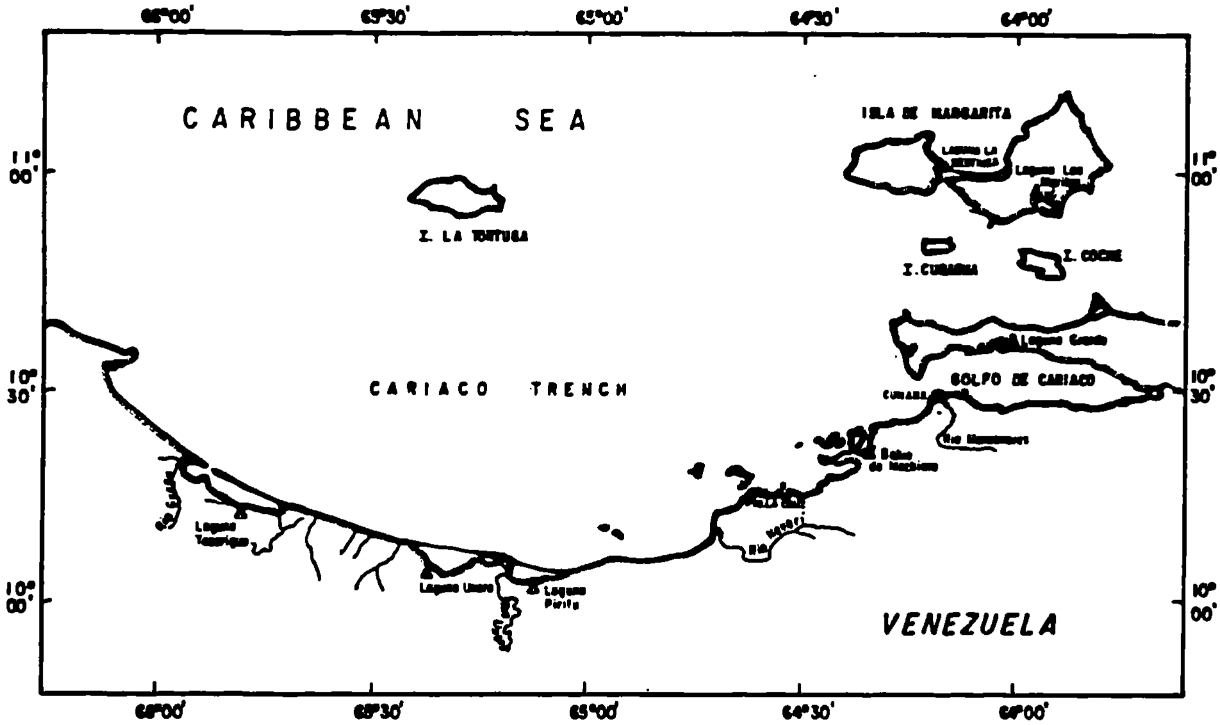

Fig. 1 Map of central-eastern Venezuela showing the location of coastal lagoons

Some factors, such as the stagnant inner water caused the restriction of water exchange with the open sea, the supply of fresh water, and high evaporation, are responsible for high variation in salinity of the three coastal lagoons.

The annual precipitation (Fig. 2) in the area of Laguna Tacarigua shows surprisingly high values (1,300-1,800 mm) as compared with the other areas (less than 800 mm). The lowest rainfall is in the area of Laguna Grande. In contrast with the precipitation, the annual evaporation (Fig. 3) in the area of Laguna Grande (3,400-3,800 mm) stands out sharply above the other areas, and the values of Laguna Tacarigua are the lowest (1,600-1,800 mm). Thus, the evaporation in the areas of study is more than the precipita-

Table 1. Summary of geographic and hydrographic conditions

Location	Mean depth m	Surface area km^2	Vol. of water x 10 km^3	Temp. ^{0}C	Salinity parts per thousand
Laguna Unare	0.47-1.52	45-64	13 x 97	24-37	17-95
Laguna Tacarigua	1.03-1.38	63	75	26-34	7.7-37.9
Laguna Las Maritas	2.4	9.4	23	25-31	36-44
Bahía de Mochima	19	10.5	196	19-29	36-37
Laguna Grande	11.5	3.2	37	19-28	36-37

tion with the exception of the area of Laguna Tacarigua for which there is not a big difference between the values for evaporation and precipitation. The inner water mass of these coastal lagoons tends to be a hypersaline whenever there is no supply of river water into the lagoons and not enough exchange of water with the open sea.

Prevailing winds in the areas of study are from the northeast all the year round, with strong sea breezes during daytime which decrease after sunset.

Laguna Unare

Laguna Unare is separated from the Caribbean Sea by a sand barrier, having a width of 200-600 m. The long axis extends from east to west, about 22 km, and the short axis is about 5.5 km in a north-south direction. Most areas of Laguna Unare have a flat bottom with less than 2 meters depth, even in the rainy season. Of the three rivers connecting the lagoon, the Unare River is most important for inflow of fresh water (Fig 4).

There is considerable annual variation of the surface area and the volume of water of the lagoon between the dry and rainy seasons (Table 1): the mean temperature and salinity range from 24^{0}C to 37^{0}C and from 17 per thousand to 95 per thousand respectively.

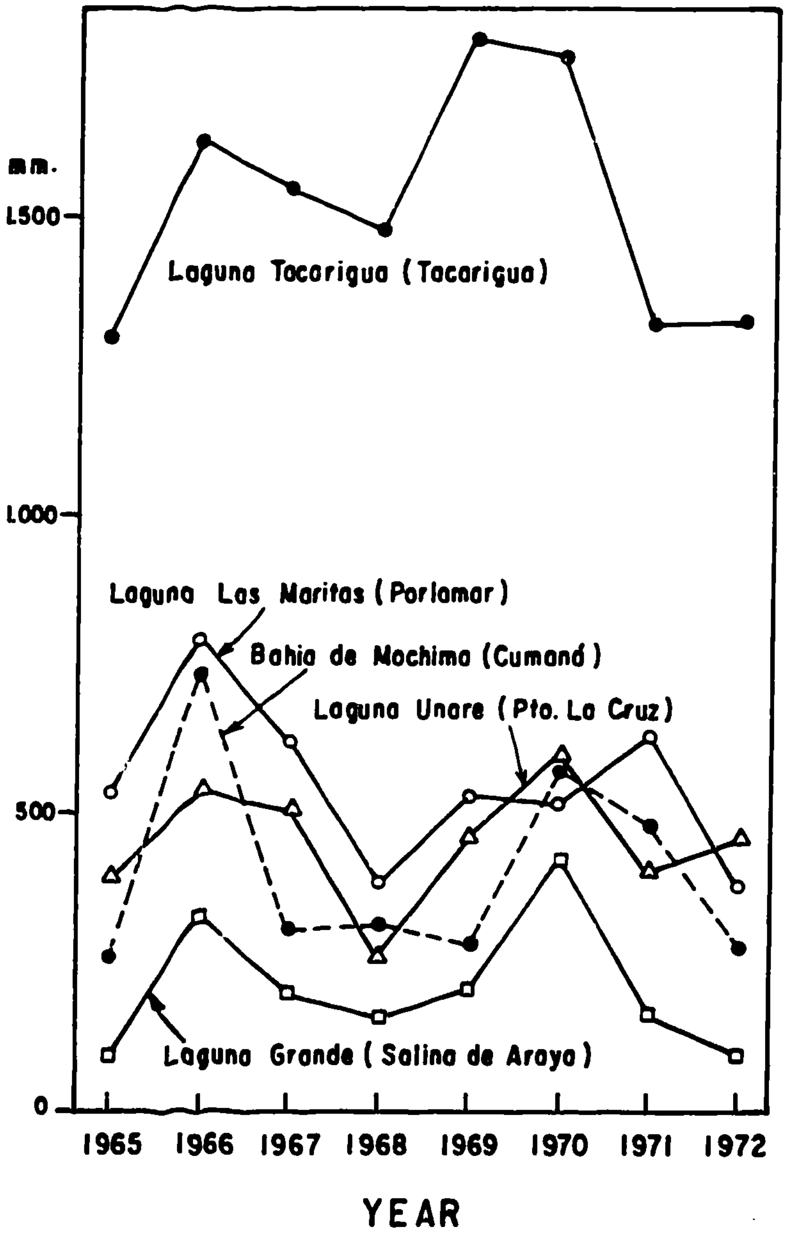

Fig. 2 Annual variation of precipitation.

Laguna Unare has a high rate of fish production (8–20 ton km^{-2} $year^{-1}$). However there is occasional fish mortality during the dry season. From the analysis of environmental conditions and the occurrence of fish mortality, the principal cause of such mortalities in Laguna Unare was attributed to hypersalinity (Okuda, 1965).

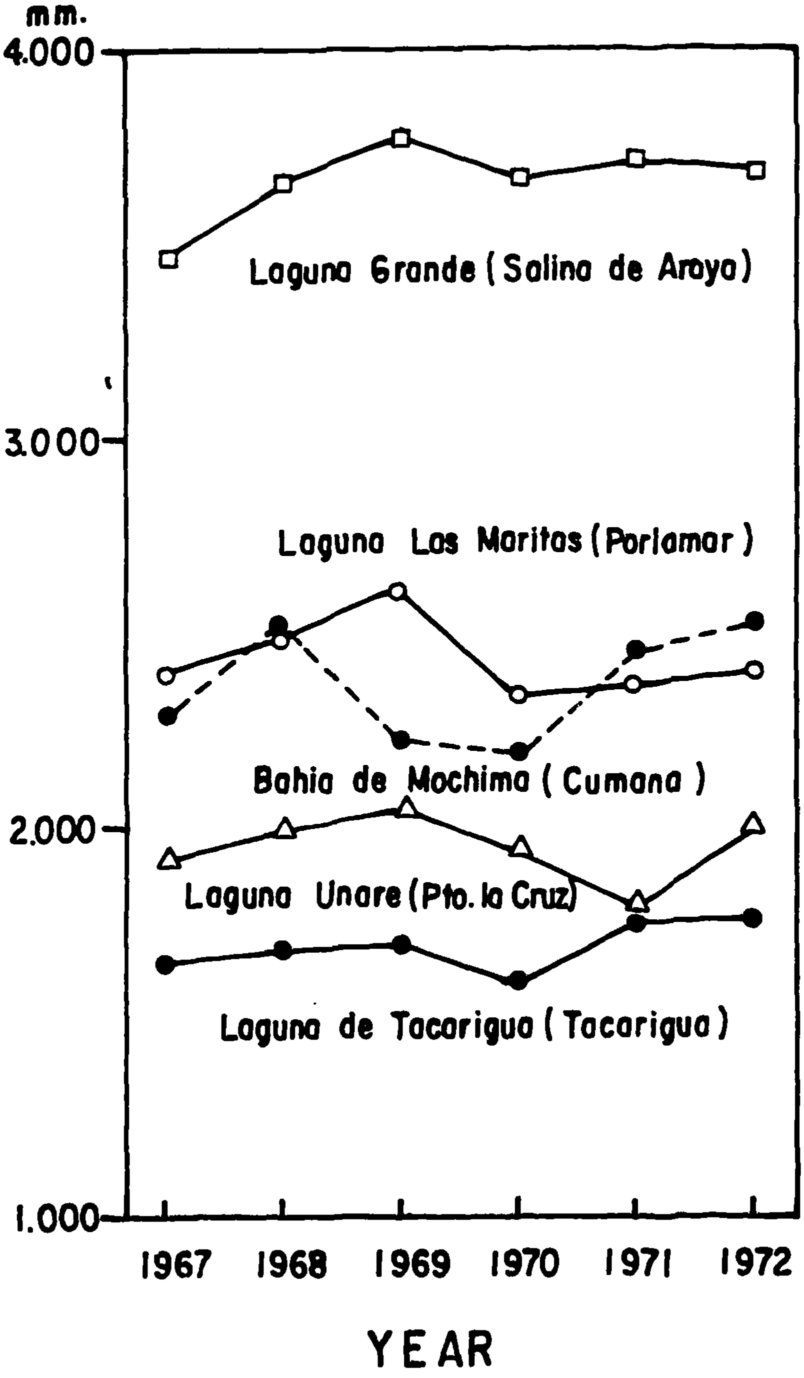

Fig. 3 Annual variation of evaporation.

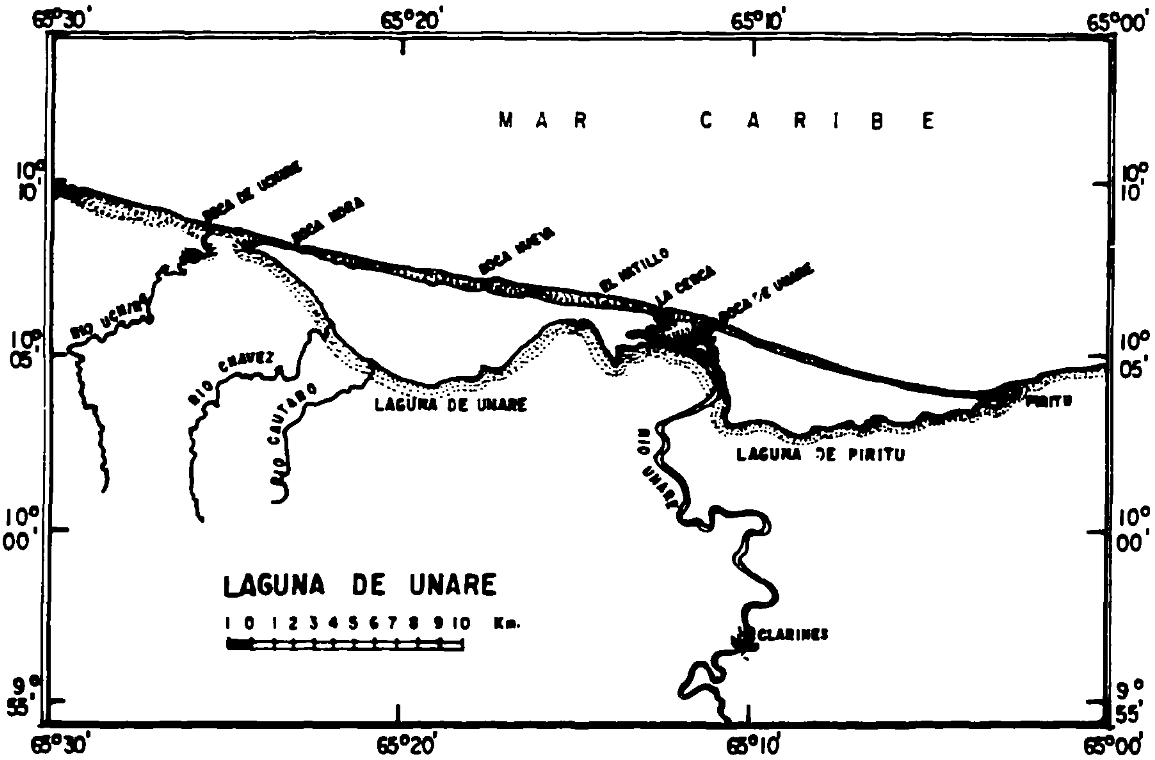

Fig. 4 Map of Laguna Unare.

Laguna Tacarigua

The long sand barriers develop in the northern part and separate the lagoon from the Caribbean Sea. The width of the sand barrier varies from 300 m to 1 000 m. The lagoon has a length of 28 km in a northwest-southeast direction with a maximum width of 5 km. The average depth of water of the lagoon ranges from 1.0 m to 1.4 m (Fig. 6). One of the characteristics of the lagoon is an exten-

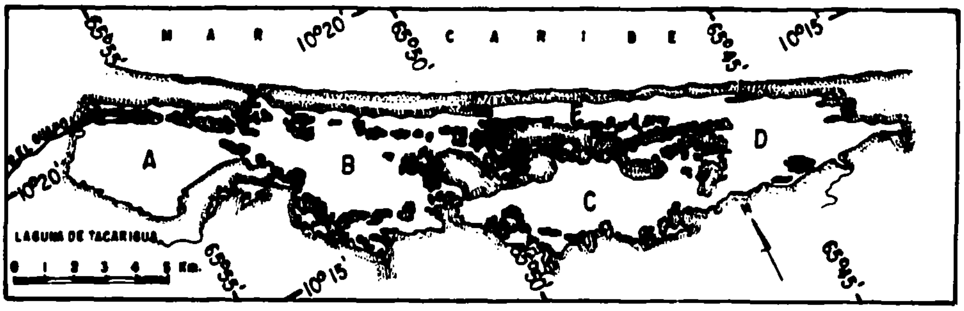

Fig. 5 Map of Laguna Tacarigua

sive development of mangrove vegetation in such a pattern that the central part and an area in the inner border of the lagoon look like an island. Such mangrove development in the central part may cause a great regional difference in the physical and chemical properties of water due to the restricted water circulation in the region of the lagoon.

It is reported that Laguna Tacarigua also has high rate of fish production (5-16 ton km^{-2} $year^{-1}$, from Gamboa *et al.*, 1971).

Laguna Las Maritas

Laguna Las Maritas lies on the south coast of Margarita Island. It extends for 6 km in a northwest-southeast direction and has a maximum width of 3.6 km. The deepest waters on the east and west sides of the lagoon are about 5 m to 4 m. It is notable that the maximum water depth in the central part of the inlet reaches 9 m. There is a development of a dense population of *Thalassia* in the major parts at the bottom of the lagoon. Mangroves have also developed along the inner border of the lagoon and oysters grow there abundantly (Fig. 6).

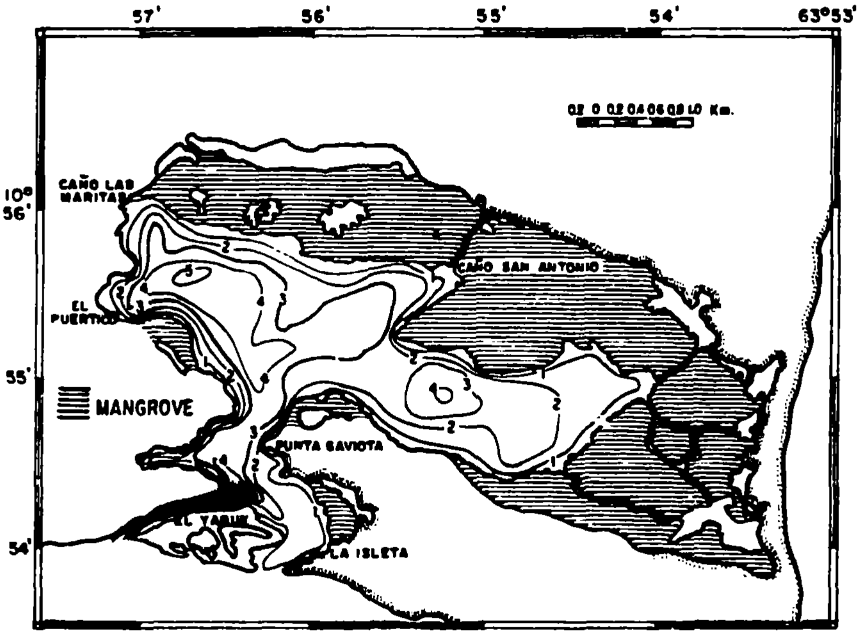

Fig. 6 Map of Laguna Las Maritas

Bahía de Mochima and Laguna Grande

Bahía de Mochima (Fig. 7) and Laguna Grande (Fig. 8) are generally deeper than the three lagoons. The entrances to these areas are

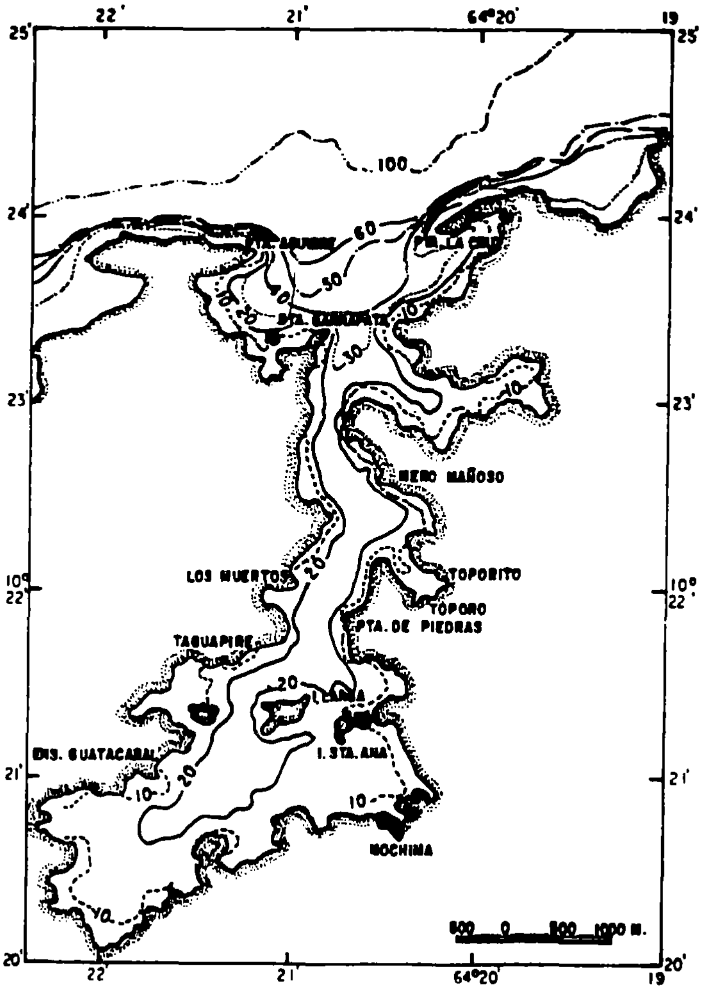

Fig. 7 Map of Bahía de Mochima

relatively narrow and the water depth tends to increase from the inner part towards the entrance, and reaches 60 m in Bahía de Mochima and 40 m in Laguna Grande. There is free exchange of the inner water mass with the open sea by the tides and the winds.

Bahía de Mochima has a length of 7.6 km extending from north to south and a width of 0.3 to 1.7 km. Laguna Grande extends to 4.2 km long and 2.2 km wide. There is mangrove vegetation along the inner coast of the both areas.

In general, hydrochemical characteristics in both areas show a similar pattern.

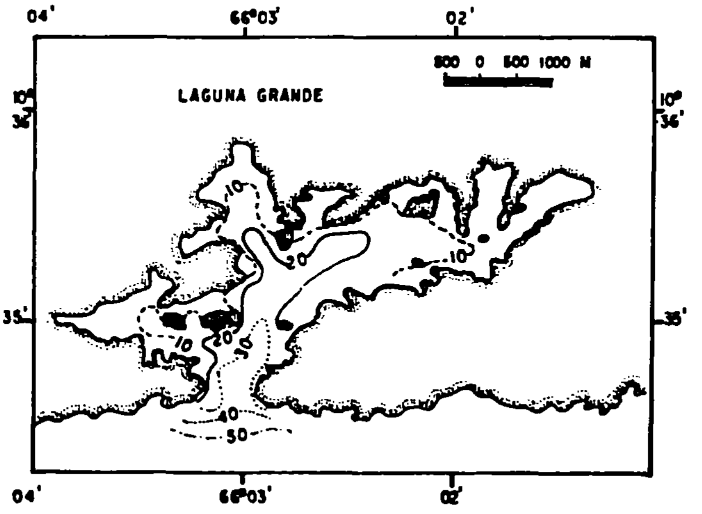

Fig. 8 Map of Laguna Grande

INORGANIC AND ORGANIC NITROGEN CONTENTS

The average annual nitrogen content in different forms in the areas of study, which were tabulated on the basis of monthly observation for 2-3 years, are shown in Table 2.

It is clearly noted that Laguna Unare has the highest nitrogen content in all forms and Mochima and Laguna Grande have the lowest. There is no definite difference in the nitrogen content of various forms between Bahía de Mochima and Laguna Grande. The content of organic nitrogen in the three coastal lagoons is remarkably high as compared to that of the other areas (Bahía de Mochima and Laguna Grande), especially in Lagunas Unare and Tacarigua. The organic content is much higher than inorganic nitrogen content in all areas of this study. The difference between organic and inorganic nitrogen contents in the three lagoons is much greater than that of the other two areas, that is, the organic nitrogen is 5 to 11 times higher than inorganic nitrogen in the three lagoons and about twice as much in Bahía de Mochima and Laguna Grande.

The inorganic nitrogen content of Lagunas Unare and Tacarigua are high but Laguna Las Maritas shows little difference from that in Bahía de Mochima and Laguna Grande. Amongst the various forms of inorganic nitrogen in the areas of this study, ammonium shows the highest content, followed by nitrate and nitrite. The content of ammonium in the three lagoons are much higher than the other areas, specifically, this type of inorganic nitrogen in Lagunas Unare and Tacarigua is remarkably high.

TABLE 2. Annual average of nitrogen content, ug-atom litre^{-1}

Location	Inorganic Nitrogen			
	Ammonium	Nitrite	Nitrato	Total
Laguna Unare	21.6	0.39	2.18	24.17
Laguna Tacarigua	9.37	0.05	0.81	10.23
Laguna Las Maritas	3.71	0.05	1.14	4.90
Bahía de Mochima	2.46	0.12	1.65	4.23
Laguna Grande	2.61	0.16	1.50	4.27

TABLE 2 continued

Location	Organic Nitrogen			Total Nitrogen
	Dissolved	Suspended	Total	
Laguna Unare	232.	36.5	268.5	292.7
Laguna Tacarigua	53.2	9.40	62.6	72.8
Laguna Las Maritas	19.9	5.01	24.9	29.8
Bahía de Mochima	5.64	3.43	9.07	13.3
Laguna Grande	6.29	3.33	9.62	13.9

TABLE 2 continued

Location	Phosphate-P	N/P*
Laguna Unare	0.49	49.3
Laguna Tacarigua	0.76	13.5
Laguna Las Maritas	0.34	14.4
Bahía de Mochima	0.23	18.4
Laguna Grande	0.34	12.6

* These values were calculated from total inorganic nitrogen and phosphate-P

Observations were carried out in: Laguna Unare from 1962 to 1964, Laguna Tacarigua from 1967 to 1969, Laguna Las Maritas from 1967 to 1969, and Bahía de Mochima & Laguna Grande from 1964 to 1966.

Generally the content of dissolved organic nitrogen is considerably higher than the suspended organic nitrogen in areas of study; 4 to 6 times higher in the three lagoons and 1.5 to 2 times higher in the other areas.

The content of organic nitrogen in Laguna Las Maritas is 2 times higher than that of Bahía de Mochimas and Laguna Grande, although there is no significant difference in the inorganic nitrogen content amongst the above three areas. These three areas have no supply of fresh water from rivers. However, there is a free flow of open sea water through an entrance in Bahía de Mochima and Laguna Grande. On the other hand, there is a restriction of exchange of the lagoon water with the open sea water in Laguna Las Maritas.

The shallow areas which prevent the water circulation generally have a high rate of organic productivity, and tend to accumulate organic matter. In Laguna Las Maritas, the high rate of evaporation reduces the quantity of the lagoon water. This decreased volume of the lagoon water is compensated for by an inflow of tidal sea water. Such a process over a long period may contribute to the accumulation of nitrogen in the lagoon water, although the nitrogen content in the open sea water is not so high.

The high content of organic nitrogen in Laguna Unare and Laguna Tacarigua may be caused by the inflow of river water into these lagoons. However, the inorganic and organic nitrogen contents in Laguna Unare are much higher than the Laguna Tacarigua. As mentioned before, Laguna Tacarigua communicates with the open sea through an inlet throughout the year, but Laguna Unare has limited communication through the mouth of the River only during the rainy season.

NITROGEN CONTENT IN THE DRY AND RAINY SEASONS

Table 3 shows the nitrogen content in the different forms in Laguna Unare River (Okuda et al., 1965). It is noted that the greatest part of total nitrogen consists of dissolved nitrogen. Suspended organic nitrogen predominates in the river water in the rainy season. Of the three types of inorganic nitrogen in the lagoon and in the river, the content of nitrate is highest in the rainy season and that of ammonium in the dry season. The content of total inorganic nitrogen in the lagoon and in the river in the dry season is lower than that of the rainy season.

On the other hand, the content of organic nitrogen in the lagoon in the dry season is remarkably high compared with that of in the rainy season; however, the contents of dissolved and suspended organic nitrogen in the river water in the rainy season are higher than those of the dry season. The contents of dissolved organic nitrogen in the river and suspended organic nitrogen in

Table 3. Comparison of Hydrochemical values of the Unare Lagoon and river between the dry and rainy seasons (1964)

Season	End of dry season		Beginning of rainy season	
	Lagoon	River	Lagoon	River
Salinity - parts per thousand	88.60	13.38	23.40	0.09
Oxygen ml litre^{-1}	6.31	3.20	8.68	3.45
Inorganic nitrogen (in ug-atom litre^{-1})				
Ammonium	6.7	4.2	4.1	1.9
Nitrite	0.17	0.12	0.15	0.48
Nitrate	0.28	0.82	7.7	32.3
Total	7.15	5.14	11.95	34.7
Organic nitrogen (in ug-atom litre^{-1})				
Dissolved	318.	24.3	145.	47.3
Suspended	29.2	12.1	43.7	66.5
Total	347.	36.4	189.	114.
Total Nitrogen (in ug-atom litre^{-1})	354.	41.5	201.	149.
Phosphate-P (in ug-atom litre^{-1})	0.54	0.47	0.41	0.91
T.O.N/T.I.O.N *	48.5	7.1	15.8	3.3
D.O.N/S.O.N. **	10.9	2.0	3.3	0.71
N/P ***	13.2	10.9	29.1	38.1

* Total organic nitrogen/total inorganic nitrogen

** Dissolved organic nitrogen/suspended organic nitrogen

*** These values were calculated from total inorganic nitrogen and phosphate-P the lagoon and the river in the rainy season are higher than those in the dry season.

In the lagoon, the organic nitrogen content is much higher than that of the inorganic nitrogen; the former is about 49 times greater than the latter in the dry season and about 16 times greater in the rainy season. Whereas, in the river water, this relation is 7.1 times in the dry season and 3.3 times in the rainy season.

The river water entering the lagoon has a high concentration of nitrate and suspended organic nitrogen. In the beginning of the rainy season, the ratio of dissolved and suspended organic nitrogen is 0.71 and 3.3 in the river water and in the lagoon water respectively. However, this ratio increased to 10.9 in the lagoon water at the end of the dry season.

From these observations it is likely that the Unare River supplies nitrogen in the forms of nitrate and suspended organic nitrogen to Laguna Unare. Then, through the organic production and the decomposition processes in the lagoon, the nitrogen is finally transformed into ammonium and dissolved organic nitrogen.

REGIONAL VARIATION OF NITROGEN CONTENT

Fig. 9 shows average annual nitrogen contents in the different zones of Laguna Tacarigua. "A" zone receives fresh water from the Guapo River. Therefore the water of this zone has a low salinity and a relatively high concentration of nitrite and nitrate. The contents of organic and inorganic nitrogen tend to increase from "A" zone to "E" zone in alphabetical order but nitrite and nitrate in "A" zone do not follow the same pattern where higher values were obtained.

Laguna Tacarigua has an inlet in "B" zone which maintains the exchange of water with the open sea by the tidal action. "C, "D" and "E" zone are located on the eastern part of the lagoon and have a restricted circulation.

High ammonium and organic nitrogen contents and low oxygen content in these zones (C, D and E) may be caused by the accumulation of nitrogen resulting from the restriction of free flow of inner water mass due to the development of mangrove. The annual average of physical and chemical properties in different zones of Laguna Tacarigua are shown in Fig. 9

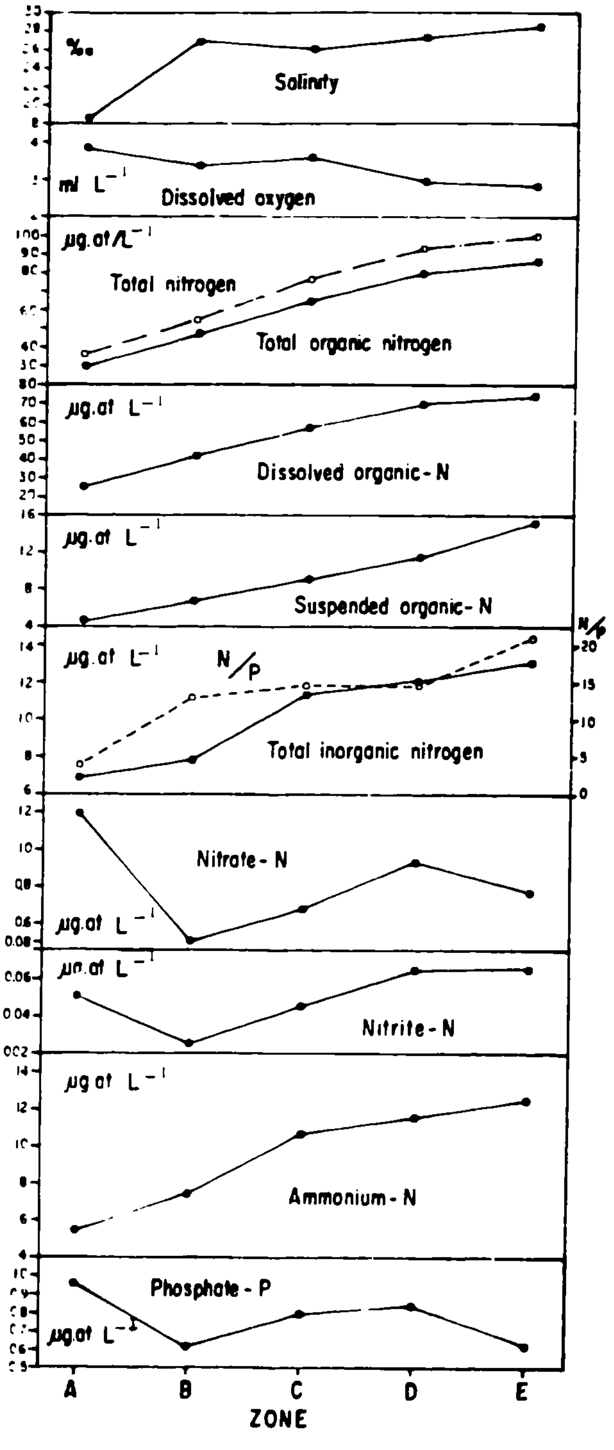

Fig. 9 Annual average of physical and chemical properties in different zones of Laguna Tacarigua.

NEW SITUATION OF LAGUNA TACARIGUA

For the last few years, the flow of the Guapo River into Laguna Tacarigua has been remarkably reduced by the construction of a dam; communication with the open sea has been closed by piling of sand. This new situation in Laguna Tacarigua has brought about a notable increase of salinity in the lagoon which has created occasional fish kills. Because of this, hydrochemical observations were carried out in Laguna Tacarigua on 16 June 1978 to investigate what some of the environmental changes in the lagoon have been in the last 10 years.

Our salinity date obtained from monthly observations during the years 1967-1969 never show a value of more than 40 parts per thousand. On this occasion, salinity of the lagoon shows a maximum of 51 and 45 parts per thousand as average. In 1967-1969, there was a great regional difference of salinity as well as of other chemical properties, but the observations of 1978 do not show a wide difference in these properties throughout the lagoon.

Another notable feature is that organic nitrogen content (174 ug-atom litre^{-1} as an average) was very high compared with the former dates (less than 80 ug-atom litre^{-1} as a maximum) and inorganic nitrogen content was extremely low. Of the three forms of inorganic nitrogen, nitrite and nitrate are almost exhausted and the ammonium content is also only 2.5 ug-atom litre^{-1} as average.

One of the reasons for a considerable increase of organic nitrogen content in the past 10 years may be attributed to an accumulation of organic matter in the lagoon, due to a restricted water change with the open sea through an inlet and a stagnation of the inner water due to the development of mangrove vegetation in the lagoon.

An extremely low content of inorganic nitrogen and a very high content of organic nitrogen may indicate that there is a considerably high organic production and a relatively low rate of mineralization in the lagoon.

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COASTAL LAKES OF THE NILE DELTA. LAKE MANZALAH

by

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A number of shallow but wide depressions extend from east to west along the Nile Delta, forming a chain of six coastal lakes (Fig. 1). Ancient Egyptian reliefs and paintings showing the aquatic vegetation, the fish fauna and the abundance of bird and other predators bear witness both to the fresh water character and to the high productivity of these so-called "Northern Land" swamps. They were periodically flooded by Nile waters at which time their area was greatly expanded. Until the late middle-ages, the two north Sinai lakes, Lake Port-Fouad and Lake Bardaweel, were also related to the complex pattern of the Nile branches (Fig. 2). The silting up and ultimate disappearance of the Pelusiac branch, about 5 centuries ago, led to their final isolation from the Delta.

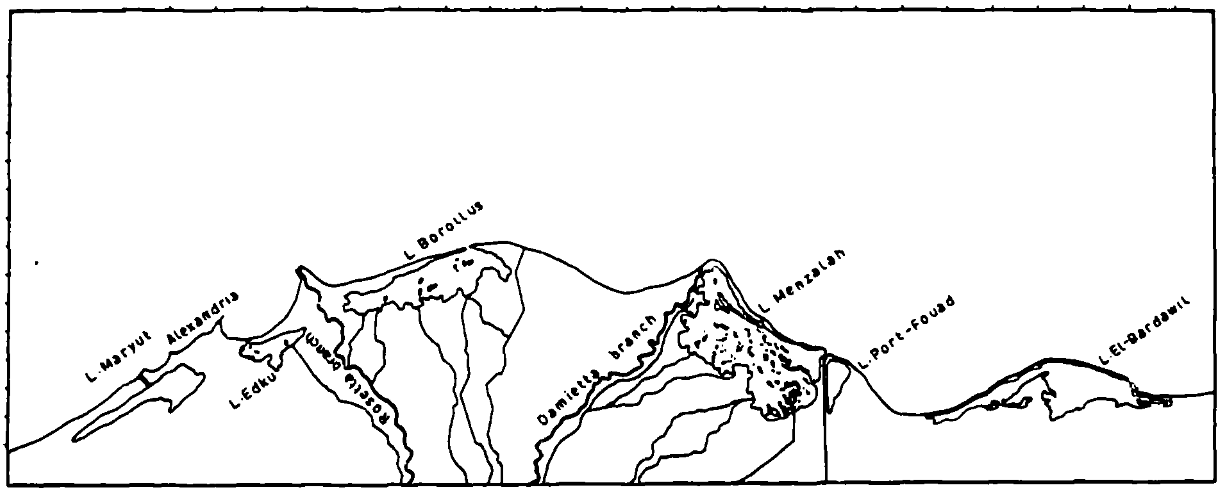

Fig. 1 The Nile Delta and the coastal lakes.

The present Delta lakes, reduced to four, are still highly productive. Although they are an integral part of the Nile Delta system their waters are not fresh but slightly brackish. Located

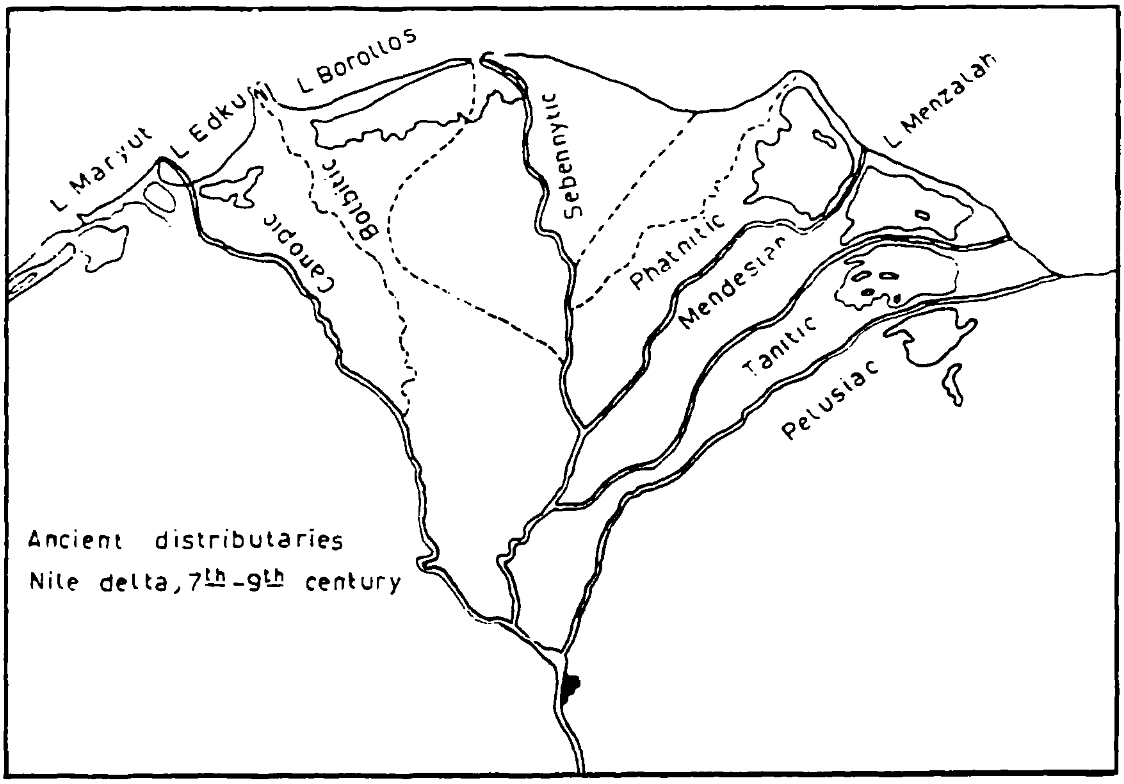

Fig. 2 The Nile delta in the Middle Ages (from various sources).

at the northern rim of the cultivated lands, they depend mostly on agricultural drainage for their water supply. Except for the easternmost Lake Mariut, which is land-locked, there is also a limited mixing with sea water through lake-sea connections on their northern side. All the lakes, including Lake Mariut, which has water continuously pumped to the sea, are transition basins where active transformations occur between land drainage and the coastal Mediterranean waters.

Land drainage feeding the lakes derives indirectly from the Nile. Irrigation water is collected by a system of drain canals after infiltration through the subsoil and, in this process, its composition is affected by the type of soil through which it permeates (Fig. 3.). The most obvious changes are the rise in chloride content, the enrichment in nutrient salts and in dissolved humic material (Table 1). As a rule, it is very poorly oxygenated. Soil silicates and nitrates from chemical fertilizers dissolve in large amounts. Both the silicate to phosphate (Fig. 4) and the nitrate to phosphate ratios are abnormally high, respectively about 400:1 and 40:1. Further changes subsequently take place within the lake basins. The chloride content rises due to evaporation and mixing with sea water. Dissolved oxygen also

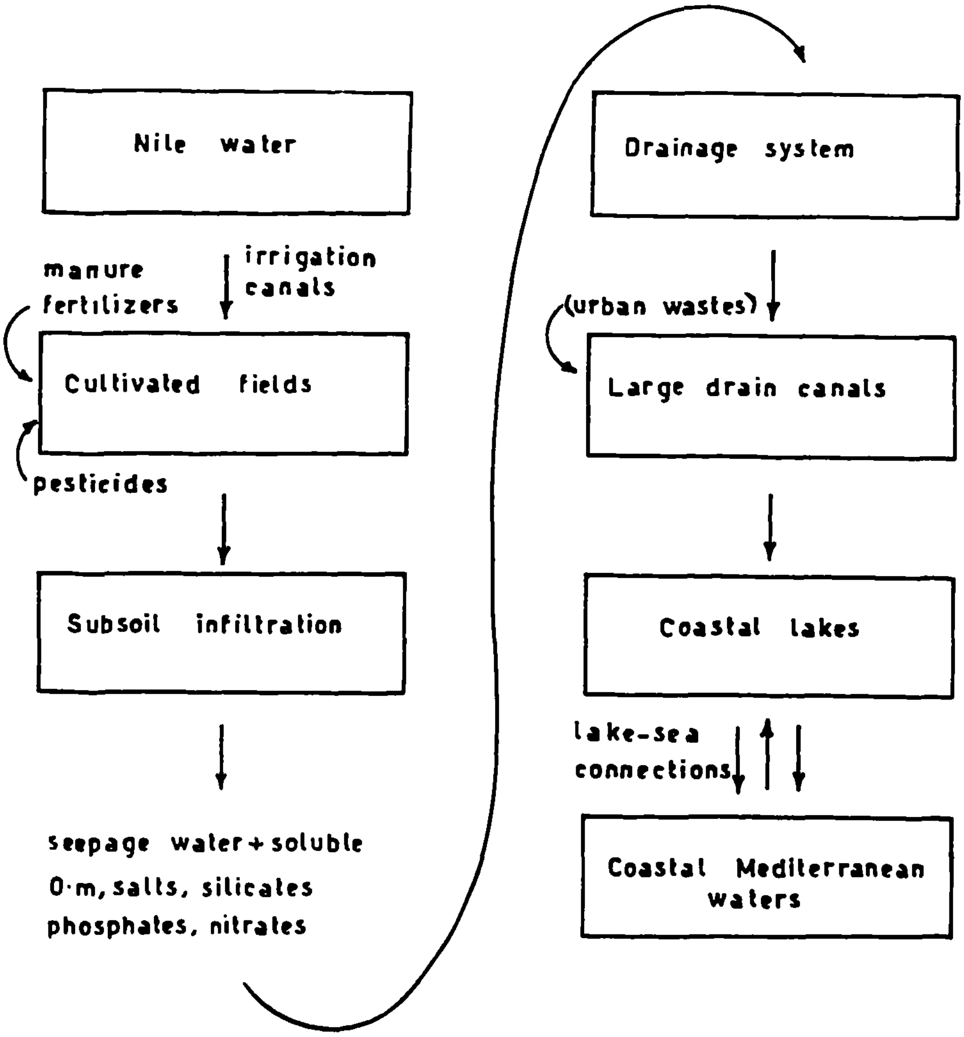

Fig. 3 Flow diagram. Nile water to coastal Mediterranean.

rises due to saturation. The demand on nitrates by the lake primary producers appears to be relatively greater than on phosphates and much greater than on silicates. Although the absolute concentrations of the three salts are decreased relative to the drain water level, the silicate ratios to both phosphate and nitrate are significantly higher (Fig. 4).

The outlined flow pattern, land drainage to lake basins and to the coastal belt of the sea, is the same for all lakes. The type of primary producers, the food-web and the composition of the fish population are also similar, but there are differences in the level of nutrient salts in particular, washed down by land drain-

Table 1. Some characteristics of Nile, Drain and lake waters. All values represent the average of 12 months measurements

	Nile (1)	Drain (2)
Cl g liter^{-1}	0.03-0.07	0.44
Oxygen % sat.	77	41-73
PO4 ug-atom litre^{-1}	0.4(0.2-0.8)	0.59
NO3 ug-atom litre^{-1}	-	22
Silicate	18-38	300-200
N/P	-	41:1
Si/P	53:1	425:1

(1) Halim et al. (1976)
(2) Darrag (1974)

Table 1 continued

	Lake		
	Menzalah	Borollos (2)	Edku (3)
Cl g litre^{-1}	0.79-3.5 (4)	1.31(2.6-0.58)	0.61
Oxygen % sat.	40-110 (4)	76 (54-104)	92
PO4 ug-atom litre^{-1}	1.36 (4)	0.39	0.78
NO3 ug-atom litre^{-1}	19 (5)	6.5	1.4 (21-0.02)
Silicate	350 (5)	218	106
N/P	31 (5)	16:1	2:1
Si/P	562:1	545:1	132:1

(3) Kenawi (1974)
(4) Guerguess (unpublished)
(5) El Wakeel and Wahby (1970a)

age. Lake Mariut is heavily polluted in its eastern basin due to its proximity to the city of Alexandria. Limited eutrophication is also observed in the south-east basin of Lake Menzalah.

The lake basins provide shelter and feeding grounds for some marine fish (*Chrysophrys* sp., *Morone* sp., and grey-mullets) and

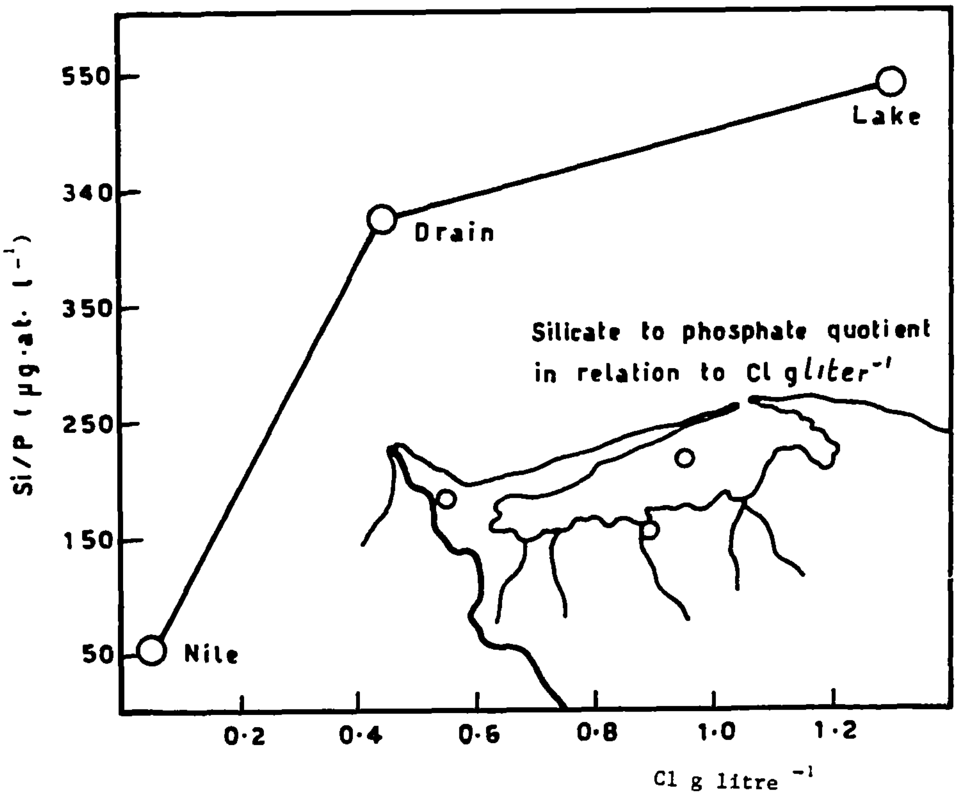

Fig. 4 The silicate to phosphate index in relation to the chloride content in three types of inland waters, the river Nile at Edfina, drain water and lake Borollos.

crustaceans (*Penaeus kerathurus*, *Callinectes sapidus*) mixing with euryhaline Nile fish (*Tilapia zilli*) and brackish *Palaemon* shrimps. Being shallow basins not exceeding 1.5 m at their greatest depths, they constitute a suitable breeding ground for Nile fish and for *Palaemon elegans* shrimps. Their fish yield per unit area, about 24 tons km^{-2}, compares favourably with most Mediterranean brackish lagoons (excluding fish culture ponds). The average yield of the latter ranges from 0.4 to 20 ton km^{-2} (Levi and Troadec, 1974). The continental shelf in the south-east Mediterranean is much poorer, its yield averaging 1 ton km^{-2}.

LAKE MENZALAH

Lake Menzalah (Fig. 5) is the largest of the four Delta lakes, with a surface area of 1350 km^2, or about 60% of their total area. Located east of the Damietta branch of the Nile, it is connected to the river by the small fresh water Enaneya canal (E, Fig. 5), supplying its western basin with 5.00 x 10^8 m^3 per year. The total inflow from its drain tributaries amounts to a little less than 6 billion m^3 per year (Fig. 6), 0.9 of which are dilute sewage water flowing into the south east basin through the El-Bakar

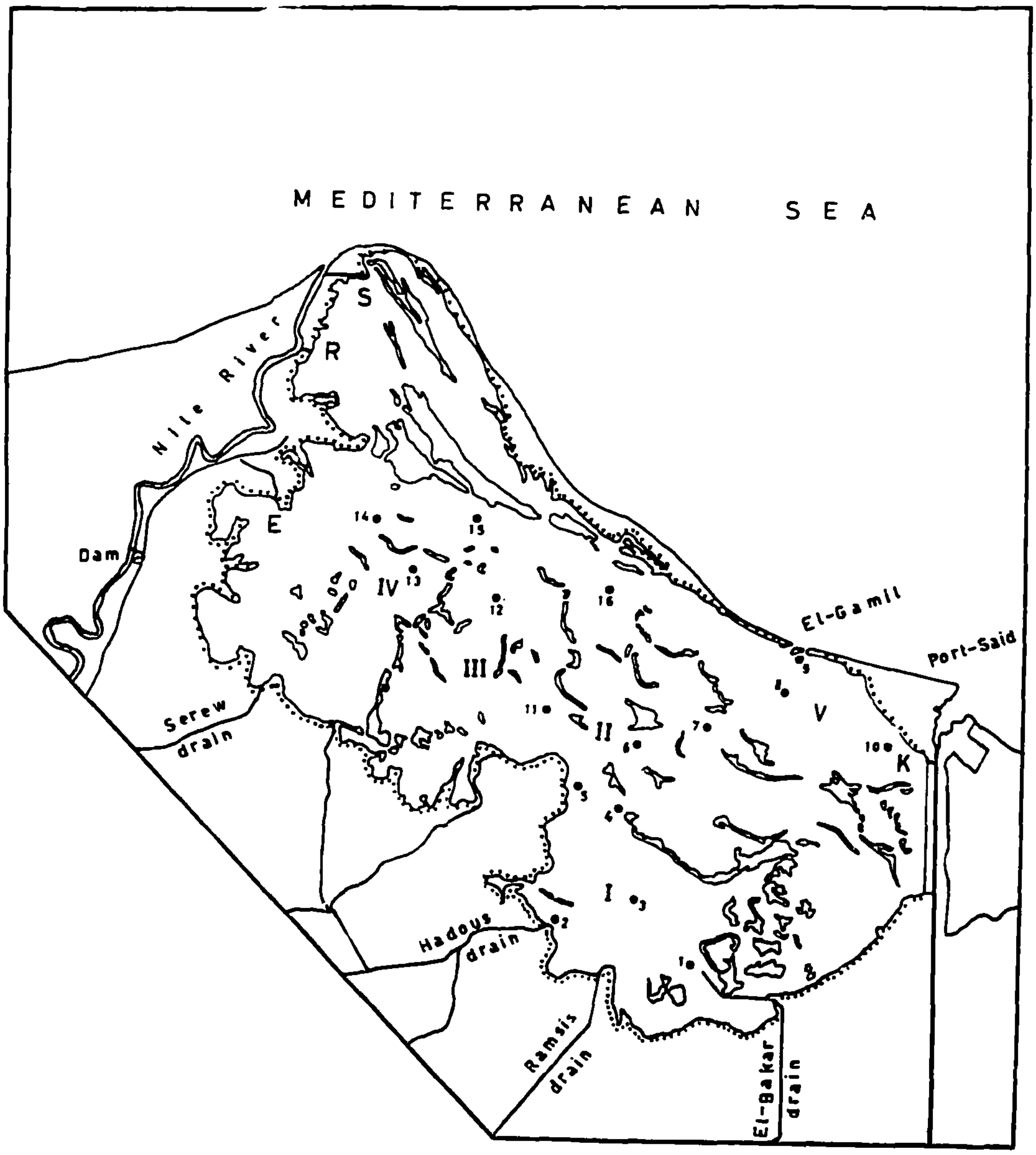

Fig. 5 Lake Menzalah. Showing the investigated stations (1971-1973), the major basins, the inlets and outlets. S,R and K, indirect connections to the sea. E's inlet of fresh-water canal. El-Gamil is major lake-sea connection.

canal (station 1). The lake has several northern connections to the sea (at S, R and K, Fig. 5), the largest being at El-Gamil. The low sandy embankment separating the lake basin from the sea has given way several times in the last decades, leading to the inrush of sea-water (Fig. 7) and a complete change in the environment. Contemporary records of plankton show the dominance of the euryhaline marine form Acartia latisetosa (Gurney, 1927; El-Magha-

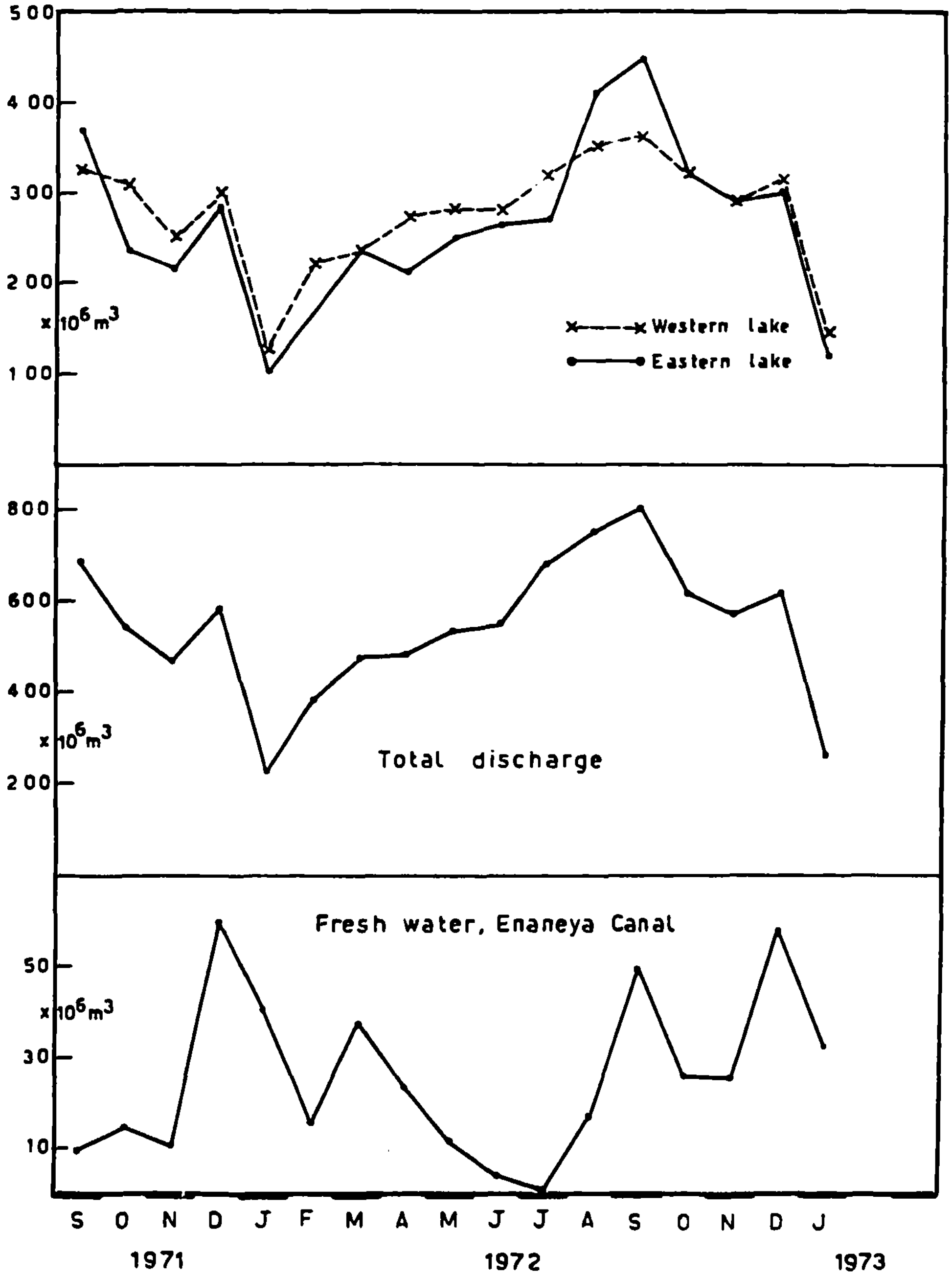

Fig. 6 Monthly discharge of drainage and fresh-water to Lake Menzalah.

raby *et al.*, 1963). Accumulations of dead shells of marine bivalves, are also found in abundance. In the last few years

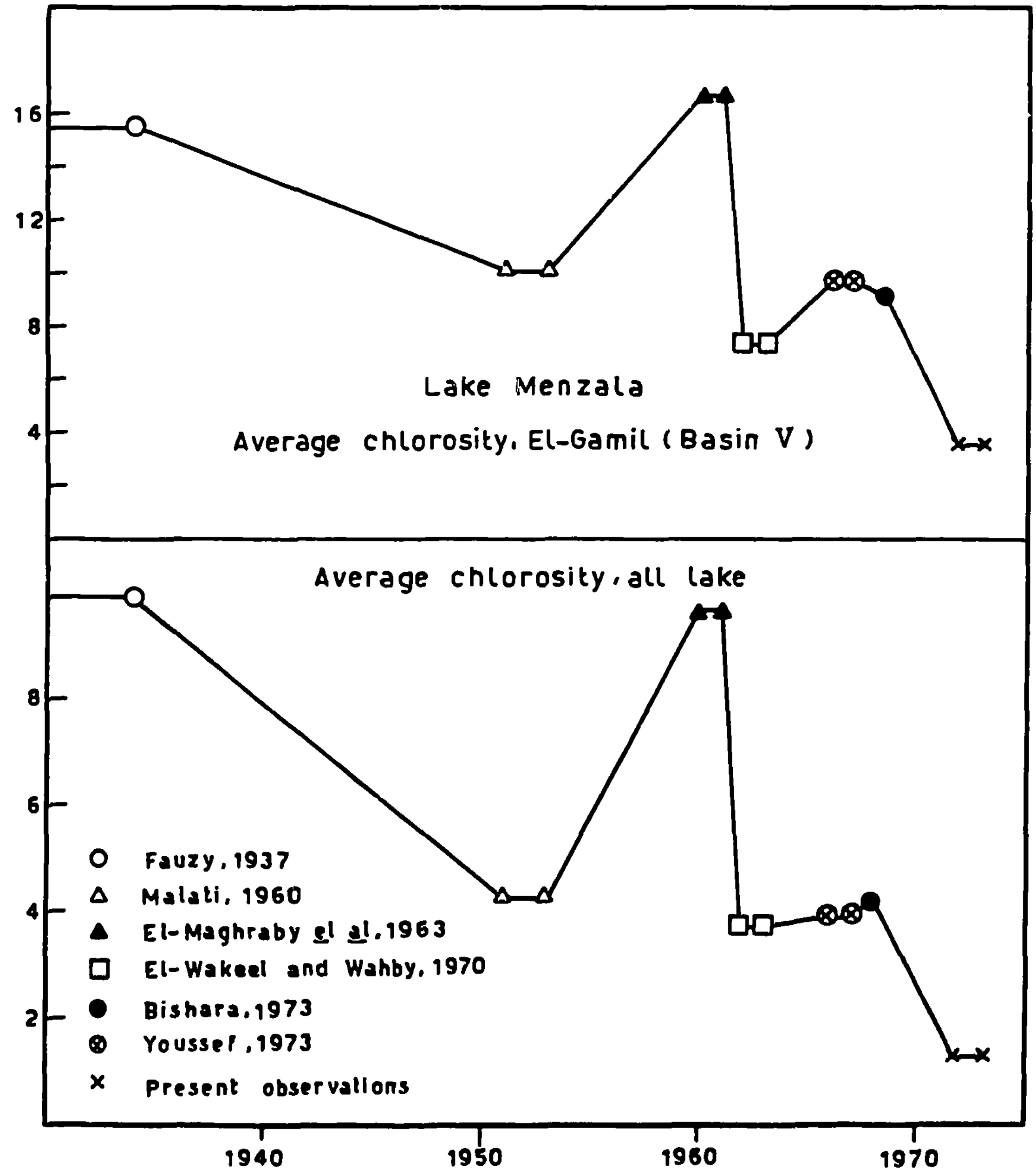

Fig. 7 Lake Menzalah average chlorosity since 1934.

chlorosity showed a steady decrease as a result of increased land drainage input.

Lake Menzalah can be dealt with as one system with pronounced north-south and less pronounced east-west gradients in its environmental characteristics. This gradation is largely determined by the respective locations of the inlets and outlets and by the clockwise pattern of wind induced circulation. On dealing with trophic relations, however, subsystems will be distinguished.

The predominant type of sediment is the complex type sand-clay-silt, followed in abundance by the clayey sand and silty clay respectively (El-Wakeel & Wahby, 1970,b). The lake peripheries, except on the north, are covered with silty clay. This changes basinwards into sand-silt-clay. The sand fraction spreading along the northern side is mainly derived from the Mediterranean beach sands penetrating through the lake-sea connection, as well as from wind blown sand and Cardium shells. Such a distribution of sediment types reveals the influence of drains and fresh-water connections and the proximity of the sea. The areas affected by the drainage inflow have a finer sediment unit.

The distribution of organic matter on the bottom follows the sediment distribution, higher organic matter being found in the peripheral zones of silty-clay and lower in the sandy areas. The range is from 1 to 7% The highest content, 7.3% is found near the

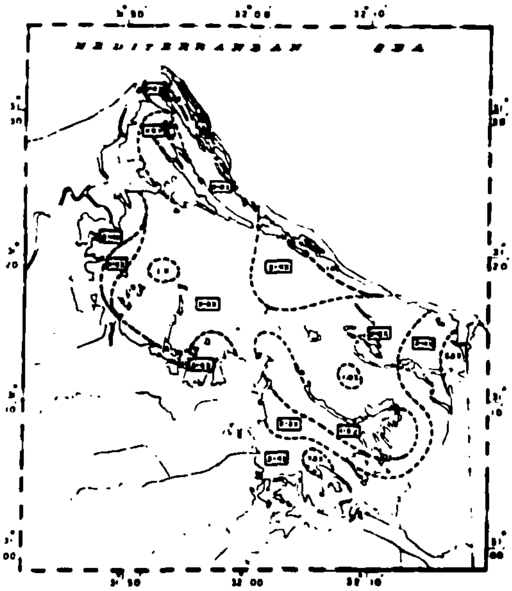

Fig. 8 Distribution of sediment organic matter in Lake Menzalah (after El-Wakeel and Wahby, 1970b)

inlet of El-Bakar canal (Fig. 8). The phosphorous content of the lake sediments ranges from 0.016% to 0.103%. Its distribution in the bottom sediments shows a relation to the median grain size and follows more or less the same pattern of distribution of sediments in the lake. The highest values are located along the lake peripheries (Fig. 9).

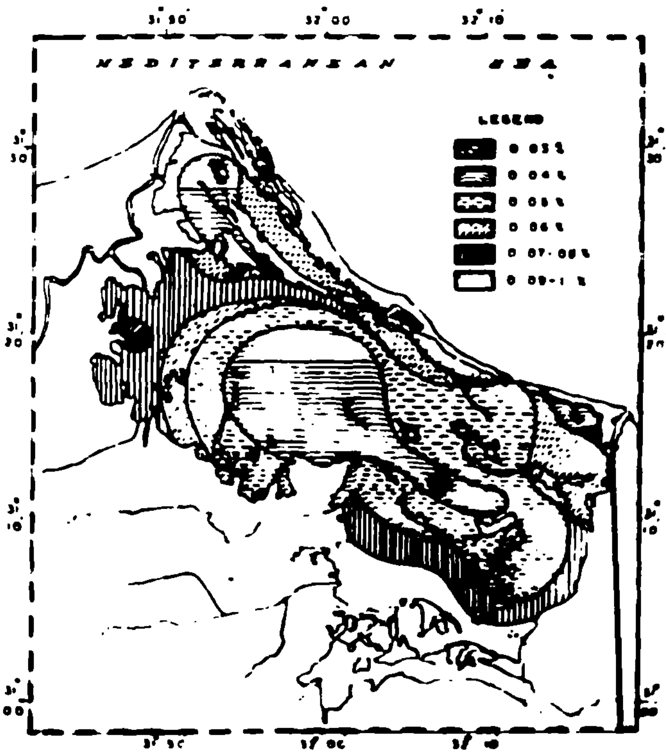

Fig. 9 Sediment phosphate in Lake Menzalah (after El-Wakeel and Wahby, 1970b).

Chlorosity near El-Gamil lake-sea connection is much higher than elsewhere in the lake. Due to small differences in tidal elevation, sea-water mixes with lake water in basin V (Fig. 10). This mixed water, with its associated plankton forms, is often displaced eastward and southward, becoming trapped between basin V and basins I and II (Fig. 11-13). An abrupt chlorosity decrease is observed everywhere after the peak of the drainage inflow, in September-October. By mid-winter, the drainage volume falls to a minimum and chlorosity rises to a peak except in the western-most basin IV (Fig. 11). Basin V is the most affected by the east-south displacement of the mixed waters. This pattern of circulation is reflected in most other characteristics.

The phosphate supplied with drainage water largely exceeds the demands of the primary producers (Fig. 14). While nitrate is depleted in spring and summer, phosphate rarely falls below 0.5 ug-atom litre^{-1} (Fig. 15). The northward and westward gradients are particularly obvious for nutrient salts. The abnormally high concentrations supplied by the outlet at station 1 maintain a high level in basins I and II, but the decrease is rather abrupt (Fig. 16, Table 2). This is due to the screening effect of the dense growth of submerged vegetation in basin I.

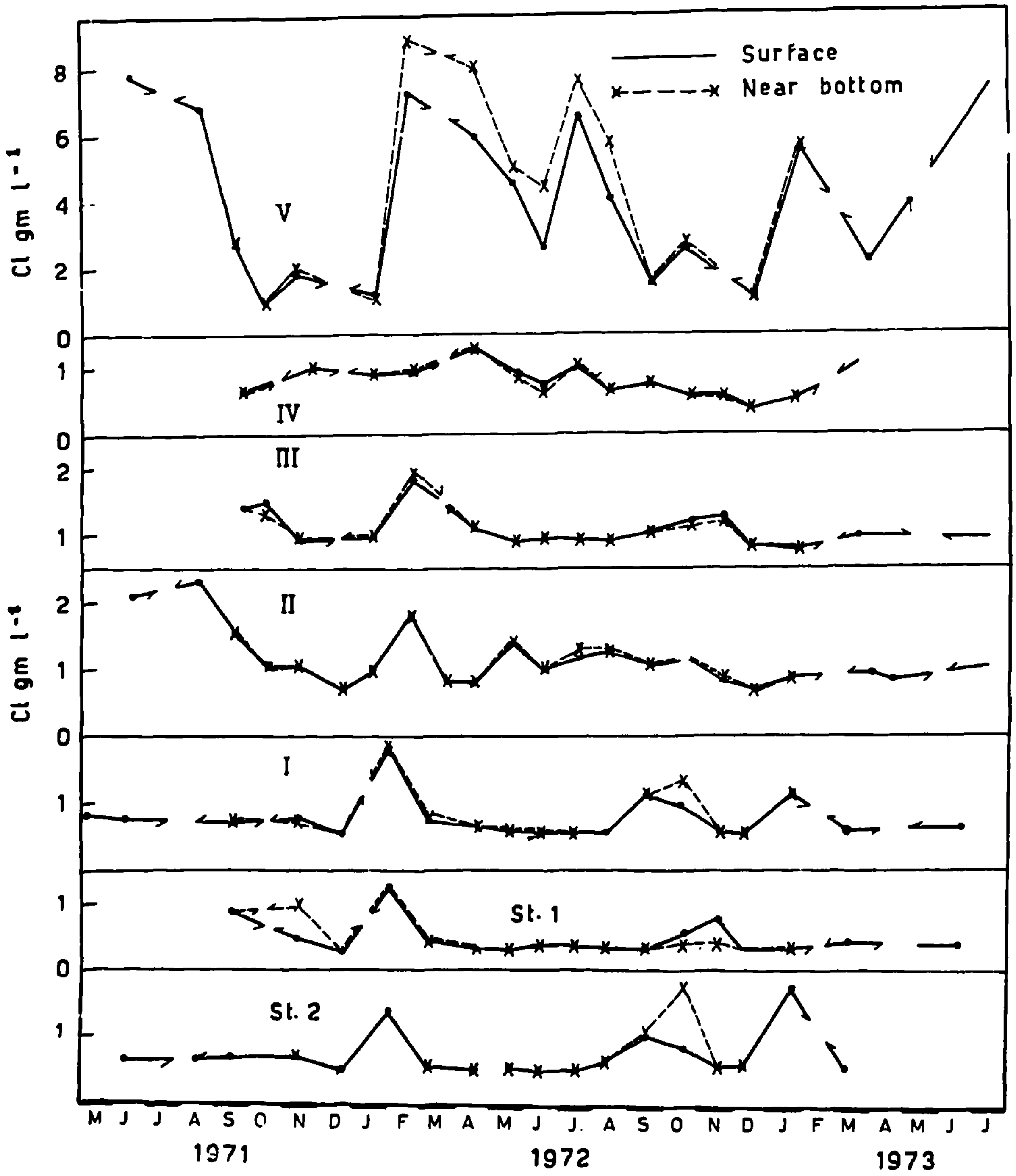

Fig. 10 Monthly average chlorosity in Lake Menzalah, basins I to V and drain stations 1 and 2.

A significant east to west variation in the phytoplankton composition is observed, although the main species are ubiquitous:

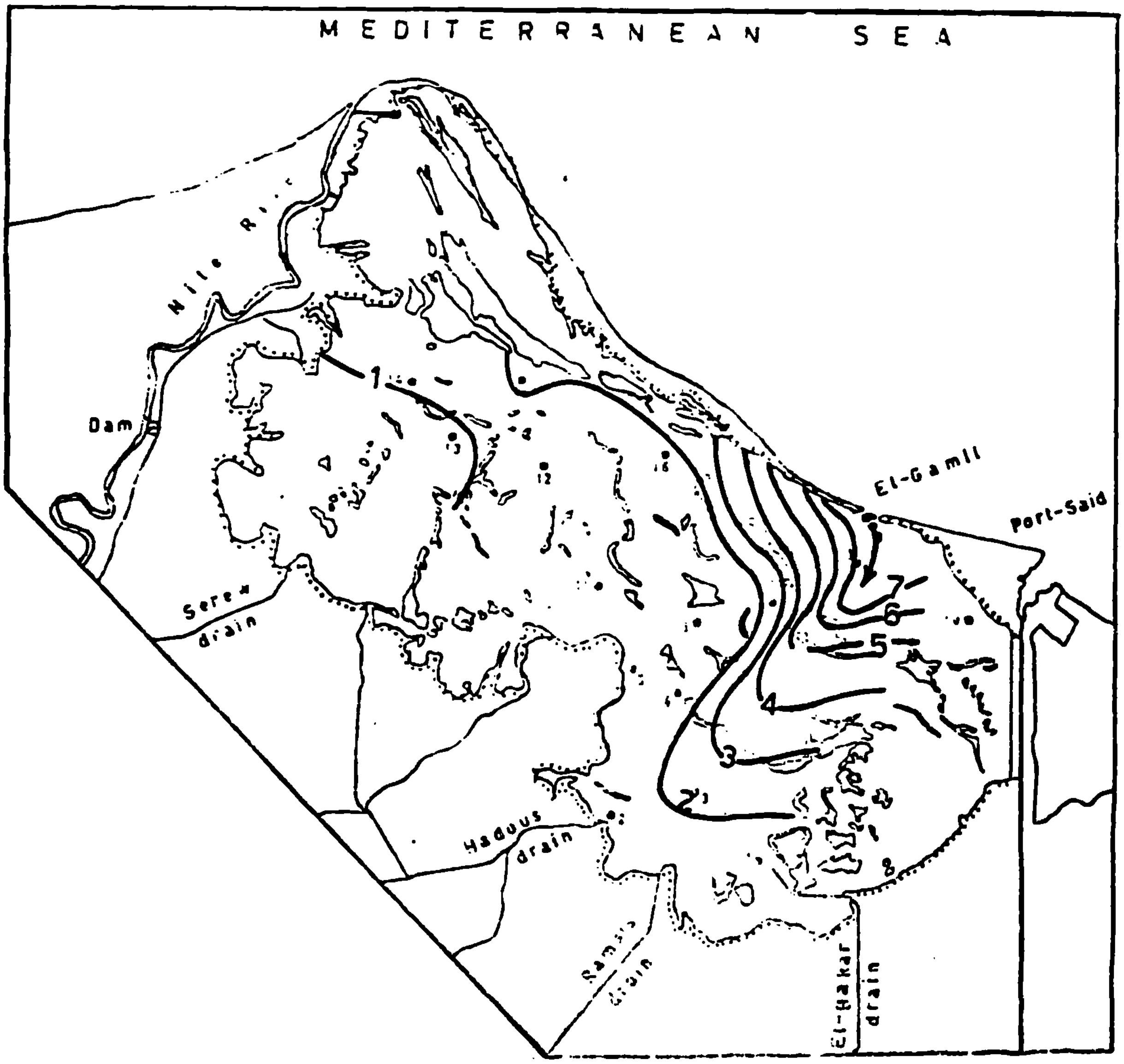

Fig. 11 Chlorosity distribution in February, time of minimum drain discharge.

Cyclotella meneghiniana, *Melosira granulata angustissima*, *Ulothrix* sp., *Microspora* sp. The eutrophic basin I is characterized by an abundant and varied population of *Euglena* spp. Up to 20 euglenophyte species are recorded from this basin. Many are known to be indicators of organically rich waters: *Phacus tortus*, *P. triqueter*, *P. pleuronectes*, *Euglena acus*. Their numerical ratio to

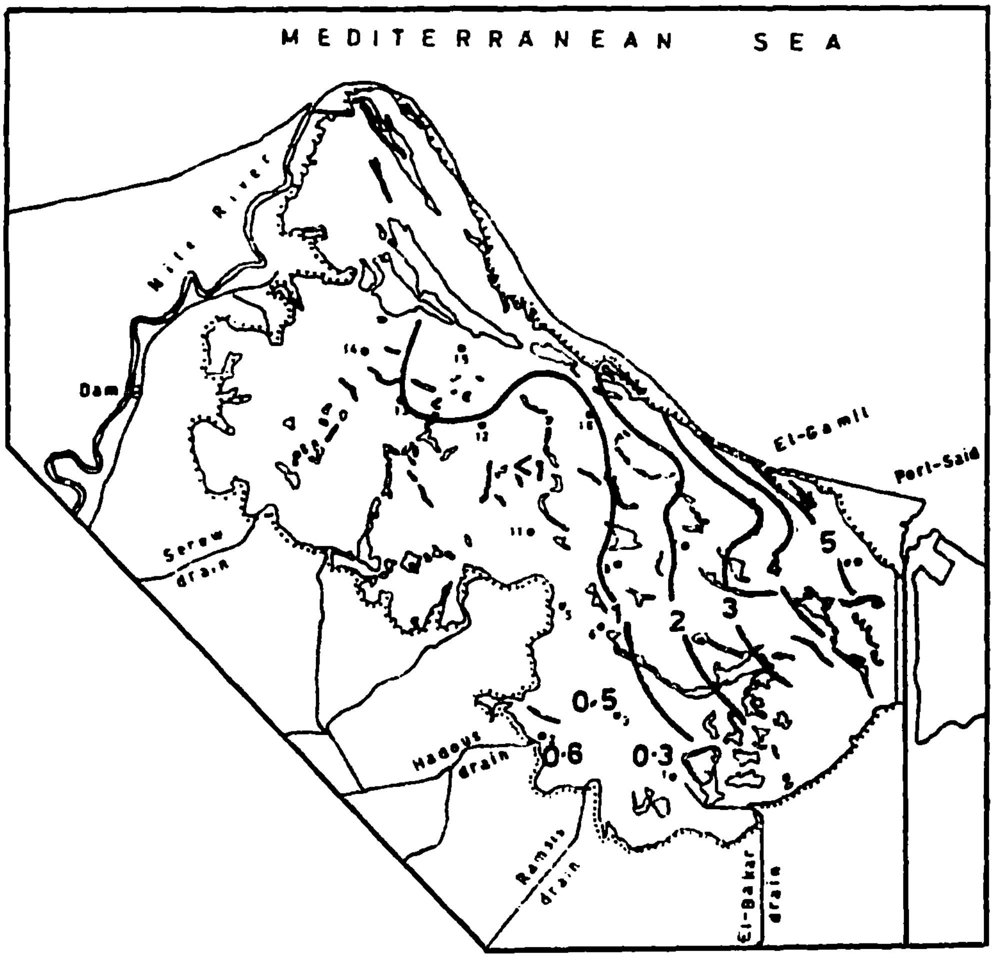

Fig. 12 Chlorosity distribution, May.

other phytoplankters decreases rather abruptly from basin I westward (Table 3). Diatoms are leading in basin I, but from basin II westward, green and bluegreen algae, characteristic of Nile phytoplankton (Halim *et al.*, 1976), become predominant (Table 4).

The zooplankton population is typically estuarine. Characteristic of this type of transitional environment is the intermixing between populations of very different biogeographic origins. Fresh-water cladocerans and copepods, extending in their distribution to the Central African lake-sources of the Nile, mix with brackish rotifers and various coastal Mediterranean forms (Table 5). The distribution pattern and the relative abundance of

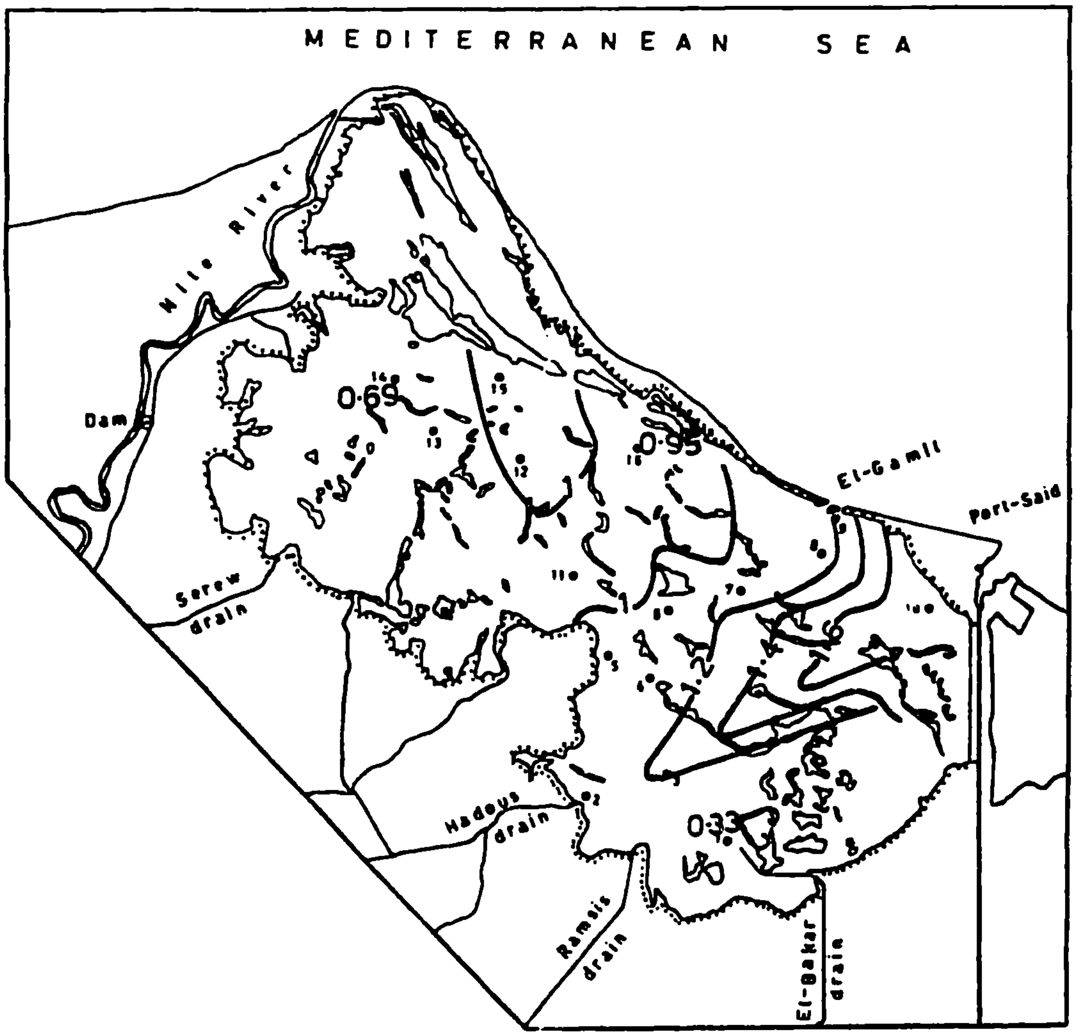

Fig. 13 Chlorosity distribution in August at maximum discharge.

such populations is not only governed by their varying tolerance to salinity variations but also by the water quality and the type of phytoplankton food available. The marine mysid *Mesopodopsis slabberi* shows a clear-cut distribution, as it remains restricted to the mixed water mass trapped in basin V. Although the east-west chlorosity variations along the south zone of the lake are limited, the zooplankton communities are different. Rotifers, copepods and the cladoceran *Moina micrura* are concentrated in the eutrophic basins I and II where they feed on diatoms and green algae. In the western lake, free from pollution, and where fresh-water phytoplankton is more abundant, *Diaphanosoma excisum* and cladocerans in general predominate. Rotifers and copepods are often insignificant (Fig. 17).

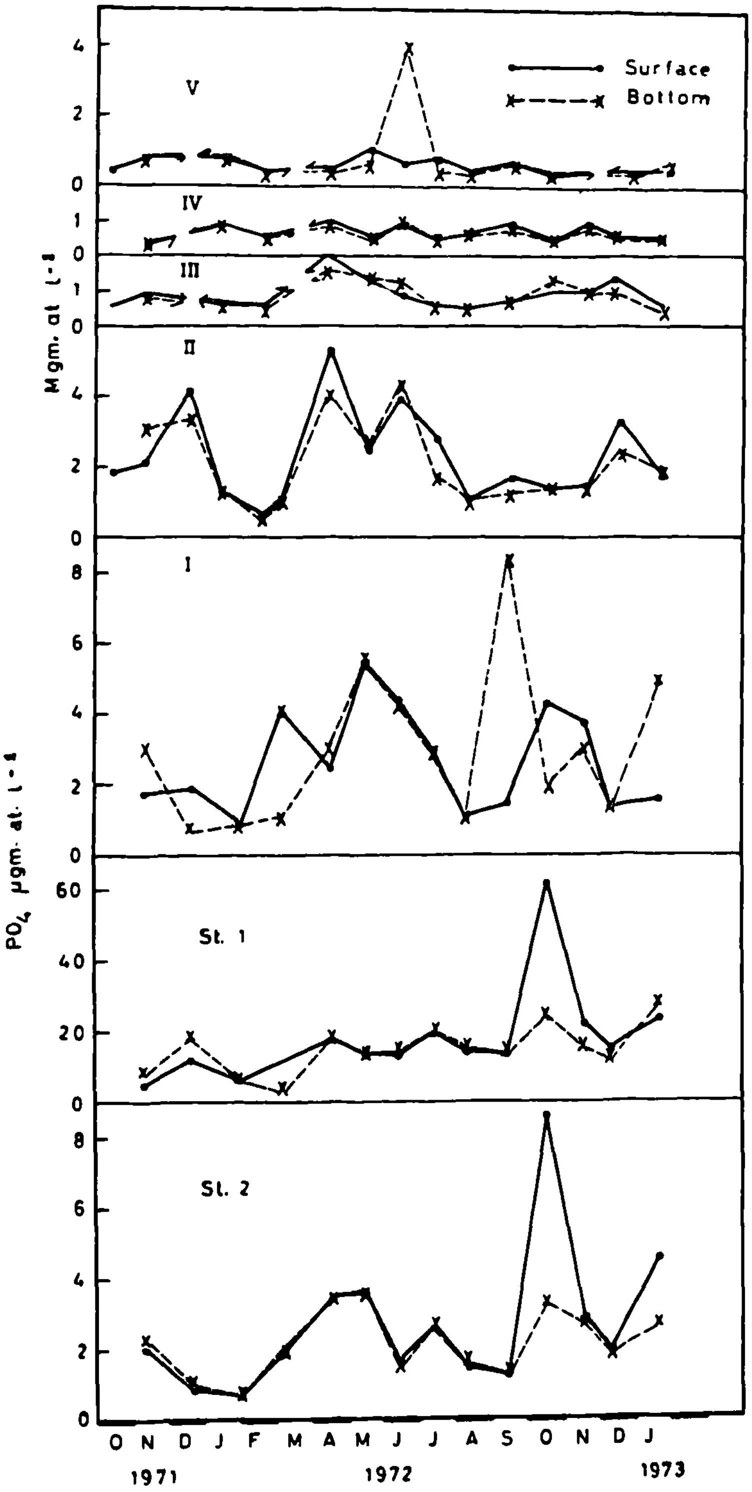

Fig. 14 Monthly average phosphate in Lake Menzalah basins I to V and drain stations 1 and 2.

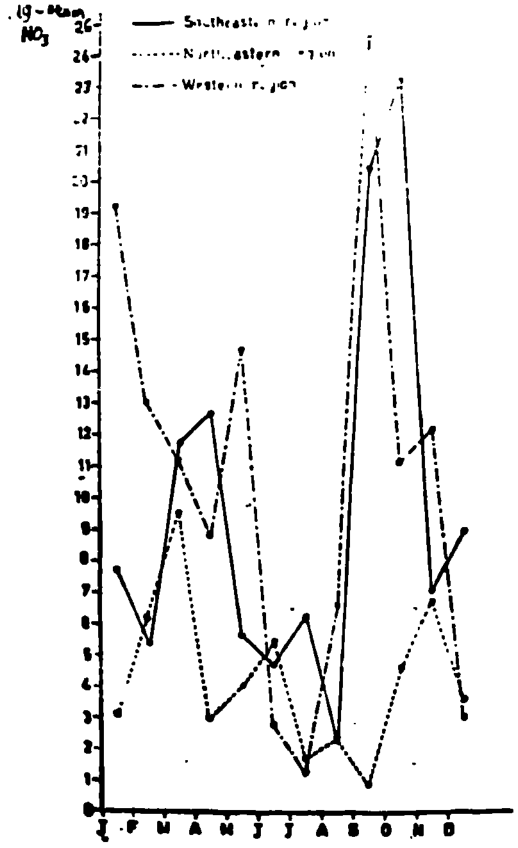

Fig. 15 Nitrate variations in Lake Menzalah (after Wahby *et al.*, 1972)

The ecosystems

The primary producers include the phytoplankton and the submerged higher plants with their epiphytes. In consequence, two main subsystems of trophic relations have to be distinguished, the pelagic and the semibenthic or macrophyte subsystems.

The macrophyte subsystem

The macrophyte subsystem constitutes the so-called "plant-belt" of submerged higher plants covering roughly the whole southern half of the lake. Represented by *Potamogeton pectinatus*, *Ceratophyllum demersum* and *P. crispus*, the macrophytes are flowering plants growing from rhizomes embedded in the bottom sediment and rising up to the water surface. Although seeds are produced and released in spring the plants appear to propagate mainly by their rhizomes. Their wet-weight biomass ranges from 1.7 to 7.1 kg m^2. Spring is the main growth period, followed by a smaller one in early autumn

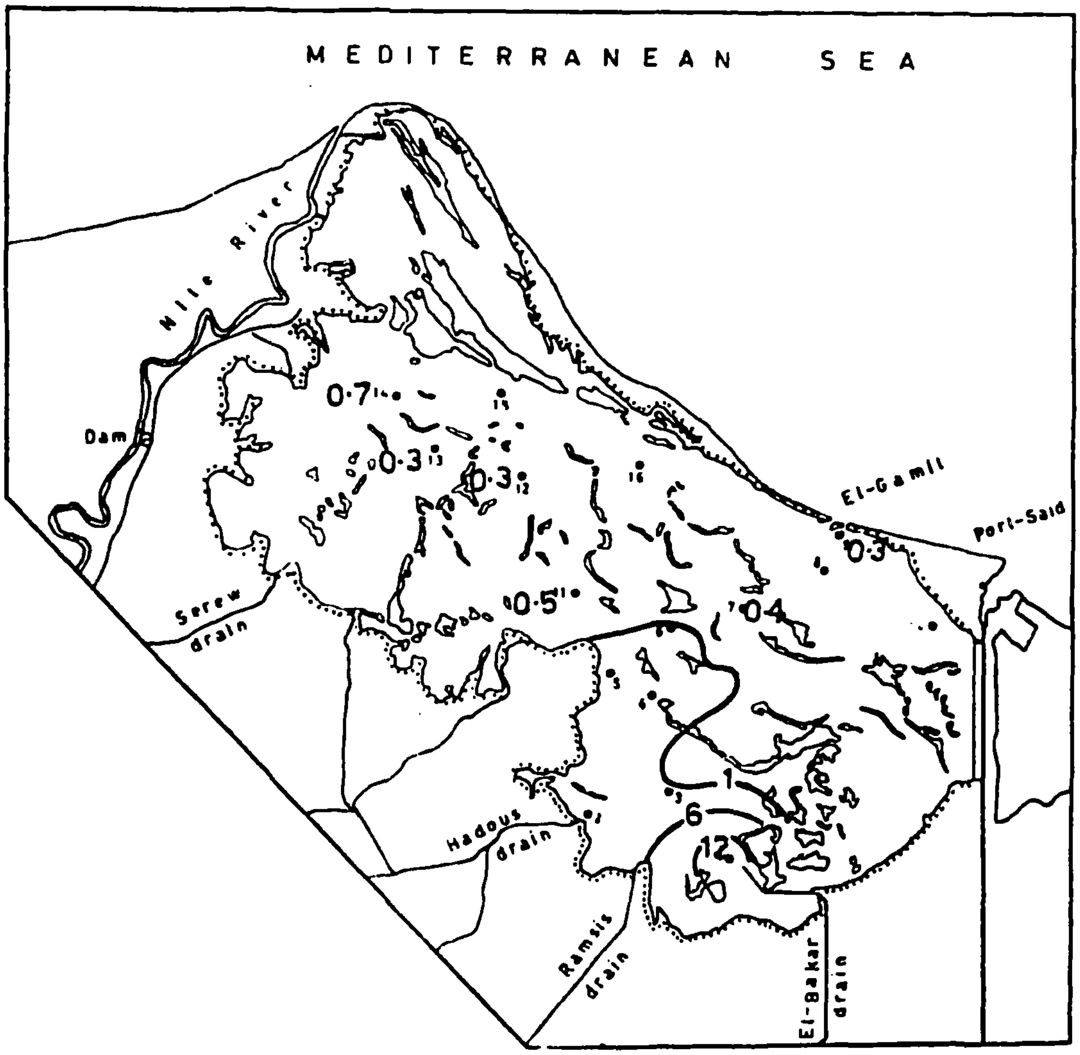

Fig. 16 Phosphate distribution, August 1972.

Table 2. Average phosphate concentration (ug-atom litre^{-1}) in Lake Menzalah basins

Station 1	Basin I	Basin II	Basin III	Basin IV	Basin V
15	2.5	2.2	0.7	0.6	0.5

(Aleem and Samaan, 1969). In winter, the plants deteriorate, settling and decomposing with production of reducing conditions over the bottom. A notable increase in the oxidizable organic

Table 3. Euglena quotient (Total phytoplankton minus Euglena to total Eugena) and frequency (percentage presence in samples).

	Station 1	Basin I	Basin II	Basin III	Basin IV
Quotient	25:1	50:1	280:1	325:1	250:1
Presence in samples, %	87	93	65	60	35

Table 4. Relative importance of the phytoplankton groups in Menzalah basins (percent)

	St. 1	Basin I	Basin II	Basin III	Basin IV	Basin V
Cyanophyoea	8	4	3	9	16.5	11.4
Bacillariophyceae	84	52	25	11.8	18.7	17.2
Chlorophyceae	8	42	72	7.9	64.6	70
Dinophyceae	0.2	2	0.1	0.2	0.2	1.4

matter follows, accompanied by a lowering of the pH (Badawi, 1978). During the growth period, diurnal variations in dissolved oxygen and in the pH are very pronounced (Fig. 18). In the afternoon, the pH exceeds 9, falling to 7.5 at dawn. The concentration of nutrient salts is drastically reduced within the plant-belt (Elster and Vollenweider, 1961). The productivity was estimated to be about 1.3 gm C m^{-2} per day throughout the year in Lake Edku (Samaan, 1974).

As plant material, the macrophytes do not seem to be consumed by herbivores. Fragments of leaves are only accidentally found in the stomach of fish browsing on epiphytes. The macrophyte plant-belt, however, has an essential function in the lake ecosystem. Beside restoring healthy oxygen conditions at the drain inlets (Fig. 19), it provides a substratum for a variety of sessile organisms and a shelter and a feeding ground for many others. The <u>Potamogeton</u> leaves are densely packed with diatoms, mostly <u>Campy-</u>

Table 5. Zooplankton of Lake Menzalah

A. Species in common with the Nile and its upper lakes

Brachionus calyciflorus
B. angularis
B. caudatus
B. falcatus
B. plicatilis
B. quadridentatus
Filinia longiseta
F. limnetica
Keratella quadrata
Lecane luna
Polyarthra dolichoptera
P. vulgaris

Platyias quadricornis
Rotaria reptantia
Trichocerca sp.
Diaphanosoma excisum
Moina micrura
Ceriodaphnia cornuta rigaudi
Bosmina longitostris
Ceriodophnia reticulata
Macrothrix laticornis
Lynceus bukobensis
Mesocyclops leuckarti
Thermocyclops crassus

B. Marine species

Evadne tergestina
E. spinifera
Corycaeus sp. (copepodites)
Oithona sp.
Paracalanus parvus
Clausocalanus furcatus
Labidocera brunescens
Euterpina acutifrons

Microsetella norvegica
Canuella perplexa
Sagitta friderici
Sagitta sp.
Oikopleura sp.
Zoea larvae
Cirrepede larvae
Mesopodopsis slabberi

Iodiscus, *Mastogloia* and *Navicula*, and with filamentous blue-green algae. In spring, three to seven million diatom cells are attached per gram of macrophyte. Two invertebrate species are important browsers on the epiphytes, the amphipod *Gammarus locusta* and the small snail *Theodoxus nigricans*. *Gammarus* appears to perform some vertical migration in relation to the diurnal oxygen cycle and is often found in the plankton. The sessile protozoan *Vorticella microstoma* is mostly abundant in the polluted zone. *Tilapia zilli* fish are attracted to the plant belt where they feed on a mixed diet. Their fry are herbivorous, but the adults, though having a preference for plant food, will also feed on the associated epizoans. Next to diatoms, filamentous algae and detritus, 20% of their stomach content is constituted by Gammarida, gastropods and copepods (Abdel-Malek, 1972).

The pelagic subsystem

The occurrence of successive pulses of abnormally high density should not mask the fact that the lake waters sustain a continuous bloom of phytoplankton. Except for the polluted zone near station

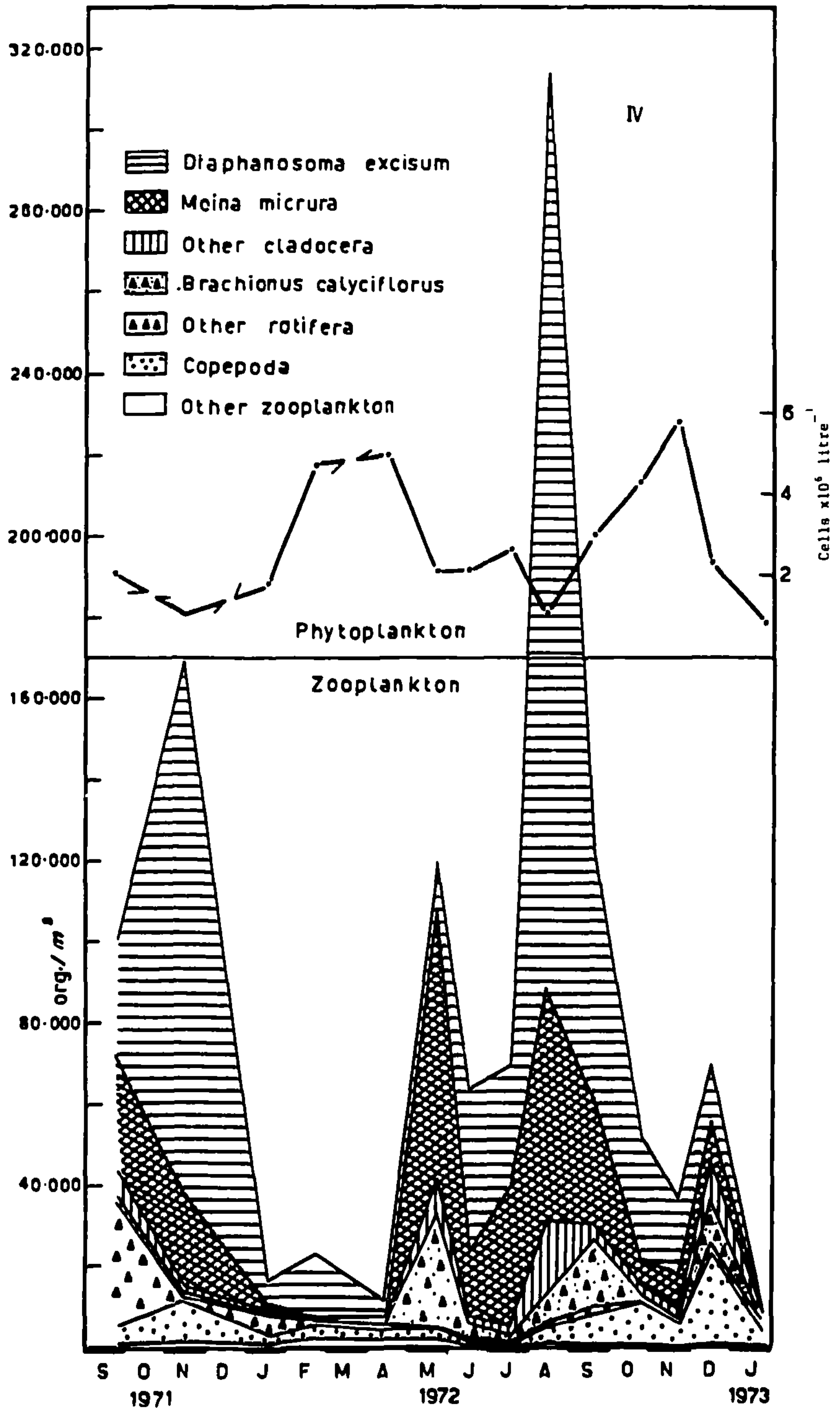

Fig. 17 Phytoplankton and zooplankton standing crops by number. Basin IV.

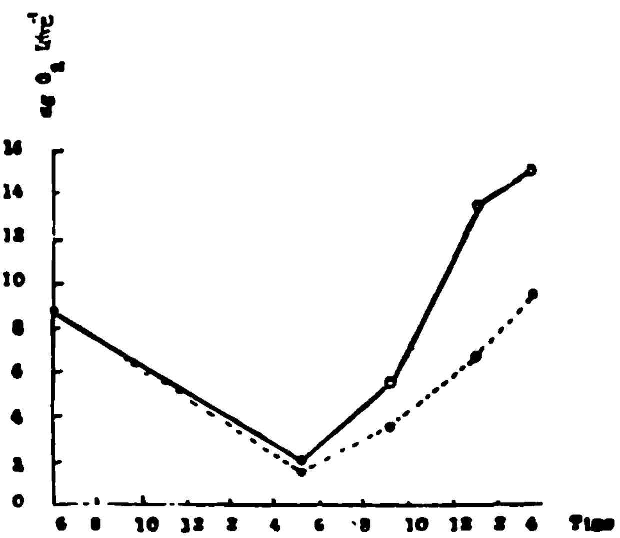

Fig. 18 Diurnal oxygen variations at a position within the plant belt, Lake Mariut (after Wahby, 1961).

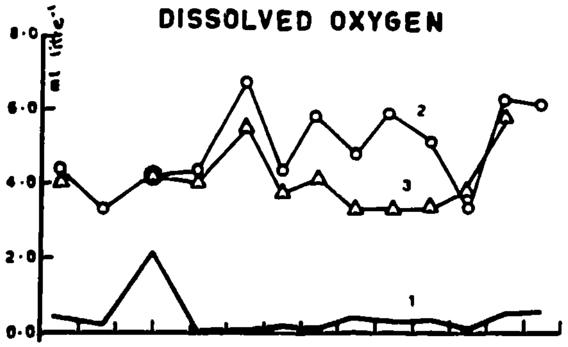

Fig. 19 Monthly dissolved oxygen at stations 1 to 3. (December 1971-December 1972).

1 and for the north-east margin, basin V, the standing crop, even when at a minimum, always exceeds 1 million cells litre^{-1} (Figs. 17, 20, 21, 22 and 23). Large patches of outstanding density develop, reaching up to 6 to 34 million cells litre^{-1}. They are usually centered at the margin of the eutrophic basin I, extending to basin II (Figs. 24 and 25). Although basin I provides the maximal levels of nutrient salts, the heavier growth of submerged hydrophytes appears to limit the development of phytoplankton blooms. The dense meadows of Potamogeton filamentous leaves rising to the surface, reduce light penetration and are likely to limit the photosynthetic zone to a thin layer. The sequence of the blooms, as shown by their successive peaks, is

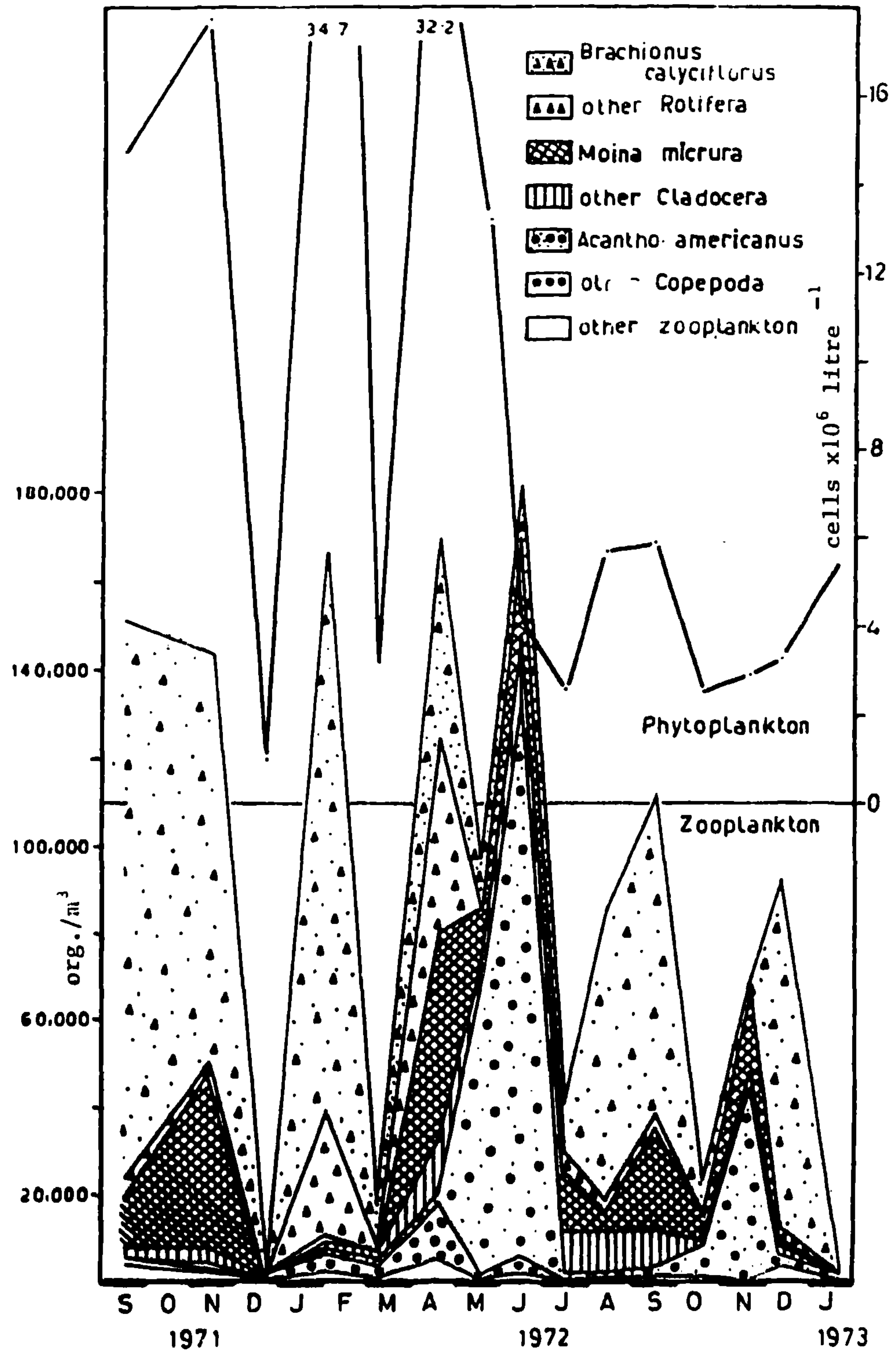

Fig. 20 Phytoplankton and zooplankton standing crop and composition by number. Basin I.

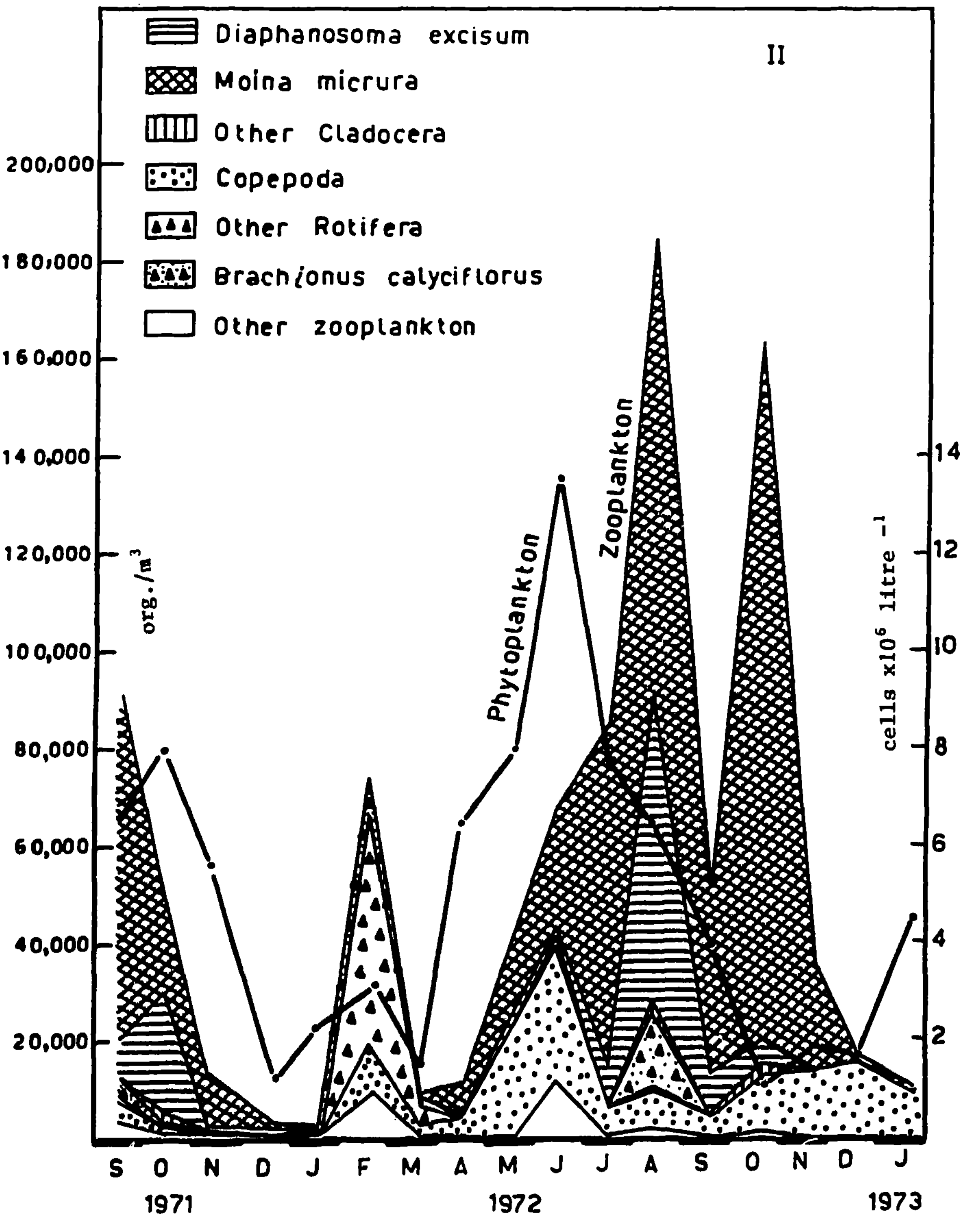

Fig. 21 Phytoplankton and zooplankton standing crop and compositon by number. Basin II.

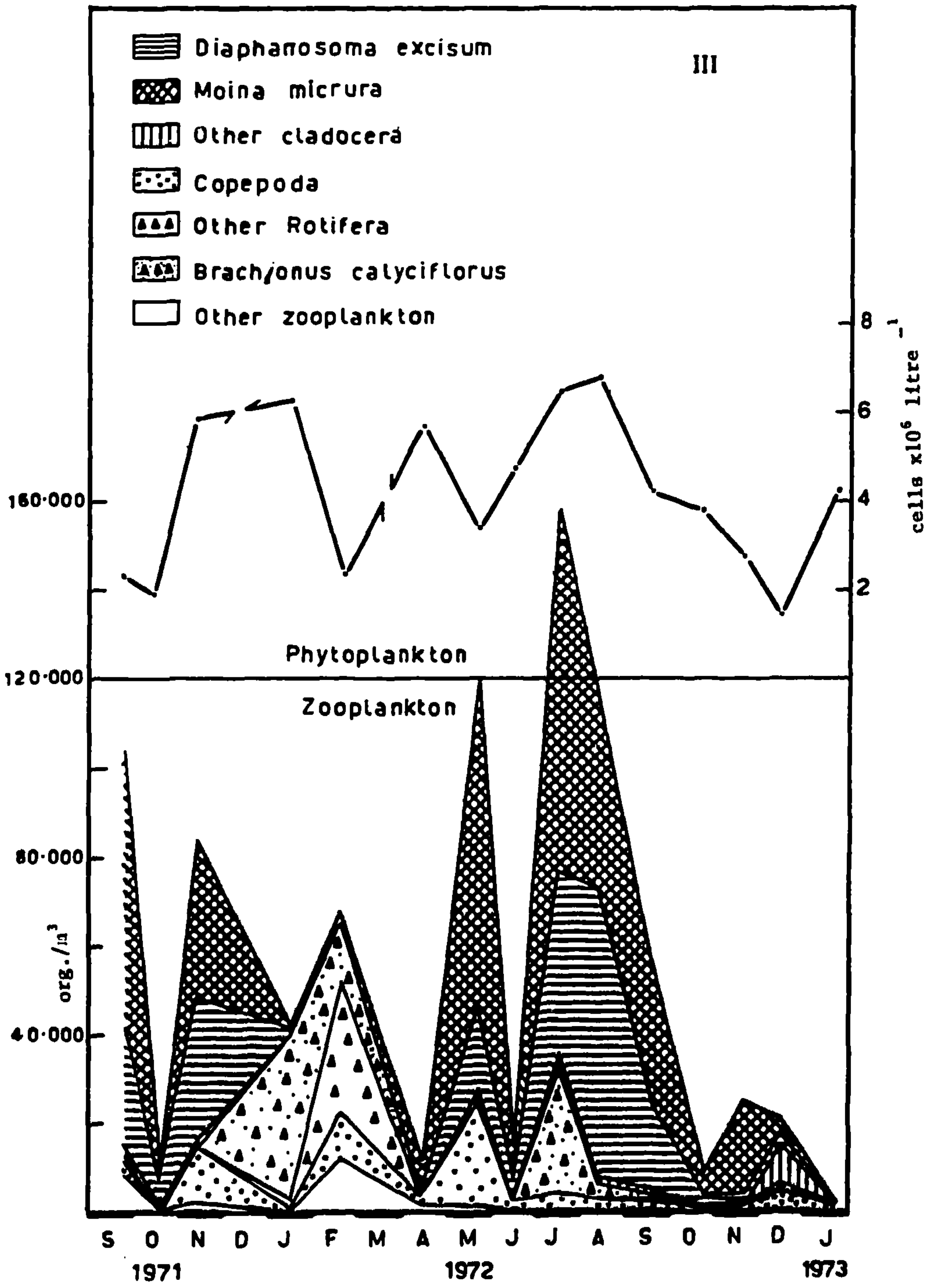

Fig. 22 Phytoplankton and zooplankton standing crops by number. Basin III.

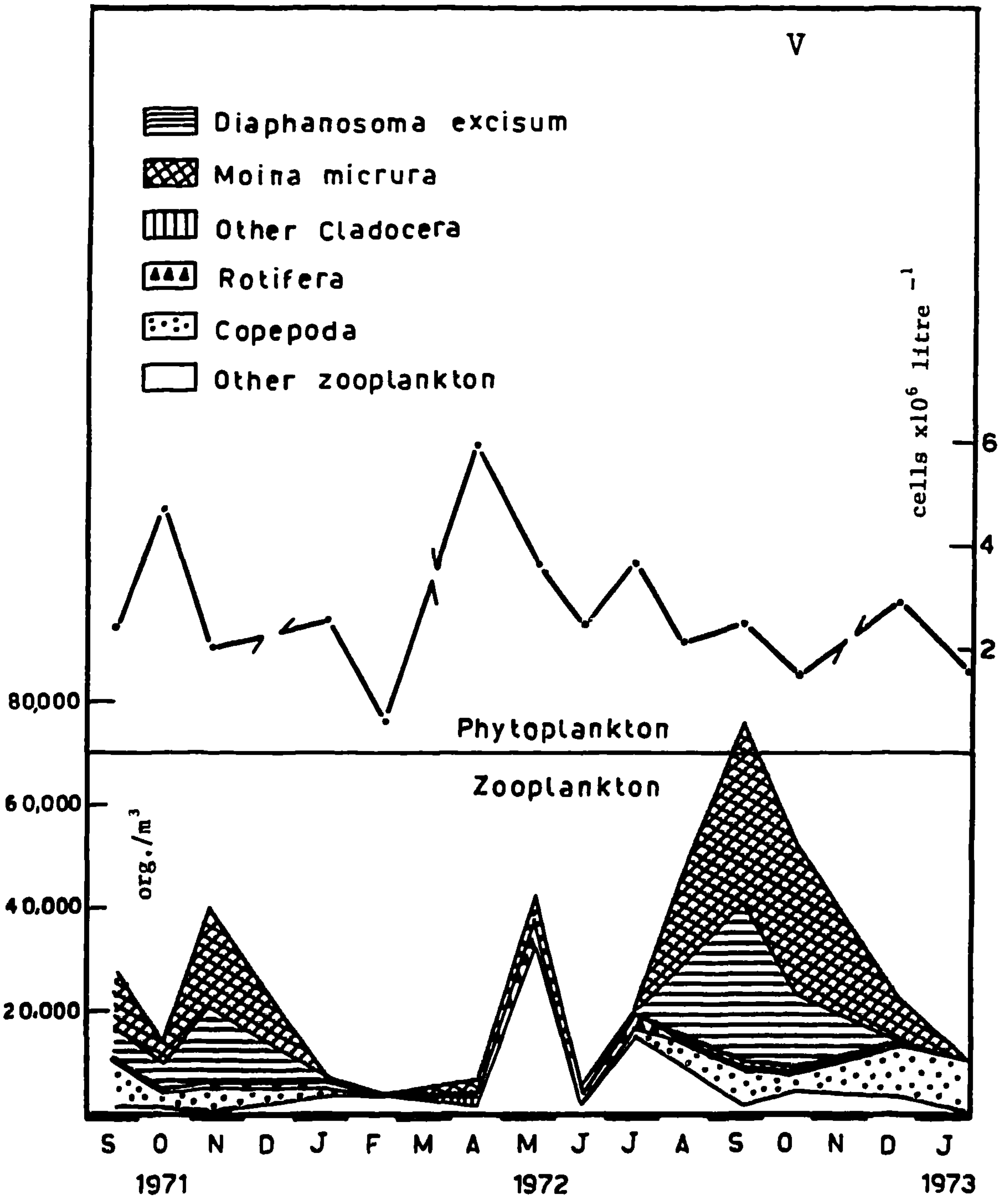

Fig. 23 Phyto- and zooplankton standing crops by number Basin V.

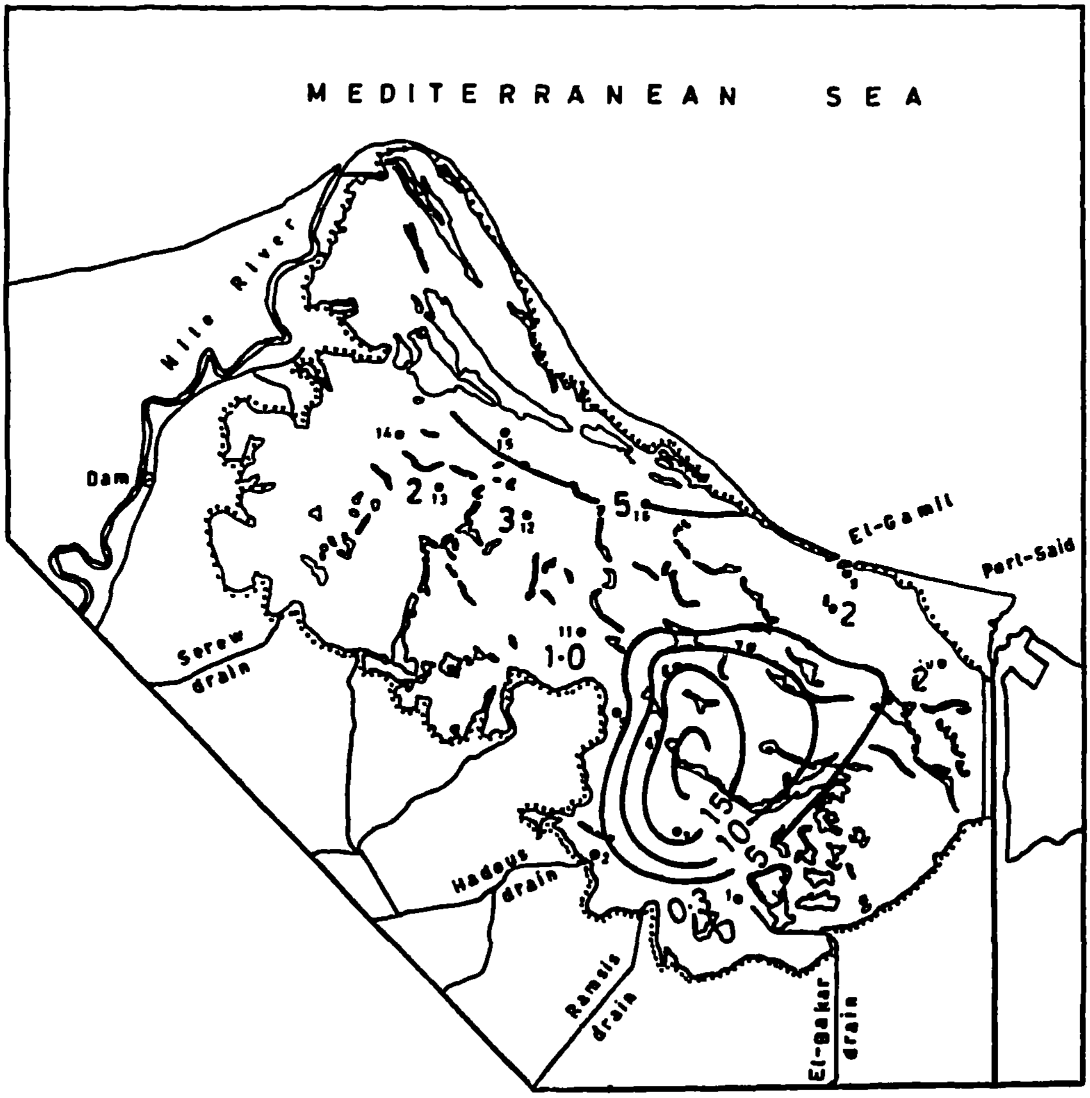

Fig. 24 Distribution of phytoplankton, May 1972. (10^6 cells m^{-3})

independent from the cycle of seasons. Blooms occur at all times in the lake, irrespective of variations in temperature or incident light. Neither the reduction in the rate of drainage inflow in mid-winter, nor its increase in August-September appear to reduce or induce the blooms. The lake environment provides steady optimum conditions for the planktonic producers. The shallowness of such lagoon environments, in itself, creates a situation where seasonal variations are damped and a vigorous production enhanced. Seasonally inhibiting factors in deeper bodies of water, such as deep mixing in winter removing the phytoplankton cells from the photosynthetic layer, or stable stratification in summer, are eliminated. The most important feature in this situation is the

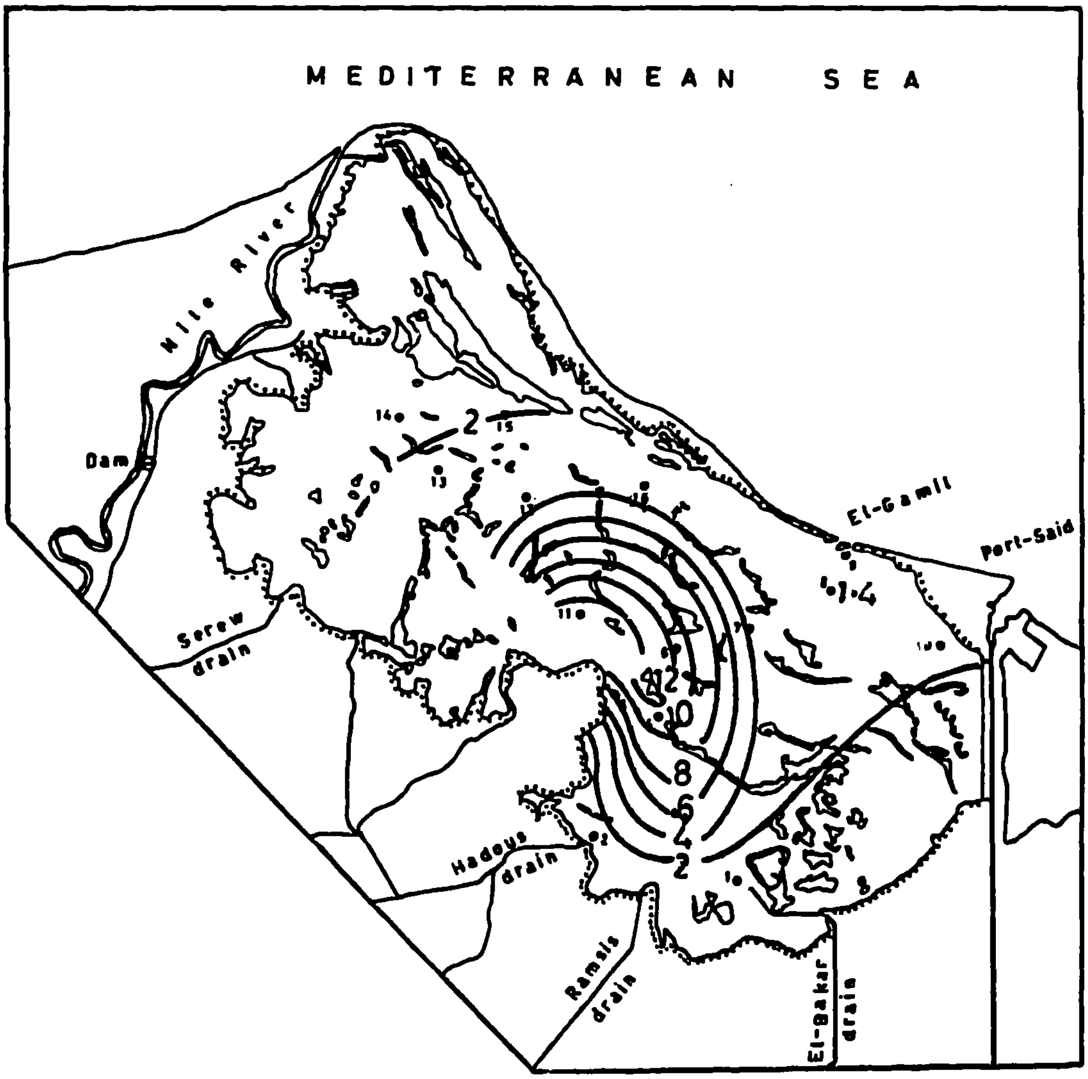

Fig. 25 Phytoplankton distribution, August 1972. (10^6 cells m^{-3})

immediate proximity of the photosynthetic layer to the layer of organic decomposition and to the sediment store. The regenerated nutrients and the nutrients released by wind stirring are immediately available to the producers. The respective contributions of the *in situ* recycling processes and of replenishment from the external supply remain to be investigated.

Heavy grazing by the massive proliferation of pelagic herbivores appears to be the major factor controlling the time sequence as well as the extension in space of the blooms in a simple pattern. As a rule the peaks of abundance of zooplankton are followed by a drop in the phytoplankton standing crop. On the other hand, the respective patches of zooplankton and phytoplankton are not concentric, their cores of maximum abundance are displaced

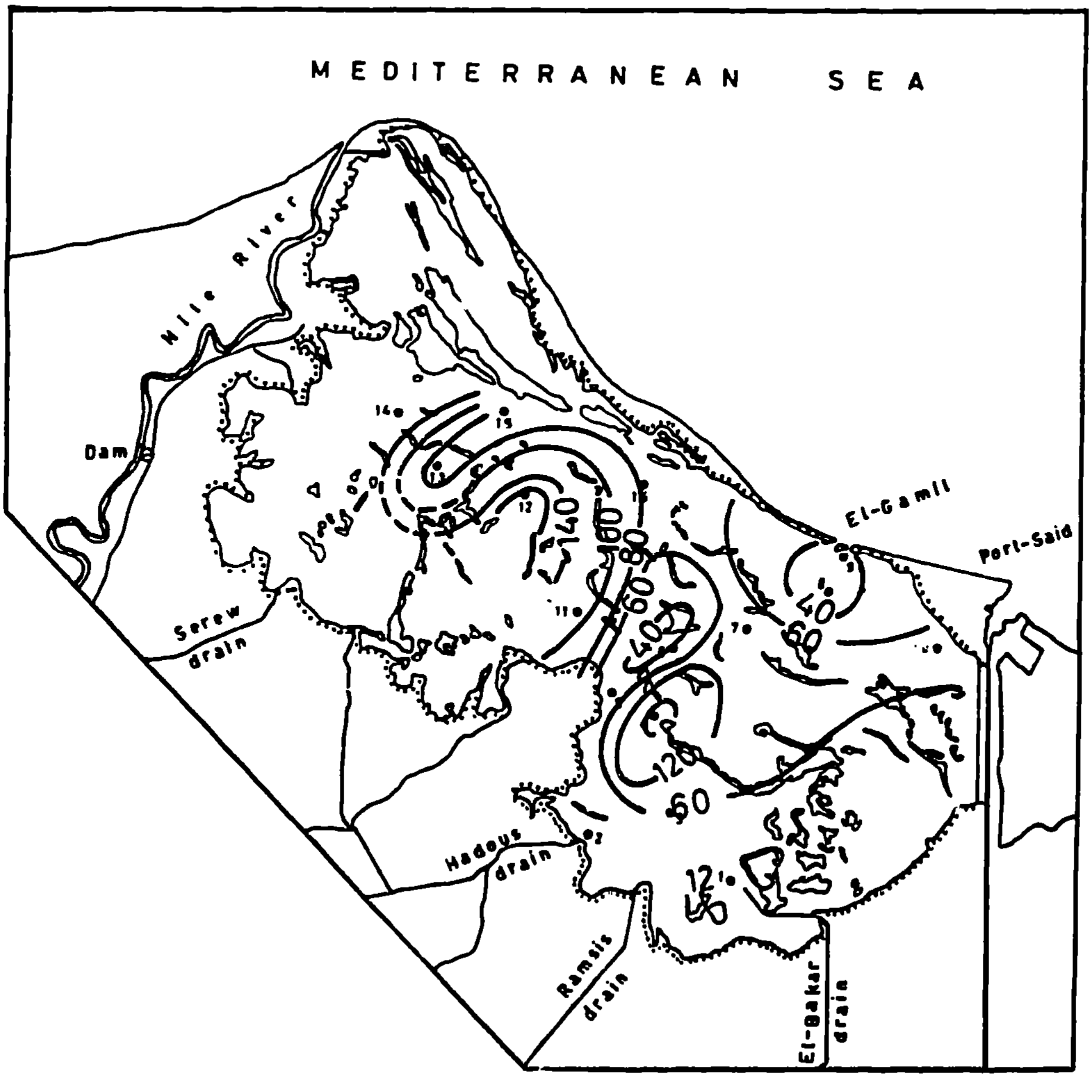

Fig. 26 Zooplankton distribution, May 1972. (10^3 org. m^{-3}).

relative to each other (Figs. 26 and 27). Examination of the stomach content of the predominant forms confirmed their herbivorous habit. The copepod *Acanthocyclops americanus*, the cladocerans *Moina micrura*, *Diaphanosoma excisum* and *Bosmina* and the rotifer *Brachionus calyciflorus* feed indiscriminately on the available planktonic diatoms, green and blue-green algae. *Ulothrix* chains, *Microspora* sp and *Nitzschia* sp are regular items in their stomach content.

The measured volume of the various herbivores shows a significantly wide size range providing for a more efficient use of the available particulate food materials (Table 6). The importance of

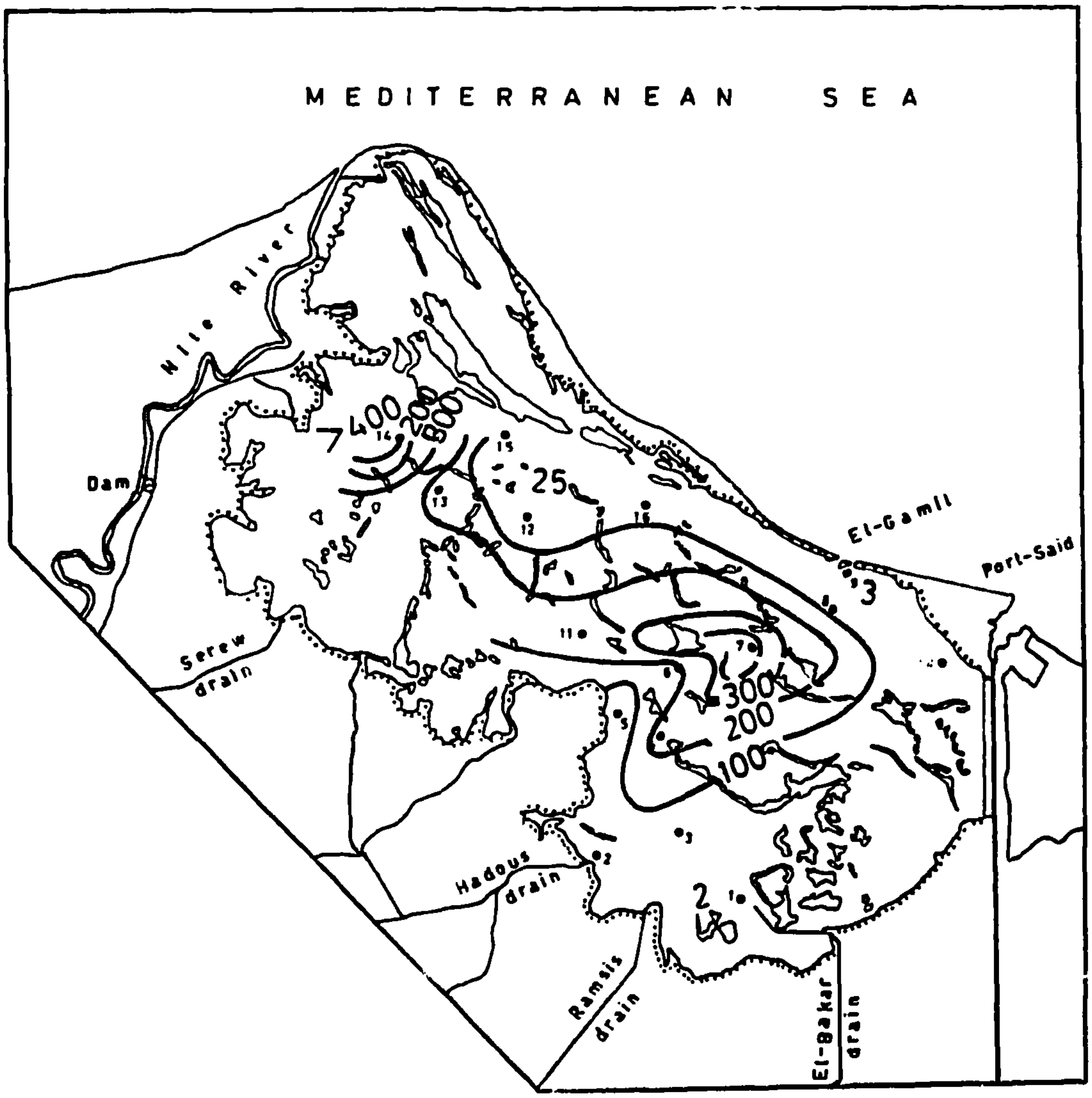

Fig. 27 Zooplankton distribution, August 1972. (10^3 org. m^{-3})

two larger sized, though less numerous, organisms, the mysis larvae of *Palaemon* shrimps and the mysid *Mesopodopsis slabberi*, is revealed (Fig. 28, 29, 30, 31 and 32). Both are phytoplankton feeders but not exclusively so. They also prey on the smaller sized cladocerans and copepods, *Ceriodaphnia* and *Thermocyclops*. Mullet fish are associated with the pelagic ecosystem and Tilapia fish with the macrophyte system. Their juveniles feed on phytoplankton as well as on cladocerans and mysis larvae. With the steady decrease in chlorosity in the last decade and the increased extension of the macrophyte ecosystem, the conditions are more and more favorable to the latter fish. Their relative yield increased from 60 in 1963 to 82% in 1974. In the meantime, mullets dropped from 11% to 7%. Carnivorous fish contribute only 3% to the total (Shaheen and Yosef, 1978).

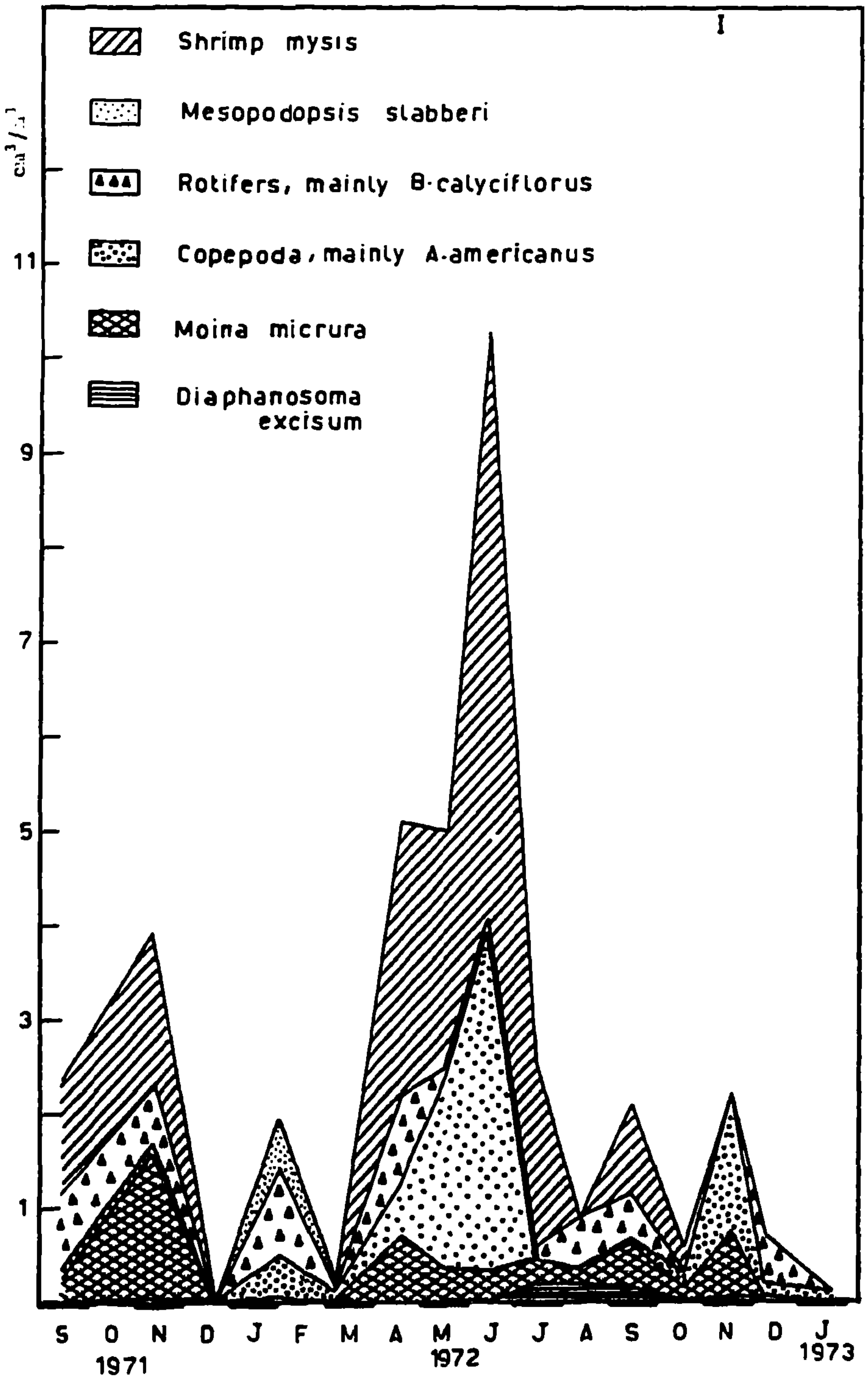

Fig. 28 Zooplankton standing crop and composition by volume. Basin I.

Table 6. Average volume of major zooplankton species in Lake Manzalah (in cubic millimeters)

Species	Average volume (mm^3)
Gammarus sp.	15
Mysis larva of Palaemon	3
Mesopodopsis slabberi	1.25
Mesocyclops leuckarti	0.164
Acanthocyclops americanus	0.001-0.333
Moina micrura	0.0036-0.317
Diaphanosoma excisum	0.00169-0.288
Ceriodaphnia reticulata	0.094
Diacyclops bicuspidatus	0.078
Eucyclops speratus	0.055
Acartia latisetosa	0.046
Macrothrix laticornis	0.032
Ergasilus sp. (male)	0.024
Canuella perplexa	0.023
Thermocyclops crassus	0.021
Ceriodaphnia cornuta rigaudi	0.019
Bosmina longirostris	0.019
Cypris larvae of Balanus	0.018
Halicyclops magniceps	0.016
Lynceus tenuicaudis	0.015
Thersitina gasterostei, copepodite	0.015
Lynceus bukobensis	0.0070
Onychocamptus mohammed	0.0075
Brachionus calyciflorus	0.0068
Nauplii of Balanus	0.0065
Schizopera clandestina	0.0050
Nitocera lacustris	0.0052
Brachionus plicatilis	0.0030
Nauplii of copepoda	0.0012
Brachionus caudatus	0.00067
Brachionus angularis	0.00047

In both ecosystems the plant production largely exceeds the herbivore consumption, but no dystrophy has been observed as yet. The organic matter in the sediment remains relatively low except at the effluent outlet. Oxygen shows a positive gradient from the drain outlets basinward (Fig. 17). Productivity, as judged by the total fish catch, has doubled in the last 20 years. Both the apparent healthy condition of this basin and the steady increase

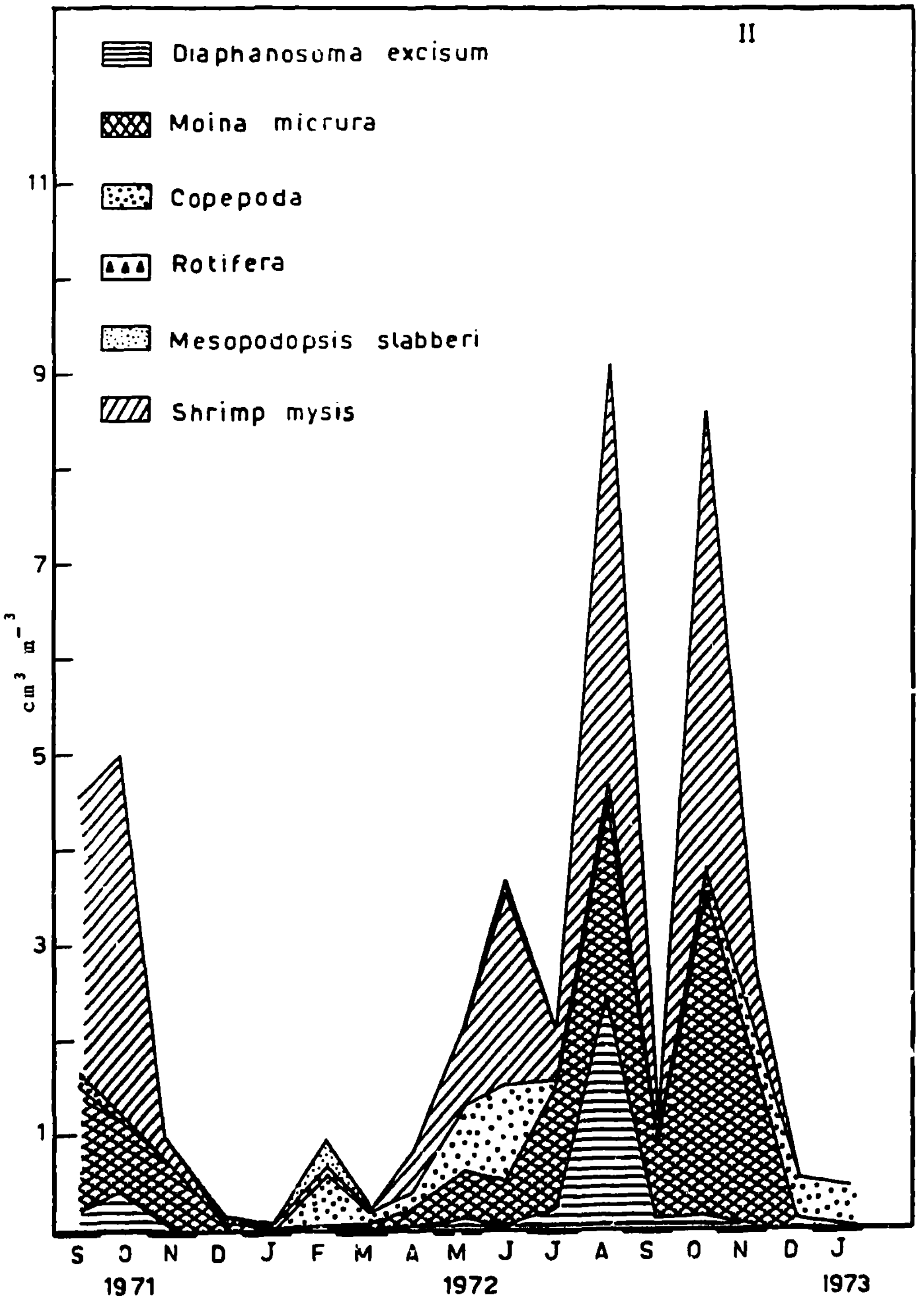

Fig. 29 Zooplankton standing crop and composition by volume. Basin II.

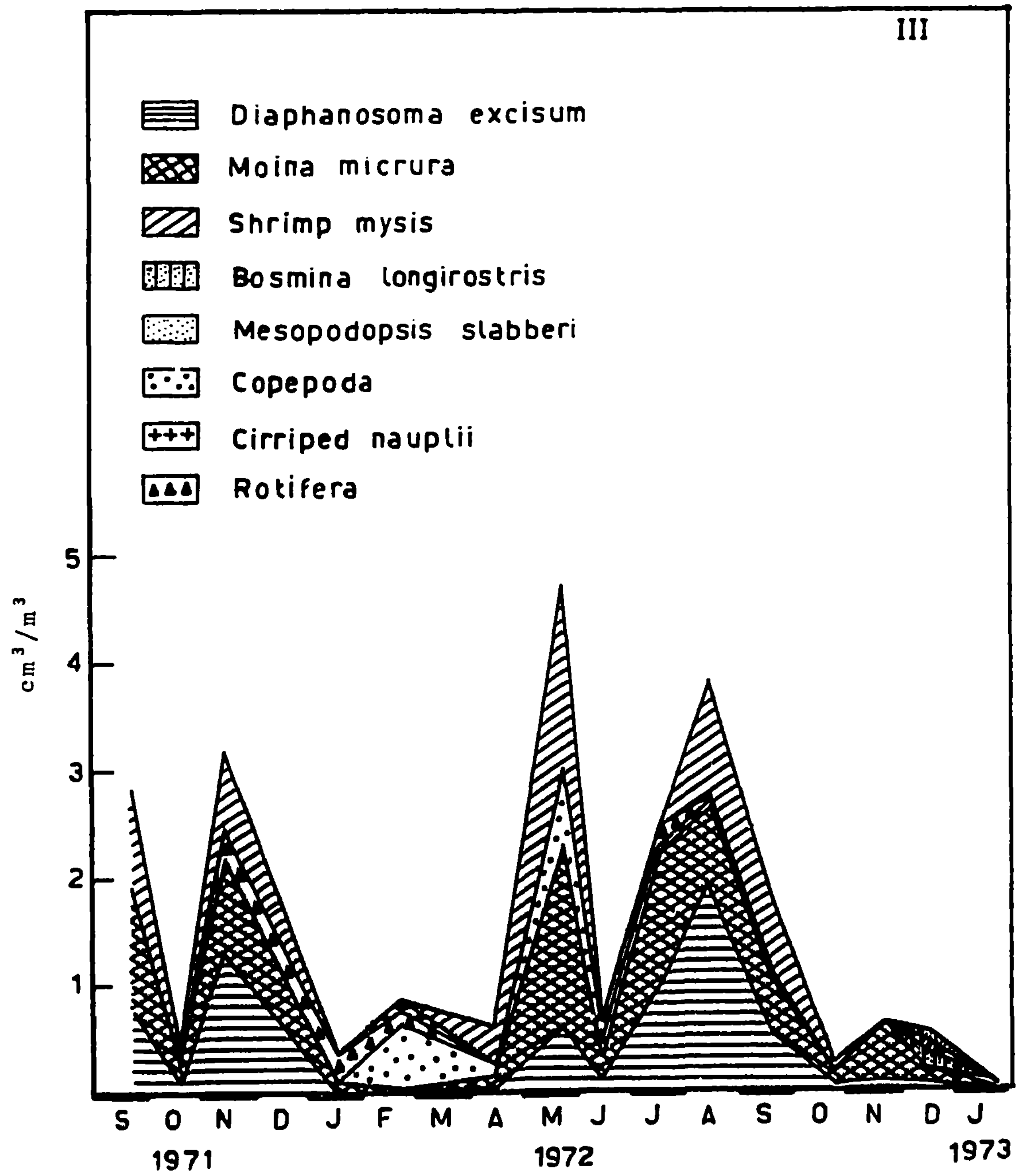

Fig. 30 Zooplankton standing crop and composition by volume. Basin III.

in its productivity are largely determined by the parallel decrease in the residence time from 9 months in 1935 to 3 months in 1956 and finally a month and a half in 1974.

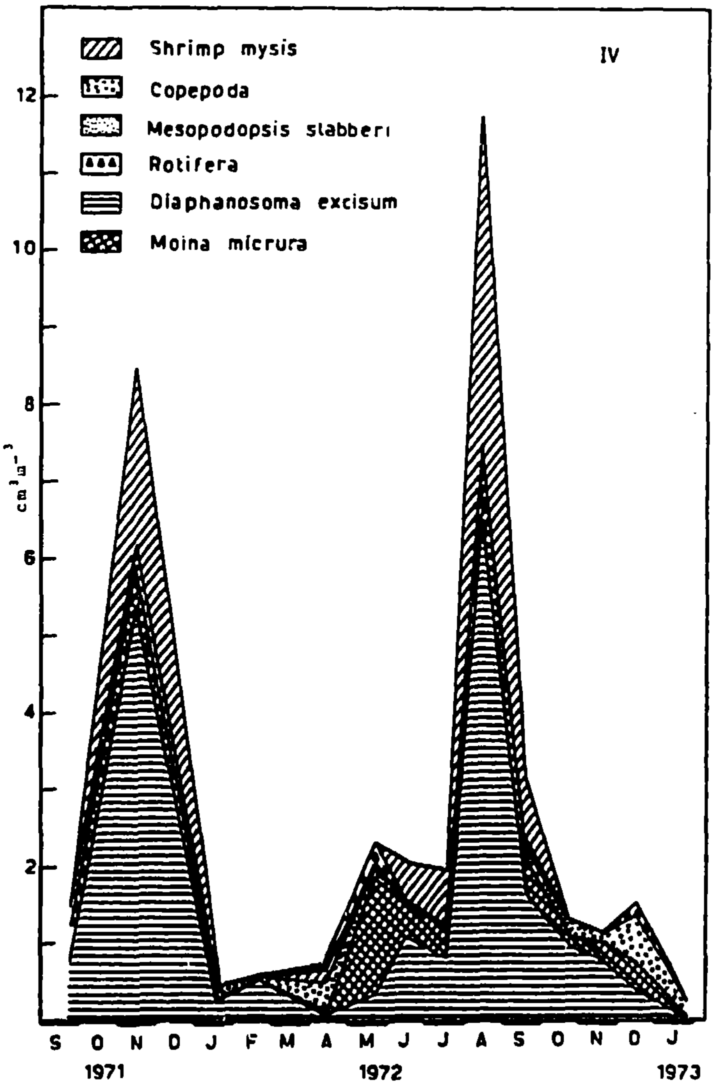

Fig. 31 Zooplankton standing crop and composition by volume. Basin IV.

There are, however, alarming signs when the trend of evolution of phosphate and oxygen over the last two decades is followed. There appears to be a steady decrease in the relative oxygen saturation over the years accompanied by a no less steady increase in the average phosphate. The mean oxygen saturation in 1962-63 was 80-90% and values less than 70% were never observed (El-Wakeel and Wahby, 1970,a). It was 88% in 1967 (Yosef, 1973), with a minimum of 54.4% recorded from Basin I. During the present observations, values of less than 40% were recorded from Basins I, II and IV. In the mean time, phosphate increased from 0.54 ug-atom litre^{-1} in 1963 (El Wakeel and Wahby, 1970,a), 0.54 in 1967 (Yosef, 1963) and 0.47 in 1968 (Bishara, 1973) to 1.36 in the present observations.

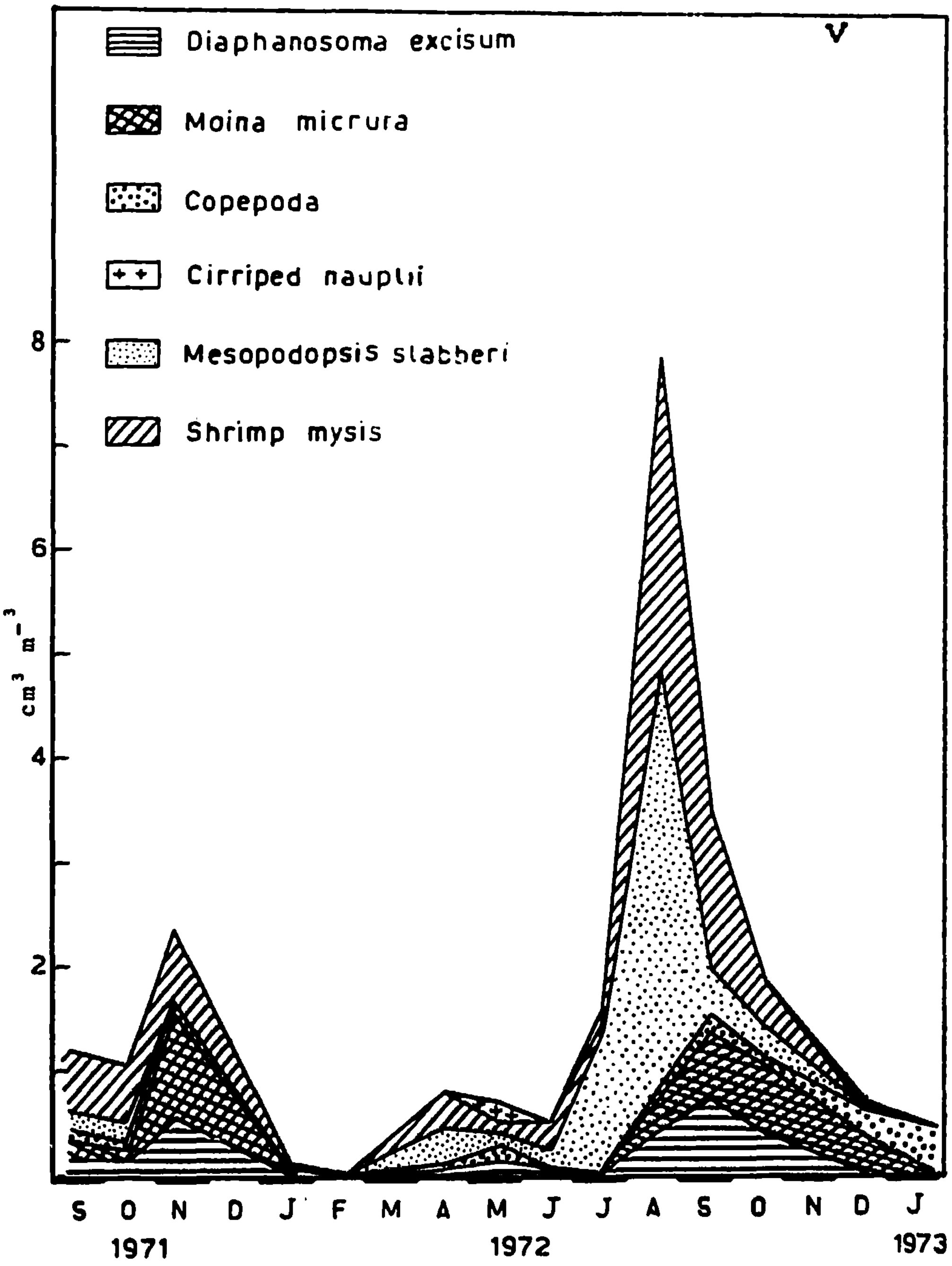

Fig. 32 Zooplankton standing crop and composition by volume. Basin V.

The decrease in dissolved oxygen accompanied by an increase in dissolved phosphate is an indication of a heavier eutrophication load. This trend in Lake Manzalah appears to be acclerated since 1962.

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SPATIAL AND TEMPORAL VARIATIONS OF PHYTOPLANKTON PRODUCTION IN LAGOONS

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INTRODUCTION

Lagoon, as a generic term, has perhaps many meanings and a precise definition is hard to formulate since the characteristics of each are different. Coastal lagoons should be viewed as ephemeral modified estuaries with little or no freshwater inflow. They are shallow, semi-enclosed bodies of water, lying parallel to the coastline and separated from the open sea by barrier islands. A shallow euphotic zone where environmental conditions are significantly modified by strong wind-driven turbulence and periodic tidal exchange are also prominent features. Coastal lagoons, which constitute about 13% of the total world coastline, are highly productive and contribute large quantities of organic matter to the adjacent seas. In contrast to coastal lagoons, which are also used for aquaculture and recreation, oceanic lagoons, particularly those enclosed by coral reefs and atolls, are usually in a relatively natural state due to lesser input of domestic agricultural and industrial wastes.

Considerable progress has been made in our understanding and management of estuaries through conceptual modelling studies and it would be desirable to extend a similar approach to the lagoons. However, the necessary data is scarce, being mostly limited to qualitative and quantitative abundance of phytoplankton and to scattered primary production measurements for only short time intervals. These data have shown that their phytoplankton populations exhibit strong spatial and temporal fluctuations (Voltolina, 1973a, b) and that the magnitude of primary production was high (Vatova, 1961).

The purpose of this paper is to use available information from lagoons to identify the mechanisms that lead to spatial and temporal variations in phytoplankton populations and to compare their photosynthetic functioning. A few guidelines on the methodology for future research are also provided.

PHYTOPLANKTON COMMUNITY AND SUCCESSION

The phytoplankton community of the lagoons is represented by a great number of taxa including diatoms such as *Chaetoceros* sp., *Coscinodiscus excentricus*, *Navicula pygmaea*, *Nitzschia closterium*, *N. delicatissima*, *N. seriata*, *Phaeodactylum tricornutum*, *Rhizosolenia hebetata f. semispina*, *Skeletonema costatum*, *Thalassionema nitzschioides* and *Thalassiosira fluviatilis* and dinoflagellates such as *Ceratium furca*, *C. fusus*, *Cochlodinium* sp., *Goniaulux digitale*, *Gymnodinium splendens*, *Peridinium divergens*, *Prorocentrum micans* and *Pyrodinium bahamense*. A few of these taxa, due to their ubiquitous distributions, have been isolated from environments other than lagoons and brought into laboratory cultures and studied in considerable detail.

Phytoplankton species composition in the lagoons depends to a great extent on the hydrological conditions. Under brackish or hypersaline conditions of Mukwe Lagoon, Ghana, fewer species were present than in the adjacent estuarine Sakumo Lagoon (Kwei, 1977). In Lake Edku, an Egyptian lagoon which receives considerable freshwater run-off, most of the species were either freshwater or brackish water forms (Samman, 1974). Lagoons that receive rich dissolved organic matter as Lake Mariut, Egypt (Aleem and Samaan, 1969), Venice Lagoon (Voltolina, 1973a) and the Lagoon of Alvarado, Mexico (Margalef, 1975) have members of Eugleninae. Information on the seasonal blooms of different phytoplankton groups in lagoons is summarized above.

A typical succession such as that described by Margalef (1960) for smaller bays, i.e., initial growth of small-celled diatoms of Chlorophyta followed by a mixed community of bigger diatoms and finally by dinoflagellates, is not seen in any of the five lagoons. In the Egyptian lagoons *Gymnodinium Lohmanni* was the only dinoflagellate out of 64 taxa reported (Aleem and Samaan, 1969).

Commonly, a single taxonomic group constitutes the bulk of the phytoplankton. For example, in the oceanic lagoons of Faaa and Vairo of the 580 phytoplankton species reported 314 were diatoms (Ricard, 1977) while in Puttalam Lagoon, Ceylon, 70 out of 75 taxa were diatoms. Here *Chaetoceros lascinosus*, *Rhizosolenia alata*, *R. imbricata*, *Thalassionema nitzchioides*, *Thalassiosira subtilis* and *Thalassiothrix frauenfeldii* bloomed at different times of the year (Durairatnam, 1963). In Bahía Fosforescente, Puerto Rico five dinoflagellate species *Pyrodinium bahamense*, *Peridinium divergens*, *Ceratium furca hircus*, *C. fusus* and *Dinophysis caudata* usually dominated the phytoplankton crop (Seliger *et al.*, 1971). Monospecific blooms of microplankton such as euglenoids, pennate diatoms, *Cochlodinium* sp., *Goniodoma* sp. and *Dunaliella salina* were common in the southern coastal inlets of Puerto Rico (Burkholder *et al.*, 1967). In the barrier island lagoons of the Gulf of California,

LAGOON	SEASON			
	Spring	Summer	Fall	Winter
Edku[1]	Chlorphyta	Cyanophyta & some diatoms	Chlorophyta	Diatoms
Mariut[2]	Diatoms	Cyanophyta	Diatoms	Chlorophyta
Venice[3]	Diatoms Coccolithophores Euglenoids	Dinoflagellates	Diatoms & coccolithophores	Coccolithophores end dinoflagellates
Faaa[4]	Diatoms	Dinoflagellates	Diatoms	Dinoflagellates
Vairao[5]	Diatoms	Dinoflagellates	Diatoms	Dinoflagellates

[1] Samman, 1974
[2] Aleem and Samman, 1969
[3] Voltolina, 1973a
[4] Ricard, 1977
[5] Ricard, 1977

microflagellates (2-5um) generlly dominated the nanoplankton. In these waters smaller pennate diatoms constituted about 25% of the nanoplankton in the eutrophic eastern lagoons whereas in oligotrophic western lagoons, where the contribution of pennate diatoms never exceeded 1%, Myxophyceae and a large number of dinoflagellates occurred as co-dominants (Gilmartin and Revelante, 1978).

SPATIAL DISTRIBUTION

As shown in Fig. 1, the species diversity index in the lagoon proper is low (<1.0) and increases in the direction of the open sea where it reaches a maximum of 4.5. The pattern of primary production is just the opposite with a maximum in the lagoon decreasing to about 5% along a section moving offshore perpendicular to the coast. In the vertical scale, surface phytoplankton populations from temperate and tropical lagoons generally have lower species diversity, evenness and richness than the sub-surface populations (Manzi *et al.*, 1977). In the Lagoon Estero de Urias the minimum species diversity index (0.42) is associated with the maximum primary production (136 mg C hr^{-1} m^{-3}) and a minimum production (4 mg C) is associated with a high species diversity index (3.76) in the Lagoon Bahía Concepción (Gilmartin and Revelante, 1978). Because of certain abiotic and biotic factors some of the phytoplankters, especially the motile flagellates and

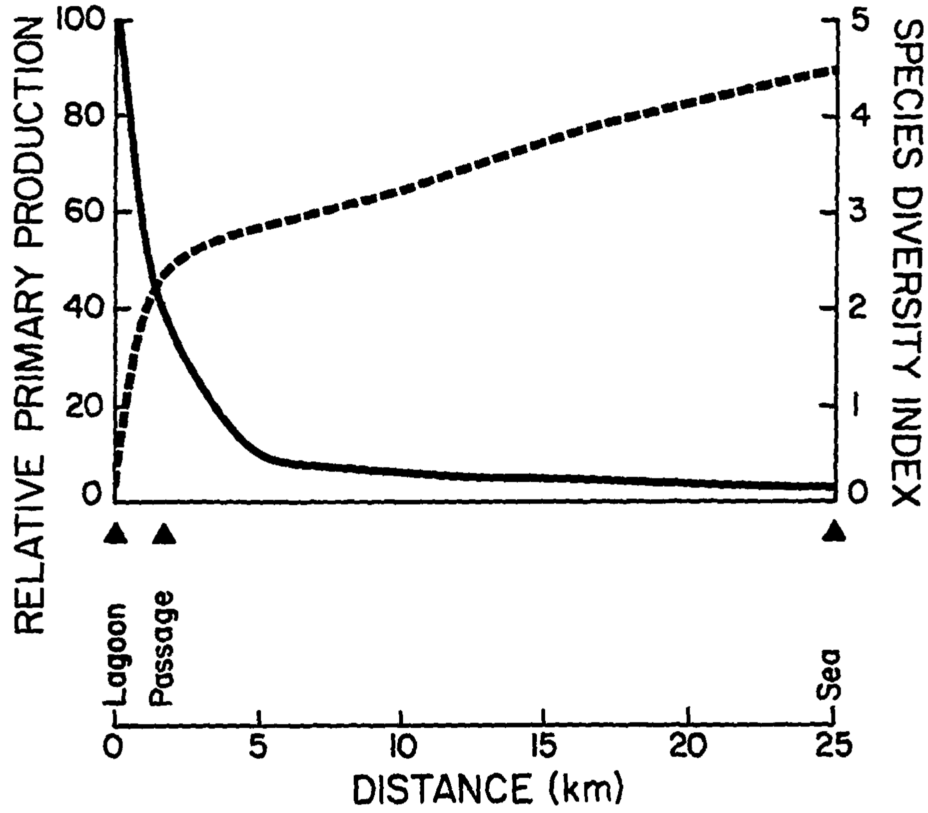

Fig. 1 Schematic illustration of the relationship between species diversity index and primary production along a section perpendicular to the coast starting in a coastal lagoon.

dinoflagellates, usually occur in patches on a scale of few to several hundred meters and thus introduce both spatial and temporal heterogeneity.

We might then ask what mechanisms generate a patchy spatial and temporal distribution of phytoplankton in coastal lagoons. As direct observations on the mechanisms for the accumulation of certain phytoplanktons in lagoons are lacking, perhaps observations from the tidal creeks on Sapelo Island, Georgia and Oyster Bay, Jamaica may be considered as analogous because of similarities such as shallow depth and similar phytoplankton composition. Two categories of accumulation mechanisms are operative: 1) abiotic or vectorial factors, such as the transportation and displacement of *Pyrodinium bahamense*, by differential movement of diurnal wind-driven water layers of different densities, as in Oyster Bay (Seliger *et al*., 1970) or convergences of *Gymnodinium* sp. between wind-driven convection cells, as in Sapelo Island (Pomeroy *et al*., 1956); 2) biotic factors, such as positive phototaxis towards light during day and nocturnal downward migration of *Pyrodinium bahamense* in Oyster Bay and *Gymnodinium* sp. in the tidal creeks of Sapelo Island.

PRIMARY PRODUCTION IN LAGOONS

Three types of temporal variations, diurnal, tidal and seasonal variations in primary production will be considered here. Variations in primary production due to transient meteorological conditions such as cloud cover and rapid fluctuations in irradiance are reported from coastal waters (Dera *et al.*, 1975). For want of similar direct observations from lagoons this aspect is not considered. Nor is there information on long-term observations.

Diurnal variations

Diurnal variations in photosynthetic activity in the low and mid-latitude lagoons are similar. In Minicoy and Oyster Pond waters photosynthesis increased steadily in the morning hours to attain a maximum at about 1200 hrs and decreased gradually in the afternoon (Fig. 2). The photosynthesis maximum:minimum ratio in both these lagoons was about 12, similar to that reported from coastal waters (Sournia, 1968).

Tidal variations

In Venice lagoon, primary production during low tide was higher than that during high tide (Vatova, 1961) (Fig. 3). Vatova (1961) showed that during low tide individual production values ranged between 4 and 1078 mg C day^{-1} m^{-2} and during high tide between 10 and 313 mg C day^{-1} m^{-2}. Using 24 pairs of data (see Table 1, Vatova), the affect of the phase of tide on production was tested by the Wilcoxon matched-pairs signed - ranks test (Siegel, 1956). The smaller of the sums of the like-signed ranks (T) was 39. For N-24, a T of 39 is significant at <0.005 level which allows us to conclude that the phase of tide does affect primary production. Such differences were attributed to the shallow photosynthetic layer, containing higher levels of nutrients during low tide. In the same lagoon, Voltolina (1973a, b) also showed a similar difference in the total phytoplankton abundance, during low tide the cell numbers ranging between 5.1 and 70.6 x 10^6 cells litre^{-1} and during high from 0.45 to 23.6 x 10^6 cells. Comparison of carbon assimilation ratios (mg C hr^{-1} mg Chl *a*) during low and high tide would be interesting but chlorphyll *a* data are lacking. However, the association of higher production and higher cell concentrations suggests that production:biomass (P/10^6 cells) ratios during the two tidal phases may not be significantly different.

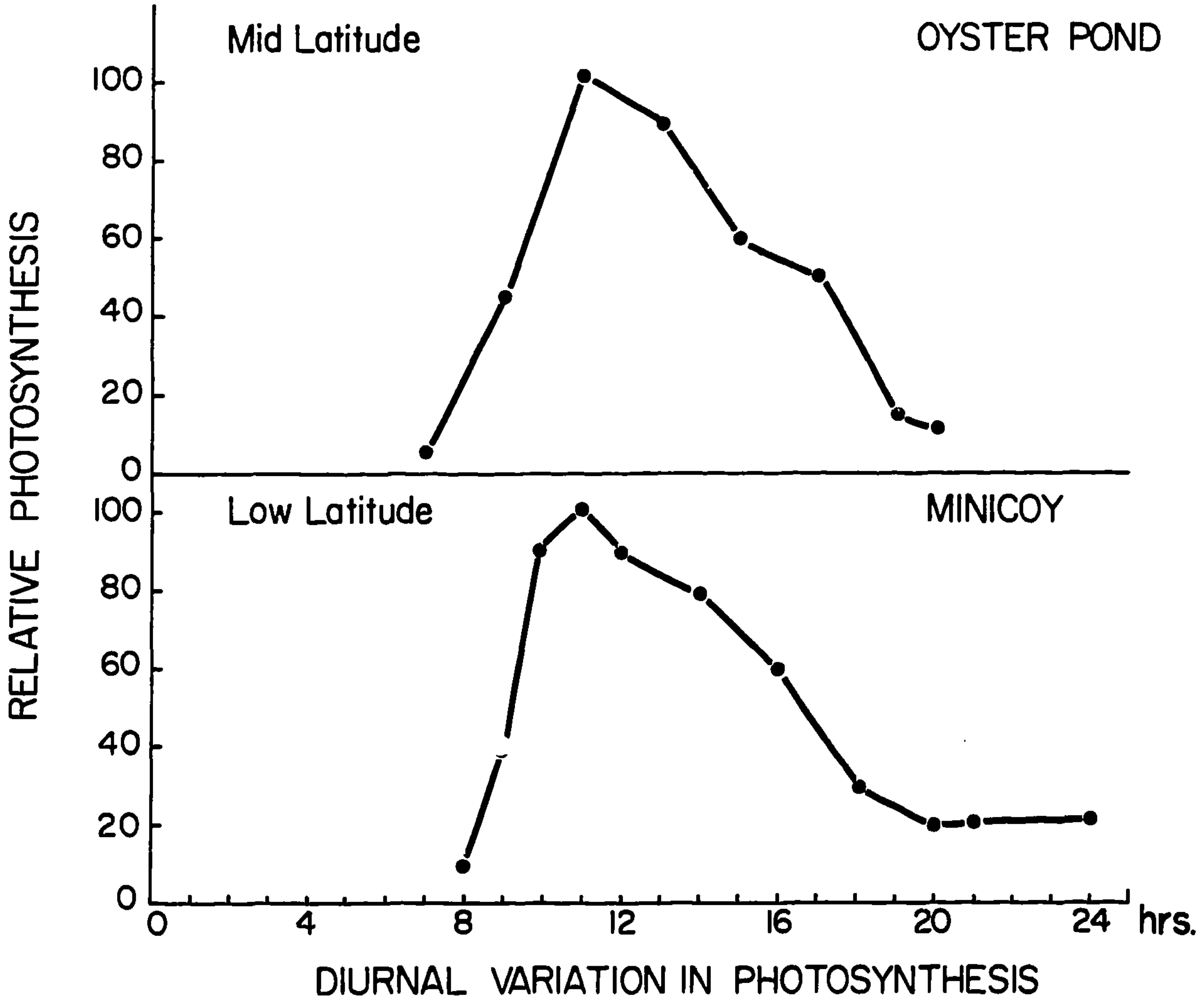

Fig. 2 Diurnal variations in photosynthesis in Oyster Pond and Minicoy waters. Data for Oyster Pond are from Emery (1975) and for Minicoy from Nair and Pillai (1972).

Seasonal variations

Fig. 4 summarizes primary production in five lagoons from mid-latitude regions only as data from low and high latitudes are lacking. In Venice Lagoon and Lake Mariut which receive nutrient rich effluents an unimodal peak production was noticed. Production was initially low during January-February and gradually increased to attain a peak during July-August. The production pattern in Lake

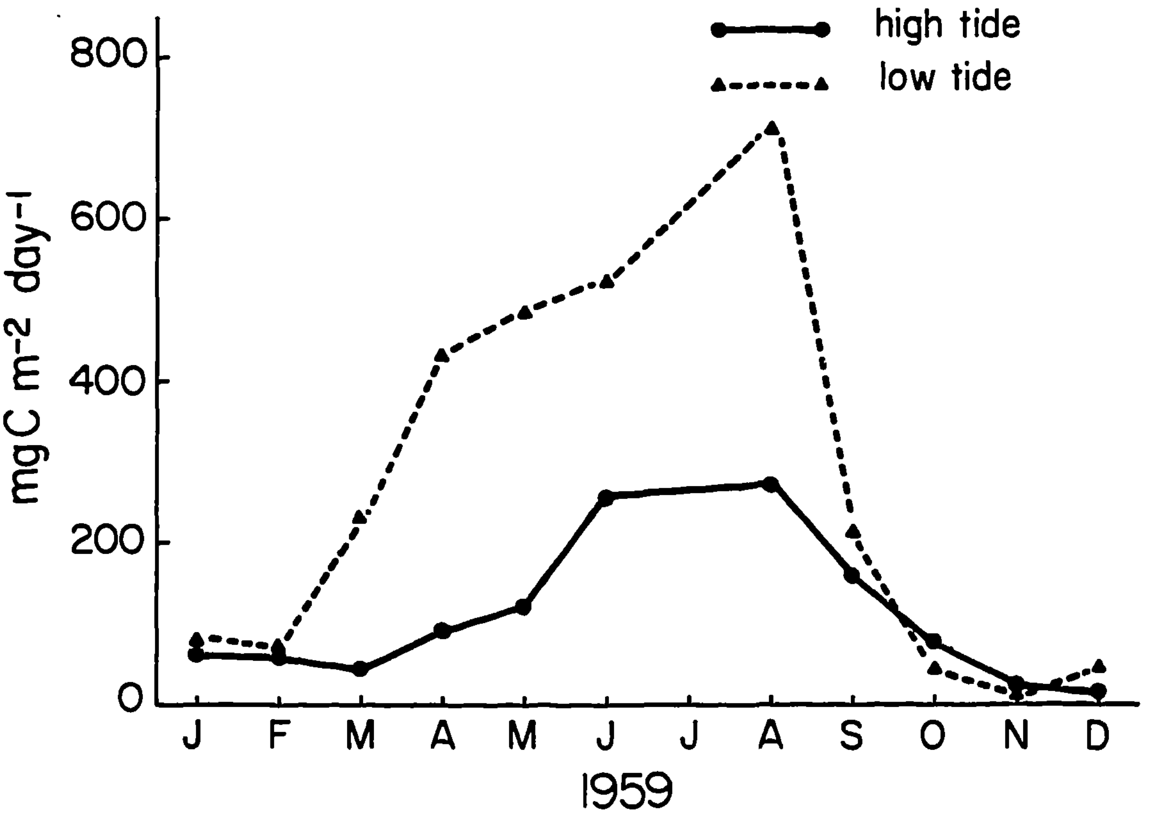

Fig. 3 Tidal variations in primary production in Venice lagoon. Data are from Vatova (1961).

Mariut ran parallel to the level of incident solar radiation and annual temperature curve (Aleem and Samaan, 1969). These authors concluded that in Lake Mariut neither phosphate, nitrate nor nitrite limit primary production. In Venice Lagoon, which is about four times more concentrated than Lake Mariut, nutrients presumably do not restrain production either.

In both lagoons, changes in temperature seem to effect production. Thus in Lake Mariut the fall of temperature below 17°C during winter resulted in a sudden drop in primary production. In Venice Lagoon production was high only during spring and summer when the water temperature was above 10°C. and low during autumn and winter when the temperature was below 10°C.

Seasonal production data from Cananeia Lagoon, Oyster Pond and Lake Edku (Fig. 4) show a biomodal distribution. In these lagoons the primary peak was during February-March and the secondary peak during August. In Lake Edku and Oyster Pond production was low

Table 1. Primary production characteristics for mid-latitude lagoons based on year round observations.

Region	Latitude	Temperature °C	Salinity °/oo	Primary peak of production			Secondary peak of production			Annual production g C/m²/yr	References
				Range mg C/m²/day	Amplitude	Duration months	Range mg C/m²/day	Amplitude	Duration months		
Venice Lagoon	45.15N	6-25	32-34	133-1387	10	8	None	-	-	147	Vatova 1961
						12	None	-	-		
Lake Mariut	31.15N	12-29	2.76-10.23								
Stn I				3596-10572	3					2667@	Aleem and Samaan 1969
II				2175-9821	4.6					2861@	
III				2005-9685	5					1967@	
IV				1524-4961	4					1355@	
V				383-7965	31					1805@	
VI				110-5181	47					630@	
VII				11-3179	289					1886@	
VIII											
Oyster Pond	40N	2-22	1.7-11	101-710	7	4	296-527	1.8	3	140	Emery 1975
Lake Edku	31.15N	14.2-28.5	0.79-18.43								Samaan 1974
Stn I				150-377	2.5	6	223-403	2	2	118@	
II				408-1395	3	5	914-1331	1.5	3	254@	
III				195-824	4	6	684-1489	2	4	288@	
IV				180-1634	9	4	677-1609	2	4	283@	
V				165-528	3	6	191-875	4.6	4	159@	
Cananeia Lagoon	25.01S	17.5-28.1	3.4-24.4	199-2044	10	5	117-825	7	3	180@	Tundusi 1969

@Calculated. Amplitude and duration of production cycle are calculated using Cushing's method (1975).

during the winter months, December and January, coinciding with low water temperatures. In Cananeia Lagoon, Brazil, changes in salinity seem to regulate production more than temperature; thus production was low during February and May when there was a sudden drop in salinity to 3.54-4.80 parts per thousand (Tundusi, 1969). Of these three lagoons, nutrient data are available only from Lake Edku and Samman (1974), concluded that nutrients in general do not limit production.

In Langebaan Lagoon, South Africa, phytoplankton production, probably triggered by the influx of nutrient rich waters, attained a maximum during spring. In late summer, owing to low nutrient levels, production decreased (Henry et al., 1977). A gradient in production was also observed with high values close to the source of nutrients near the entrance to the sea and low values at the head of the Langebaan Lagoon farthest from source.

In the tropical Puttalam Lagoon, Ceylon, where seasonal range in temperature and salinity were 27.6-30.8°C and 20.0-36.4 parts per thousand respectively, primary phytoplankton maximum during May-June and a secondary maximum during October were observed (Durairatnam, 1963). As temperature and salinity conditions were fairly stable during the periods of high phytoplankton production, Durairatnam assumed that enrichment by an influx of nutrient laden river waters was responsible.

Besides nutrients, marine phytoplankton require light for their growth. Although light intensity decreases exponentially with depth, at least in some lagoons such as Lakes Edku and Mariut, light does not seem to limit algal growth as evident by active photosynthesis carried out by both benthic micro- and macrophytes

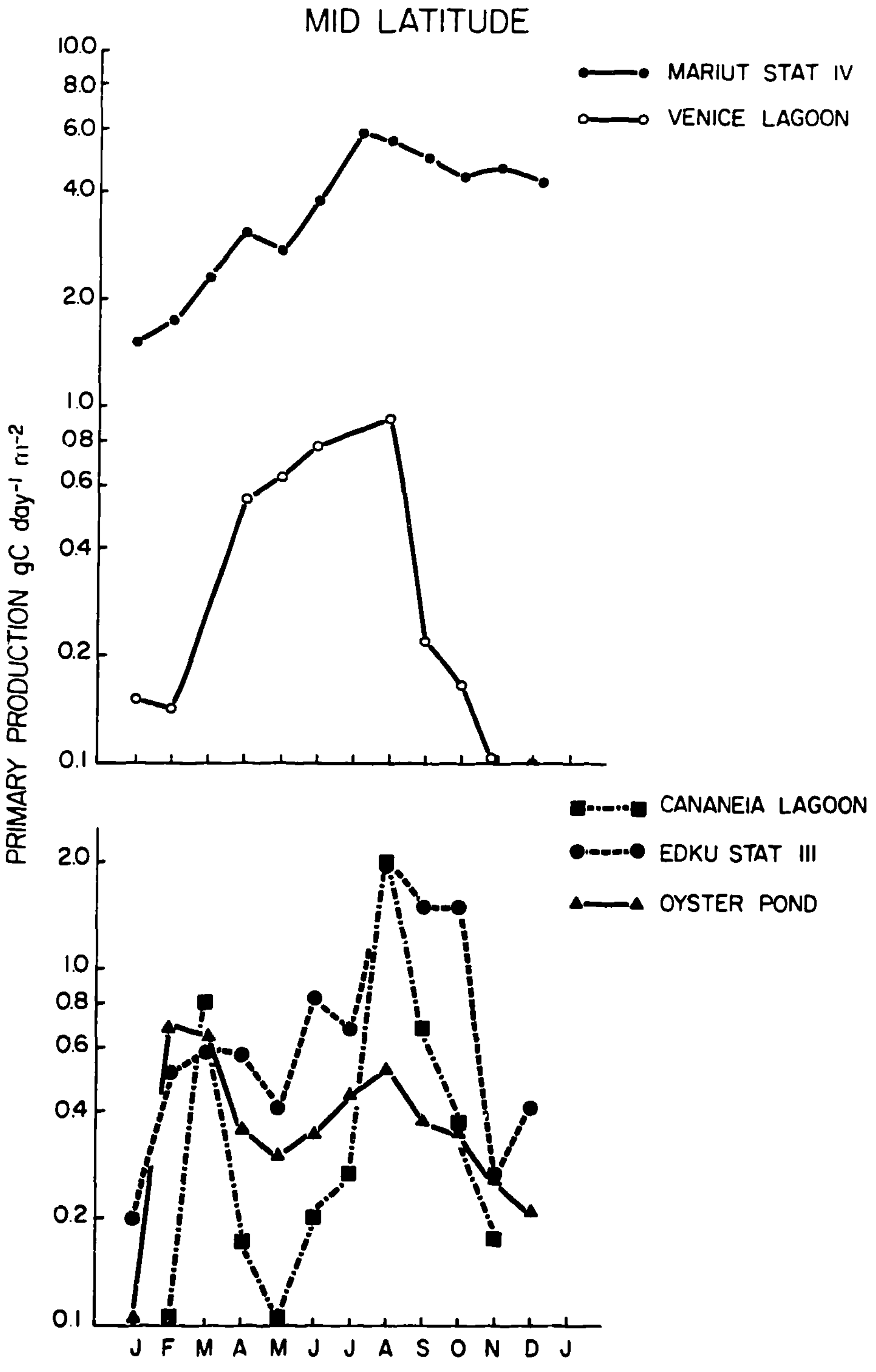

Fig. 4 Seasonal variations in primary production in mid-latitude lagoons. Data are from: Mariut Stat IV, Aleem and Samaan (1964); Venice lagoon, Votova (1961); Cananeia lagoon, Tundusi (1969); Edku Stat III, Samman (1974) and Oyster Pond, Emery (1975).

(Samman, 1974; Aleem and Samaan, 1969). In most of the barrier island lagoons of the Gulf of California, where the euphotic zone depths markedly exceeded the mean depth of the lagoon, incident radiation was not a limiting factor (Gilmartin and Revelante, 1978). In Venice Lagoon and Cananeia Lagoon due to freshwater drainage and stirring up of the bottom, the water takes on a brownish-yellow colour. Vatova (1961) reported a temporary reduction in the depth of the euphotic zone in Venice Lagoon under such conditions.

Lagoons being shallow, the degree of tidal exchange of water between them and the sea regulates the nutrient concentrations and the dependent populations. Although seasonal data on both the flushing index and primary production from the same environment are lacking, in the barrier island lagoons of the Gulf of California standing crop, primary production and nutrient levels were positively related to flushing indices thus suggesting some form of internal recycling of nutrients (Gilmartin and Revelante, 1978). In Bahía Fosforescente, which is analogous to a lagoon, restriction of exchange of water through urban development increased the nutrient load which encouraged the growth of ultraplankton and consequently eliminated _Pyrodinium bahamense_, once a dominant dinoflagellate in the bay (Seliger _et al._, 1971). Although no nutrient data for the coastal lagoons of Ghana are available during the dry season a higher rate of production attributable to greater exchange, was observed in those open to the sea than in those which were not (Kwei, 1977).

Results of Brown and Parsons (1972) on the impact of flushing on primary production are relevant here. Under controlled experimental conditions in a fibre glass tank (1.0 m deep and 2.4 m in diameter), 100% flushing per day resulted in a maximum production of 1.5 g C day^{-1} m^{-2} compared to 0.252 g C day^{-1} m^{-2} obtained with 10% flushing rate. Under low flushing (10%) rates the population consisted largely of flagellates < 20 um but at higher flushing (100%) rates, larger diatoms such as _Skeletonema costatum_, _Thalassiosira_ sp., _Nitzschia_ sp. and _Chaetoceros_ sp. dominated.

PHOTOSYNTHETIC FUNCTIONING OF LAGOONS

Because of spatial heterogeneity of phytoplankton in the horizontal and vertical scales, production estimates per unit area, rather than per unit volume, give a better comparison of two environments or of the functioning of any ecosystem in time. Two approaches are suitable for this purpose: a) comparison of the amplitude and duration of production following Cushing's (1975) method; and b) comparison of rate of light-saturated photosynthetic production per unit chlorophyll _a_, i.e., assimilation index. In the former, the production cycle is described as a bell shaped curve, symmetrical around its peak, so that the magnitude can be described as an amplitude and the duration, as the time interval between initial and terminal phases. Table 1 summarizes the range of primary production, amplitude and duration characteristics in mid-latitude lagoons where year-round observations were made. The daily production ranged from 0.011 to 10.572 g C day^{-1} and the annual production between 140 and 2861 g C yr^{-1} m^{-2} which compare well with productive areas summarized by Platt and Subba Rao (1975). The amplitude of production ranged between 2 and 289 and the duration from 2-12 months which are similar to the ranges summarized by Cushing (1975) for marine phytoplankton even though his values are based on extrapolation from cell numbers on chlorophyll as well as direct estimates of production rates using C^{14} method.

On the basis of short-term surveys, mostly from oceanic lagoons, the daily production ranged between 0.004 and 12.200 g C day^{-1} m^{-2} and the amplitude from 2 to 197 (Table 2). Production rates on individual samples ranged between 0.004 and 0.236 g C hr^{-1} m^{-3} with an amplitude ranging from 2 to 225. Assimilation numbers of lagoons ranged between 1.3 and 24 which are also similar to those for marine phytoplankton data summarized by Platt and Subba Rao (1975). Assimilation numbers over 5 were

Table 2. Primary production characteristics of some oceanic and coastal lagoons based on short-term surveys.

Region	Period of study	Primary production values					Reference
		Individual Range mg C/m^3/hr	Amplitude	Daily mg C/m^2/day	Amplitude	Annual production g C/m^2/yr	
Pacific							
Rongelap atoll		0.42					Sargent and Austin 1949
Eniwetok		1.67					Sargent and Austin 1949
Fanning	January	7.30-11.6	1.5	588*			Gordon *et al.* 1971
Majuro atoll		4.10-51.7^{+}	13	30			Sorokin 1973a
Ninigo		1.70-12.1^{+}	7	160-720	5		Sorokin 1973 b
St. Andrews		5.10-13.8^{+}	3	440-560	-		Sorokin 1973b
Lizard Island Reef	April			270-290			Scott and Jitts 1977
Tiahura-Moorea	April, July, August	4.30-22.3^{+}	5	4.3-850	197	15	Ricard 1977
Takapoto	April, July, August	4-31^{+}	8	19-395	21	45	Ricard 1977
Vairao-Tahiti	April, July, August	8.60-58.1^{+}	7			231	Ricard 1977
Faaa	April, July, August	15.40-44.1^{+}	3				
Fiji		9.60-28.6^{+}	3	26-190	7		Ricard 1976
Takapoto	August			125-275	2		Sournia and Ricard 1975
Tiahura	July, August	4.30-22.3^{+}	5	4-645	161		Sournia and Ricard 1976
Vairao	July, August	8.60-1[illegible].7^{+}	2	103-420	4		Sournia and Ricard 1976
Gulf of California Lagoons	July, August	1-184	184				Gilmartin and Revelante 1978
Atlantic							
Bahia Fosforescente	January			885			Odum et al. 1959
Bahia Fosforescente	February, July	4.0-900.0	225	800-8300	10		Burkholder *et al.* 1967
Bahia Fosforescente	December	1.0-139.4	139	43-965	23		Subba Rao *et al.* (unpubl.)
Alvarado Mexico	December	6.0-34.0	6				Margalef 1975
Sonora-Mexico	Spring, Summer			700-12200	17		Nichols 1966
Corpus Christi-Texas	June, July			3300			Odum and Wilson 1962
Madre-Texas				1110-2140	2		Copeland and Jones 1965
North Lagoon-Bermuda	March 64-April 66	2.0-30.0^{+}	15				Beers and Herman 1969
Sakumo-Ghana	July, September	378-2834^{+}	7				Kwei 1977
Mukue-Ghana	September, December	463-1823^{+}	4				Kwei 1977
Unrae-Venezuela	October			2600-2900	-		Gessner and Hammer 1962
Langebaan-Saldhana	February 71-February 72	261.6-885.3	3				Henry *et al.* 1977
Indian							
Karavatti	December			890-1212*			Qasim and Sankaranarayanan 1970
Karavatti	April, November, December	0.43-2.49	6				Qasim *et al.* 1972

*Hourly rates are multiplied by 12. + values are per day. Amplitude is calculated using Cushing's method (1975).

Table 3. Summary of assimilation numbers (mg C hr^{-1} mg^{-1} Chl *a*) from lagoons

Region	Period	mg C/hr/mg Chl *a*	References
Pacific			
Fanning	January	2.4-14.9	Gordon *et al.* 1971
Moorea	April, July-August	3.4-10.3	Ricard 1977
Vairao	April, July-August	2.4-9.3	Ricard 1977
Faaa	April, July-August	8.3-11.7	Ricard 1977
Takapoto	August	7.5[a]	Sournia and Ricard 1975
Tiahura	July-August	6.7-24[a]	Sournia and Ricard 1976
Vairao	July-August	11-1.9[a]	Sournia and Ricard 1976
Lizard Island Reef	April	14.4	Scott and Jitts 1977
Gulf of California Lagoons	July-August	5.7-13.4	Gilmartin and Revelante 1978
Atlantic			
Bahia Fosforescente	February-July	2.3-13.0	Burkholder *et al.* 1967
Alvarado, Mexico	December	1.3-5.1	Margalef 1975
Indian			
Karavatti	April, November, December	4-12	Qasim *et al.* 1972

[a] Calculated assuming 12 hrs day light.

observed in most lagoons, indicating that the phytoplankton are not dormant populations (Table 3).

Scope of future research

On the basis of these data, it is evident that spatial and temporal variations in phytoplankton production are characteristics of lagoons and that these variations are caused by a combination of abiotic and biotic factors. Because of their small size, spatial heterogeneity and high productivity, coastal lagoons offer convenient systems for production efficiency studies. However, there are serious gaps in the information from the low and high latitudes. Systematic data encompassing tidal and seasonal variations in flushing rates, nutrient cycles, phytoplankton biomass and production are desirable.

A critique of individual methods to be used in lagoons is beyond the scope of this paper but a few suggestions might be offered. If the carbon-14 method is used for primary production measurement, variations in the total carbon dioxide concentration could introduce errors up to 120% in coastal waters (Table 4). Where borate sulfate concentrations and boron:silicon ratios are different from that of sea water, the pH, total alkalinity, buffering capacity and solubility of carbon dioxide will be affected so that total carbon dioxide should be determined routinely in lagoons. In coastal inlets, dark assimilation of carbon dioxide ranges between 20 and 200% of that assimilated in light, and could be about 25% of the annual photosynthetic assimilation (Taguchi

Table 4. CO_2 concentration and primary production in coastal waters.

Region	Range Temperature (°C)	 Salinity (‰)	Total CO_2 mg/L	PRI · PRO based on determined CO_2 mgC/hr/m^3 A	PRI · PRO if 90 mg CO_2/L used B	Error [100(B–A)/A]	Reference
Adriatic	7.16	26.61	96	-	-	will be under-estimates	Fossato, 1970
	9.98	38.64	120	-	-		
Caribbean	27.26	35.0	65.6	1.364	1.802	32	Bunt *et al.*, 1972
	28.42	36.0	99.9	0.738	0.819	11	
Gulf of Thailand	27.05	30.68	41	1.49	3.28	120	Subba Rao, 1965
	31.13	33.84	102	2.11	1.86	12	

and Platt, 1977). Hence measurement of the dark assimilation is necessary in lagoons. Mapping and vertical profiling of chlorophyll by continuous fluorometric techniques (Loftus et al., 1972) can be used in the studies of phytoplankton dynamics. As phytoplankton bloom communities are known to be satisfactory analogues of monospecific cultures, lagoon populations would be a suitable experimental material. A few of the dominant phytoplankton species from the lagoons can also be brought into culture. Studies on the growth response of such cultures to simulated environmental perturbations would be interesting and instructive.

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ECOLOGICAL STUDIES IN PUERTO REAL INLET, LAGUNA DE TERMINOS, MEXICO:

Discussion on the Trophic Structure of Fish Communities on *Thalassia testudinum* Banks

by

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INTRODUCTION

Boca de Puerto Real is a particular place within the area of the Laguna de Términos. Because of its environmental dynamics (Phleger and Ayala-Castañares, 1971; Cruz-Orozco *et al.*, 1977), the nature and characteristics of its communities (Bravo-Nuñez and Yáñez-Arancibia, 1979) and the fact that it is the entry way for numerous marine animal groups, it can be considered to be the most important in productivity and in composition of the communities in all the internal environments of the lagoon. The circulation pattern as it exists in the lagoon originates in this section; a horizontal gradient that diminishes, caused by the major marine influence in the lagoon, also begins in this area. The existence of a tide flow delta is the consequence of net transportation toward the interior of the lagoon. This zone is in no way a model of a typical estuary. The work that has been done in this area shows that the light thermic and saline stratification together with the apparent shallowness are not incidental in the vertical distribution of the communities.

The study of the food and feeding habits of the species is important for many reasons: 1) it indicates the trophic relationships of the different species and indirectly an aspect of the energy flow; 2) it indicates the relationship between producer-consumer, which is particularly valuable when there are different groups of economic importance in the environment; and 3) it indicates the ecological relationship of the organisms, which helps in a better interpretation of the general dynamics of the ecosystem studied and more sound recommendations for the adequate administration of its fishing resources.

Numerous studies have shown that in marine ecosystems the main source of energy for the consumers comes from the phytoplankton. Nevertheless, in the estuarial environment this role is shared by a large diversity of primary producers (i.e., phytoplankton, micro-phytobenthos and epiphytes, sea grasses, marsh grasses, mangroves and eventually macroalgae), which have a high primary productivity and are "seasonally programmed" to assure a good level of production practically all year around.

The contribution of aloctone organic matter, which comes from the runoff of associated fluvial systems, and autochthonic organic matter, which is derived principally from the decomposition of primary producers, is high and one of the typical features of the estuary environment. This detritus (organic matter in any state of microbic decomposition, potentially representing a source of energy for consumption by species) can be the basis of numerous trophic complexes in the estuarine ecosystem.

In Boca de Puerto Real, the macrofauna communities associated with the fields of *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme* are a very significant characteristic feature in the ecology and structure of the communities (Bravo-Nuñez and Yáñez-Arancibia, 1979). At least some knowledge of the macrofauna community is very important in the understanding of the whole community and in this way the study intends to report on the macrofauna associated with the communities of *Thalassia testudinum* of the area and in a preliminary way to discuss several common trophic relationships. This approach is partly based upon work done by the International Study Group on Marine Grasses carried out in Leyden, Holland (Mcroy, 1973).

The sea grass communities represent interesting ecosystems because, as many studies have shown, they are fundamental to the control and modification of a habitat (Fergusson Wood *et al.*, 1969): 1) they can serve as food for direct grazing by such organisms as fish, turtles, gasteropods and sea-urchins, even when not all of them can be digested; 2) they serve as substrata for numerous epiphytes which in their turn are grazed upon; 3) they provide large quantities of detritus which serve as food for different species and micro-organisms, which in their turn can be consumed by higher animals; 4) they provide organic matter to initiate the reduction of sulfates and to activate the sulfur cycle; 5) they retain sediments of the water-sediment interphase; 6) they tend to collect the organic and inorganic matter in suspension through the diminution of the flow of current and the stabilization of sediments; 7) they have a rapid growth rate and can produce between 2.2 and 10 g dry weight m^{-2} day^{-1}.

In the Gulf of Mexico the marine grass communities are found to be represented mainly by *Thalassia testudinum* Konig. Phillips (1960), Humm (1973) and Buesa (1974) show several values which demonstrate that the *Thalassia* communities are among the most productive ecosystem reaching up to 18.1 g dry weight m^{-2} day^{-1} (Buesa, 1974). The recent studies by Heald (1971), Hoese and Jones (1963), W.E. Odum (1971), W.E. Odum and Heald (1972 and 1975), Zieman (1970), Jones (1968), Brook (1977), Carr and Adams (1973), D'Croz *et al.*, (1977), Kikuchi and Pérès (1977) and Hutomo and Martosewojo (1977) show that the high primary productivity of the *Thalassia* grass which is transformed into detritus sustains a large variety of consumer groups. At the same time, sources of detritus other than from the sea grasses can be more important in the trophic structure of the estuarial lagoon environment, for example the swamp grasses and mangroves (Heald *et al.*, 1974; Day *et al.*, 1973a and 1973b; Yáñez-Arancibia and Nugent, 1977; Yáñez-Arancibia, 1978a and 1978b; Odum *et al.*, 1973).

AREA OF STUDY

The area of study is in Boca de Puerto Real (91°30'E-18°50'N) in

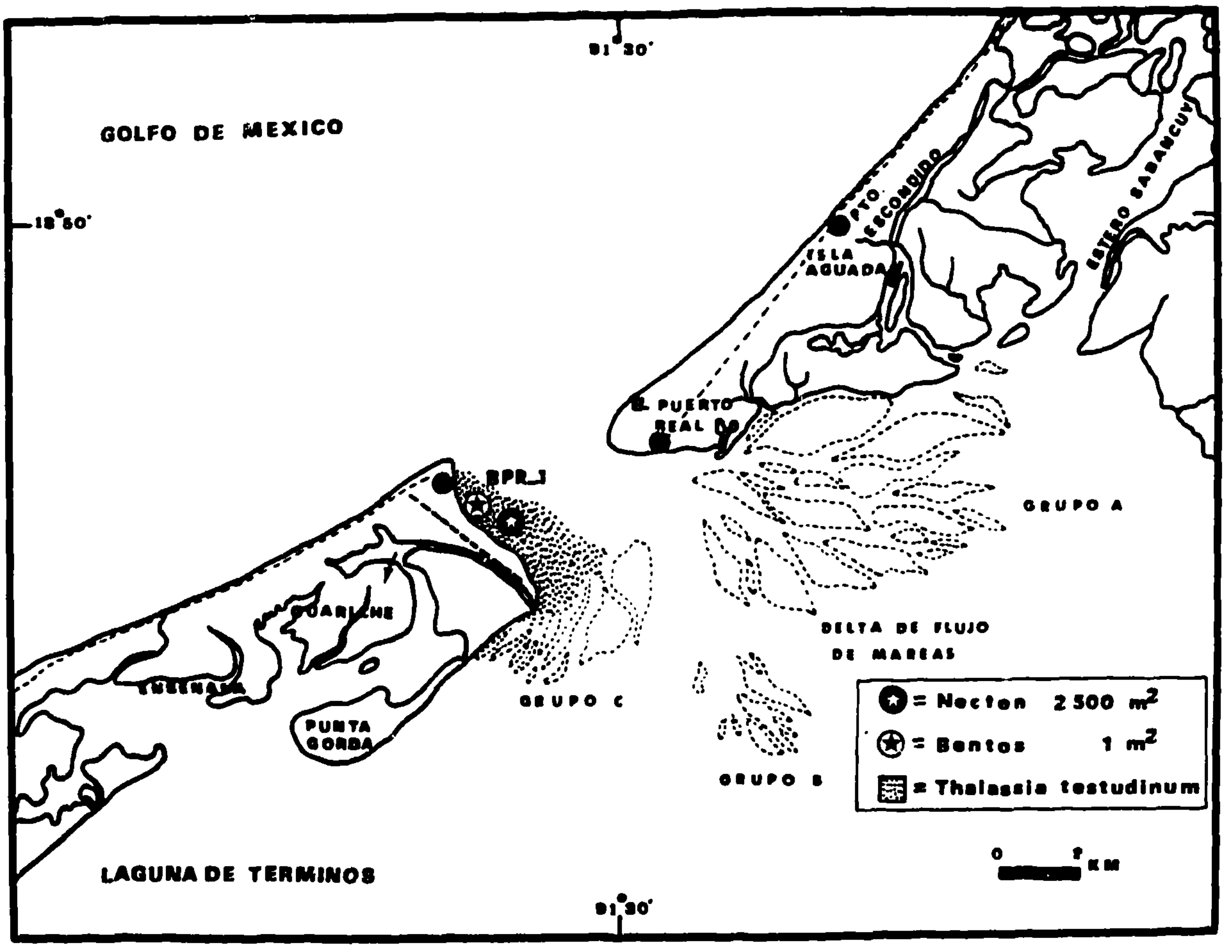

Fig. 1 Inlet of Puerto Real, Términos Lagoon, South Gulf of Mexico. The principal topographic and geomorphological features are indicated. BPR-1 is the name of station sampling.

the Laguna de Términos (Fig. 1). It has been described in detail by Bravo-Nuñez and Yáñez-Arancibia (1979). These authors indicate the following general characteristics for the banks zone of *Thalassia testudinum* in Boca de Puerto Real: salinity of 28 to 38%, temperatures of 21 to 29°C, oxygen of 2.6 to 6.4 ml litre^{-1}, muddy substrata of a fine slime clay area with 50% to 60% $CaCO_3$ and a high organic content, depths up to 4 m, varied and abundant macroepifauna, transparency of 64%, high availability of food and a moderate succession of waves.

MATERIAL AND METHODS

Bimonthly collections were taken between September 1976 and August 1977. The benthonic macrofauna was collected in a one m^2 area (Fig. 2) and photographs were made with an underwater NIKKONOS camera of the *Thalassia* patches (Fig. 2, 3). The nekton was collected in the morning and at not more than a depth of 4 m with a shrimp dragging net 10 m long with a 9 m opening (5 m of drag opening and mesh 3/4"). This kind of net also collected benthonic macroepifauna. The draggings covering a distance of 500 m which gives a sampling area of 2 500 m^2. The samples were fixed with formol of between 7-10% neutralized with sodium borate.

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Fig. 2 Sampling benthonic macrofauna in a 1 m^2 area. Banks of *Thalassia testudinum* in Puerto Real.

Fish were determined at specific levels and the benthonic macrofauna at the level of phylum, family, genus and/or species, depending on the taxonomic difficulties which presented themselves. The analysis of the fishes' stomachs was made in accordance with the methods discussed by Yáñez-Arancibia *et al.*, (1976). The observations on feeding of the macroinvertebrates were carried out qualitatively and the discussion based on the existing bibliographic information in the studies by W.E. Odum (1971), Odum and Heald (1972) and Day *et al.*, (1973a and 1973b).

Fig. 3 a) Underwater photograph showing folliage density and epiphytes. (Photograph taken by Manuel Guzman Arroyo).
b) Photograph showing circular beds of *Thalassia testudinum* in the inlet of Puerto Real.

The diversity of the fish was calculated in accordance with the statement by Shannon and Weaver (1963) in order to evaluate the diversity of all fish communities in the *Thalassia testudinum* pasture area. Both the number and weight were used to calculate the diversity. (Wilhm, 1968; Marshall Adams, 1976a; Bravo-Nuñez and Yáñez-Arancibia, 1979). Many scientists agree that it seems to be more logical to calculate the index of diversity in the biological mass, since the energy of the ecosystem is governed in terms of biomass and/or calorimetric units.

In the conceptual, models of the trophic structures, only the groups in the fishes stomachs are considered.

RESULTS

PRIMARY PRODUCERS

At Boca de Puerto Real the following groups are evident: 1) *Thalassia testudinum* marine grasses, secondarily associated with *Halodule wrightii* and *Syringodium filiforme* 2) epiphytes on *Thalassia* leaves, 3) not very abundant Phaeophicea and Rhodophiceae macroalgae with a predominance of *Gracilaria confervorides* and *Murrayela*, 4) microphytobenthos which include benthonic and epiphytic diatoms, filamentous algae, and 5) phytoplankton. Primary productivity values that consider all primary producers in this ecosystem are presently unknown.

Nothing is yet known about epiphytic and benthonic diatoms, but previous studies of other similar areas indicate that the diversity and the biomass of these groups could be very important (J.W. Day *et al.*, 1973b; Humm, 1973). For plankton studies in the area, see Silva-Barcenas (1963), Gomez-Aguirre (1965a, 1965b, and 1974), Suarez-Castro and Gomez-Aguirre (1965), Loyo-Rebolledo (1965 and 1966), and for studies on marine grasses, see Hornelas (1975) and Botello and Mandelli (1978).

Detritus

The concept of detritus has been fully discussed by E.P. Odum and De la Cruz (1963) and the groundwork laid down by Darnell (1967a and 1967b), Heald (1971) and Heald *et al.* (1974). Detritus represents a significant store of available energy as food in many ecosystems such as: estuaries, salt water swamps, ground communities, woods, temperate lakes, tropical lakes, rivers, and even the open ocean (W.E. Odum, 1971). This organic matter undergoes transportation, varied processes and uses, and correspondingly, as its rate of decomposition increases, its level of nutrition increases (E.P. Odum and De la Cruz, 1967; Fergusson Wood *et al.*, 1969; Heald, 1971; Fenchell, 1970 and 1977).

The microbic process of decomposition of detritus and its subsequent use as a food source can be summarized in the following manner (Fig. 4) for Boca de Puerto Real. The detritus is attacked by bacteria and fungus which begin the oxidation, hydrolysis and assimilation of the basic structural carbon of the detritus particles. As this process continues the bacteria are continually grazed by protozoa (generally ciliate) generating a relationship

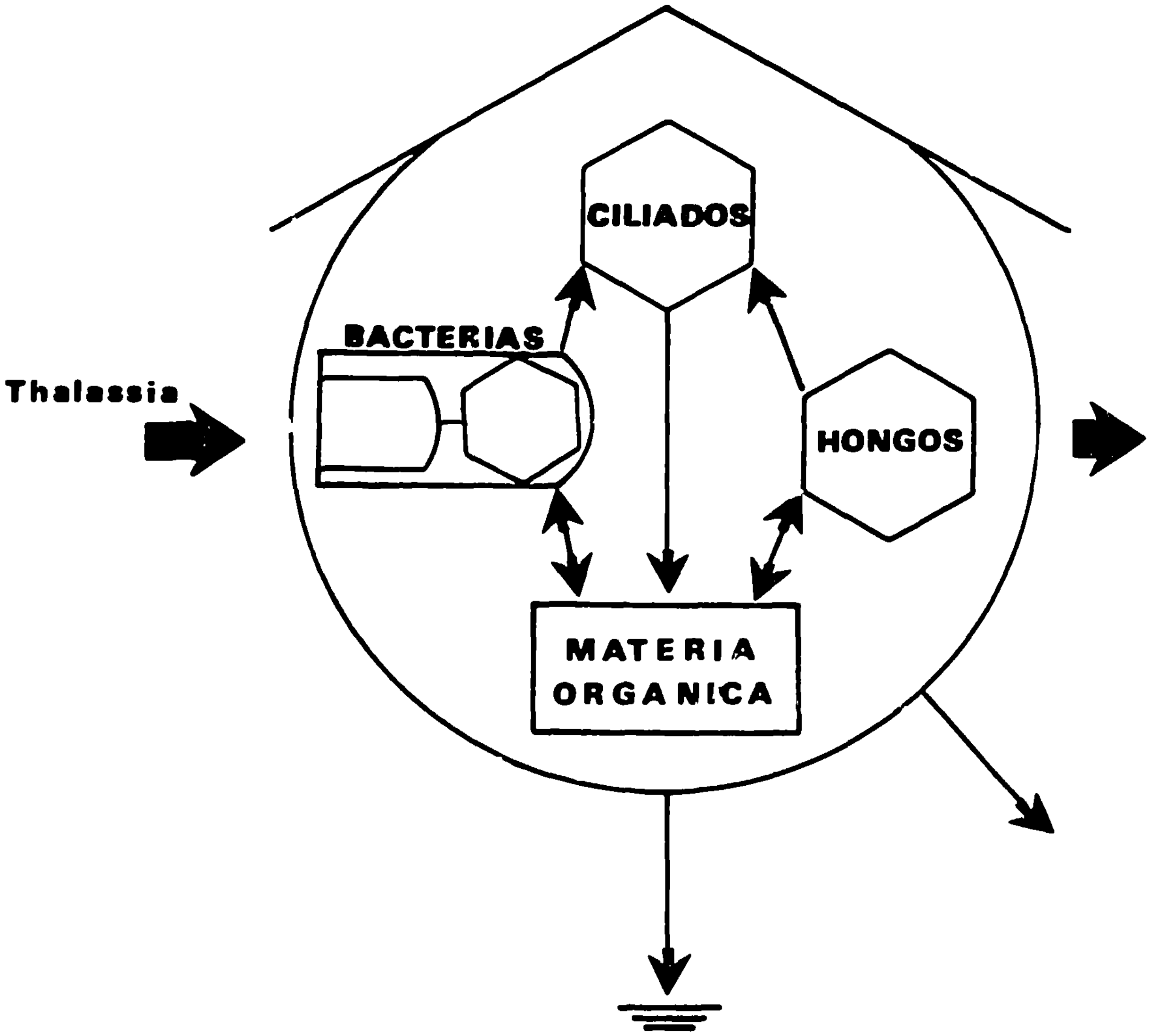

Fig. 4 Diagram showing a conceptual model of path-way of energy flow throughout the common trophic relationships among the components of the detritus in the inlet of Puerto Real. The relationships between "Protozoa-Bacteria-Fungi-Detritus" is really a microtrophic structure within the general food web. The origin of detritus, processes, and results are indicated. (Ciliados=Ciliates; Hongos=Fungi).

(protozoa-bacteria-fungi-detritus) which represents a potential valuable food source for other members of the community. This relationship is really a "microtrophic structure" within the general trophic structure of the ecosystem in question since the whole microscopic complex is ingested by the detritus eating organisms and sea bottom feeders in general.

The trophic significance of the bacteria and fungi in fish, crabs, insect larvae, amphypods, molluscs, and others has been studied by numerous authors, and W.E. Odum (1971) and Yáñez-Arancibia (1978a) give a summary of the majority of these studies. Some animals consume bacteria and fungi directly as food but others ingest them as a digestive aid in order to metabolically reduce another type of food.

Zooplankton

In estuary environments the main diet of the copepods is composed of microalgae and detritus and, by definition, bacteria, ciliate protozoa and fungus associated to it (Green, 1968; J.W. Day et al., 1973a and 1973b; W.E. Odum and Heald, 1972 and 1975; Reeve, 1975; Heinle et al., 1976; Yáñez-Arancibia and Nugent, 1977). As well as the herbivorous and/or detritus eating copepods, there are carnivorous copepods. Jellyfish, quetognats, ctenophores and several fishes (larvae and young) are the most important carnivores of the zooplankton in Boca de Puerto Real (Fig. 5).

Fig. 5 schematically represents zooplankton of five main groups present in the area (copepods, meroplankton, ctenophores and scifozoa, ichthyoplankton and chaetognaths) as "consumption unit; competition and predator". The main energy source for this unit comes from phytoplankton and from detritus which originates fundamentally from Thalassia testudinum. For studies on zooplankton in the area, see Laguarda-Figueras (1967), Gomez-Aguirre (1974) and Canudas Gonzales (1979).

Zoobenthos

Foraminifers

Very recent studies have considered their significance in the lagoon-estuarial trophic chains, among them, the studies by Lipps and Valentine (1970), Lee and Muller (1973), Le Furgey and St. Jean (1977). At Boca de Puerto Real Ayala-Castañares (1963) and Phleger and Ayala-Castañares (1971) determined a group of foraminifers which gave the name to "Biofacies de Golfo Abierto", characterized by many species.

Bacteria, benthonic diatoms, algae and organic detritus (Fig. 4) constitute the main food of the foraminifera. Fig. 6 schematically represents the probable common trophic relationships among the groups of benthonic micro and meiofauna. J.W. Day et al. (1973b) discuss numerous studies on the productivity of the foraminifers in estuarial environments and suggests that the

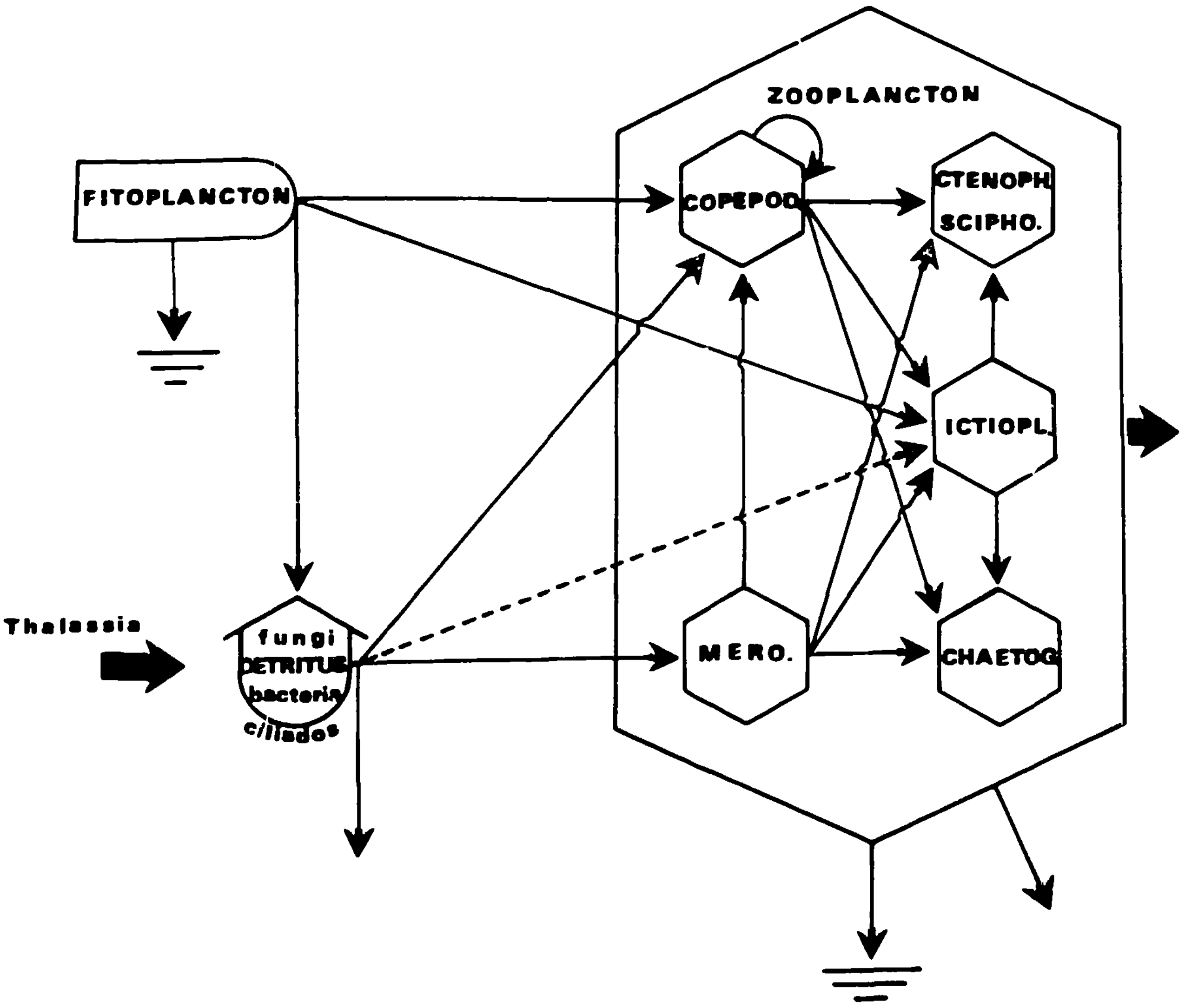

Fig. 5 Diagram showing a conceptual model of path-way energy flow throughout the common trophic relationships among the components of the zooplankton in the inlet of Puerto Real. The five principal groups inside a "consumption-competition-and predation unit" have been indicated. The "unit" has two principal entrances of energy, i.e., phytoplankton and detritus.

organic matter is found in direct relationship to a large number of foraminifers in the sediments. Nichols (1974) on the other hand, demonstrates the great value of the foraminifers not only in the trophic structure but also in the "classification of estuaries".

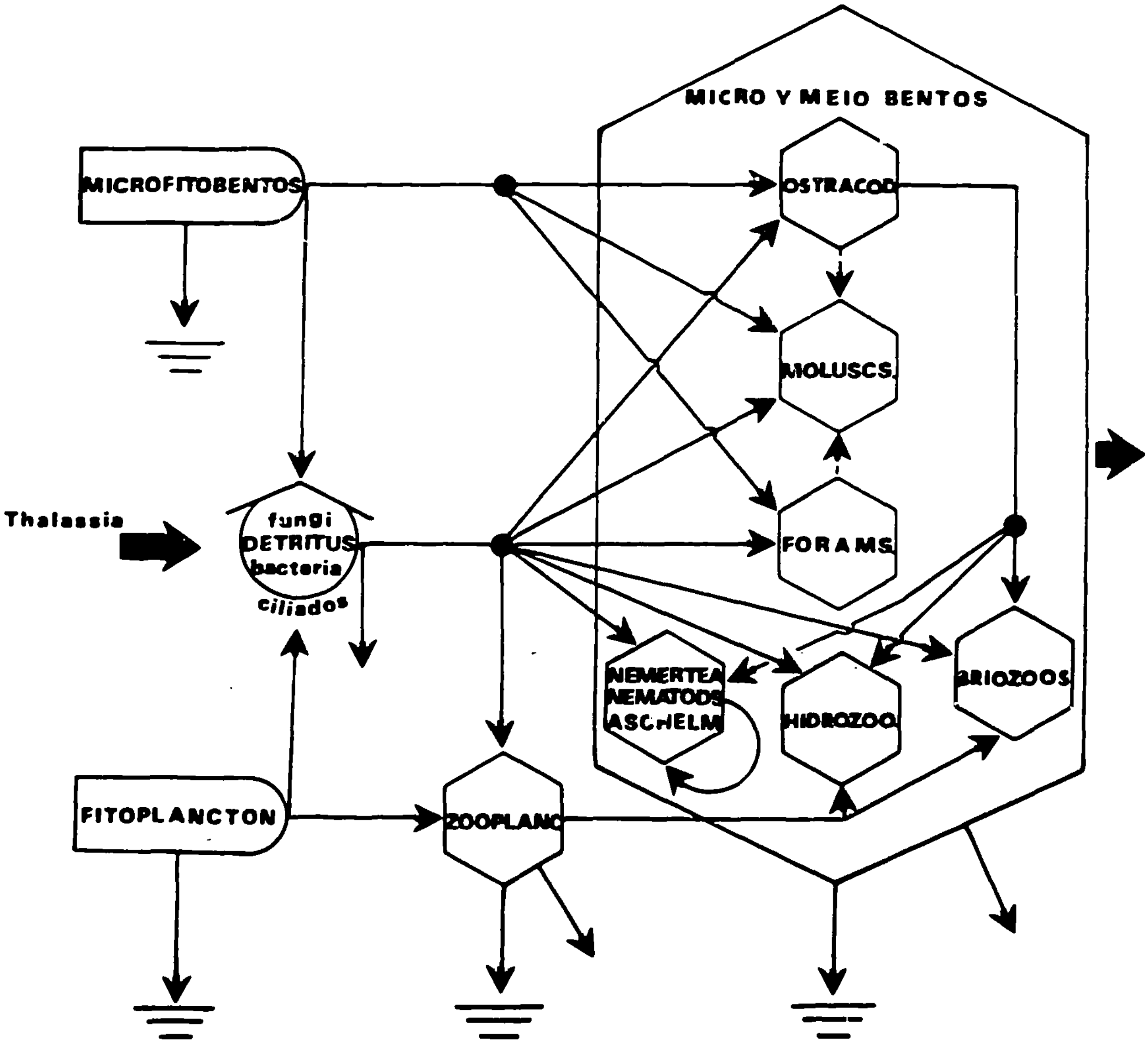

Fig. 6 Diagram showing a conceptual model of path-way of energy flow throughout the common trophic relationships among the components of the *micro-* and *meio* *benthos* in the inlet of Puerto Real. The six principal groups inside a "consumption-competition-and predation unit" have been agrupated. The "unit" has three principal entrances of energy, i.e., detritus, zooplankton and microphytobenthos.

Ciliate Protozoa

The ciliates are found associated with sediments and detritus of vascular plants. Probably the protozoa in general are eaten by higher organisms when these ingest detritus and particles of sediment. W.E. Odum (1971) and W.E. Odum and Heald (1972) give information on feeding habits of Florida ciliates in an estuary with a salinity of 12%. Marron-Aguilar and Lopez-Ochoterena (1969) in May 1964 found numerous species of ciliates in Boca de Puerto Real in a salinity of 38%.

The trophic relationships of the ciliates and their relationships with other components of detritus are schematically represented in Fig. 4.

Ostracods

In general, the meiobenthos (i.e., nematodes, ostracods, small poliquets and oligoquets, amphypods and copepods harpacticoids) are poorly known in estuarial systems. Nevertheless, J.W. Day *et al.* (1973b) synthesizes what is known on these groups in estuaries.

At Boca de Puerto Real, Morales (1966) found numerous species of ostracods. Pennak (1953), W.E. Odum (1971) and W.L. Odum and Heald (1972) have shown that ostracods eat bacteria, fungi, algae and fine particles of vegetable detritus (Yáñez-Arancibia, 1978a).

Micromolluscs

Small bivalves and gastropods are common on *Thalassia testudinum* leaves in the Boca de Puerto Real. Garcia-Cubas (1963) has found numerous species. These species commonly feed on benthonic diatoms, epiphytes, filamentous algae, detritus and small animals that colonize the films of epiphytes.

Nematodes (Asquelmints)

Undetermined nematodes have been found as parasites in some kinds of fish. Others have appeared inside the abdominal cavity and since they don't have any mouth skeleton nor cuticle resistent to digestive juices, it is suggested they are free living nematodes which fish obtain as food from the meiofauna. They are not abundant as food and are difficult to quantify and analyze taxonomically because of the rapid digestion they undergo. Heald (1971) and W.E. Odum and Heald (1972) consider that the nematodes ecological role in the estuary communities is most important as an agent in the processes of decomposition of the vascular aquatic plants' leaves. J.W. Day *et al.* (1973b) synthesizes the most possible information on estuarine meiobenthos in general. Detritus and bacteria are the nematodes' main food. Other undetermined acanthocephalan, apparently carnivorous, can be found among the benthonic meiofauna in the area. It is not possible to state precisely the trophic value of nematodes for higher groups.

Hydrozoan

Some unidentified, colonizing hydrozoan were found in the stomachs of certain fish. These colonies are common on Thalassia testudinum Thalassia testudinum leaves, but they are not usually very dense. They are not significantly important in the diet of most fishes. The hydrozoans eat copepods, ostracods, meroplancton, detritus, bacteria and ciliate. The genus Obelia seem to be the best represented among these unidentified hydrozoans.

Bryozoan

Undetermined bryozoan (Ectoprocta) have been frequently found on the Thalassia testudinum leaves in very characteristic colonies. They are difficult to quantify and to determine taxonomically and their value as a trophic group can't be precisely stated for several fishes, though it is thought that it must be insignificant. The distribution and ecology of these groups has been studied by Sandberg (1961) and Winston (1977). The bryozoans eat copepods, meroplancton, detritus, bacteria and ciliate.

Nemertean

Some unidentified nemertean were found on the stems or foliage groups of Thalassia testudinum and also in the nearby sediment. They are usually not abundant and also are difficult to determine taxonomically. Certain earlier observations indicate that the nemerteans' principle food is detritus and the associated micro flora and fauna. It is not possible to state precisely its trophic value for higher groups.

Poriferan

Studies on sponges in estuarial systems are practically unknown (Nuñez-Fernandez, 1978). This author reports different species at the Boca de Puerto Real and from other areas of Thalassia testudinum.

The poriferans' main food is bacteria and particles of organic material in suspension. Fig. 7 schematically represents the probable common trophic relationships among the benthonic macrofauna. Many of these groups can be situated within "unit of consumption, competion, and predation".

The study of the stomachs of some fish has revealed the presence of sponges among the macrofauna. Nevertheless, sponges do not seem to be quantitatively a very important part of the diet of fish.

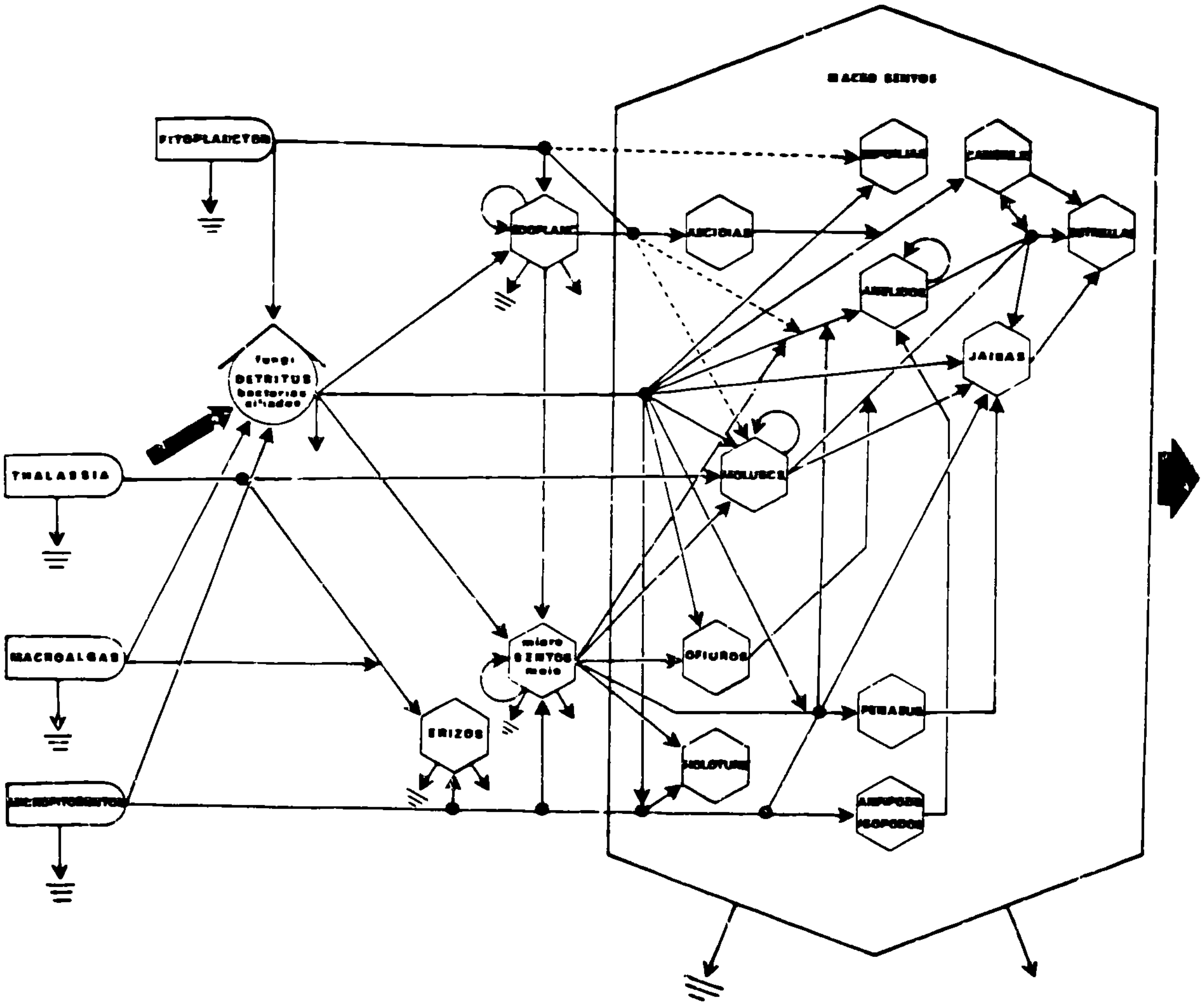

Fig. 7 Diagram showing a conceptual model of path-way of energy flow throughout the common trophic relationships among the components of the *macro benthos* in the inlet of Puerto Real. Many different groups inside a "consumption-competition-and predation unit" have been indicated. The "unit" has seven principal entrances of energy, i.e., phytoplankton, macroalgae, microphytobenthos, *Thalassia testudinum*, detritus, zooplankton and micro- and meiobenthos. (Erizos=Sea Urchins; Esonjas=Sponges; Cangrejo=Prawns; Estrellas=Sea Stars; Jaibas=Crabs; Ofiuros=Ophiuroids; Holotura=Holothurians; Ascidias=Ascidians).

Annelida

Some polychaetes appear relatively frequently in fishes' stomachs. They have predominantly been from the families of Nereidae, Cirratulidae, Serpulidae, Arenicolidae, Sabellidae, Spionidae, Orbiniidae, Syllidae, Onuphidae.

W.E. Odum and Heald (1972) suggest that some polychaetes nereids characteristic of estuarial environments in Florida are omnivorous and eat vegetable detritus, algae and occasionally small crustaceans (copepods and amphypods). At Boca de Puerto Real serpulids and sabelids are generally carnivorous and arenicolids and nereids are omnivorous.

Very little information exists about polychaetes in estuarial systems. J.W. Day et al. (1973b) synthesizes what is known about them in estuaries in the Gulf of Mexico from the point of view of standing crop and respiration. Marron-Aguilar (1975) enumerates numerous species of polychaetes for Boca de Puerto Real.

The polychaetes represent one of the most important macrofauna groups among the benthonic macrofauna for their diversity, density and biomass.

Macromolluscs

Bivalves and gastropods have been common but not in great densities in the fields of Thalassia testudinum in Boca de Puerto Real. The bivalves eat detritus and organic matter in suspension and/or sedimentation, phytoplankton, epiphytic diatoms and inorganic sediment. The gastropods generally are omnivorous feeding on detritus, phanerogams, epiphytic algae and small organisms of micro and meiobenthos. Some gastropods are carnivorous being predators of other molluscs.

Numerous fishes feed upon benthonic molluscs in Boca de Puerto Real. Two species of cephalopods (an Octopus sp. and a squid Lolliguncula brevis) are common at Boca de Puerto Real. Both are considered among the components of nekton and have exclusively carnivorous habits feeding on Penaeus spp., other macroinvertebrates and small fish including larvae. In Fig. 8 the position of the cephalopods in the 4th trophic level of the structure of the communities of Thalassia testudinum is schematically represented.

Crustacean

Copepods, ostracods, isopods, amphypods, decapods (Portunidae, Penaeidae, Paguridae, Xanthidae, Grapsidae, Alpheidae, Porcelanidae, and Majidae predominanting) were found in this group.

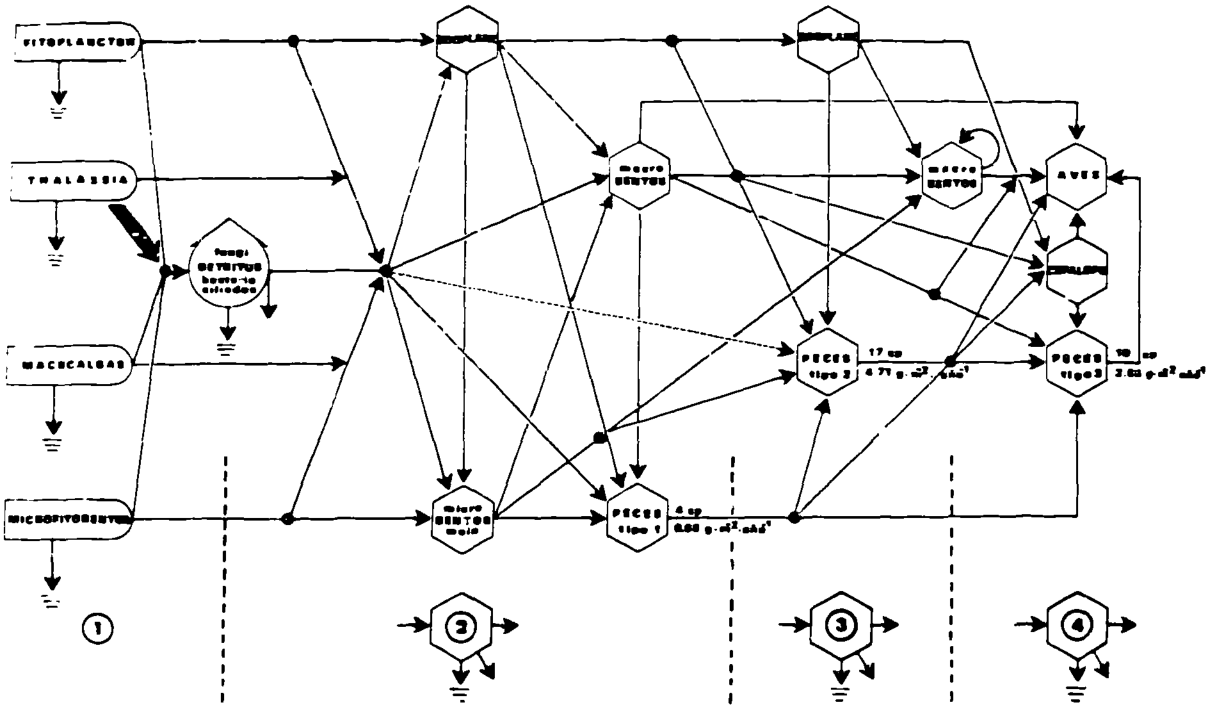

Fig. 8 Diagram showing a conceptual model of general food web of communities associated with banks of *Thalassia testudinum* in the inlet of Puerto Real. The path-way of energy flow throughout the common trophic relationships is indicated. The food web has four trophic levels. The values of fish biomass correspond to the addition of biomass obtained in each month. (Aves=Birds).

Copepods

These were considered earlier among the components of the zooplankton (Fig. 5).

Ostracods

These were considered earlier among the benthonic micro and meiofauna (Fig. 6).

Isopods

Some isopods have been found living among the *Thalassia testudinum* leaves, but even more frequently on the macroalegae *Gracilaria confervoides* which are occasionally found among the patches of *Thalassia*. Studies in Florida estuaries have shown that the digestive tract of some isopods contains microalgae and particles of detritus and feed mainly at night. Other species in that same area feed on small particles of vegetable detritus, inorganic sediments and some benthonic diatoms. Yáñez-Arancibia (1978a and 1978b) also found isopods but did not record either genus or species in the coastal lagoon of Guerrero. Those in Boca de Puerto Real have not been determined either.

Amphipods

Some amphipods living among the _Thalassia testudinum_ leaves have been found, but even more frequently on the macroalga _Gracilaria confervoides_ which are occasionally found among the patches of _Thalassia_. On certain occasions they are very numerous and may be important in some fishes' diets. They mainly feed on vegetable detritus and benthonic microalgae, with associations of microfauna of detritus. W.E. Odum (1971), W.E. Odum and Heald (1972) and Hargrave (1970) suggest that this feeding habit is due to the ability of gamarid amphipods to nourish themselves on the microorganisms associated with detritus.

Neither genus nor species were determined at Boca de Puerto Real.

Decapods

Different families were found within this group.

Palemonidae. Few examples of Palemonidae have been found in the _Thalassia testudinum_ fields of Boca de Puerto Real and Ensenada Punta Gorda. The food of this group in estuarial systems is based on microfauna, vegetable remains and detritus. W.E. Odum and Heald (1972) have discussed Hunt's study (1953) and Kawanabe _et al._ (1965). They have indicated that in general, the species of Palaemonetes feed on five trophic groups: 1) inorganic particles, 2) organic and inorganic particles of the size of clay, which probably contain organic colloidal substances, 3) benthonic diatoms, dinoflagellates, green and blue-green filamentous algae, 4) particles detritus of vascular plants coming from rushes and mangrove bushes and 5) animal remains such as ostracods, amphypods and copepods. The fungi, bacteria and protozoa are ingested together with numbers 1) and 2). This group of decapods can be considered scarce in Boca de Puerto Real and hasn't been represented in Fig. 7.

Penaeidae. According to Signoret (1974) four species of shrimp have been detected in Laguna de Términos.

It is deduced from studies by Idyll (1967), Dall (1968), Farfante (1969) Sastrakusumah (1971), W.E. Odum and Heald (1972) and Yáñez-Arancibia (1978a and 1978b) that shrimp are omnivorous, that they feed on small animals they can easily capture (ostracods, foraminifers, micromolluscs, polychaetes and harpacticoides copepods, unicellular and filamentous algae, particles of sediment and detritus such as bacteria, yeast and fungi).

Portunidae. There are at least three species of this family in the area (Cedeño, 1976). From the studies by Darnell (1958), Tagatz (1968), W.E. Odum and Heald (1972), J.W. Day *et al.* (1973) and Yáñez-Arancibia (1978a and 1978b) it is known that portunids behave preferentially as carnivores but they also ingest some detritus. They can eat molluscs, crabs, fish, other crustaceans, annelids, insects, briozoa and amphypods.

Crabs. Different crabs of the Porcelanidae, Paguridae, Gecarcinidae, Grapsidae, Xanthidae and Majidae families are found among the *Thalassia testudinum* fields. Neither genus nor species have been determined at Boca de Puerto Real; the diversity and distribution of this group in the area has been given greater attention. Yáñez-Arancibia (1978a and 1978b) considers some crabs in the coastal lagoons of Mexico's Pacific Ocean, finding that they feed on small organisms they can catch, vegetable remains and detritus. Like Cuban crabs, these crabs tend to behave as carnivores. W.E. Odum and Heald (1972) found in Florida estuaries that some crabs fed on vegetable detritus, amphipods and harpacticoids copepods. In Fig. 7 the decopods and their common trophic relationship in Boca de Puerto Real are schematically represented, based on the fact that the crabs which live there behave predominantly like carnivores, but without dismissing the fact that, depending on the availability of food they can also ingest detritus. It is important to consider hermit crabs in this last respect.

Echinoderms

This is exclusively a marine group and for that reason their distribution in the Laguna de Términos would delineate the zones of major marine influence and relative stability in relation to the salinity. In Boca de Puerto Real numerous examples of *Thalassia testudinum* fields still buried in sediment (holothurians) have been found. With the reference of Caso (1961), the collection, in a preliminary form, of representatives of Asteroidea, Ophiuroidea, Echinoidea and Holcthuroidea has been revised.

Matsui (1968) and Fuji (1967) have found that the echinoderms preferably feed at night. Buckle *et al.* (1977) studied the feeding of sea urchins in captivity and found that they prefer macroalgae.

Of the four coastal echinoderm groups, sea urchins are predominantly herbivores in lagoon-estuarial systems. Several earlier observations indicate that they graze on macroalgae (Phaeophiceae and Rhodophiceae), microphytobenthos and marine grasses of the *Zoostera* and *Thalassia* type. (Ferguseon Wood *et al.*, 1969).

Others feed on microorganisms of micro- and meiobenthos and eventually on detritus. Starfish are predominatly carnivorous, feeding on different macroinvertebrates that they can capture. Holothurians are omnivorous, feeding on micro- and meiobenthos, microphytobenthos and detritus.

Urocordads (Ascidias)

This has been one of the most characteristic groups in the fields of *Thalassia testudinum* in Boca de Puerto Real. Nevertheless little is known about these species in estuarial systems. (See the study by Solis-Wolfowitz, 1973 in Laguna de Términos). This author initially reported diverse solitary and colony species for Boca de Puerto Real. As well as the stems (folliage groups) and leaves of *Thalassia*, the ascidium ses other substrata such as macroalgae *Murrayela* sp., *Gracilaria confervoides*, *Caulerpa* sp., but they can also grow on mollusc shells and polychaete tubes.

The Ascidias' food is based on microorganisms that are able to filter out from the phyto- and zooplankton some micro- and meiobenthos organisms and organic matter in suspension.

Nekton

Thirty-one species of fish and 2 cephalopods (one *Octopus* sp. and one squid *Loliguncula brevis*) were collected during the year in accordance with the three ichthyotrophic categories proposed by Yáñez-Arancibia (1978a and 1978b) for the nektonic lagoon estuarine communities (fish). The species studied here are grouped in this manner (see Bravo Nuñez and Yáñez-Arancibia, 1979).

1) First Order Consumers (Type 1 Fish)

Included in this category are: a) planktophags (phyto- and/or zoo-), b) detritus eaters (and other vegetable remains), and c) omnivores (detritus, vegetable amd small sized animals). This group includes: *Anchoa hepsetus hepsetus*, *Eucinostomus gula*, *Chaetodon ocellatus*, and *Novaculichthys infirmus*.

2) Second Order Consumers (Type 2 Fish)

Included in this category are predominantly carnivorous fish, even when they eat small amounts of vegetables and detritus. This group includes: *Arius felis*, *Gobiesus strumosus*, *Orthopristis chrysopterus*, *O. poeyi*, *Anisotremus surinamensis*, *A. virginicus*, *A. spleniatus*, *Haemulon plumieri*, *Archosargus probatocephalus*, *A. unimaculatus*, *Bairdiella chrysura*, *Equetus acuminatus*, *Odontoscion dentex*, *Corvula sanctaeluciae*, *Monacanthus hispidus*, *M. ciliatus*, *Laectophrys tricornis and* and *Diodon hystrix*.

3) Third Order Consumers (Type 3 Fish)

Included in this category are fish which are exclusively carnivorous. This group includes: *Urolophus jamaicensis*, *Hippocampus hudsonius punctulatus*, *Syngnathus rousseau*, *S. mackayi*, *Scorpaena plumieri plumieri*, *Epinephelus guttatus*, *Lutjanus synagris*, *L. griseus*, *Cynoscion nebulosus*, *Sphoeroides testudinus*, *S. marmoratus* and *Chilomycterus schoepfi*.

This categorization demonstrates that in Boca de Puerto Real there are four primary consumers (13%), 17 secondary consumers (55%) and 10 third order consumers (32%). This annual balance changes seasonally (Fig. 9) basically for two reasons: 1) when under the circumstances some secondary consumers behave as third order consumers due to the availability of food, competition, age of fish, etc., 2) due to the succession of species during the year. Nevertheless, throughout the year the communities are sustained by structure and function of the second order consumers (Fig. 9).

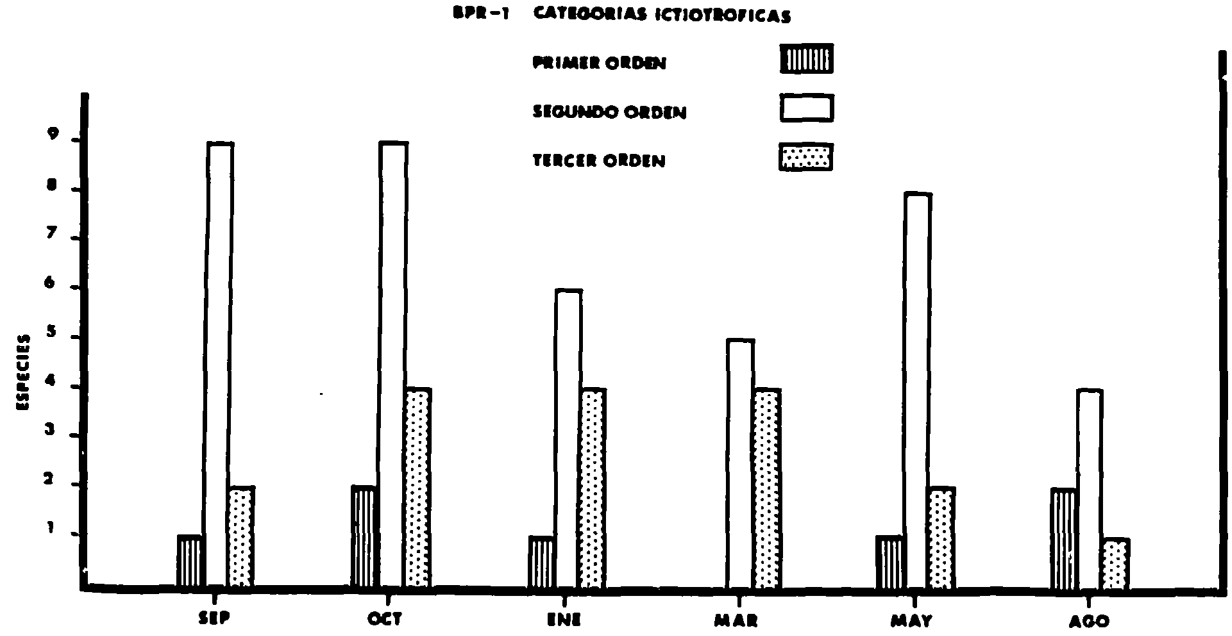

Fig. 9 Temporal variations and proportions between the three ichthyotrophic groups inside the trophic structure of fish communities associated with banks of *Thalassia testudinum* in the inlet of Puerto Real. (Categorias Ictiotróficas=Ichthyotrophic Categories; ENE=January; AGO=August).

Bravo-Nuñez and Yáñez-Arancibia (1979) discuss these ichthyotrophic categories in detail, their community components and their seasonal variations, comparing them with other communities in the area.

The community components have been characterized in accordance with their frequency in the samples and their seasonal variation thus being determined in three categories in the following manner.

1) Occasional Visiting Species

This category includes those fish with less than 20% frequency in the samples. This group includes: *Urolophus jamaicencis*, *Anchoa hepsetus hepsetus*, *Hippocampus hudsonius punctulatus*, *Syngnathus rousseau*, *Lutjanus synagris*, *Orthopristis poeyi*, *Anisostremus spleniatus*, *Equetus acuminatus*, *Chaetodon ocellatus*, *Novaculites infirmus*, *Monacanthus ciliatus*, *Lactophrys tricornis*, *Sphoeroides marmoratus* and *Gobiesus stromosus*.

2) Species in Transit

This category includes fish between 30 and 70% frequency in the samples. This group includes: *Arius felis*, *Epinephelus guttatus*, *Lutjanus griseus*, *Eucinostomus gula*, *Anisostremus surinamensis*, *Archosargus probatocephalus*, *Bairdiella chrysura*, *Cynoscion nebulosus*, *Odontoscion dentex*, *Monacanthus hispidus*, *Sphoeroides testudinus* and *Chilomycterus schoepfi*.

3) Permanent Inhabitants

This category includes those fish which appear at a frequency of 80% in the samples. This group includes: *Orthopristis chrysopterus*, *Haemulon plumieri*, *Archosargus unimaculatus* and *Corvula sanctae-luciae*.

This categorization shows that in Boca de Puerto Real 15 occasional visitors are present (48%), 12 species in transit (39%) and 4 permanent residents (13%). This annual balance changes seasonally (Fig. 10) and partly explains the quantitative seasonal variation of the ichthyotrophic categories. In accordance with Figs. 8 and 9 the communities are sustained throughout the year by structure and function of the second order consumers and species in transit.

Bravo-Nuñez and Yáñez-Arancibia (1979) discuss in detail the succession of nektonic communities, their species, ichthyotrophic categories and community components.

In Fig. 8 the probable common trophic relationships among the component groups of the four trophic levels considered in Boca de Puerto Real are schematically represented. Fig. 8 (see Discus-

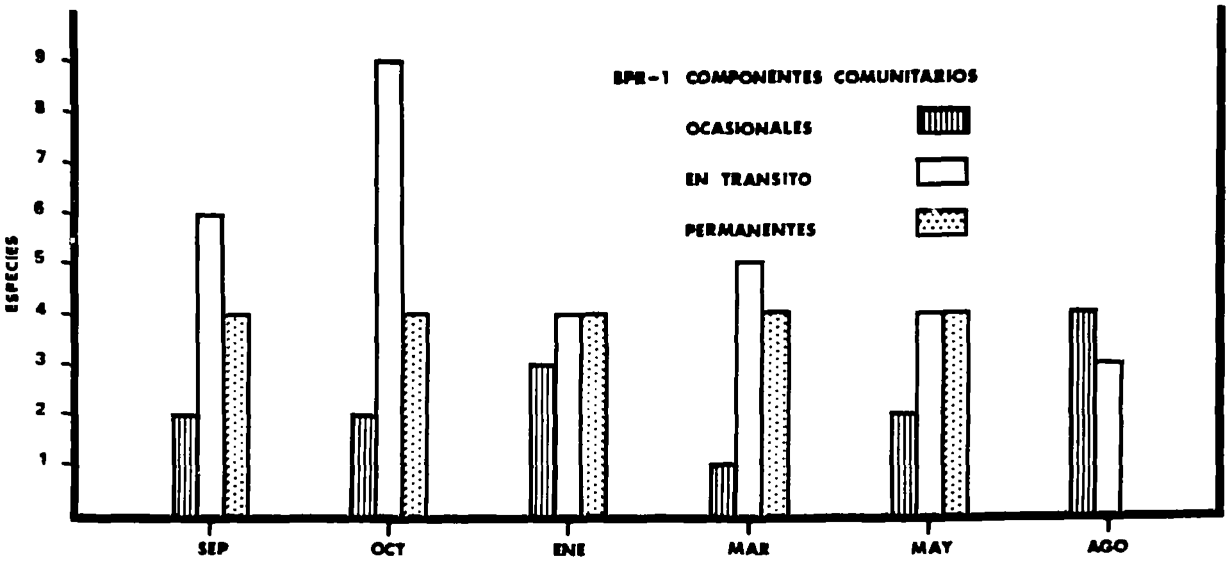

Fig. 10 Temporal variations and proportions between the three kinds of community components (Occasional visting fish species, fish species in transit, and permanent inhabitants). Fish communities associated with banks of *Thalassia testudinum* in the inlet of Puerto Real. (Componentes Comunitarios = Community Components; ENE = January; AGO = August).

sion) represents a synthesis of Fig. 4, 5, 6 and 7 considering nekton also as one of the principle community components.

DISCUSSION

In Mexico there are very few previous studies on *Thalassia testudinum* in general. Lot (1968, 1971 and 1973) emphasizes the importance and present knowledge of the marine phanerogams in Mexico. Chavez *et al.*, (1970) includes information on marine grass fields in his studies on benthonic reef communities in Veracruz. Hornelas (1975) in the same area of study looks at folliage density, biomass (dry weight), index of leaf area and morphometric differences in the length and width of the leaf. Jordan *et al.* (1978) and Nugent *et al.* (1978), in studies on the Mexican Caribbean coast has introduced new observations for *Thalassia testudinum* in relation to the ecology of the area.

The latter study is one of the most interesting because the biomass obtained (13.1 to 92.8 g m^{-2}, with an average of 42.9 g m^{-2}, dry weight) is considerably lower than that obtained by other investigators in other regions of the Gulf, Caribbean and adjacent zones (Table 1). Nevertheless, the biological mass val-

Table 1. Values of biomass of _Thalassia testudinum_ in the Gulf of Mexico and Caribbean Sea

Leaves ($g\ m^{-2}$)		Roots ($g\ m^{-2}$)		Total biomass	Locality	References
Range	Avg.	Range	Avg.			
10-740	340				Cuba	Zieman (1975)
138-857	450	540-7390	2800	3250	Puerto Rico	Zieman (1972)
700-1800	830	2200-4300	2830	3660	Florida (1)	Zieman (1975)
30-230	126				Florida (1)	Zieman (1975)
80-650	280				Florida (2)	Zieman (1975)
				700	Veracruz	Lot (1968, 1971)
	198		597	795	Texas (3)	Hornelas, _et al._, 1975
	157		402	559	Texas (4)	Hornelas, _et al._, 1975
119-214	164	247-463	341	505	Texas	Hornelas 1975
56-94	75	49-244	118	193	Veracruz	Hornelas 1975
73-117	112	168-406	270	382	Campeche (5)	Hornelas 1975
0.92-4.4	3.21			3.21	Florida (1)	Thorhaug & Roessler (1977)
13-93	43			43	Quintana Roo	Nugent _et al._ (1978)

(1) = near coast
(2) = far off coast
(3) = Ranson Island
(4) = Pin and Feader
(5) = Laguna de Términos *

ues of _Thalassia testudinum_ are quite variable even in the same area (Zieman, 1975; Thorhaug and Roessler, 1977; D'Croz _et al._, 1977); and normally are difficult to compare.

Determination of the biomass as a measure of productivity is very important for the determination of the amount of energy that flows through a food chain. In the case of *Thalassia* it is known that more than 90% of its energy is transferred to different trophic levels through detritus. Its growth and defoliation is as rapid as its decomposition, which is very high, and predacity (grazing) reduced, (Jones, 1968; Zieman, 1968 and 1970; Fergusson Wood *et al.*, 1969). On the other hand, some marine grass systems produce more organic matter than is able to be used by the consumer populations and it is reasonable to think that there is a large exportation of detritus toward neighboring ecological sytems (see Thayer and La Croix, 1971; Thayer *et al.*, 1975).

The importance of marine grass as modifiers and controllers of ecology in their areas is brought out, and in this aspect it is interesting to emphasize again the importance as epiphyte and epizoa environments (Humm, 1973; Orth, 1973; Marsh, 1973) as testimony of some pollutants (Botello and Mandelli, 1978) and as modifiers by biological action in the general marine geology of their areas (Thom, 1969; Phleger and Ayala-Castañares, 1971; Cruz-Orozco *et al.*, 1977). These latter studies refer in particular to the area of these studies and are very good observations on the ecological aspects of "*Thalassia* vs. geological habitat". Nevertheless, nothing is known about the epiphytes of *Thalassia* in Laguna de Términos (i.e., microphytobenthos in general) but it is reasonable to suppose that for the variety and size of biomass, they have a very important significance in the ecology of the lagoon. Humm (1973) states that the large diversity of epiphytes is evident and also in biomass can be greater than the leaf which serves them as substrata.

The primary producers in Boca de Puerto Real are represented by marine grasses (i.e. *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme*), macroalgae (i.e. Phaephiceae and Rhodophiceae predominating *Graciliaria confervoides*), phytoplankton (numerous species) and microphytobenthos (i.e. benthonic diatoms, epiphytic diatoms and filamentous algae, presumably well represented in diversity and biomass).

Of the earlier known observations on *Thalassia testudinum* on Mexican coasts, none refers to trophic structure of the communities (Yañez-Arancibia, 1975, 1978a and 1978b; Yañez-Arancibia and Nugent, 1977), which makes it difficult to make comparisons with trophic structures in tropical lagoon-estuarine ecosystems of other latitudes as in the studies by J.H. Day (1967), Qasim (1970), De Sylva (1975) and Brook (1977). Similar studies in Mexico refer to characteristic ecosystems of mangroves (also present in Laguna de Términos but not in Boca de Puerto Real) and in them is found a comparative bibliographic review of similar studies in other latitudes (Yañez-Arancibia 1978a and 1978b; Yañez-Arancibia and Nugent, 1977; Amezcua-Linares and Yánez-Arancibia, 1980).

Because of the environmental dynamics of the area, the net transportation in Boca de Puerto Real is toward the interior of the lagoon. This situation lets us assume that the major portion of detritus in suspension and that the sedimentation present there both come from the decomposition of _Thalassia testudinum_. The detritus which comes from Rhizophora mangle has its origin and distribution toward the interior of the lagoon.

From Figs. 4, 5, 6 and 7 a trophic structure characterized by 4 trophic levels (Fig. 8) can be synthesized.

Primary producers are located in the 1st level of the marine grasses, phytoplankton, macroalgae and microphytobenthos. The origin and output of detritus is also included.

In the 2nd level the primary consumers are located in complex trophic relationships (Figs. 4, 5, 6 and 7). From the microbiots associated with the process of formation of detritus: bacteria, fungi and nematodes, as well as macro-, micro- and meiobenthos including ostracods, foramniphers, nemertins, asquelmints, gastropods, bivalves, crayfish, shrimp, holothurians, ophiurs sea-urchins, annelids, polychaetes, ascidia, porifers, amphipods, isopods, crabs, herbivorous copepods, bryozoa, fish larvae, meroplankton and primary consumer fish (type 1 fish) with 4 species.

In the 3rd level are the carnivorous invertebrates of zooplankton (copepods, jellyfish, ctenofers and quetognats), and of the benthos (gastropods, polychaetes, annelids, starfish, crabs, hydrozoa). The main components in this level are coposed of 17 species of secondary consumer fishes (type 2 fish).

In the 4th level are 10 species of consumer fish of the third order (type 3 fish) and aquatic birds of the area and cephalopods. This trophic structure (Fig. 8) is present during the whole year, but it is probable that some insignificant seasonal variations are manifested by succession of several species, a situation that unfortunately was not detected in this study. The stability of the components is characteristic of the communities of _Thalassia_, reflecting the relative stability of the environment. This contrasts notably with the coastal lagoons with ever-changing entrances where the trophic structure rarely varies cyclically. The only reference with respect to the latter is constituted in the study by Yáñez-Arancibia (1978a and 1978b). Fish are one of the components in the trophic structure of the coastal lagoons and estuaries and their ecological role has been fully discussed by De Sylva (1975) and especially by Yáñez-Arancibia and Nugent (1977).

In Table 2 the biomass of the fish communities in different marine grass ecological systems of North America can be compared. Two aspects are interesting to discuss in this sense: 1) appar-

Table 2. Values of biomass of fish communities in estuarine systems of North America

Range	Avg.	Locality	Reference
0.76 g dry w m^{-2}	0.76	Long Island Sound	Richard (1963)
1.20 g dry w m^{-2}	1.20	Laguna Madre, Texas	Hellier (1962)
0.40 g dry w m^{-2}	0.40	Guadalupe Bay, Texas	Moseley & Copeland (1969)
0.04-0.40 g dry w m^{-2}	-	Rhode Island	Nixon and Oviatt (1972)
1.20 g dry w m^{-2} 5.90 g wet w m^{-2}	- -	New Port River, North Carolina (marsh areas)	Kjelson *et al.* (1973)
0.30 g dry w m^{-2} 1.50 g wet w m^{-2}	- -	New Port River, North Carolina (estuary)	Kjelson *et al.* (1973)
0.08-2.18 g dry w m^{-2}	1.33	New Port River, North Carolina (Phillips Is.)	Thayer *et al.* 1975)
1.50 g dry w m^{-2}	1.50	New Port River, North Carolina	Marshall Adams (1976a, b, c)
0.60-15.2 g wet w m^{-2}	3.10	Card Sound, Florida	Brook (1977)
0.97-2.23 g wet w m^{-2}	1.33	Puerto Real (BPR-1) Campeche, Mexico	Bravo Nuñez & Yañez-Arancibia (1978) & this study
0.18-10.92 g wet w m^{-2}	2.02	Puerto Real (BPR-3) Campeche, Mexico	Bravo Nuñez & Yañez-Arancibia (1978)
38.8-66.7 g wet w m^{-2}	49.9	Chautengo Lagoon Guerrero, Mexico	Yañez-Arancibia (1980)
21.5-43.1 g wet w m^{-2}	29.3	Tres Palos Lagoon Guerrero, Mexico	Yañez-Arancibia (1980)

ently the marine grass fields are efficient ecological systems to convert energy from solar radiation to that of a form capable of sustaining important fish populations, and 2) the biological mass of fish is considerably less than the biological mass of *Thalassia testudinum* in Laguna de Términos (Table 1). Therefore it is reasonable to suppose that an excess of *Thalassia* organic matter unable to be used by consumers is produced, which is deposited and retained in sediments but must also be exported to neighboring ecological systems. Thayer *et al.* (1975) and Marshall Adams

(1976a, 1976b and 1976c) have discussed the quantitative results of the latter aspect for a similar problem in fields of *Zostera marina*.

The temporal distribution of the total standing crop of the fish communities (gram humid weight per square meter) is discussed in the study by Bravo-Nuñez and Yáñez-Arancibia (1979). In this study an animal range of biomass of 0.97 g m^{-2} (January) to 2.23 g m^{-2} (May) is valued with an annual average of 1.33 g m^{-2}. This biological mass doesn't necessarily follow a direct relationship to the density (Fig. 11). This can be explained because the organisms are young, sexually immature and therefore small. In turn the relationship between the total biomass and the index of biomass (H'g) is more direct and relatively uniform, but some eventual inverse relationship can present itself when isolated examples of considerable size appear (Fig. 12).

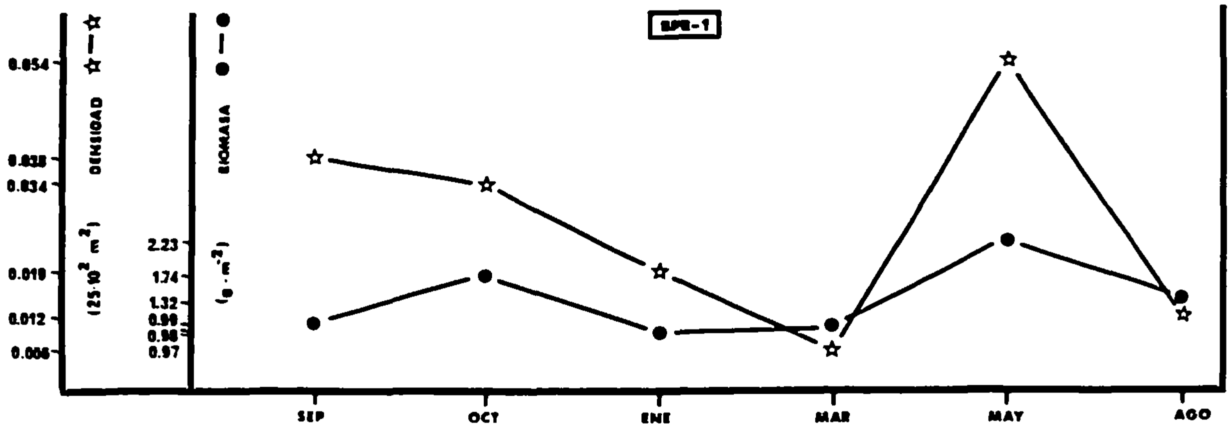

Fig. 11 Temporal variations and relationships between density and biomass of fish communities associated with banks of *Thalassia testudinum* in the inlet of Puerto Real. Density = specimens x 2 500m^2. (Densidad=Density; ENE=January; AGO=August).

The calculated diversity as numerical index (H'n) and biomass index (H'g) also shows temporal variation (Figs. 12 and 13). These indexes are low and in accordance with other categories found in other areas of marine grasses and mangroves (Table 3). These indices permit the summary of information concerning the populations' numerical structure. Its isolated empirical value is vague and should be considered as additional information within a very ample ecological context.

Pianka (1966), Dahlberg and E.P. Odum (1970) and Yáñez-Arancibia (1978a) consider at least 11 factors that can regulate the diversity in fish communities: 1) variety of niche, 2) size and

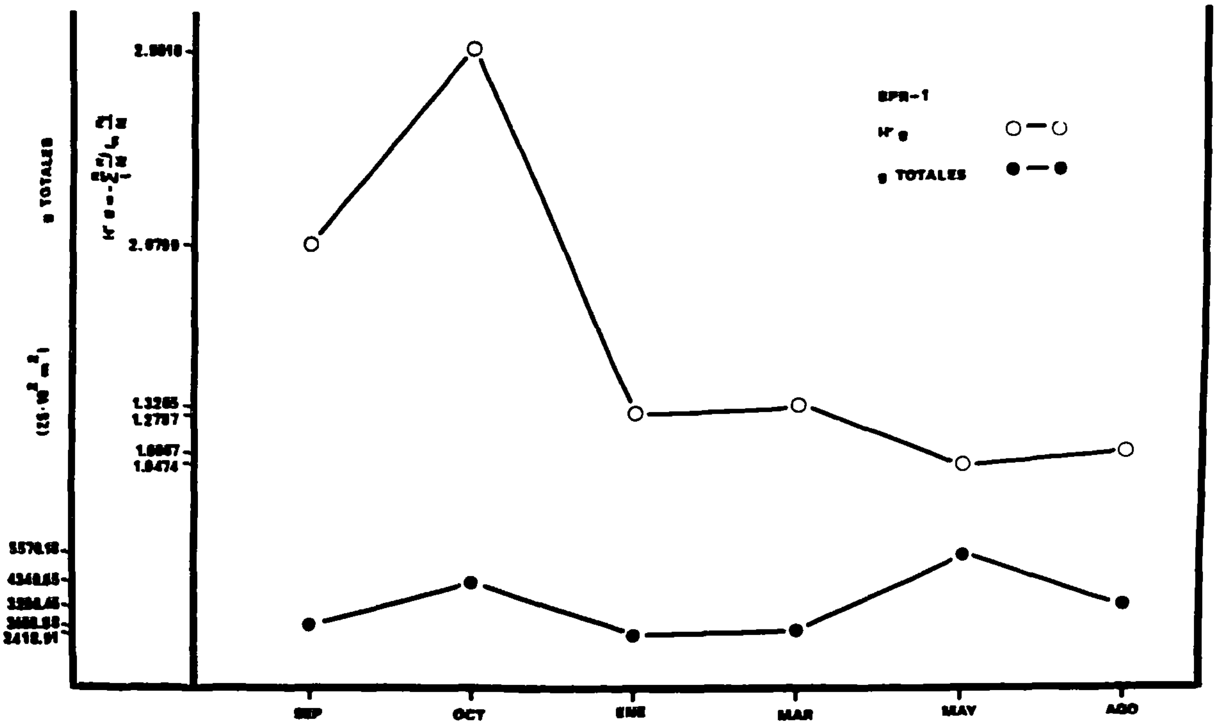

Fig. 12 Temporal variations and relationships between total weight and biomass indice (H'g=H'w) of fish communities associated with banks in *Thalassia testudinum* in the inlet of Puerto Real. (ENE=January; AGO=August).

superposition of niches, 3) stability of the environment or climate, 4) rigour of environment, 5) succession or geological weather, 6) productivity, 7) accumulation of biomass, 8) competition, 9) space, 10) size of the organisms, and 11) length of food chains. Without analyzing those aspects at the present (such a study is presently being carried out for Puerto Real), it is evident that the study of the diversity by means of indices is very problematic and complex for nektonic communities of active displacement and generally difficult to interpret.

An analysis of frequency allowed the grouping of 3 categories of community components (Fig. 10), that is, 1) 15 occasional components (48%), 2) 12 species in transit (39%) and 3) 4 permanent residents (13%). This categorization is slightly similar to that found by Kikuchi (1966) in which he recognizes for marine grasses: 1) permanent residents, 2) seasonal residents 3) temporary visitors which feed in a larger area than that occupied only by marine grasses, and 4) occasional migratory species.

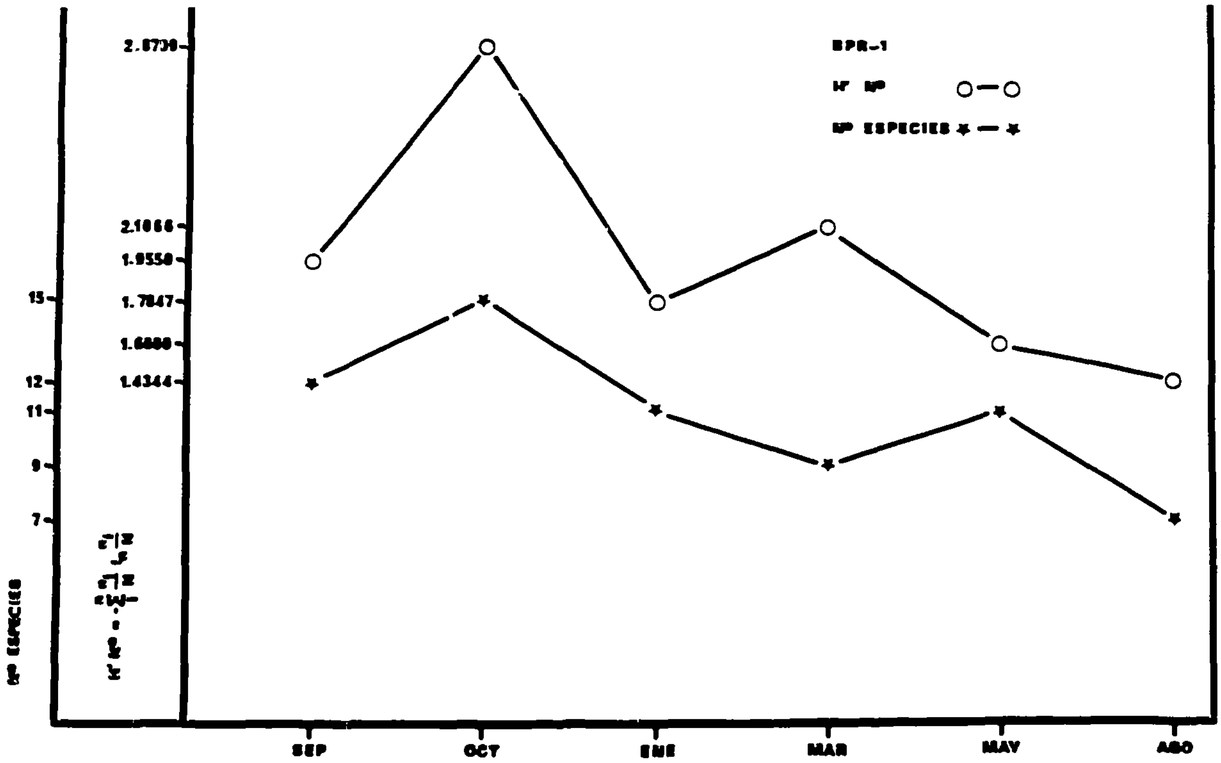

Fig. 13 Temporal variations and relationships between number of species and diversity indice (H') in fish communities associated with banks of *Thalassia testudinum* in the inlet of Puerto Real. (ENE=January; AGO=August).

CONCLUSIONS

From the results presented and the discussion established:

1. The biomass of *Thalassia testudinum* found in one place in the Laguna de Términos (382 g dry weight m^{-2}, Table 1) is much higher than of the total ichthyoconsumers (8.0 g weight m^{-2} yr^{-1}).

2. There is a high diversity of animal groups in Boca de Puerto Real, associated with banks of *Thalassia testudinum*.

3. This determines the large availability of food to sustain nektonic communities characterized by at least 31 species of fish and 2 cephalopods.

4. These ichthyofaunistic communities present a range of biomass of 0.97 to 2.23 g wet weight m^{-2} with an average of 1.33 g dry weight m^{-2}. (Table 2) and a total biomass of 8.0 g wet weight m^{-2} $year^{-1}$.

Table 3. Values of diversity (H'n = number; H'w = weight) of fish communities in estuarine systems of North America

H'n	H'w	Locality	Reference
1.31	2.71	Galveston Bay, Texas	Bechtel & Copeland (1970)
0.92-2.09	1.51-1.97	Aransas Bay, Carolina	Hoese *et al.* (1968)
2.02	1.85	Cape Fear, N. Carolina	Copeland & Birkhead (1972)
0.65-1.42	0.21-5.46	Albermale Sound, N. Carolina	Hester & Copeland (1975)
1.79-3.73	-	Wakulla & St. Marks, Florida	Subrahamanyam & Drake (1975)
0.03-0.11	-	Colorado Lagoon, California	Allen & Horn (1975)
0.36-1.52	0.34-1.87	Phillips Is., N. Carolina	Marshall Adams (1976a, b, c)
0.23-1.23	0.50-1.28	Bogue Sound, N. Carolina	Marshall Adams (1976a, b, c)
1.43-2.18	1.05-2.31	Puerto Real (BPR-1) Campeche, Mexico	Bravo Nuñez & Yáñez-Arancibia (1978) & this study
1.17-1.65	1.06-1.76	Puerto Real (BPR-3) Campeche, Mexico	Bravo Nuñez & Yáñez-Arancibia (1979)
1.52-2.28	-	Chautengo Lagoon Guerrero, Mexico	Yáñez-Arancibia (1978)
1.69-2.53	-	Tres Palos Lagoon Guerrero, Mexico	Yáñez-Arancibia (1978)

5. These 31 species of fish are categorized from the point of view of their permanence in the community: 12 transit species (39%), 15 occasional visiting species (48%), 4 permanent resident species (13%). (From the point of view of ichthyotrophic categories: 4 first order consumers (13%) with a biomass range of 0 to 0.04 g wet weight m^{-2} (i.e. 0.6 g wet weight m^{-2} yr^{-1}). 17 second order consumers (55%) with a biomass of 0.14 to 1.20 g wet weight m^{-2}. (i.e. 4.71 g wet weight m^{-2} yr^{-1}). 10 third order consumers (32%) with a biomass of 0.12 to 1.63 g wet weight m^{-2} yr^{-1} (i.e. 2.65 g wet weight m^{-2} yr^{-1}).

6. The diversity indice (H'n) presents a range of 1.43 to 2.18; and the biomass indice (H'g) presents a range of 1.05 to 2.31 (Table 3).

7. These biomass and diversity values are relatively low and reinforce the idea that Boca de Puerto Real is a dynamic ecosystem, of transitional ichthyofauna and not favorable for the establishment of permanent communities of these species. The system represents one of the entrances to the lagoon estuarine ecosystem of the interior of Laguna de Términos.

8. The trajectory of the energy flow can be included throughout the common trophic relationships of the conceptual descriptive model proposed for the ecosystem (Fig. 8).

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THE OCCURRENCE, DIVERSITY, AND ABUNDANCE OF FISHES IN TWO TROPICAL COASTAL LAGOONS WITH EPHEMERAL INLETS ON THE PACIFIC COAST OF MEXICO

by

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INTRODUCTION

Studies on occurrence, diversity, and abundance of fish communities are common. For semi-enclosed coastal areas we can consider as selected references the papers of Springer and McErlean (1963), Harrel *et al.*, (1967), Betchel and Copeland (1970), Dahlberg and Odum (1970), McErlean *et al.*, (1973), Oviatt and Nixon (1973), Turner and Johnson (1973), Wiley *et al.*, (1973), Harima and Mundy (1974), Headrich and Headrich (1974) Hester and Copeland (1975), Allen and Horn (1975), Saila (1975), Subrahmanyam and Drake (1975), Horn and Allen (1976), Livingston (1976), Marshall Adams (1976), Hoff and Ibara (1977), Hillman *et al.*, (1977), Kjelson and Colby (1977), Moore (1978), and others, considered in the Discussion.

Mexico has an exceptional geographic situation with 1.5 million hectars of estuarine environment, potentially productive and poorly known. According to Lankford (1977) the country has 123 or 125 coastal lagoons, which constitute a third of the Mexican coast line. They represent its principal and most durable geographic feature, as well as a cultural and economic patrimony becoming more important in the future development of the fishing sector. A lot of lagoons are located in tropical and subtropical areas. Nevertheless, there are few studies on ecology and structure of fish communities in these areas. The only references are the papers of Yáñez-Arancibia (1978a, 1978b), Yáñez-Arancibia and Nugent (1977), Bravo Nuñez and Yáñez-Arancibia (1979), and Yáñez-Arancibia (1978).

The study of Yáñez-Arancibia (1978b) must be considered complementary with the results discussed here: both papers refer to the most significant aspects of the ecology in many coastal lagoons with ephemeral inlets in the central Pacific coast of Mexico; and both give information which can help to understand the natural cycle of these lagoons as part of an inventory designed to establish bases for the future detection, evaluation, and control of pollution that might result from new industries and tourism. In this context it is a priority to consider the importance of the pattern of diversity in the time and space, if possible, prior to the advent of stress.

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STUDY AREAS

Both lagoons, Chautengo 34 km^2 (99°05'W and 16°06'N), and Tres Palos 50 km^2 (99°09'W and 16°06'N) have been described from an ecological point of view by Yáñez-Arancibia (1978a, 1978b). They are located near Acapulco in a tropical area with a four or five month rainy season, precipitation ranging from 1,900 to 2,200 mm per year. In addition, there is a very high rate of evaporation during the entire year and runoff is not significant, at least in Chautengo.

Chautengo Lagoon

During period 1 Chautengo Lagoon communicates with the sea from August to November, the marine influence occurs throughout the entire lagoon (Fig. 1). The lagoon is characterized by a mean depth of 1 m, temperatures from 29 to 31°C, salinities from 15 to 34 parts per thousand, a high phytoplanktonic biomass with a maximum of 43 x 10^6 cell $litre^{-1}$, a zooplanktonic biomass with a maximum of 10^5 indiv. m^{-3} and 1.0 g m^{-3}, a variable amount of detritus in sediments, few mangroves, variable macrobenthic biomass with some populations of *Mytella strigata*, *Callinectes toxotes*, *C. arcuatus*, and *Penaeus* spp. During period 2, when the lagoon is isolated from the sea during the dry season, November to May; the temperatures range from 28 to 40°C, salinities from 25 to 45 parts per thousand. During period 3 when the lagoon is isolated from the sea during the rainy season, May to August; the temperatures range from 29 to 35°C, and the salinities from "zero" to 15 parts per thousand, exceptionally up to 20 parts per thousand.

Tres Palos Lagoon

This lagoon has a channel (estero) which connects the lagoon with the sea. During period 1 when the barrier bar is open, from September to October, exceptionally until November, the marine influence occurs only in the estero zone (Fig. 1). Characteristics during this time include a mean depth of 2 m, temperatures from 29 to 31°C, salinities from "zero" to 3.5 parts per thousand, a very high phytoplanktonic biomass with a maximum of 10^9 to 10^{11} cell $litre^{-1}$, zooplanktonic biomass with a maximum of 10^3 indiv. m^{-3} and 3.0 g m^{-3}, large quantities of detritus in sediments due to input of phytoplankton and leaves of *Rhizophora mangle* (numerous mangroves), and macrobenthic biomass almost absent but with important fisheries of *Macrobrachium tenellum*. During period 2 when the lagoon is isolated from the sea during the dry season, Novem-

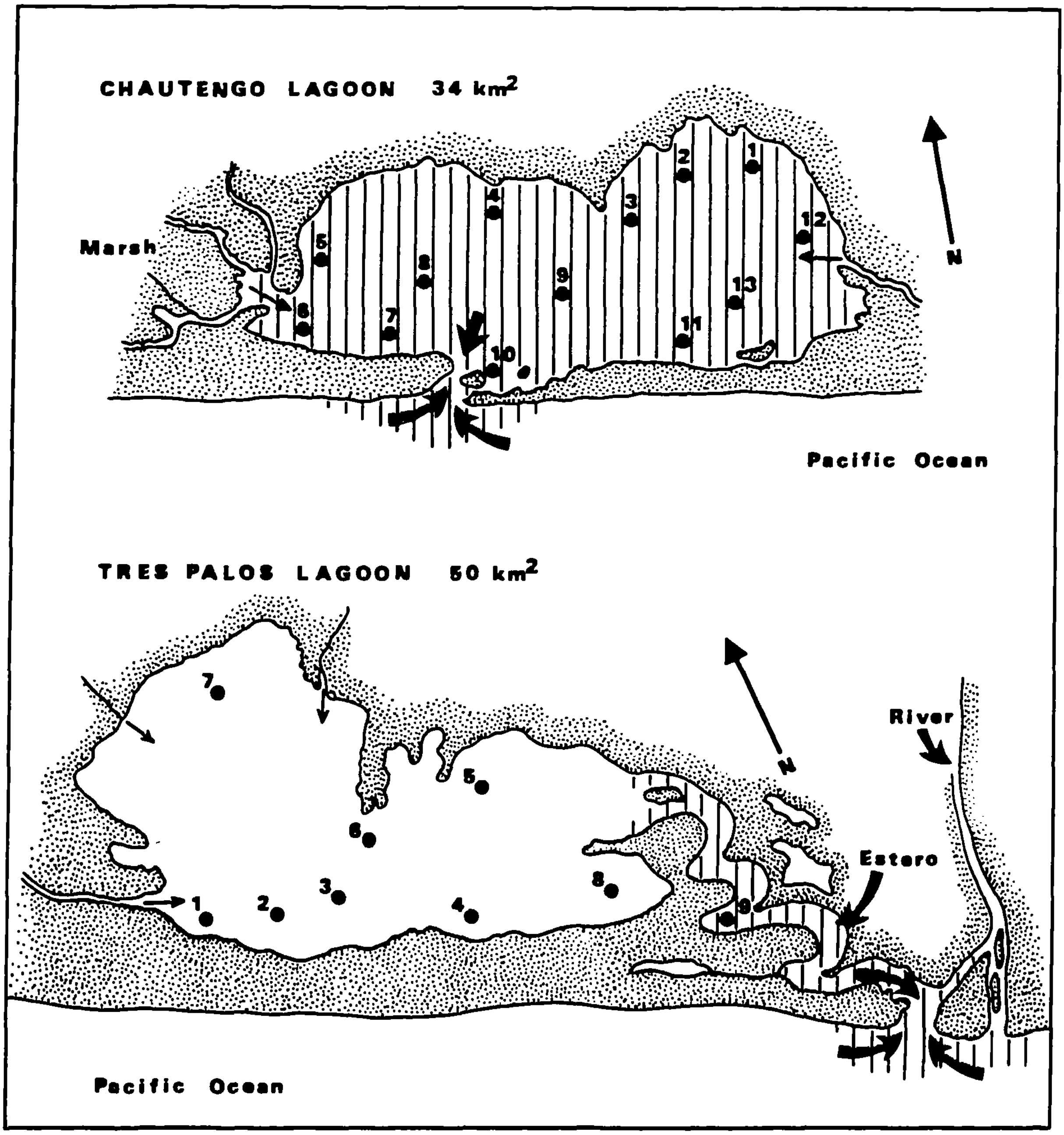

Fig. 1 Geomorphological diagram of Chautengo Lagoon (99°05'W-16°06'N) and Tres Palos Lagoon (99°09'W-16°06'N), showing the marine influence zone during the ecological period 1, and stations of fish collections.

ber to May, the temperatures range from 30 to 35°C, and salinities from "zero" to 4 parts per thousand. During period 3 when the lagoon is isolated from the sea during the rainy season, May to August, the temperature ranges from 29 to 33°C, and salinities from "zero" to 3 parts per thousand. Only in the estero zone during period 1 are the salinities as high as 12 parts per thousand.

MATERIAL AND METHODS

Fishes were sampled during the early morning from September 1973 until July 1975 during the best representative months of each ecological period. Ten collections in each station were realized: Chautengo 13 stations and Tres Palos 9 stations for period 1 (September and October 1973 and 1974), period 2 (May 1974 and 1975), and period 3 (July 1974 and 1975). All collections were within 2.0 m of the surface.

A total of 8,245 individuals were collected: Chautengo, 4,325, and Tres Palos, 3,920.

The atarraya net was used. It has a 5.0 m diameter, net 1/2", and collected in a 19.5 m^2 area.

To compare the lagoons, salinities, temperatures, amount of detritus, phytoplankton biomass, zooplankton biomass, benthos (Yáñez-Arancibia, 1978b), diversity and biomass composition of fish communities were studied. Three diversity indices were calculated. The Shannon-Weaver (1963) information function:

$$H' = - \quad Pi \log Pi \qquad (1)$$

where Pi is the proportion of individuals in the i-th species. This formula has been used widely as a species diversity index in fishes, as suggested by Dahlberg and Odum (1970). The Shannon-Weaver function increases as both the number of species (richness) and the equitability of species abundance (evenness) increase. It is desirable to consider indices that treat these aspects separately since the two components of diversity may react differently to certain types of factors.

For the "species richness" component of diversity, we selected the following:

$$D = \frac{(S-1)}{\log N} \qquad (2)$$

where S is the number of species and N is the numbner of individuals. This index was also used by Margalef (1969) and in many other studies in estuarine areas.

The "evenness" index of Pielou (1966) was the third ratio used, for the equitability of species abundance:

$$J' = H'/H_{max} = H'/\log S \qquad (3)$$

in which log S is the maximum possible value of H'. Then $H'=H_{max}$ when all species are equally abundant.

All diversity calculations are based on the use of natural logs (log). The abundance of fishes was determined by density and biomass (standing crop), as indiv. m^{-2}, and g wet weight m^{-2}.

RESULTS

Chautengo Lagoon

Diversity and Dominant Species

4,325 individuals were studied out of which 85 species were determined (Table 1) with an H' of 2,1588. This diversity changes in time (Table 2). The fishes during period 1 are predominantly marine fishes and the fisheries production is very important. Fresh water fishes reach 9.8% in September and 10% in October in total fish communities. The best representatives species according H' has been *Diapterus peruvianus*, *Mugil curema*, *Galeichthys caerulescens*, *Anchovia macrolepidota*, *Mugil cephalus*, *Gerres cinereus*, and *Centropomus* spp.

During period 2 the volume of water decreases inside the lagoon. Fresh water fishes reach 16.6% of the total fish communities as a consequence of a reduction of marine fishes. *Diapterus peruvianus*, *Galeichthys caerulescens*, *Mugil curema* and *Anchovia macrolepidota* are predominant.

During period 3 the diversity increases relative to the second period, due to fresh water fishes. *Galeichthys caerulescens* and *Mugil curema* are abundant. Likewise, *Lile stolifera*, *Astyanax fasciatus*, *Melaniris crystallina*, *Diapterus peruvianus*, *Cichlasoma trimaculatum*, *Mugil cephalus*, *Eleotris pictus*, *Dormitator latifrons* and *Gobionellus microdon* are characteristic of this period. Fresh water fishes reach 50% of the total fish communities.

Very few species are present throughout the entire year. The most important are: *Elops affinis*, *Astyanax fasciatus*, *Galeichthys caerulescens*, *Centropomus robalito*, *Diapterus peruvianus*, *Cichlasoma trimaculatum*, *Mugil cephalus*, *Mugil curema* and *Gobionellus microdon*. These fishes represent 11% of the total diversity. During period 2, *Astyanax*, *Cichlasoma*, and *Gobionellus* are collected only near the distributaries.

Table 1. Occurrence, relative abundance, and temporal distribution of fishes in Chautengo Lagoon

Species	Period 1 Sept. 73		Period 2 May 74		Period 1 Oct. 74		Period 3 July 75		Total No.
	No.	%	No.	%	No.	%	No.	%	
Heterodontus francisici					1	0.06			1
Pristis zephyreus					1	0.06			1
Urotrygon nebulosus					1	0.06			1
Urotrygon asterias	1	0.1							1
Urotrygon aspidurus	1	0.1							1
Urotrygon goodei					1	0.06			1
Urotrygon chilensis					1	0.06			1
Urotrygon sp A					1	0.06			1
Elops affinis	2	0.2	4	0.4	19	1.2	3	0.33	28
Alibula vulpes	1	0.1			4	0.2			5
Lile stolifera					3	0.19	28	3.1	31
Ophistonema libertate	2	0.2			4	0.2			6
Ophistopterus dovii	1	0.1							1
Pliosteostoma lutipinnis *									
Anchovia macrolepidota	19	2.2	68	6.8	96	6.1			183
Anchoa panamensis	2	0.2			8	0.5			10
Anchoa mundeoloides	2	0.2	1	0.1	2	0.12			5
Anchoa curta					2	0.12			2
Anchoa scofieldi	3	0.35			3	0.19			6
Chanos chanos	3	0.35	1	0.1	2	0.12			6
Astyanax fasciatus	5	0.6	2	0.2	8	0.5	37	4.0	52
Galeichthys caerulescens	72	8.5	340	34.0	458	29.1	412	45.6	1282
Galeichthys gilberti	3	0.35			1	0.06			4
Arius liropus *									
Hyporhamphus unifasciatus	3	0.35			10	0.6			13
Strongylura stolzmanni	1	0.1			2	0.12			3
Tylosurus fodiator	1	0.1			2	0.12			3
Poecilia sphenops							6	0.66	6

Species	Period 1 Sept. 73		Period 2 May 74		Period 1 Oct. 74		Period 3 July 75		Total No.
	No.	%	No.	%	No.	%	No.	%	
Melaniris crystallina	1	0.1			2	0.12	19	2.1	22
Prionotus ruscarius	1	0.1							1
Centropomus nigrescens	2	0.2	6	0.6	10	0.6			18
Centropomus robalito	6	0.7	18	1.8	95	6.0	3	0.33	123
Centropomus pectinatus	6	0.7							6
Diplectrum pacificum	1	0.1							1
Caranx hippos	4	0.97			16	1.0			20
Caranx marginatus			2	0.2	4	0.2			6
Caranx medusicola					1	0.06			1
Caranx latus	1	0.1			1	0.06			2
Caranx caballus *									
Selene brevortii	3	0.35			4	0.2			7
Oligoplites mundus	3	0.35			2	0.12			5
Oligoplites altus					4	0.2			4
Oligoplites saurus					10	0.6			10
Oligoplites refulgens	1	0.1							1
Trachynotus rhodopus	1	0.1							1
Lutjanus novemfasciatus	2	0.2			6	0.38			8
Lutjanus argentiventris	1	0.1	2	0.2	2	0.12			5
Lutjanus guttatus	1	0.1			2	0.12			3
Diapterus peruvianus	413	48.7	346	34.6	473	30.1	26	2.87	1258
Gerres cinereus	14	1.6	1	0.1	4	0.2			19
Eugerres lineatus	7	0.8	2	0.2	9	0.57			18
Eugerres axillaris	1	0.1			2	0.12			
Eucinostomus currani	2	0.2			9	0.57	2	0.22	13
Eucinostomus entomelas			1	0.1	1	0.06			2
Eucinostomus dowii	2	0.2			1	0.06			3
Pomadasys macracanthus	8	0.9			12	0.76	1	0.11	21

Species	Period 1 Sept. 73		Period 2 May 74		Period 1 Oct. 74		Period 3 July 75		Total No.
	No.	%	No.	%	No.	%	No.	%	
Pomadasys leusiscus					4	0.2	1	0.11	5
Pomadasys branickii	2	0.2			4	0.2			6
Umbrina xanti	2	0.2			2	0.12			4
Micropogon altipinis	2	0.2			3	0.19			5
Micropogon ectenes	3	0.35			2	0.12			5
Cynoscion stolzmanni	3	0.35			1	0.06			4
Cynoscion annulus					3	0.19			3
Cynoscion reticulatus					3	0.19			3
Menticirrhus elongatus	2	0.02							2
Menticirrhus nasus	1	0.1			2	0.12			3
Kyphosus elegans	1	0.1							1
Cichlasoma trimaculatum	1	0.1	4	0.4	8	0.5	18	1.99	31
Mugil cephalus	18	2.1	12	1.2	26	1.65	46	5.0	102
Mugil curema	179	21.1	186	18.6	163	10.3	202	22.3	730
Polydactilus approximans *									
Sphyraena ensis	1	0.1			1	0.06			2
Eleotris pictus	3	0.35			8	0.5	22	2.4	33
Gobiomarus maculatus					2	0.12	11	1.2	12
Dormitator latifrons	2	0.2			8	0.5	19	2.1	29
Bathygobius soporator	1	0.1					1	0.11	2
Microgobius miraflorensis							3	0.33	3
Giobionellus microdon	6	0.7	3	0.3	8	0.5	22	2.4	39
Gobionellus sagittula							8	0.88	8
Scomberomorus maculatus *									
Cyclopseta querna	2	0.2			1	0.06			3
Citarichthys gilberti	4	0.47			12	0.76	11	1.2	27
Achirus mazatlanus	2	0.2			6	0.38			8
Achirus panamensis	2	0.2			1	0.06			3

Species	Period 1 Sept. 73		Period 2 May 74		Period 1 Oct. 74		Period 3 July 75		Total No.
	No.	%	No.	%	No.	%	No.	%	
Achirus klunsingeri					0	0.06			1
Trinectes fonsecensis	2	0.2			2	0.12			4
Sphoeroides annulatus	3	0.35			3	0.19			6
Sphoeroides lobatus					1				1
Diodon hystrix	2	0.2			1	0.06			3
No. of specimens	847		999		1577		901		4325
No. of Species (85)	61 (73%)		18 (21%)		70 (81%)		22 (26%)		

* Species collected during August, 1976.

Table 2. Analysis of variations of effects of ecological periods on composition and diversity of fishes from atarraya net samples in Chautengo Lagoon.

Indices	Period 1 Sept.	Period 1 Oct.	Period 2 May	Period 3 July
S (species)	61	70	18	22
N (specimens)	847	1572	999	901
H'	19848	22798	15237	18776
D	88998	93748	24613	30856
J'	.4828	.5366	.5271	.6074

Abundance

At the beginning of period 1 in September, 847 individuals in 70 collections were captured. The surface sampled was 1,365 m^2. The density average was 12 indiv. 19.5 m^{-2}. From this density, as shown in Table 1, 52% are Gerridae, 23% Mugilidae, 3% Engraulidae, 2% Centropomidae, and 1% Carangidae, of the most important groups.

In October during the same period 1, 1,572 individuals in 130 collections were captured. The surface sampled was 2,535 m^2. The density average was 12 indiv. 19.5 m^{-2}. From this density, as shown in Table 1, 32% are Gerridae, 29% Ariidae, 12% Mugilidae, 7% Engraulidae, 6% Centropomidae, 2% Carangidae, and 1% Elopidae, of the most important groups.

During period 2, 999 individuals in 130 collections were captured. The surface sampled was 2,535 m^2. The density average was 8 indiv. 19.5 m^{-2}. From this density it is considered, as shown in Table 1, that 35% are Gerridae, 34% Ariidae, 20% Mugilidae, 7% Engraulidae, and 2% Centropomidae, from the most important groups.

During period 3, 901 individuals in 130 collections were captured. The surface sampled was 2,535 m^2. The density average was 7 indiv. 19.5 m^{-2}. From this density, as shown in Table 1, 46% are Ariidae, 27% Mugilidae, 9% Gobiidae, 4% Characinidae, and 3% Gerridae, of the most important groups.

The standing crop ranges as following: During period 1 the average was 1,300 g 19.5 m^{-2} (i.e., 66.7 g m^{-2}). During period 2 the average was 864 g 19.5 m^{-2} (i.e., 44.3 g m^{-2}). During period 3 the average was 756 g 19.5 m^{-2} (i.e., 38.8 g m^{-2}).

Tres Palos Lagoon

Diversity and Dominant Species

3,930 individuals were studied out of which 32 species were determined (Table 3) with an H' of 1,9898. This diversity changes in time (Table 4). During period 1 the fishes are predominantly marine fishes in the estero zone, but fresh water fishes are dominant in the rest of the lagoon. In general, during period 1 the fresh water fishes reach 43.3% in September and 41.7% in October of the total fish communities. The best representative species according to the H' index were *Poeciliopsis balsas*, *Galeichthys caerulescens*, *Poecilia sphenops*, *Mugil curema*, *Melaniris crystallina*, *Diapterus peruvianus*, *Dormitator latifrons*, *Gobiomorus maculatus*, *Eugerres lineatus*, and *Cichlasoma trimaculatum*.

During period 2, fresh water fishes reach 52% in total fish communities. The best representative species according to the H' index were *Galeichthys caerulescens*, *Poeciliopsis balsas*, *Eugerres*

Table 3. Occurrence, relative abundance, and temporal distribution of fishes in Tres Palos Lagoon

Species	Period 1 Sept. 73		Period 2 May 74		Period 1 Oct. 74		Period 3 July 75		Total No.
	No.	%	No.	%	No.	%	No.	%	
Elops affinis	3	0.17			6	0.72	1	0.13	10
Lila stolifera	3	0.17	7	1.12	5	0.06	28	3.74	43
Anchovia macrolepidota	1	0.05			3	0.36	1	0.13	5
Chanos chanos					2	0.36			2
Astyanax fasciatus	21	1.21	6	0.96	14	1.69	38	5.08	79
Galeichthys caerulescens	238	13.7	314	50.6	275	33.2	185	24.7	1012
Poecilia sphenops	12	0.69	7	1.12	188	22.7	38	5.08	245
Poeciliopsis lucida	9	0.51	4	0.64			12	1.60	25
Poeciliopsis porosus	11	0.63			2	0.36	13	1.73	26
Poeciliopsis balsas	1220	70.4	142	22.9	96	11.6	133	17.8	1591
Melaniris crystallina	38	2.19	23	3.70	54	6.52	29	3.87	144
Centropomus robalito	3	0.17			1	0.12			4
Caranx hippos					2	0.36			2
Oligoplites saurus					2	0.36			2
Lutjanus guttatur	5	0.28							5
Diapterus peruvianus	30	1.73	6	0.96	27	3.26	11	1.47	74
Gerres cinereus	8	0.46	11	1.77	6	0.72		0.93	32
Eugerres lineatus	16	0.92	33	5.31	22	2.65	11	1.47	82
Eugerres axillaris	2	0.11					1	0.13	3
Eucinostomus currani	3	0.17	1	0.16	1	0.12	1	0.13	6
Cichlasoma trimaculatus	8	0.46	13	2.09	18	2.17	40	5.34	79
Tilapia mossambica	2	0.11					1	0.11	3

Species	Period 1 Sept. 73		Period 2 May 74		Period 1 Oct. 74		Period 3 July 75		Total No.
	No.	%	No.	%	No.	%	No.	%	
Mugil cephalus	11	0.63	3	0.48	7	0.84	21	2.80	42
Mugil curema	38	2.19	21	3.38	54	6.52	77	10.3	190
Eleotris pictus	9	0.51	3	0.48	1	0.12	18	2.40	31
Gobiomorus maculatus	17	0.98	8	1.28	24	2.89	30	4.01	79
Dormitator latifrons	20	1.15	14	2.25	6	0.72	21	2.80	61
Microgobius miraflorensis	3	0.17					2	0.26	5
Gobionellus microdon					12	1.44	18	2.40	30
Gobionellus sagittula			1	0.16			3	0.40	4
Achirus mazatlanus	2	0.11	4	0.64			7	1.06	14
Achirus sp.							1	0.13	1
No. of specimens	1733		621		828		748		3930
No. of species(32)	26 (81%)		19 (59%)		24 (75%)		26 (81%)		

Table 4. Analysis of variations of effects of ecological periods on composition and diversity of fishes in atarraya samples in Tres Palos Lagoon.

Indices	Period 1 Sept.	Period 1 Oct.	Period 2 May	Period 3 July
S (species)	26	24	19	26
N (specimens)	1733	829	621	748
H'	18580	21093	16924	25335
D	33522	34225	27987	37779
J'	.5319	.6637	.5747	.7776

lineatus, *Melaniris crystallina*, *Mugil curema*, and *Dormitator latifrons*.

During period 3 the diversity increases relative to the second period and is similar to that in period 1. The fresh water fishes reach 53.8% of the total fish communities. The best representative species according to the H' index were *Galeichthys caerulescens*, *Mugil curema*, *Mugil cephalus*, *Poeciliopsis balsas*, *Poeciliopsis* spp., *Poecilia sphenops*, *Gobiomorus maculatus*, *Astyanax fasciatus*, *Lile stolifera*, *Cichlasoma trimaculatum*, *Eugerres lineatus*, *Dormitator latifrons*, and *Gobionellus microdon*.

Many of fishes are present throughout the entire year. The most important are *Lile stolifera*, *Astyanax fasciatus*, *Galeichthys caerulescens*, *Poecilia sphenops*, *Poeciliopsis lucida*, *Poeciliopsis porosus*, *Poeciliopsis balsas*, *Melaniris crystallina*, *Diapterus peruvianus*, *Gerres cinereus*, *Eugerres lineatus*, *Eucinostomus currani*, *Cichlasoma trimaculatum*, *Dormitator latifrons*, and *Achirus mazatlanus*. This is a 59.4% of the total ichthyofauna and is a characteristic of the environmental stability.

Abundance

At the beginning of period 1 in September, 1,733 individuals in 90 collections were captured. The surface sampled was 1,755 m^2. The density average was 19 indiv. 19.5 m^{-2}. From this density, as shown in Table 3, 72% are Poecilliidae, 14% Ariidae, 4% Gerridae, 3% Mugilidae, 3% Gobiidae, 2% Characinidae, and 1% Clupeidae, of the most important groups.

In October during the same period 1, 828 individuals in 90 collections were captured. The surface sampled was the same. The density average was 9 indiv. 19.5 m^{-2}. From this density, as shown in Table 2, 35% are Poecilliidae, 33% Ariidae, 7% Characinidae, 7% Mugilidae, 6% Gerridae, 5% Gobiidae, and 2% Clupeidae, of the most important groups.

During period 2, 621 individuals in 90 collections were captured. The density average was 7 indiv. 19.5 m^{-2}. From this density, as shown in Table 2, 51% are Ariidae, 31% Poecilliidae, 14% Gerridae, 4% Characinidae, 4% Gobiidae, and 2% Clupeidae, of the most important groups.

During period 3, 748 individuals in 90 collections were captured. The density average was 8 indiv. 19.5 m^{-2}. From this density, as shown in Table 2, 26% are Poecilliidae, 25% Ariidae, 13% Mugilidae, 12% Gobiidae, 9% Clupeidae, 4% Characinidae, and 4% Gerridae, of the most important groups.

The standing crop ranges as following: during period 1 the average was 840 g 19.5 m^{-2} (i.e., 43.1 g m^{-2}); during period 2 the average was 421 g 19.5 m^{-2} (i.e., 21.5 g m^{-2}); during period 3 the average was 480 g 19.5 m^{-2} (i.e., 24.6 g m^{-2}).

DISCUSSION

Chautengo Lagoon

Diversity and Dominant Species

The Chautengo Lagoon is dominated by the seasonal influence of euryhaline and stenohaline marine fishes. This seasonal fluctuation is reflected in the three indices calculated (Table 2).

Highly significant seasonal fluctuations occur in the distribution of numbers among species in the Shannon-Weaver Index H'. The highest value occurs during period 1. Low overall values are characteristic of the stressful conditions found in the estuary during periods 2 and 3 (Fig. 2).

During period 1 eight species out of 70 (11%) are dominant according to the H' index: *Diapterus peruvianus* (896 specimens), *Galeichthys caerulescens* (530), *Mugil curema* (342), Centropomus spp. (119), *Anchovia macrolepidota* (115), *Mugil cephalus* (44), and *Gerres cinereus* (18), which represent 85% of the total specimen number collected during this period in September and October (i.e., 2,424 specimens).

During period 2 four species out of 18 (22%) are dominant according to the H' index: *Diapterus peruvianus* (346 specimens), *Galeichthys caerulescens* (340), *Mugil curema* (186), and *Anchovia macrolepidota* (68), which represent 94% of the total specimens number collected during this period (i.e., 999 specimens).

During period 3 eleven species out of 22 (50%) are very important according to the H' index, but especially two of them (9%) are significantly abundant, i.e., *Galeichthys caerulescens* (421 specimens), and *Mugil curema* (202), which represent 69% of the total specimens number collected during this period (i.e., 901 specimens).

Eighty five species were found in Chautengo Lagoon, but only 11% occur during the entire year throughout the three ecological periods, i.e., *Elop affinis*, *Astyanax fasciatus*, *Galeichthys caerulescens*, *Centropomus robalito*, *Diapterus peruvianus*, *Cichlasoma trimaculatum*, *Mugil cephelus*, *Mugil curema* and *Gobionellus microdon*, being a consequence of the instability in the ecological system.

The Shannon-Weaver Indice calculated is not high, and it is similar to the results obtained in other estuarine areas (Table 5). The low values are not the consequence of contaminated areas, rather they are a result of stressful conditions.

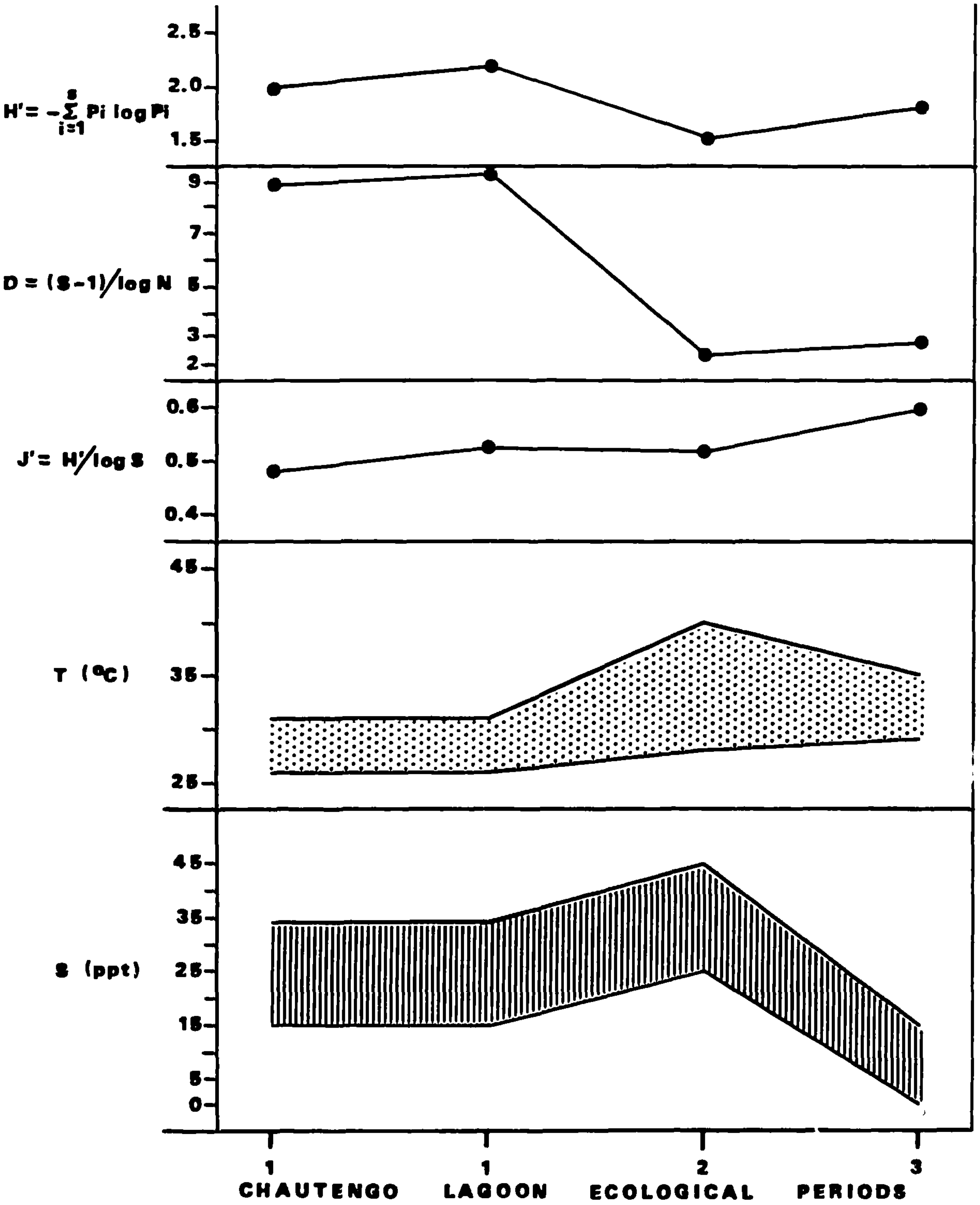

Fig. 2 Temporal variation and relations between species diversity indices, temperatures, and salinities, in Chautengo Lagoon.

Table 5. Values of diversity (H'w=weight) of fish communities in estuarine systems of North America.

H'n	H'w	Locality	Reference
1.31	2.71	Galveston Bay, Texas	Bechtel & Copeland (1970)
0.92-2.09	1.51-1.97	Aransas Bay, Texas	Hoese *et al.* (1968)
2.02	1.85	Cape Fear, N. Carolina	Copeland & Birkhead (1972)
0.65-1.42	0.21-5.46	Albermale Sound, N. Carolina	Hester & Copeland)1975)
1.79-3.73	-	Wakulla & St. Marks, Florida	Subrahamanyam & Drake (1975)
0.03-0.11	-	Colorado Lagoon, California	Allen & Horn (1975)
0.36-1.52	0.34-1.87	Phillips Is., N. Carolina	Marshall Adams (1976)
0.23-1.23	0.50-1.28	Bogue Sound, N. Carolina	Marshall Adams (1976)
1.43-2.18	1.05-2.31	Puerto Real (BPR-1), Campeche, Mexico	Bravo Nuñez & Yáñez-Arancibia (1979)
1.17-1.65	1.06-1.76	Puerto Real (BPR-3), Campeche, Mexico	Bravo Nuñez & Yáñez-Arancibia (1979)
1.52-2.28	-	Chautengo Lagoon, Guerrero, Mexico	This study
1.69-2.53	-	Tres Palos Lagoon Guerrero, Mexcio	This study

The higher species number occurs during period 1 and decrease considerably during periods 2 and 3. Because there is no contact with the sea during periods 2 and 3, the increase of species number and biomass during the last period is due to fresh water species which occur inside the estuary during the rainy season.

The actual values of H' are quite low, reflecting a skewed distribution where a few species contribute most of the number in response to the stress characteristic of the estuarine environment. Rapid fluctuation of temperature, salinity, dissolved oxygen, available food, and turbidity, limit the species of nekton able to live inside the lagoon during periods 2 and 3. Species are not able to tolerate the entire gamut of seasonal changes.

No trend is discernable using the relative species abundance or "evenness" index J'. Species certainly do move in and out of the lagoon during period 1, but it was not detectable with this index due to a readjustment by other species. Therefore, the distribution over species remained unchanged.

Further evidence suggesting replacement of species is provided by the "species richness" index, D. D relates the total number of species to the total catch and weighs each species equally. This index shows a great seasonal trend. Since seasonal activity is known to occur within the Chautengo Lagoon, this result clearly shows that species disappear and/or replacement takes place. Various species utilize the estuary during different seasons depending on each species' niche adaptation.

Only period 1 showed a higher number of species. Species replacement between period 2 and 3 and the response of the nekton community to the changing conditions within the Chautengo Lagoon produce a "stable" population as reflected by the diversity indices calculated. This "stable" period 2 and 3 population, however, is a function of dynamic processes occurring throughout the estuary over time involving numerous species.

Abundance

Diversity and biomass were calculated for the "atarraya" net used. The "atarraya" has a collection surface of 19.5 m^2. During period 1 the density was 12 indiv. 19.5 m^{-2} and the standing crop 66.7 g m^{-2}. During period 2 the density decreased 33%, being 8 indiv. 19.5 m^{-2}, and the standing crop decreased 34% being 44.3 g m^{-2}. During period 3 the density was 7 indiv. 19.5 m^{-2}; it decreased 42% relative to period 1 and 12% relative to period 2. The standing crop decreased 42% relative to period 1 and 11% relative to period 2, its value being 38.8 g m^{-2}.

These values are higher than other results in other estuarine areas (Table 5). The highest value occurs during period 1 and then decreases during period 2 and 3, as characteristic of stressful conditions. Therefore, populations remain high in density throughout the year, and apparently, energy utilization is optimized.

Tres Palos Lagoon

Diversity and Dominant Species

Whereas seasonal fluctuation is characteristic of the Chautengo Lagoon, this phenomena does not occur in Tres Palos Lagoon (Table 4). No highly significant seasonal fluctuations occur in the distribution of numbers among species, the Shannon-Weaver Index H'. When marine group species move out of the estuary (by natural mortality and/or fishing) during period 1, they are replaced by others maintaining a relatively constant H' value.

Highly significant seasonal fluctuations occur with H' between periods 2 and 3. This increase of species number, indice H', and biomass during period 3 is due to fresh water species which occur inside the lagoon during the rainy season when the area is isolated from the sea. Even in this situation the environment shows relative stability (Fig. 3).

During period 1, eleven species out of 26 (42%) are dominant according to H': *Poeciliopsis balsas* (*1,316 specimens*), *Galeichthys* (1,316 specimens), *Galeichthys caerulescens* (513), *Poecilia sphenops* (200), *Mugil curema* (92), *Melaniris crystallina* (92), *Diapterus peruvianus* (57), *Gobiomorus maculatus* (41), Eugerres lineatus (38) *Astyanax fasciatus* (*35*), *Cichlasoma trimaculatum* (*26*), *and* (35) *Cichlasoma trimaculatum* (26), and *Dormitator latifrons* (26), which represent 96% of the total specimens number collected during this period in September and October (i.e., 2,561 specimens).

During period 2, seven species of 19 (37%) are dominant according to H': *Galeichthys caerulescens* (314 specimens), *Poeciliopsis balsas* (142), *Eugerres lineatus* (33), *Melaniris crystallina* (23), *Mugil curema* (21), *Dormitator latifrons* (14), and *Cichlasoma trimaculatum* (13), which represent 90% of the total specimens number collected during this period (i.e., 621 specimens)

During period 3, 14 species of 26 (54%) are important according to H': *Galeichthys caerulescens* (*185 specimens*), *Poeciliopsis balsas* (133), *Lile stolifera* (28), *Astyanax fasciatus* (38), *Poecilia sphenops* (38), *Melaniris crystalline* (29), *Eugerres lineatus* (11), *Cichlasoma trimaculatum* (40), *Mugil cephalus* (21), *Mugil curema* (77), *Elotris pictus* (18), *Gobiomorus maculatus* (30), *Dormitator latifrons* (21) *Gobionellus microdon* (18), which represent 92% of the total specimens number collected during this period (i.e., 748 specimens).

Thirty two species were found, but only 59% exist during the entire year throughout the three ecological periods (Table 3), which is a characteristic of the stability in the ecological system.

The Shannon-Weaver Indice calculated is not high, and it is similar to the results obtained in other estuarine areas (Table 5). The low values are not a consequence of contaminated areas but are a result of stressful conditions.

The number of species present is related to the characteristics of the habitat. There are no significant fluctuations in temperature and salinity (Fig. 3), however dissolved oxygen, phytoplank-

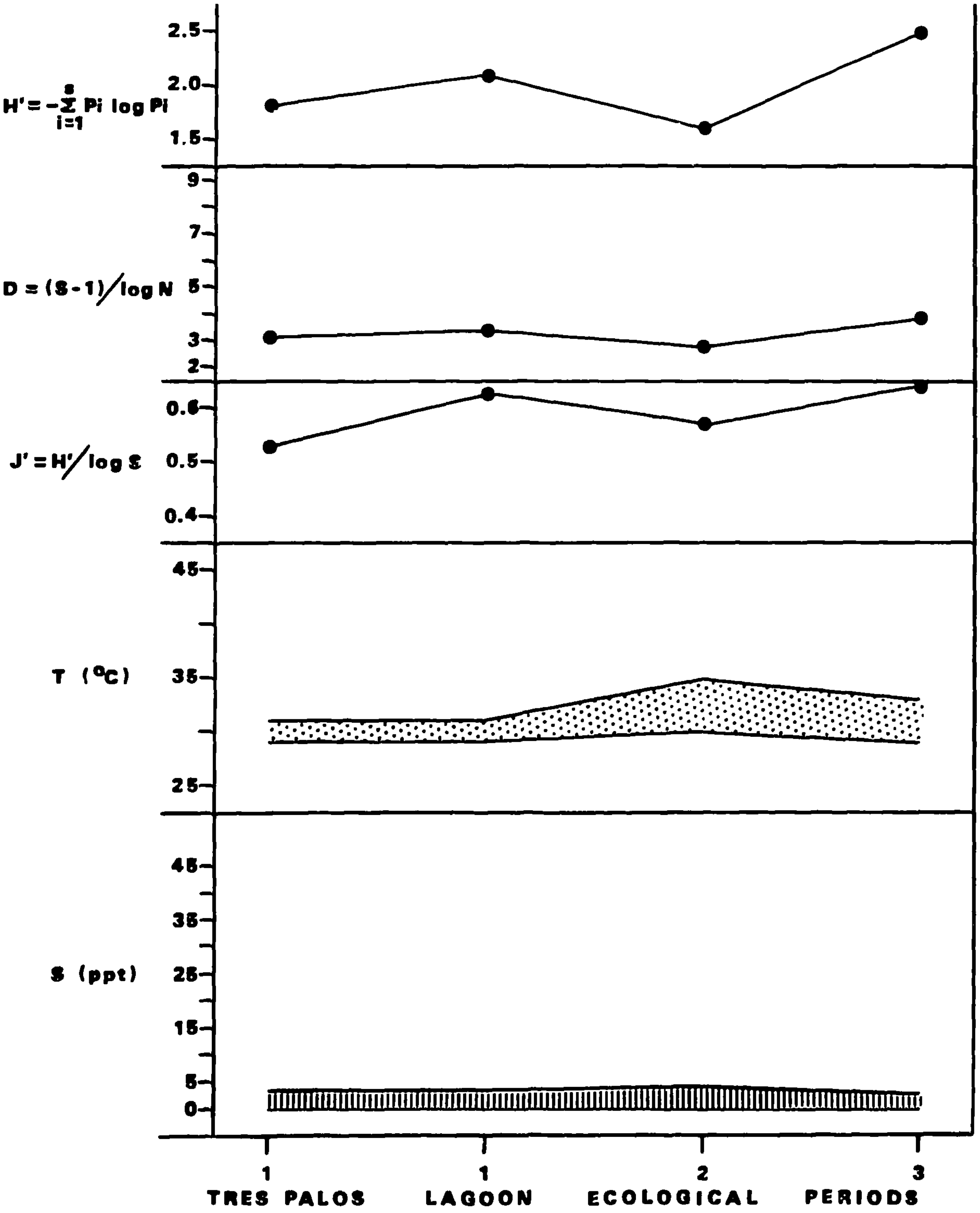

Fig. 3 Temporal variation and relations between species diversity indices, temperatures, and salinities, in Tres Palos Lagoon.

ton bloom, available food, and very low salinities, limit the nekton species able to live inside the lagoon.

The "evenness" index J', fluctuates seasonally from period 2 to period 3, due to the input of new freshwater species during the rainy season. In general, J' remains constant during the entire year.

The decrease in "species richness", D, which also occurs in period 2 is due, in part, to the same factors, temperature and salinity, but particular stress is placed on the environment by the amount of dissolved oxygen and available food.

The Tres Palos Lagoon estuarine system proved to be productive for a relatively short time, during period 1 in the estero zone. Therefore, seasonal fluctuations are clearly apparent from an analysis of the diversity indices. However, similar changes in the diversity index may result from very different processes and must be studied in conjunction with other data.

Abundance

Density and biomass was calculated for the "atarraya" net used. The "atarraya" has a collection surface of 19.5 m^2. During period 1 the density was 14 indiv. 19.5 m^{-2} and the standing crop 43.1 g m^{-2}. During period 2 the density decreases 50%, and the standing crop descreases in 49%; the density has a value of 7 indiv. 19.5 m^{-2}, and that of the standing crop's is 21.5 g m^{-2}. During period 3 the density decreases 43% relative to period 1 and increases 12% relative to period 2; its value being 8 indiv. 19.5 m^{-2}. The standing crop decreases 42% relative to period 1 and increases 12% relative to period 2; its value is 24.6 g m^{-2}.

These values are lower than Chautengo Lagoon but, in general, higher than other results in other estuarine areas (Table 6). The greatest values occur during period 1 and these decrease during periods 2 and 3, as they are characteristic of stressful conditions. Therefore, populations have low species number but high density throughout the year.

ECOLOGICAL COMPARISONS AND CONCLUSIONS

The ichthyofaunistic diversity, and the fisheries production are directly related to the marine influence in the lagoons during period 1. Coastal areas are increasingly coming under the influence of man, and that this human utilization will result in changes in the coastal lagoons of Guerrero (Acapulco) is inevitable. Increasing urbanization, channelization, and tourism may soon alter the natural cycle of the three ecological periods in these estuarine ecosystems.

Table 6. Values of biomass of fish communities in estuarine systems of North America

Range	Avg.	Locality	Reference
0.76 g dry w m^{-2}	0.76	Long Is. Sound	Richard (1963)
1.20 g dry w m^{-2}	1.20	Laguna Madre, Texas	Hellier (1962)
0.40 g dry w m^{-2}	0.40	Guadalupe Bay, Texas	Moseley & Copeland (1969)
0.04-0.40 g dry w m^{-2}	-	Rhode Island	Nixon & Oviatt (1972)
1.20 g dry w m^{-2} 5.90 g wet w m^{-2}	-	New Port River, N. Carolina, (1973) (marsh areas)	Kjelson *et al.*
0.30 g dry w m^{-2} 1.50 g wet w m^{-2}	- -	New Port River, N. Carolina, (estuary)	Kjelson *et al.* (1973)
0.08-2.18 g dry w m^{-2}	1.33	New Port River, N. Carolina (Phillips Is.)	Thayer *et al.* (1975)
1.50 g dry w m^{-2}	1.50	New Port River, N. Carolina	Marshall Adams (1976)
0.60-15.2 g wet w m^{-2}	3.10	Card Sound, Florida	Brook (1977)
0.97-2.23 g wet w m^{-2}	1.33	Puerto Real (BPR-1) Campeche, Mexico	Bravo Nuñez & Yañez-Arancibia (1979)
0.18-10.92 g wet w m^{-2}	2.02	Puerto Real (BPR-3) Campeche, Mexico	Bravo Nuñez & Yañez-Arancibia (1979)
38.8-66.7 g wet w m^{-2}	49.9	Chautengo Lagoon Guerrero, Mexcio	This study
21.5-43.1 g wet w m^{-2}	29.3	Tres Palos Lagoon Guerrero, Mexico	This study

It is possible, using the data presented in this paper and the data presented by Yañez-Arancibia (1976, 1977, 1978a, 1978 b), that the biological responses to the physical changes can be predicted with a relatively high degree of certainty.

In Chautengo Lagoon an increase in the amount of organic material in the form of leaves of *Rhizophora mangle* is exported to the shelf during period 1. In Tres Palos Lagoon an increase in the amount of organic material carried by tributaries, in the form of leaves of *Rhizophora mangle*, and of phytoplankton bloom will surely dampen the population growth inside the lagoon.

Periods of very low flow rates are often prevalent in Tres Palos Lagoon. Under these circumstances, the normal organic load from farmland, runoff, leaves of mangroves, and dead phytoplankton may create excessive demands on the supply of oxygen. In addition, these organic materials may act as a source of nutrients stimulating the growth of phytoplankton.

Nutrient concentrations would be high in response to the low flow rates resulting in rapid algal growth. This algal productivity itself may contribute to the lack of available oxygen. Night time respiration and the reducing conditions created by decaying algae in bloom proportions could cause oxygen levels to drop quite low.

Increased organic input in Tres Palos Lagoon causes two primary consequences. The biological oxygen demand is increased, resulting in a net loss of oxygen to the biological communities, especially during the night (less than 2.0 ml Oxygen litre^{-1}). Organic material also acts as a source of nutrients, especially nitrate and orthophosphate. Secondary phytoplankton growth is stimulated by these nutrients. Algal productivity is already high, and the increased productivity will likely result in phytoplankton blooms (chlorophytes and cyanophytes), and so secondary productivity is considerably less than in Chautengo Lagoon.

It seems clear that Chautengo Lagoon would not benefit from an increased organic input, at least during periods 1 and 2. On the other hand, Tres Palos Lagoon has a greatly increased organic input, discussed above, where a net loss of available oxygen to the biotic component and a very low salinity would be detrimental to nekton and benthos populations which are unable to tolerate these conditions. A demand for marine waters in Tres Palos Lagoon may be proposed.

The most important fish species in the lagoons are *Galeichthys caerulescens*, *Mugil curema*, and *Diapterus peruvianus*. The three are of commercial importance. *Dormitator latifrons* is also very important. (Yáñez-Arancibia & Diaz, 1977).

Observations on growth data indicate that the lagoons provide a nursery ground for juveniles of *Mugil curema* (mullets), and *Diapterus peruvianus* (mojarras). *Galeichthys caerulescens* (catfish) complete all their life history inside the lagoons.

The mullets enter the lagoons during period 1, in large schools of fish of an average length of approximately 70 mm. During periods 2 and 3 they remain inside, feeding and growing until they reach 230 mm or more in length (18 to 20 months old), and gonadic development of the advanced state of maturity. When the bars open again these adults leave the lagoons, entering the sea to spawn in the following months. Once again the lagoons are invaded by large schools of small fish (6 to 8 months old) which probably correspond to the product of the spawning of the previous year.

The catfish population studies reveal that the length increases very rapidly, up to 180 mm, but with little accompanying increase in weight. Thereafter, the length-weight curve shows a marked inflection caused by a sharp increase in the weight with a relatively slow increase in length. The populations reach sexual maturity (gonadal phase III) at an average of 200 mm total length, with the female maturing at a length of 180 - 190 mm (total length), smaller than that of the male (210 mm total length). Reproduction occurs in waters with salinity values of less than 15%. Tolerance ranges of temperatures are from 19 to to 35°C, and salinities from zero to 45%.

In general, the higher species number occurs during period 1 and decreases considerably during periods 2 and 3, especially in Chautengo Lagoon. Because there is no contact with the sea during periods 2 and 3, the increase of species number, indices H', and biomass during period 3 is due to freshwater species which occur inside the lagoons during the rainy season. These lagoons with ephemeral inlets can be typically characterized by having a conspicuous spatial and temporal heterogeneity of populations dynamics, successions, and migrations. The ichthyofaunistic diversity, and the fisheries production are directly related to the marine influence in the lagoons during period 1.

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A REVIEW OF THE POTENTIALITIES FOR RESEARCH AND FISH CULTURE IN THE COASTAL LAGOONS OF WEST AFRICA

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INTRODUCTION

The coastal lagoons of West Africa lie parallel to the sandy seashores of the Gulf of Guinea, stretching roughly along 5°N latitude between Sierra Leone to the west and Nigeria to the east.

Fig. 1 shows the coastal lagoons in the Ivory Coast, the Ghana/Togo border area, Benin Republic and Nigeria.

This figure is taken from Webb (1958) who describes some of the pioneering work in these lagoons in general, and Lagos Lagoon in

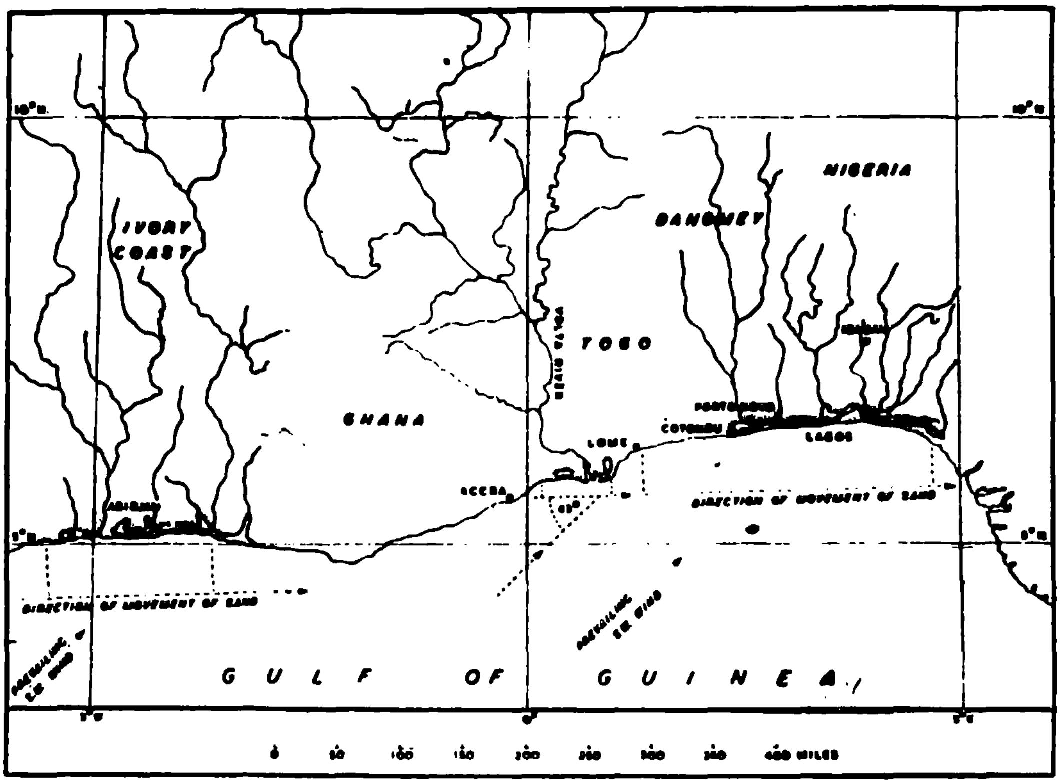

Fig. 1 The extent and position of the coastal lagoons of the Gulf of Guinea. (from Webb 1958)

particular. We note the distribution and course of the rivers which empty their waters into the lagoons, and the variable size of the lagoons themselves, from very narrow creeks of a few metres wide in parts, to bodies of water of appreciable size in other parts.

From the map we note that most of the lagoons lie parallel to the coast at an angle of about 45° to the prevailing south-west wind. Consequently they occur where the coastline runs in a west - east direction, and are absent when it runs in north - south direction.

An account of the formation of these lagoons, which are believed to be of recent origin, is best left to geologists, but a biologist can venture to remark that the movement of sand in a west - east direction would play an important role in their formation.

PHYSICAL AND CHEMICAL FEATURES

The major and unique feature of the coastal lagoons from the ecological point of view is the fluctuation in the salinity of the water which occurs in areas where they open into the sea, and its consequences on the distribution of flora and fauna. The salinity of the water varies considerably, diurnally with tidal movement of sea water, and seasonally with the rainfall. The latter swells the waters of the rivers flowing into the lagoons, consequently reducing the salinity of the water in the lagoon before discharging it to the sea at ebb tide. In areas where the influence of sea water is most noticeable, the water remains brackish all the year and the associated mangrove vegetation consists of the red mangrove Rhizophora racemosa and the white mangrove Avicennia nitida. The farther we get from the sea, the less brackish the water is, and the more freshwater conditions prevail. Consequently we have bodies of water which are part of the lagoon system in origin and location, but are in form and features similar to freshwater lakes. Examples are in the Republic of Liberia, where they are referred to as lakes, but Lekki in South West Nigeria retains the nomenclature of lagoon.

Fig. 2 shows further detail of the coastal lagoon extending from the Republic of Benin in the west to Lekki Lagoon in the east. This extent of water stretching over a distance of about 250 kilometers had a single outlet to the sea in Lagos Harbour, Nigeria, until recently when a permanent opening was constructed in Cotonou. During the last few years, an artificial barrier has once more been built cutting off the Nokoue Lagoon from the sea. On the eastern end, the Lekki Lagoon has remained closed off except for seasonal canals which permit limited entry of sea water into the lagoon.

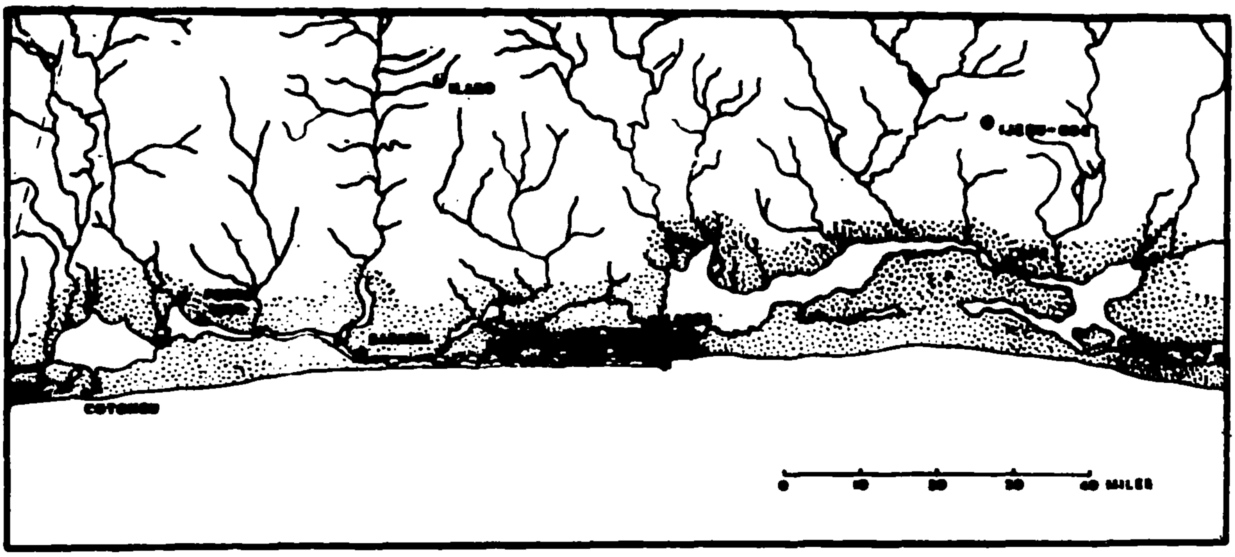

Fig. 2 River drainage into lagoon system of the Gulf of Guinea. (from Webb 1958).

As a result of the seasonal nature of rainfall along the entire subregion, the chemical characteristics of the water, as indicated by the primary characteristic, salinity, also show seasonal variation.

In the Lagos Lagoon, where studies of variation of chemical features have been carried out during the last two decades, clearly defined high salinity seasons (more than 10 parts per thousand) between December and May and low salinity (less than 10 parts per thousand) season between June and November have been identified. Further east and west of the central area, salinity differences are not as defined and at the extreme eastern end, freshwater conditions prevail throughout the year.

FAUNAL STUDIES IN GENERAL

The first faunal studies in the brackish waters centred around the Lagos Harbour and immediate vicinity were carried out in the early fifties and resulted in publications by Webb & Hill (1958) and Olaniyan (1957). The former was concerned with the study of a single animal of great taxonomic interest, the local lancelet Bran-

chiostoma nigeriense, whilst the latter was concerned with the seasonal distribution of planktonic organisms in general. One of the earliest studies on fish fauna was by Williams (1962).

In an effort to investigate the fauna of the lagoons, including the establishment of feeding interrelationships and identification of species of importance for fisheries development and culture, further studies have been carried out, and quite a number are still in progress. Due to lack of what may be described as sophisticated facilities, the investigations are simple in nature and in general are concerned with seasonal distribution and feeding interrelationships. These include studies of bottom fauna which have resulted in publications by Sandison (1966), Sandison & Hill (1966) and Oyenekan (1975). Studies on fish fauna have resulted in publication by Fagade (1971), Fagade and Olaniyan (1973), Ikusemiju (1973) and Ikusemiju and Olaniyan (1975). In addition, studies assisted by the FAO have been carried out in the delta areas of the Niger which are, strictly speaking, not part of the coastal lagoons but areas where prevalent conditions in the brackish water creeks are very similar to those in lagoons.

Studies of Fish Fauna

With the understandable emphasis on applied aspects of ecological research in developing countries, the lagoon studies have been aimed at ultimately finding scientific methods for developing the fisheries of the lagoon. As a first step, a study of seasonal distribution of the fish fauna was carried out, leading to the identification of 72 species distributed among 34 families. The fishes fell into three groups.

Group I

Those occurring throughout the year as a result of their ability to tolerate the varying salinity of the water. Of the 24 species so identified, twenty were known to be species normally resident in the sea. Of the 24 species so identified, twenty were known to be species normally resident in the sea. Of these, only 12 had sexually mature representatives. The others which were identified as primarily marine species only used the lagoon as feeding grounds for their young after undergoing reproduction in the coastal waters.

Group II

The second group are those caught between the months of December and May when the salinity fluctuates between 0.5 and 28.0 parts per thousand. The salinity range tolerated by these fishes is only slightly less than those in the first group, yet they are not found during the months of June to November when the salinity falls below 0.5 parts per thousand. There were 31 species altogether all of which were sexually immature and were therefore presumably juveniles of marine species.

Group III

The third group consisted of 17 species caught in water of salinity below 1 part per thousand. These were few in number and were generally regarded as fishes which were primarily resident in freshwater.

In seeking to identify fishes that could be suitable for culture in the lagoon, it is useful to consider those species already known to occur in large enough numbers to be of economic importance to the fisheries. Among these, the West African shad, *Ethmalosa fimbriata* was quickly identified. This fish belongs to Group I in the earlier listing, occurring in the lagoon throughout the year. *E. fimbriata* is one of the commonest pelagic species in the inshore waters of the Gulf of Guinea and yet it forms a major part of the fishery of the lagoon. A study of its spawning and development in the lagoon has been undertaken and well described in Fagade and Olaniyan (1972).

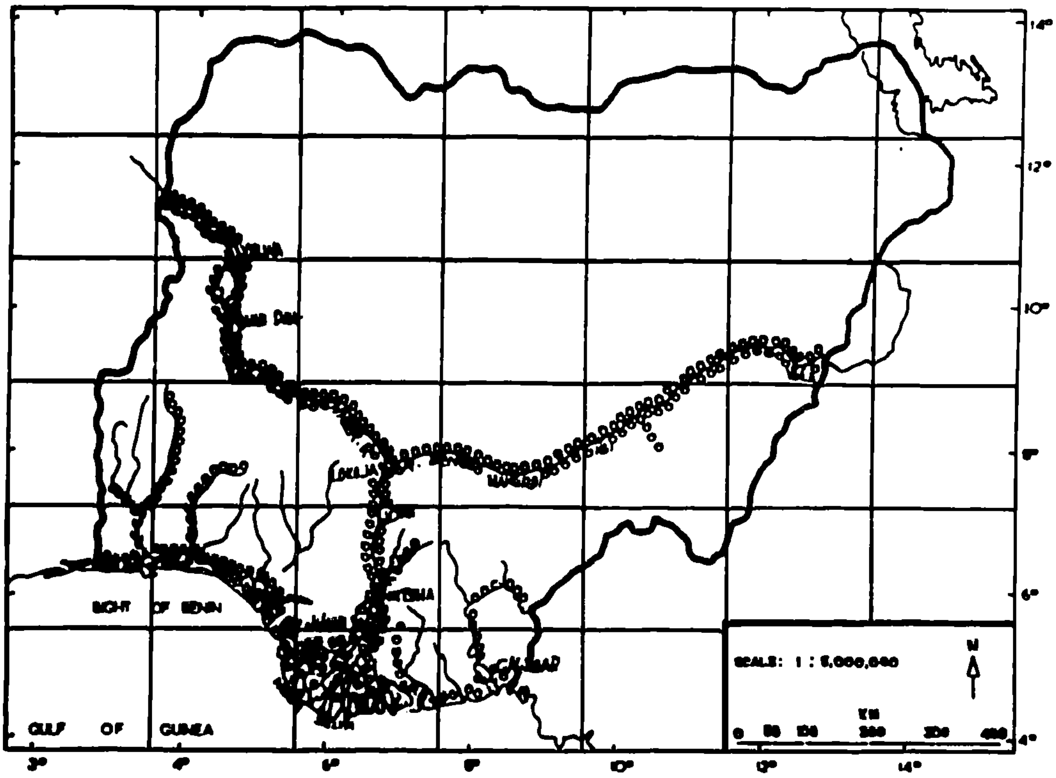

Fig. 3 Distribution of the catfish *C. nigrodigitatus* in Nigeria (from Ezenwa 1978).

A number of species of Tilapia also in Group I were considered. Two species, *T. melanotheron* and *T. guineensis* occur all the year round. The former is a well known brackish water species of economic importance and the latter is normally resident in freshwater. Thirdly we have species of *Chrysichthys*, *C. nigrodigitatus* and *C. stampflii* which also belong to Group I. Of the three types of fishes, the *Tilapia* were the most attractive to investigate for farming purposes because they are already being used as fish for culture in parts of West Africa and East Africa and outside Africa, and there is considerable amount of literature available on the subject. However, as a result of another study, this time in Lekki Lagoon, more information was provided on *Chrysichthys* and a decision to consider it in more detail was taken.

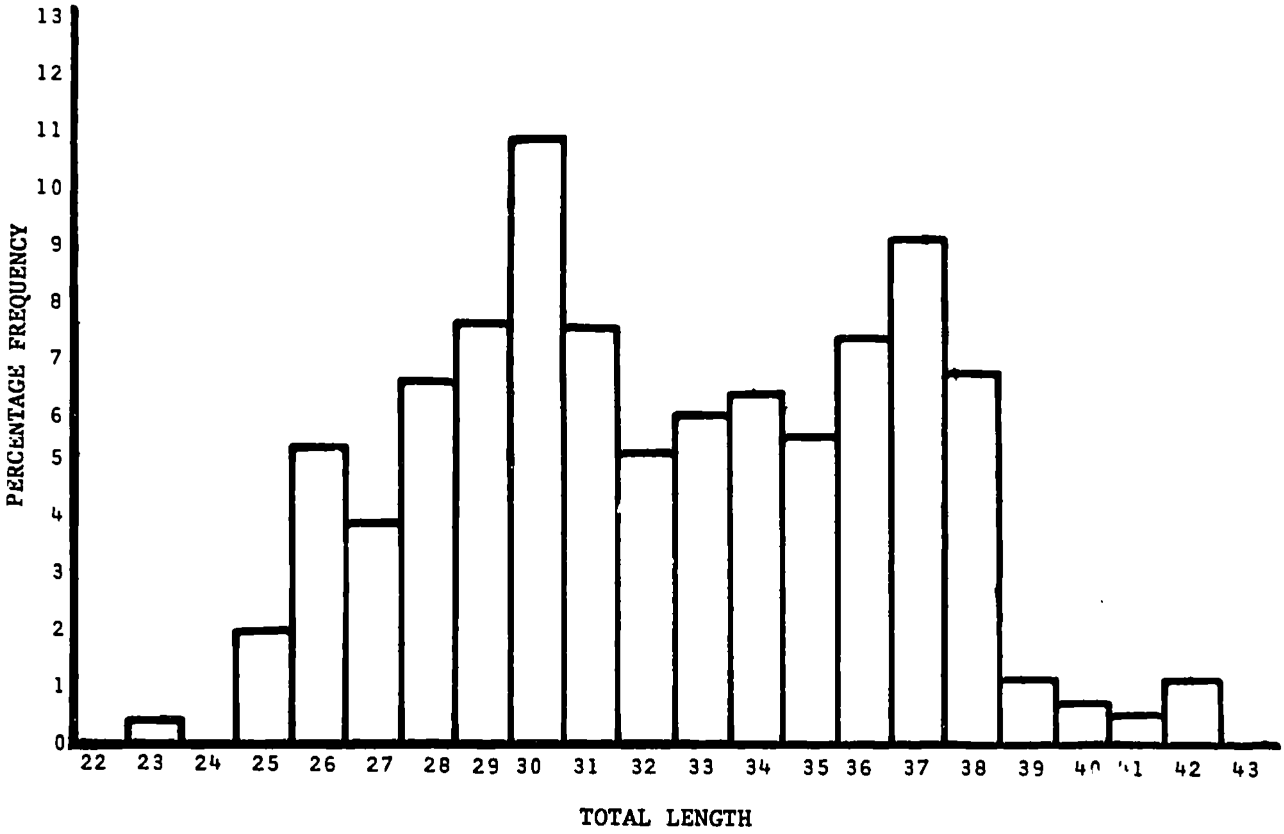

Fig. 4 Length frequency distribution of *C. nigrodigitatus*. Unfed fish (from Ezenwa 1978).

Studies on Chrysichthys species

A more detailed study of Chrysichthys, *Chrysichthys*, in particular *C. nigrodigitatus* was carried out. This included a general survey of its distribution and a comparison of the racial populations in different locations both in the major rivers and in the coastal lagoons. Furthermore, a study of the rate of growth of unfed and fed populations in the Lagos Lagoon was made.

Fig. 3 is a map of Nigeria showing the parts from which specimens of C. nigrodigitatus were obtained. Four of the seven stations were brackish water area, and station X^1 is the Lagos Lagoon

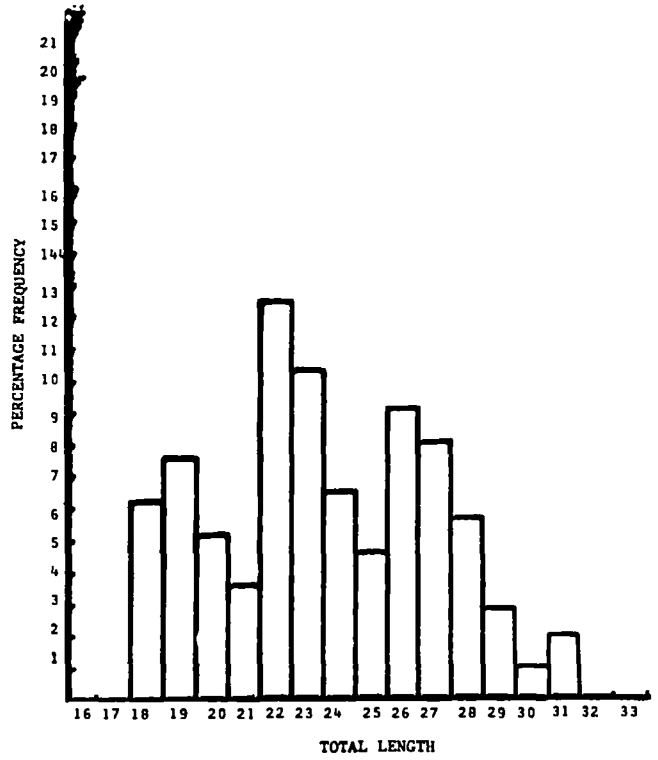

Fig. 5 Length frequency distribution of C. nigrodigitatus fed fish (from Ezenwa 1978).

where the feeding and growth studies were also carried out. The conclusions from this recent study, results of which are not yet published, indicate that there is only slight racial variation between the freshwater and brackish water populations, taking into consideration major characters such as dorsal rays, pelvic, pectoral and anal rays, upper and lower gill rakers, along with variations in morphometric characters such as head length, body length and depth, and standard length.

The following results were obtained from the feeding experiments in Lagos Lagoon ponds, using as feed stuff groundnut pellets which are a waste product from groundnut mills in the northern parts of Nigeria. Feeding at the rate of about 10% of body weight of fish stocked was applied daily both in the morning and evening. In terms of raw primary measurement of weight and length the com-

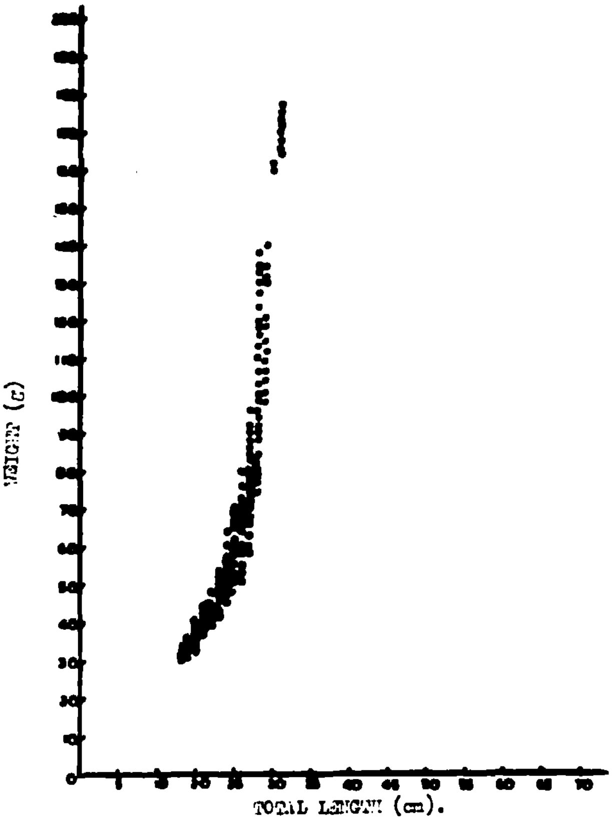

Fig. 6 Length – weight relationship for *C. nigrodigitatus* Unfed fish (from Ezenwa 1958).

parative figures for unfed and fed fish after a period of 9 months are as follows: Fig. 4 shows the length frequency distribution for unfed fish for which we have a range from 18 cm to 31 cm with a peak at 22 cm. In Fig. 5 which represents the length frequency distribution for fed fish, the comparative figures are 23 cm to 42 cm with two peaks at 30 cm and 37 cm.

Fig. 6 shows the weight length relationship for the unfed fish and Fig. 7 for the fed fish.

All the figures tell the same story, namely the clear difference between the harvest for fed and unfed fishes. It remains to compare the effect of feeding with what has been obtained for other fishes which have been used for fish culture in Nigeria, specifically the local *Tilapia* such as *T. heudiloti* and imported European carp *Cyprinus carpio*.

It is also expected that polycultures using a variety of combination of species will be attempted. This brief account is merely to emphasise how little has been done in terms of research activi-

Weight

Mean total weight of fingerlings at stocking	5.83 kg
Weight of *unfed* fish at harvest	12.47 kg
% weight increase	114%
Weight of fingerlings at stocking	5.83 kg
Weight of *fed* fish at harvest	55.86 kg
% weight increase	858.1%

Length

Mean length of fingerling	15.6 cm
Mean length of *unfed* fish at harvest	23.3 cm
% increase in length	49.0%
Mean length of fingerlings at stocking	15.6 cm
Mean length of fed fish at harvest	32.7 cm
% increase in length	109.6%

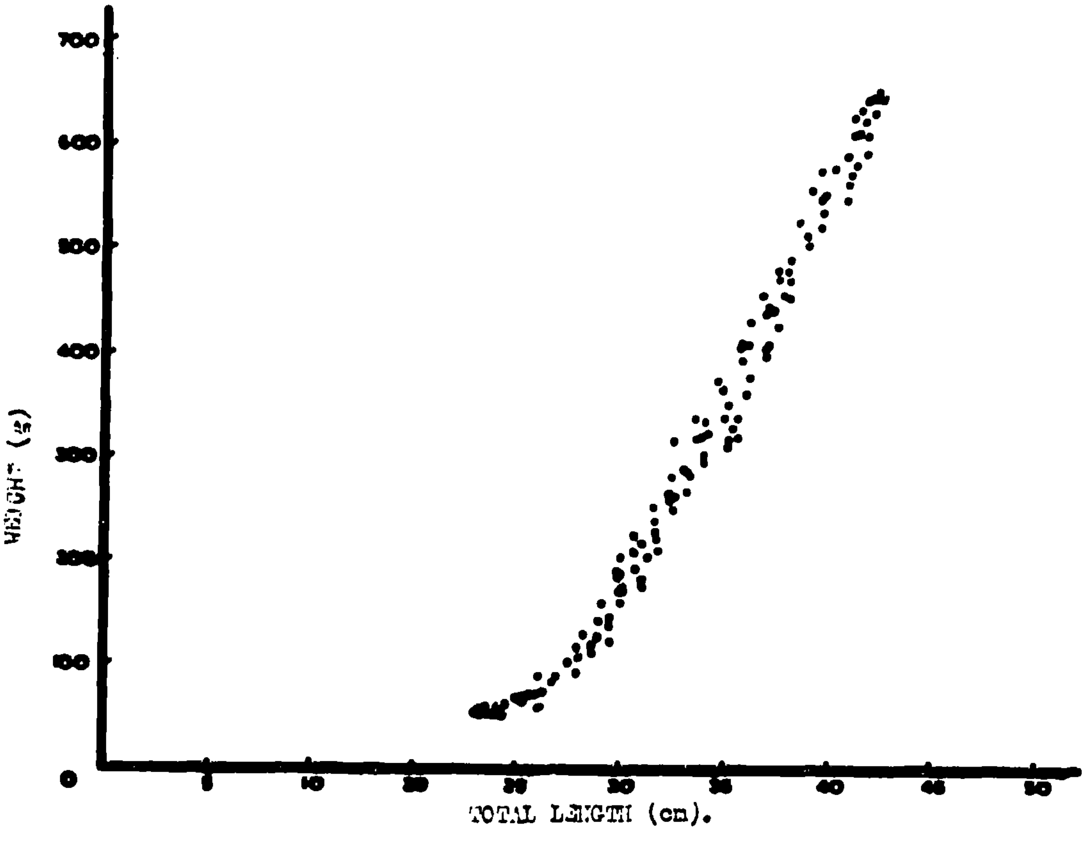

Fig. 7 Length - weight relationship for *C. nigrodigitatus* Fed fish (from Ezenwa 1978).

ties in these waters, using the Lagos Lagoon experience as an example. Similar activities are undertaken in the Ivory Coast in the Lagoon Ebrie, and in Republic du Benin in Nokoue Lagoon. All these studies attempt to emphasise one thing, namely, the need to understand the scientific basis of the existing fisheries and find ways for its scientific utilization.

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PRODUCTION DYNAMICS OF A TEMPERATE SEA - THE BALTIC

by

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INTRODUCTION

Giving the concept "coastal lagoon" a broad definition, the whole Baltic Sea might be considered as one: 1) it is to a great extent dominated by the land run off and the load of nutrients and hardous substances; 2) it shows in many areas increased productivity due to eutrophication; 3) it has large areas constituting important spawning and nursery grounds for fish. The fjord-like topography, however, leads to a stable stratification, the far-reaching effects of which makes the Baltic a special case. It is probably one of the most investigated seas of the world and the fact that we still can not predict its reaction to, for example, man's exploitation, points more to the complexity of nature than to lack of scientific efforts. There exist several bibliographies of Baltic biological literature (Segerstrale 1964, 1975; Armelius *et al.*, 1977). The informal scientific organizations "Baltic Oceanographers" and "Baltic Marine Biologists" have produced recommendations of chemical (Carlberg, 1972) and biological (Dybern *et al.*, 1976) methods to be used in the Baltic area. Several efforts to review and synthesize the knowledge of the Baltic ecosystem have been made, Magaard and Rheinheimer (1974) and Jansson (1978) being two recent ones. So much being summarized already on the Baltic ecosystem, this report on its productivity is kept short. A more detailed review is given in Jansson (1978) from which many of the illustrations here are taken.

THE STRUCTURE OF THE BALTIC ECOSYSTEM

Even a short summary of the production dynamics needs a description of the total system. Although the holistic structure and function of a natural system can never be overemphasized, a description of the Baltic characteristics for clarity is divided into: morphology, physical structure including transport of biological cycles, chemical substances and biological structure.

Morphology of the basin

With an area of 365 000 km^2, a length of 1500 km and a volume of ca. 21 000 km^3, the Baltic is the largest brackish water sea in the world. It is a shallow sea, mean depth 60 m, with shallow sounds connecting it with the North Sea (Fig. 1). Several sills divide it into natural basins and the shallow Archipelago Sea parts the stratified Baltic proper from the Gulf of Bothnia. The type of shore varies from sandy, stony in the north and south to the rocky archipelagos of the middle part. Roughly 17% of the bottoms are shallower than 10 m.

Physical structure

The annual input of solar energy varies from a temperature pulse in the South to polar conditions in the North. The temperature of the surface water may increase to slightly above 20°C in summer with a thermocline at 20 m depth. Temperatures below 5°C persist the whole year (Fonselius, 1970). Ice covers the sea in winter, in the Gulf of Bothnia for 6 months.

The Baltic water is a mixture of the inflowing saltier and denser North Sea water along the bottom and the outflowing of freshwater at the surface, mainly coming from the big rivers in Northern Sweden. The salinity of the surface water is remarkably stable (Fig. 2). The vertical stratification of the water has a primary halocline at 50–60 m depth. Intermittent inflows of the North Sea water causes periods of stagnation when oxygen is used up and nutrients diffuse to the bottom water by the bacterial activity in the sediment (Fig. 3). The simultaneous production of hydrogen sulphide kills higher life in the deeper basins (Fig. 4).

The deep water, rich in nutrients, reaches the trophic layer through vertical diffusion and through boundary mixing along the coasts. Upwelling areas along the Swedish coast act as "nutrient windows" and may induce nuclei of primary production. The absence of tide in the Baltic decreases the exchange of water with the North Sea (500 km^3 yr^{-1}) compared to the large total volume, the residence time of the Baltic water is 35-40 years.

Biological structure

The organisms

The Baltic is a young system with a past history starting as an ice-lake 12 000 years ago, switching to marine conditions and ending as a brackish water sea. This means that different types of systems were tried and rejected as the forcing functions changed. It also means that the organisms present invaded from other regimes, cold seas or freshwater lakes, where they had evolved their physiological and ecological characteristics. In the Baltic water they had to adapt or die. Today we find e.g., glacial relicts like the fourhorned sculpin Oncocottus quadricornis and the freshwater amphipod Pontoporeia affinis living in the deeper cold parts, the sculpin migrating to shallow areas in the winter to

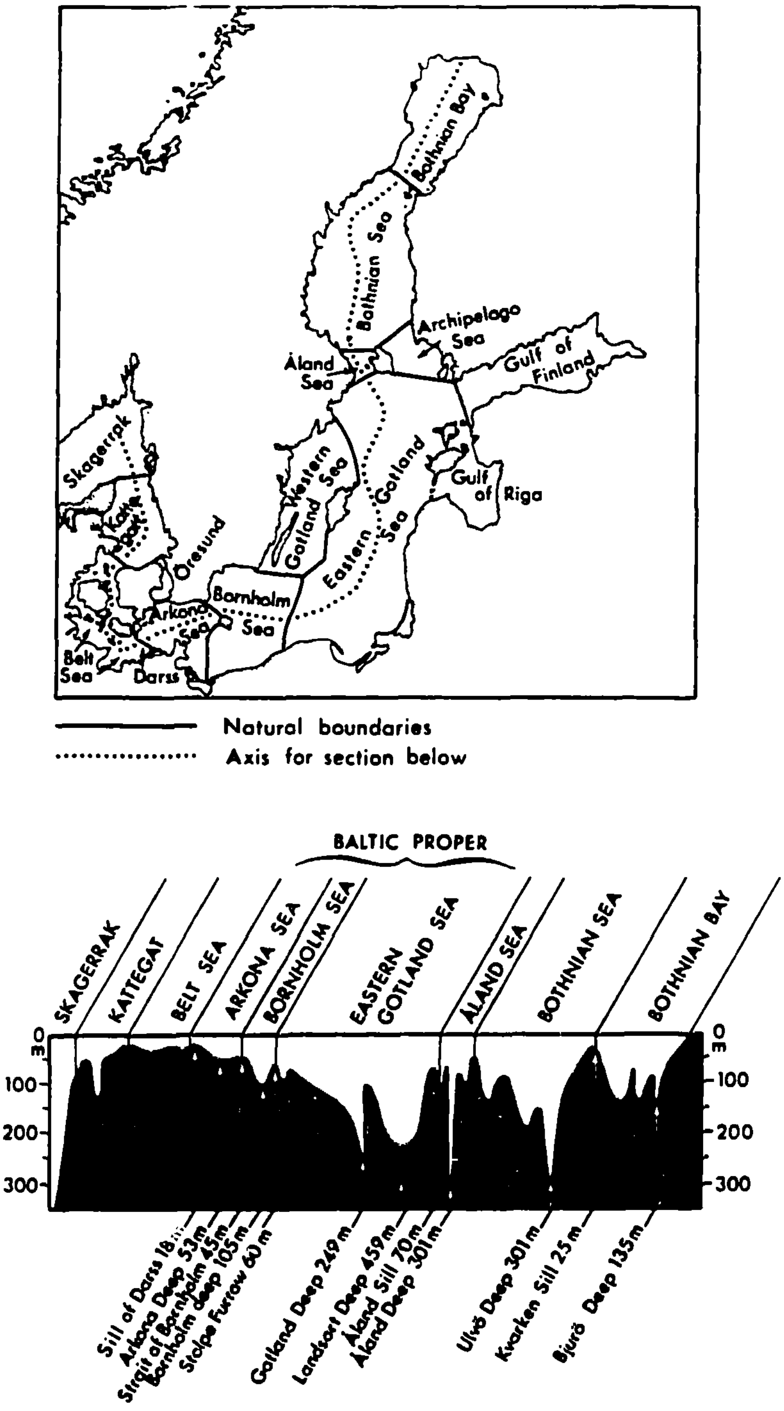


Fig. 1. The natural division of the Baltic (after Wattenberg, 1949) and the main sills and basins (after Dietrich & Kösler, 1974).

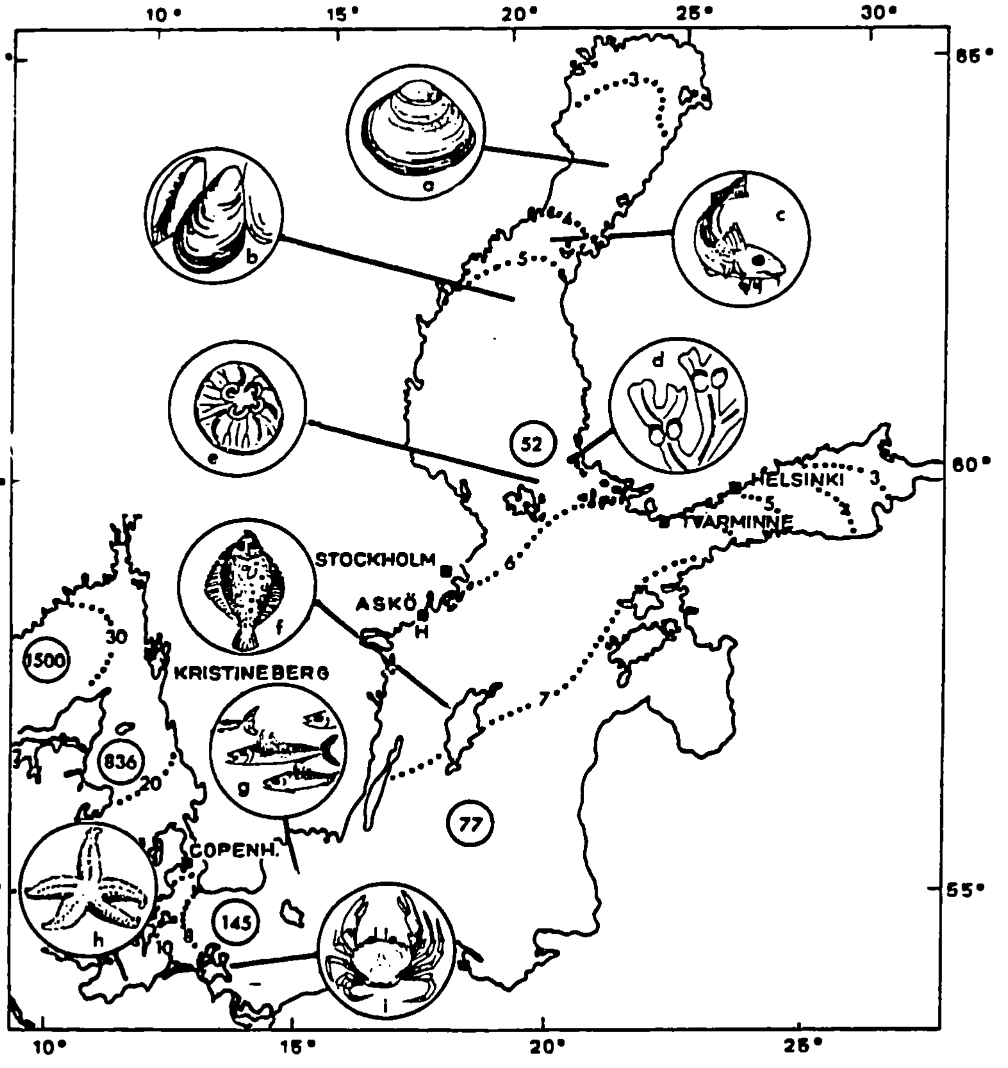


Fig. 2. The Baltic Sea. Dotted lines: surface water isohalines. Numbers within circles: number of macrofauna species. a-i distribution limits for some common marine species: a). *Macoma baltica*, b). *Mytilus edulis*, c). cod, d). *Fucus vesiculosus*, e). *Aurelia aurita*, f). plaice, g). mackerel, h). *Asterias rubens* i). *Carcinus maenas* (B.O. Jansson, 1972).

spawn. The Baltic flora and fauna is therefore a mixture of marine and freshwater organisms. In the same gillnet pike and perch can be found entangled with flounder and cod. Fig. 2 shows some marine organisms at their innermost boundaries in the Baltic.

Due to the extreme conditions the diversity is lower in the Baltic than in the adjacent North Sea. Whereas around 1500 macro-

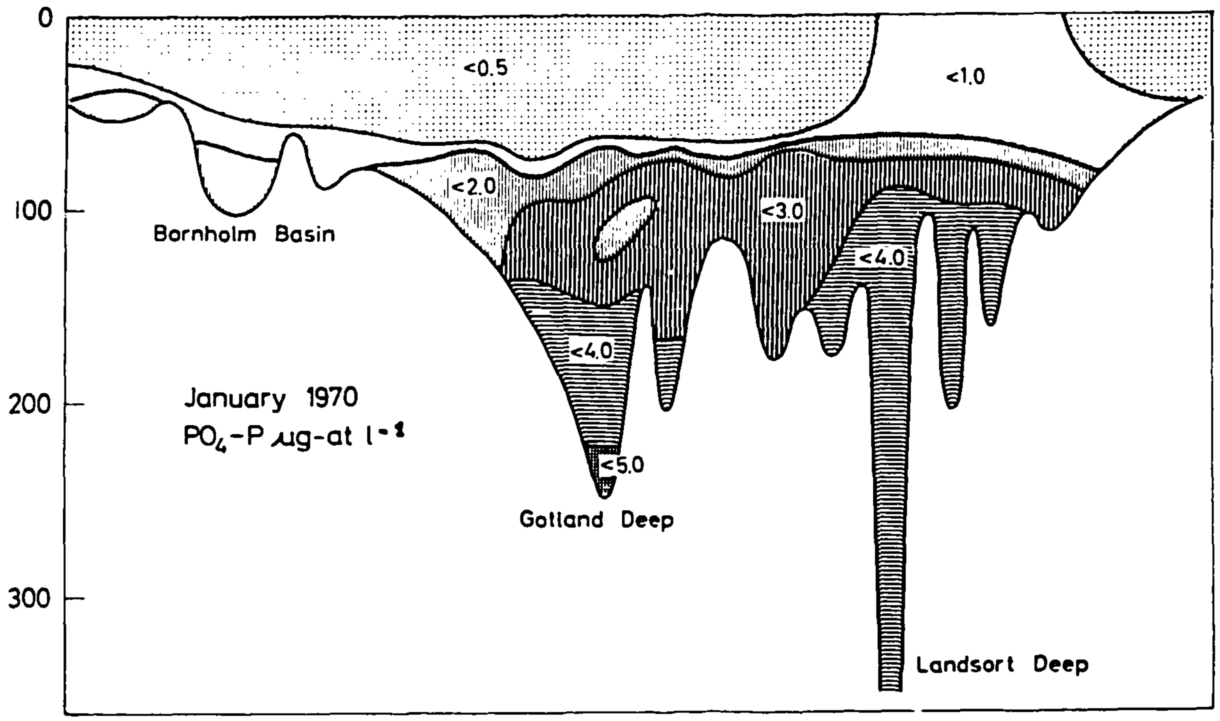


Fig. 3. Longitudinal section through the Baltic around the island of Gotland along the line: Arkona Basin, Bornholm Basin, Gothland Basin, Northern Central Basin, Landsort Deep, Karlsö Deep, showing the distribution of phosphate-phosphorus in January 1970 (from Fonselius, 1972).

scopic benthic animal species can be found off the Norwegian coast only 77 are left in the middle of the Baltic (Zenkevich, 1963). Corresponding figures for the macroalgae are 154 and 24 (off the Finnish coast) respectively (Schwenke, 1974).

Compared to a more normal coastal lagoon the Baltic diversity is probably high due to the higher stability of the salinity. Except for the Western Baltic which acts as a kind of buffer zone the salinity fluctuations in the surface water amount to 0.5 parts per thousand. The physiological stress on the marine organisms living in the diluted water leads to energy losses, however, which negatively affects the productivity. The blue mussel, *Mytilus edulis*, never attains more than 1/4 of the length of a North Sea specimen. Its filtering rate is much less in the Baltic water and its growth therefore much slower. The difference in size between Baltic and North Sea populations is valid for most macroscopic species with typical examples as flounder, cod, the clams *Mya arenaria* and *Cardium edule*, the common jellyfish *Aurelia aurita*.

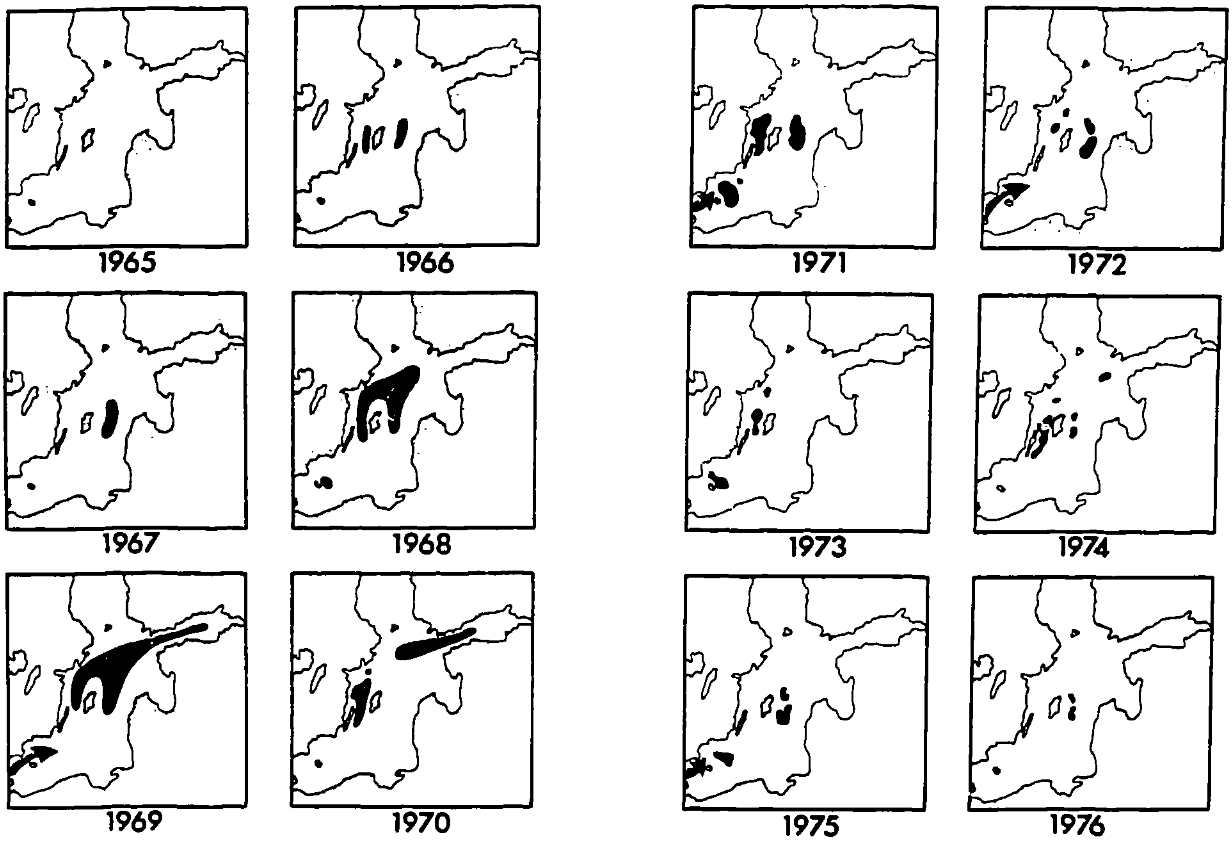

1965 1966 1971 1972
1967 1968 1973 1974
1969 1970 1975 1976

Fig. 4. The dynamics of hydrogen sulphide formation (black) in the Baltic proper. The great stagnation culminating in 1969 is broken by a saltwater inflow (arrow) through the straits in 1968/69. The following periods are characterized by shorter stagnation - inflow periods (compiled from various sources such as Fonselius, 1969, Meddelanden fran Havsfiskelaboratoriet, Lysekil) (from Jansson, 1978).

This is also, though less obvious, valid for freshwater populations, like the snails *Bithynia tentaculata* and *Theodoxus fluviatilis* which show greater size in their original medium. (Theede, 1974). Another typical feature when comparing the productivity of marine and brackish water populations is the niche breadth. Species like the Baltic clam *Macoma baltica* and the cockle *Cardium edule* which on the Swedish West Coast is restricted to sandy bottoms, occupy in the Baltic the whole range of sediment types from sandy to muddy. This has been explained by decreasing predator pressure in the Baltic partly due to the absence of echinoderms; the amphipod genus *Gammarus* totally dominates in the Baltic while they occupy more restricted niches in the North Sea.

The main subsystems

Out of the described resources Nature has built a system which can be classified into three smaller, tightly connected and open ecosystems:

A. The phytal system or phytobenthos, occupying the rocky and soft sediments within the photic layer. This is the most diversified subsystem in the Baltic with an important function as a nutrient trap, and as spawning and nursery grounds. It can be roughly classified as a producer system, producing oxygen and organic matter the excess of which is transported to the pelagic zone and the soft bottoms (Fig. 5).

B. The soft bottom subsystem occupies most of the bottom area in the Baltic. In the Baltic proper a substantial part of the sediments are mostly devoid of organisms except for heterotrophic and chemoautotrophic bacteria (Andersin et al., 1977). The soft bottom is a typical consumer system which has to be fed with organic material. The processing of this pays for the export of nutrients and fish to the other subsystems. It is also the great sink for man's wastes like heavy metals, DDT and PCB.

C. The pelagic subsystem is the largest producer unit in the Baltic. It imports nutrients from land run off and soft bottoms, is itself the main transport agency and exports organic matter, oxygen and larvae to the other subsystems (Fig. 5). Most of the commercial fish are caught in this zone.

PRODUCTION PROCESSES OF THE DIFFERENT SUBSYSTEMS

For the future management of the Baltic's natural resources, the understanding of the functions of the total system is quite necessary. Although much research has been done in the past, interest in production by organisms other than phytoplankton and commercial species is of such a recent date that little data exist. The same is valid for turnover times for the different systems and the coupling between them. In the following a short summary of our present understanding is given.

The phytal subsystem

Both in the North and the South the shallow bottom substrate with the dominance of sand and gravel makes the plant cover scarce and patchy. In the North the freshwater influence and ice erosion have caused absence of marine algae, low total biomass and production (Wulff et al., 1976). In the South the higher salinity increases the number of species but the absence of tides checks the formation of the typical zonation for marine shores (Schwenke, 1974). The Baltic phytobenthos shows the greatest development in the Swedish and Finnish archipelagos of the Central Baltic Sea.

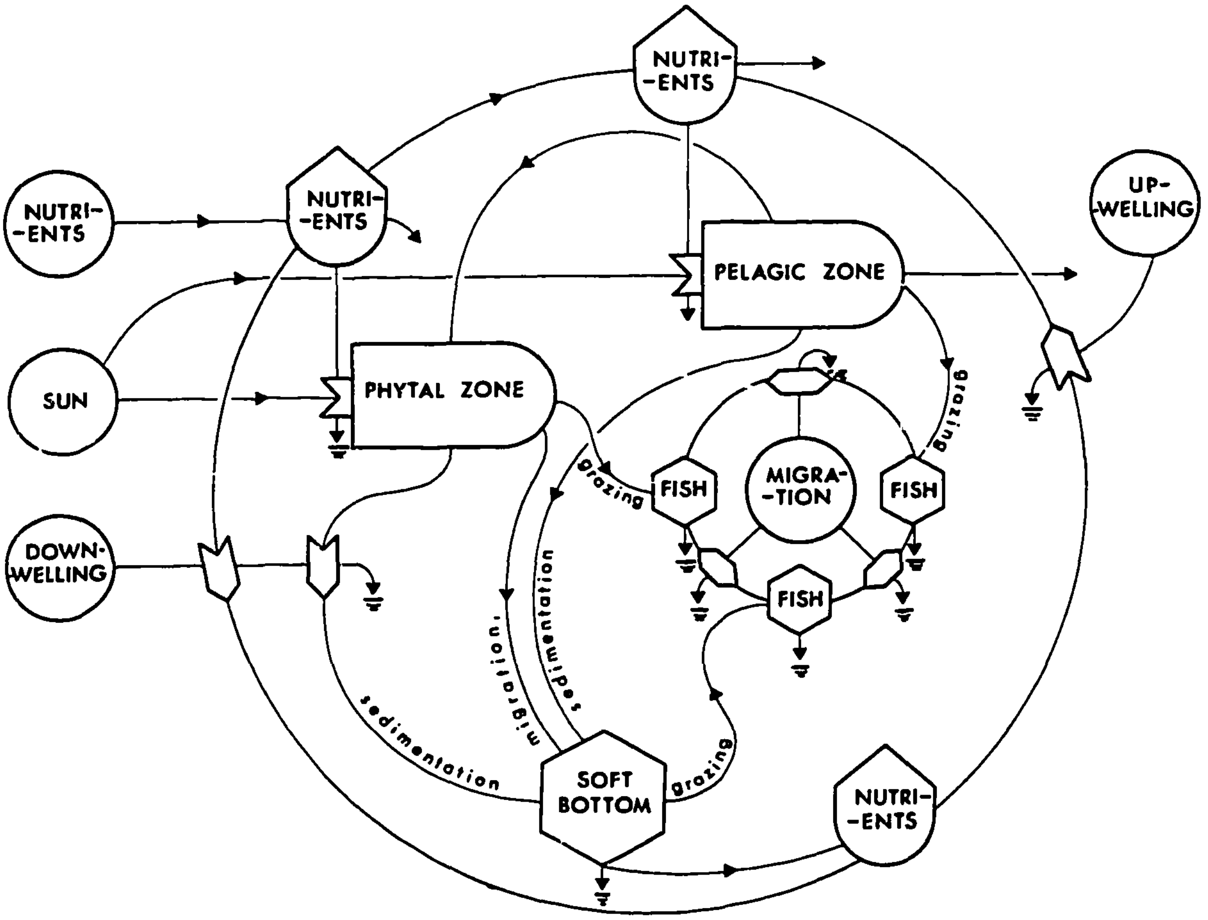


Fig. 5. Diagram showing the fish as living flows of energy and matter, moving between the main parts of the total system, taking food where it is in excess. Driven by the migration pattern the pelagic feeding might be changed for benthic feeding during winter (e.g., herring) but the early warming up of the shallow phytal region makes a migration to, and spawning in these areas favourable (from Jansson, 1978).

The Baltic archipelagos

The large network of islands (Fig. 6) means not only a greatly enlarged shallow bottom surface but also a favourable turbulence of the water - not too high to be destructive, not too low to allow stratification. With their cover of nutrient-absorbing algae like enormous intestinal villi, the archipelagos act like sieves, filtering the water from land run off, keeping the nutrients for internal use, and releasing to the offshore water lightened of its pollution burden. Adopting the maximum power

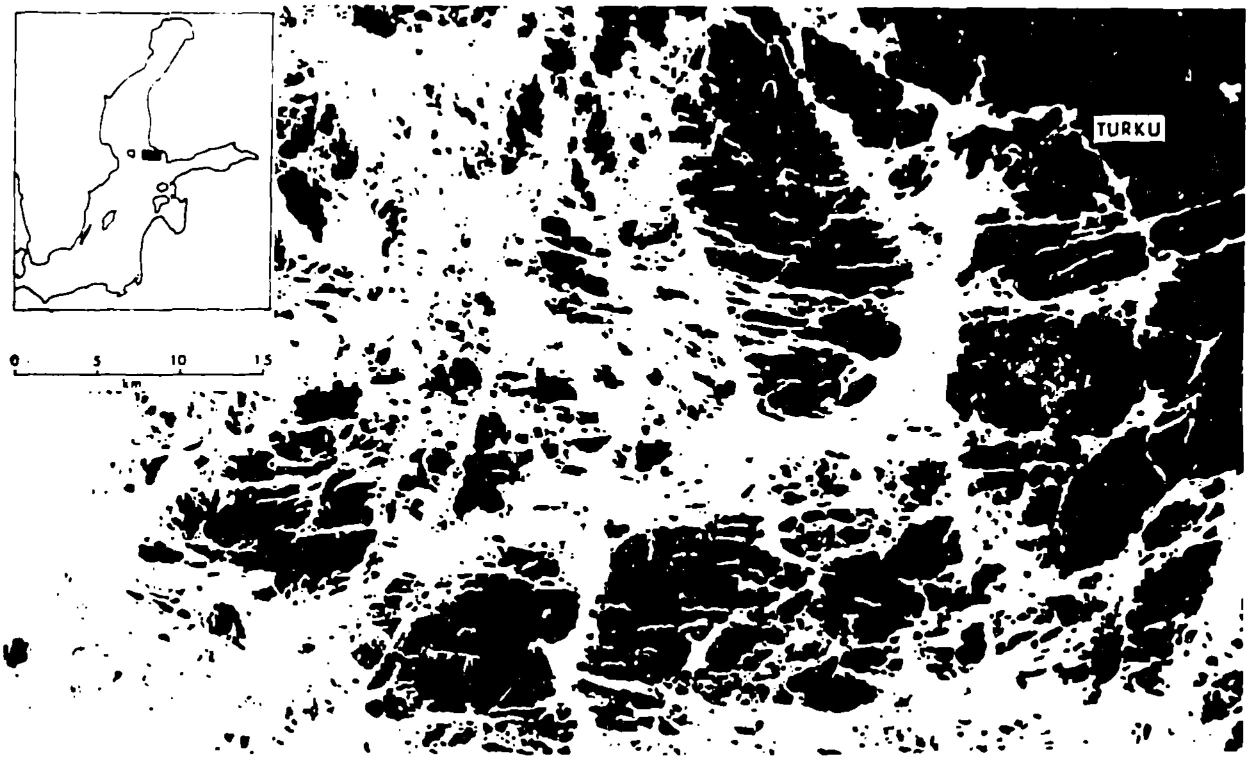


Fig. 6. The Archipelago Sea off the city of Turku – a submerged rocky landscape (from a folder of The Archipelago Research Institute, University of Turku, Finland).

principle of Lotka (Odum & Odum, 1976), the "workers" and their specialized tasks within the phytal system can be described as follows.

The rocky shores are covered by horizontal belts of algae, sorted out through competition for space and light, where generation and settling times, light optima and photosynthetic efficiency are important factors. As photosynthesis is most efficient in the complementary light spectrum, the algae are ordered due to light extinction with greens at the top, brown algae in the middle and red algae in the deepest belt.

The only detailed and extensive quantitative survey of the hard-bottoms up to now has been made by A.M. Jansson and Kautsky (1977). The 160 km^2 area is exposed with relatively few islands.

The uppermost zone is occupied by annual filamentous algae like the green *Cladophora glomerata*, the red *Ceramium* sp. and the brown *Pilayella* sp. (Fig. 7). The physical noise is great here due to turbulence, drought and ice erosion and the species have a structure which give off to the waves and a rapid turnover. Competi-

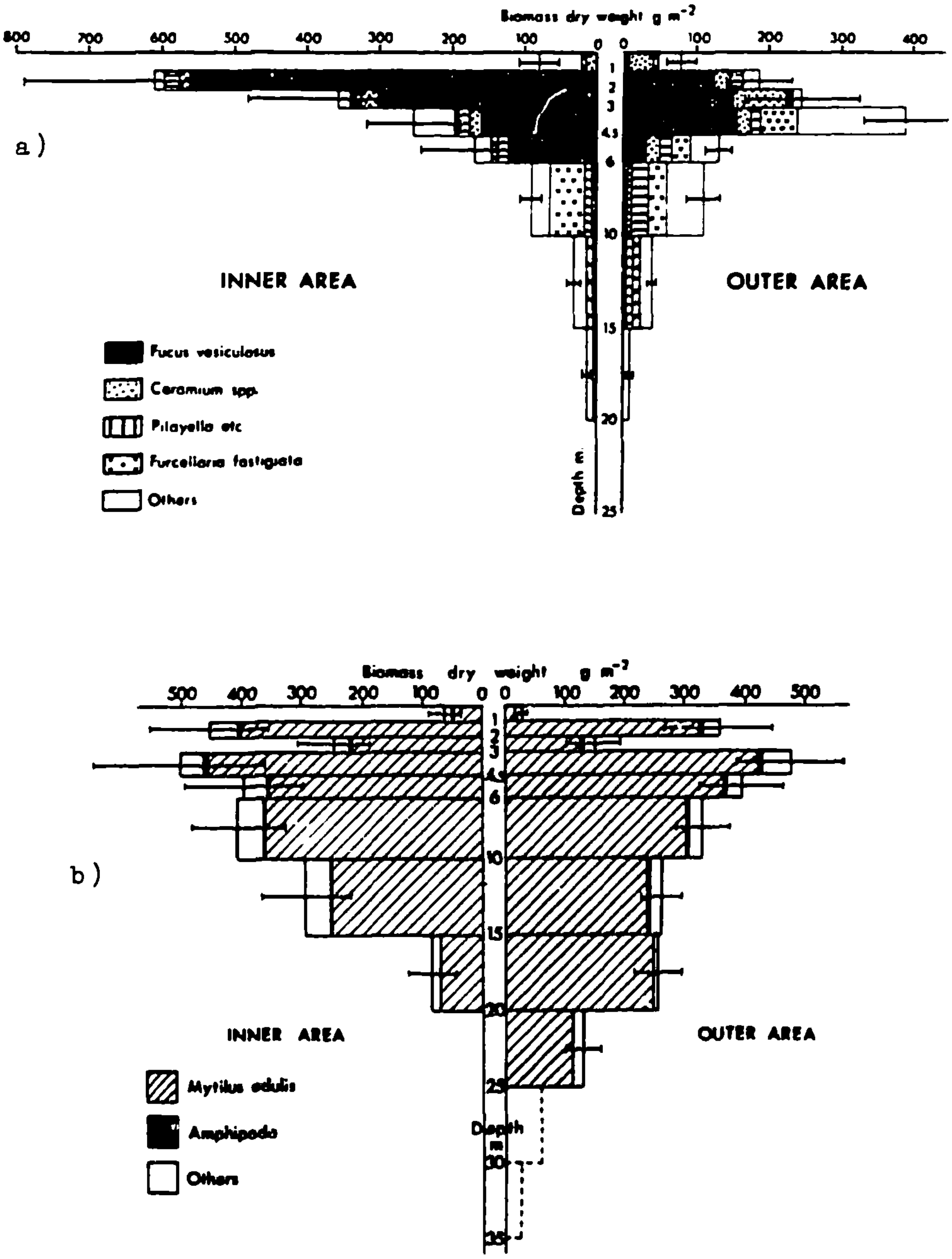


Fig. 7. The vertical distribution of plant and animal biomass in a) 160 km^2 hardbottom and b) area in the Trosa-Landsort archipelago, Northern Baltic proper (A.M Jansson and Kautsky, 1977). Standard error of mean indicated by horizontal lines.

tion for space is hard and there is a succession during the year starting when ice cover breaks up: sessile diatoms (*Amphipleura* sp.)., *Pilayella*, *Cladophora*, *Ceramium*. The zone is an important nursery ground for young crustaceans from the belts below. *Cladophora* is favoured by high nutrient levels and is particularly abundant in isolated bays and polluted areas.

The *Fucus* belt below is the most structured and diverse of all Baltic communities (Fig. 8). It is mostly covered with filamentous epiphytes and gives food and shelter to important sportfishes like perch and pike.

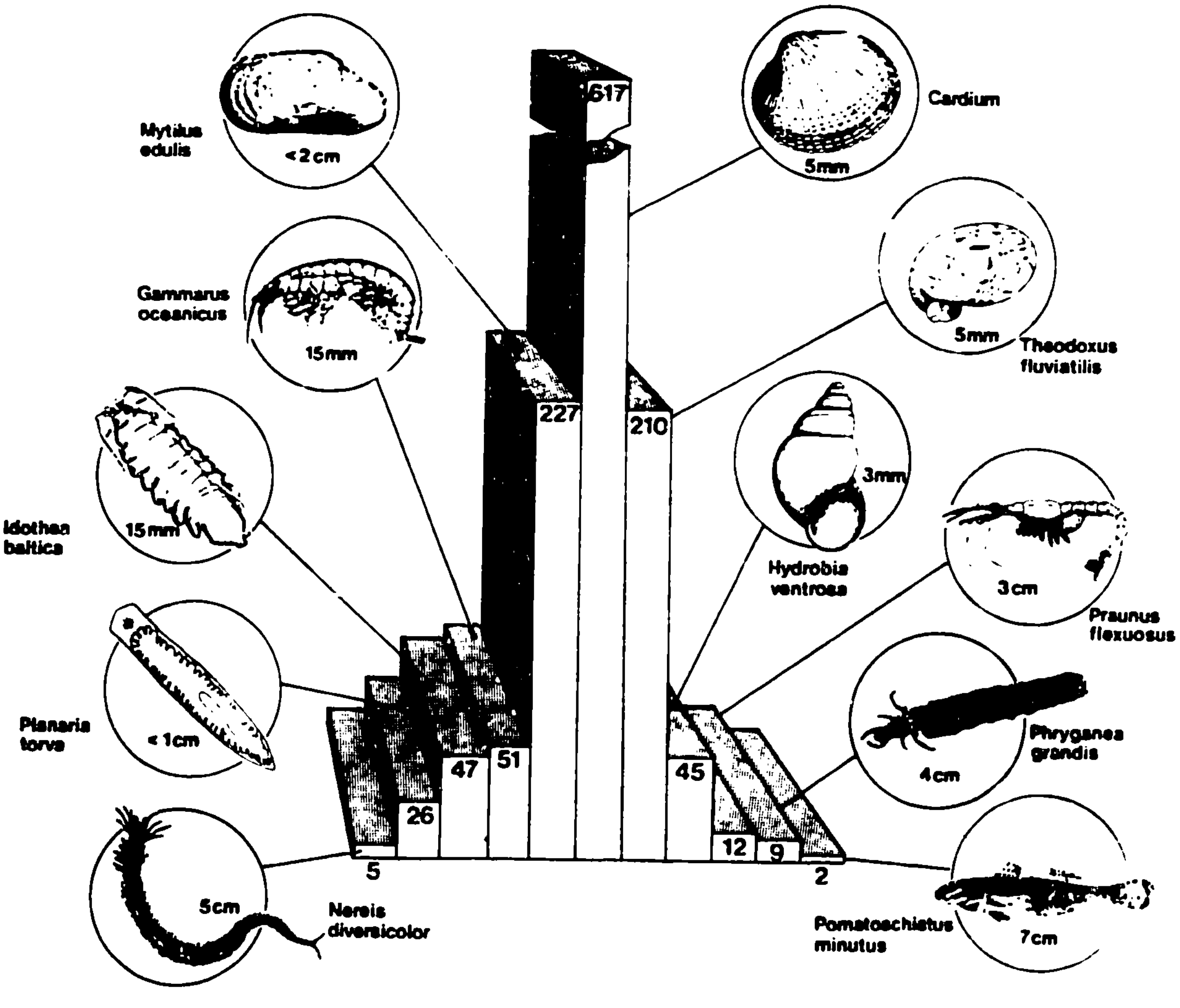


Fig. 8. The *Fucus* belt macrofauna in the Northern Baltic proper. Dominant species and their numbers per 100 g *Fucus* (dry wt.) (from A.M Jansson, 1978).

The upper zones, in spring covered with filamentous brown algae, are important spawning grounds for herring.

Further down where light is too low for *Fucus*, red algae like *Furcellaria* sp., *Phyllophora* sp. and *Rhodomela* sp. compete with the blue mussel *Mytilus edulis* for space. *M. edulis* is by far the most common animal which below the red algal belt totally dominates the bottom, often covering it like a carpet. It imports particulate organic matter by filtering the water, and exports pseudofeces and nutrient salts, especially ammonia.

The total biomass of algae within this 160 km^2 area amounted to ca. 2200 tons (dry wt) of which *Fucus* constituted 33% and the animal biomass was ca. 8600 tons (dry wt. incl. shells) of which *Mytilus* made up ca 90%. The annual net production of the plants was calculated at 1500 tons (ash-free dry wt.) of which filamentous brown algae was responsible for one third. The animal production amounted to ca. 1900 tons (ash-free dry wt.) where *Mytilus* produced 86% (A.M. Jansson and Kautsky, 1977).

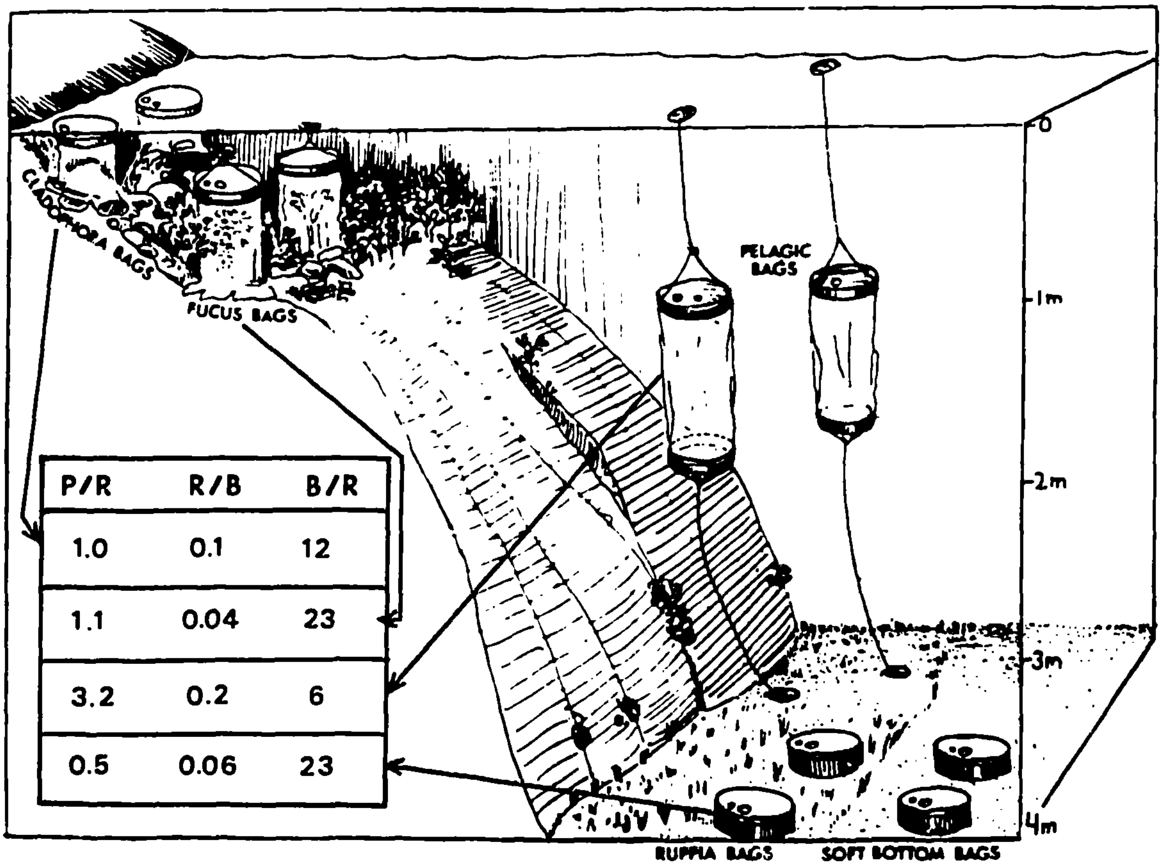
In sheltered areas with soft sediments and greater freshwater dominance, a soft bottom phytobenthos has developed with a selection of phanerogams like reed (*Phragmites* sp.), rushes (*Scirpus* spp.), pond weeds (*Potamogeton* spp.) and *Ruppia* sp. In areas with increased nutrient output, often coupled with freshwater outflow the reed belts cover large areas. The fish production, though not properly quantified yet, is probably high. As water is turbid the fish fauna is dominated by sluggish species which have close food and no need of spending energy in fast and persistent hunting. Dominating species are: rudd (*Leuciscus erythrophthalmus*), roach (*L. rutilus*) and bream (*Abramis brama*).

In sandy areas eelgrass (*Zostera maritima*) covers areas which are extensive in Southern Baltic but decreases to isolated patches in the Northern Baltic proper. The associated fauna is dominated by flat fish like flounders (*Platichtys flesus*) and by clams and snails (Lappalainen, 1973) which clear the water by filtering and clean the leaves from epiflora by browsing. More light then strikes the plant, which increases growth, which in turn gives more substrate and food for the fauna, a beautiful example of one of the numerous feedbacks in nature.

Many birds are integral parts of the Baltic archipelago. Terns (*Sterna* spp.), goosander (*Mergus merganser*) and red-breasted merganser (*M. serratus*) are to a great extent dependent on the three-spined stickleback (*Gasterosteus aculeaturs*) as a food source (Lemmetyinen and Naukki, 1975). The most characteristic bird of the archipelago, the eiderduck (*Somateria mollissima*) feeds mainly on the blue mussle. The number of eiderducks in the Baltic was calculated at 600 000 (Almqvist *et al.*, 1975).

Community metabolism

In order to roughly quantify the role of the main functional units in the dynamics of the coastal system *in situ* experiments with plastic bags have been carried out. In one extensive experiment around mid-summer, simultaneous bag experiments were run in five different communities for two 24 hr periods in a small 4 m deep sound close to the Askö Laboratory (Jansson and Wulff, 1977). The results are here (Fig. 9) concentrated to three ecological indices: the degree of selfmaintenance (P/R), the maintenance cost per unit of structure (R/B) and the turnover time (B/R). The pelagic trophic layer, the *Cladophora*- belt and the *Fucus*- belt are at this period of the year to be regarded as producers or at least autotrophs whereas the *Ruppia*- bottoms are clearly consum-



P/R	R/B	B/R
1.0	0.1	12
1.1	0.04	23
3.2	0.2	6
0.5	0.06	23

Fig. 9. Community metabolism of typical Baltic subsystems studied in situ with plastic bag technique (Jansson and Wulff 1977). Level of selfmaintenance (P/R), maintenance costs per unit structure (R/B) and turnover times are compared for the different systems.

ers. The costs for running and keeping the necessary structure are highest for the systems in zones of great physical noise like _Cladophora_ and the plankton. "Cheapest" is the _Fucus_- system with its elaborate structure (including filamentous epiphytes) and numerous niches. The turnover times are shortest in the most exposed zones, surf-zone and free water, where the need for rapid repair or total replacement of the organisms is great and nature therefore has favoured the small size scale.

The annual variation of the community metabolism in the _Fucus_-belt has been studied by Guterstam (1977, pers. comm.). During late winter the system was heterotrophic, in early spring strongly autotrophic due to high insolation, low temperature and few animals, and during summer balancing around a P/R = 1.

The annual pulse

The heavy annual pulse of solar energy and the time distribution of nutrients give the phytal system a characteristic pattern. In the Northern Baltic proper production starts already below the ice cover, stimulated by the increasing light in March-April. The uppermost zones of the rocky shores have been cleaned of their plant cover by the erosion of the ice and the naked rock is now first occupied by sessile diatoms sometime making real carpets on the rocky substrate. Also the shallow bottoms and their cover of e.g., _Ruppia_ are covered with long fringes of diatoms. A net production of 1-3 g C m^{-2} day^{-1} can be measured (Wallentinus, pers. comm.). The brown, filamentous _Pilayella_ rapidly extends over large areas of the bottom, even on _Fucus_. Few animals are there to benefit from the large amounts of produced organic matter and in May most of it successively loosens and falls to the bottom, filling depressions with loose, easily transported material. Here the algae live for some period before they decompose and go into the food web of the soft bottoms. In May-June the green algae start to grow, stimulated by the strong light and the supply of nutrients from the previous decomposition processes in the bottoms beneath. In due time the pregnant isopods and amphipods immigrate from the _Fucus_- fauna, release their broods in the _Cladophora_. This is the main reproduction period for the _Fucus_-fauna (Haage, 1976). In August the _Cladophora_ becomes detached from the substrate, heavy with sessile diatoms, and settles on the soft bottom. The _Fucus_- community shows its fullest maturity with most individuals and species in the autumn (Haage, 1975). When water is cooled in late autumn most of the _Fucus_- fauna submerges, spending the winter in the lower parts of the phytal zone. The empty space left by the _Cladophora_ is now occupied by the filamentous _Ceramium_ spp. and large numbers of small _Gammarus_ spp. can be seen sitting in the swaying tufts, their working appendages turned towards the water flow. During winter the activity is low, the light is scarce and the system is burning its organic resources. The ice cover decreases turbulence and organic matter settles on the submerged structures like dust in a closed room. Nutrients accumulate in the water and when the ice breaks, early in the year, turbulence and insolation increase and the spring bloom starts the new annual cycle.

The pelagic subsystem

The pronounced pulse of solar energy, the hydrodynamic pattern both in time and space and the quality of the water give the Baltic pelagic system its characteristics. The biological variables show a stronger marine component in the south and a freshwater one in the north but are mainly composed of hardy marine species. Evolution has favoured a succession of species during the year which is very similar to that of the Northeast American Coast described by Patten (1963). In spring, when the water is cold and dense and light is short, diatoms, which are heavy, have no mobility, a low light optima and long generation times carry out most of the primary production. In summer when water is warm, has a low density and luxurious light, green algae and other forms which are light and mobile and have a high light optima and short generation times are more efficient producers. In the autumn when water is getting colder and denser and light decreases, they are replaced by diatoms and dinoflagellates as being the more efficient "workers" for the situation.

Seasonal processes

Fig. 10 shows the course of the annual primary production and related variables in an area between the Swedish mainland and Gotland. When ice breaks up and turbulence increases the spring convection starts bringing nutrients from deeper layers into the photic zone where light now rapidly increases. The spring bloom starts, dominated by diatoms like *Scelatonema costatum*, *Thalassiosira baltica* and *Achnanthes taeniata*. The primary production rapidly reaches values of 1-2 g C m^{-2} day^{-1}. The algae actually gorge on nutrients, nitrate might be depleted in 4 days and the consumption seems to be in excess (Hobro *et al.*, in print). The first consumers to respond are the bacteria which reach biomasses in the order of 0.5 g C m^{-2} within the first 20 m. The ciliates are the next to respond, grazing on the bacteria and in this way concentrating the food for higher trophic levels. The net zooplankton are scarce at this time of the year (Ackefors, 1975); the only ones to respond are the rotifers, mainly *Synchaeta* spp. which have built-in mechanisms for fast reproduction (Fig. 11). Overwintering eggs of the copepod *Acartia* sp. now hatch, filling the water with nauplii (Hernroth, 1978). So few grazers being present up to 30% of the produced organic material sinks to the bottom (Hobro *et al*, in print), constituting an important injection of potential energy to the soft bottom subsystem.

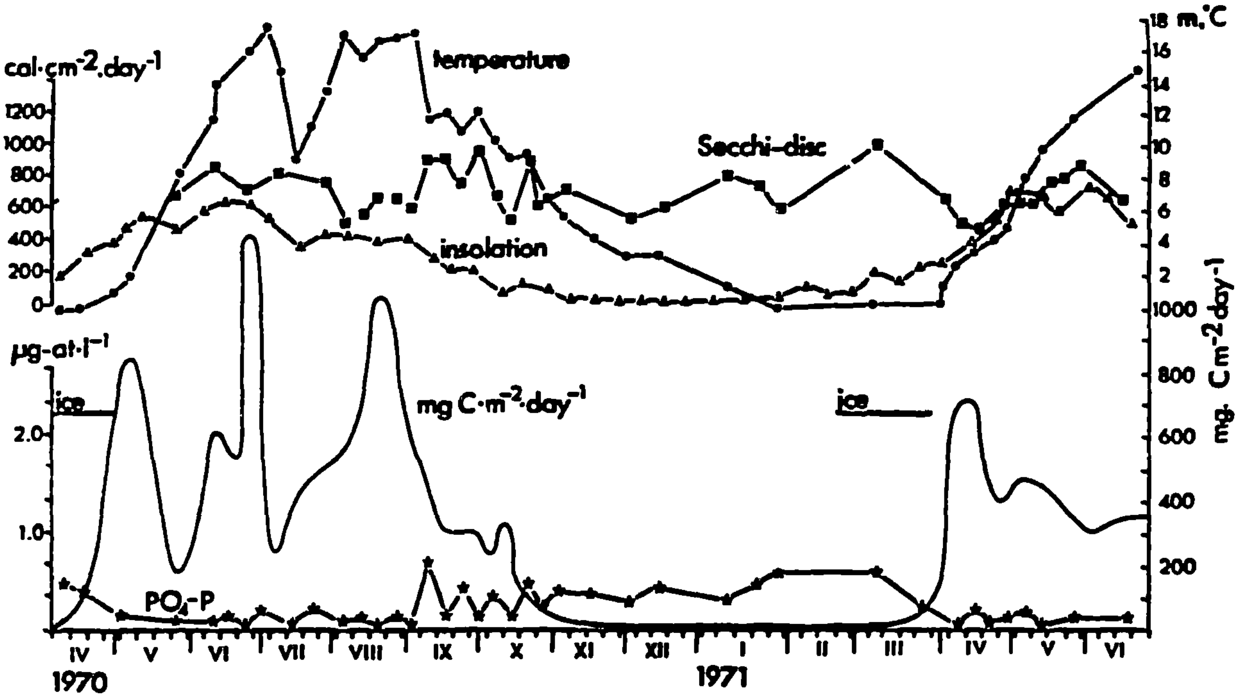


Fig. 10. Annual variation of primary production in the Northern Baltic proper with some related variables (from Hobro and Nyqvist, 1972, in Jansson, 1972).

The water has now low levels of nutrients and the summer stage of the pelagic producers is dominated by low biomasses of smaller forms with rapid turnover like dinoflagellates and monads (Bagge and Niemi, 1971). The fixation of carbon can still be intensive but primary production is checked by intensive grazing (Kaiser and Schulz, 1975). Microzooplankton increase in importance when temperature increases (Ciszewski, 1975) and the larger zooplankton like *Temora longicornis* and *Pseudocalanus minutus elongatus* show medium biomasses (Ackefors, 1975).

During this time sunlight is luxuriant but nutrients are low, however the Baltic system has an efficient "worker" for this situation: the blue-green alga *Nodularia spumigena*. Thanks to the ability to fix atmospheric nitrogen (Hübel and Hübel, 1974), this species flourishes in July-August, totally dominating the water. The positive buoyancy during one period of its life makes it concentrate on the surface where winds and currents carry it around. Using remote sensing techniques, Nyqvist (1974) was able to estimate the biomass of a two-week bloom to 1300-1700 tons C along the Swedish coast (Fig. 12) and Öström (1976) calculated the amount of fixed nitrogen to be substantial. Increased sewage flows from land is supposed to stimulate these blooms (Horstmann, 1975), which when they die, release the nutrients to the water.

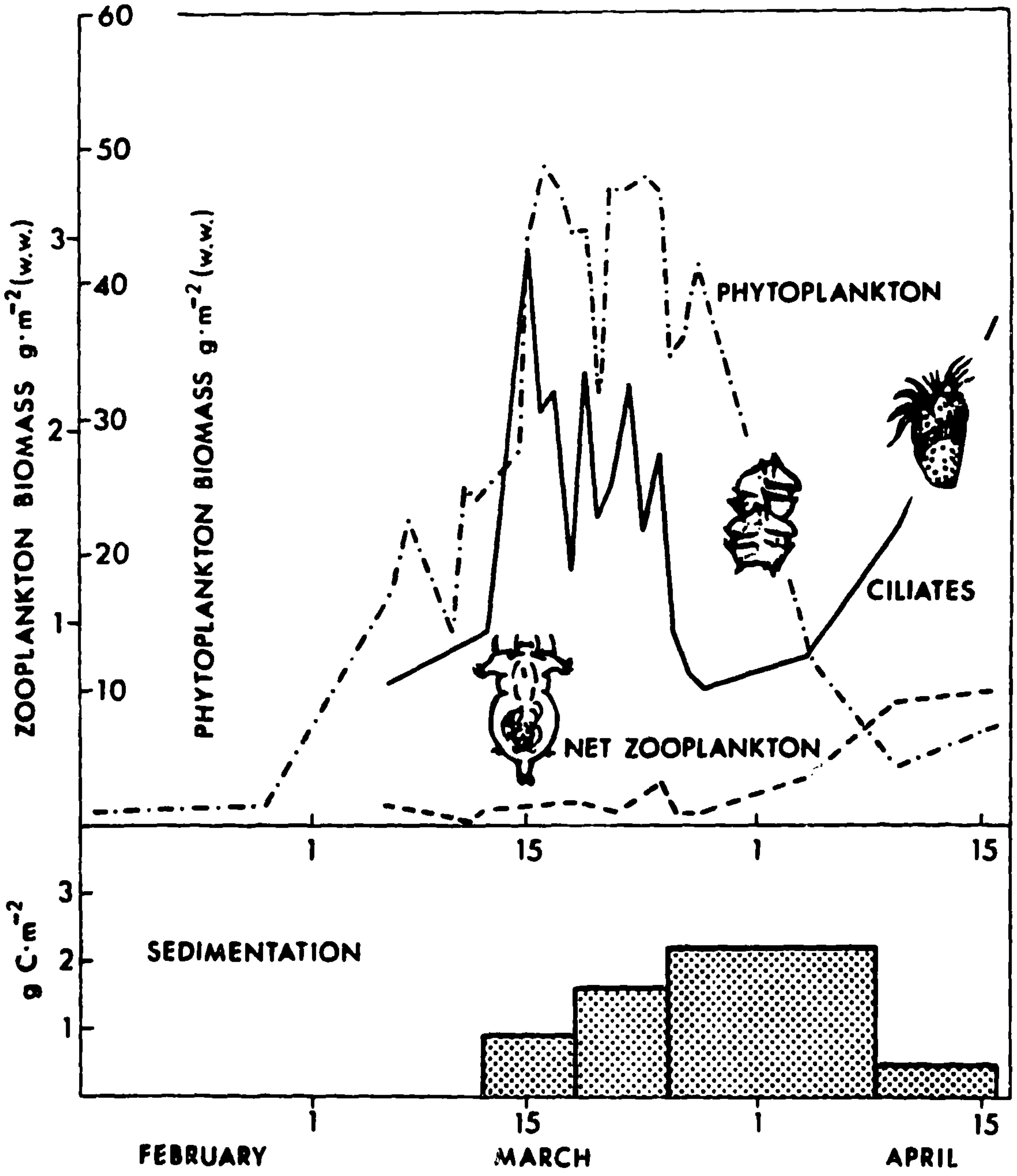


Fig. 11. The dynamics of a spring bloom in the Askö-Landsort area (from Hobro, Larsson & Wulff, in print). The ciliates rapidly respond to the increase in phytoplankton and bacteria (not shown here). Sedimentation is fast during the maximum, and decline of bloom and net zooplankton has a time lag.

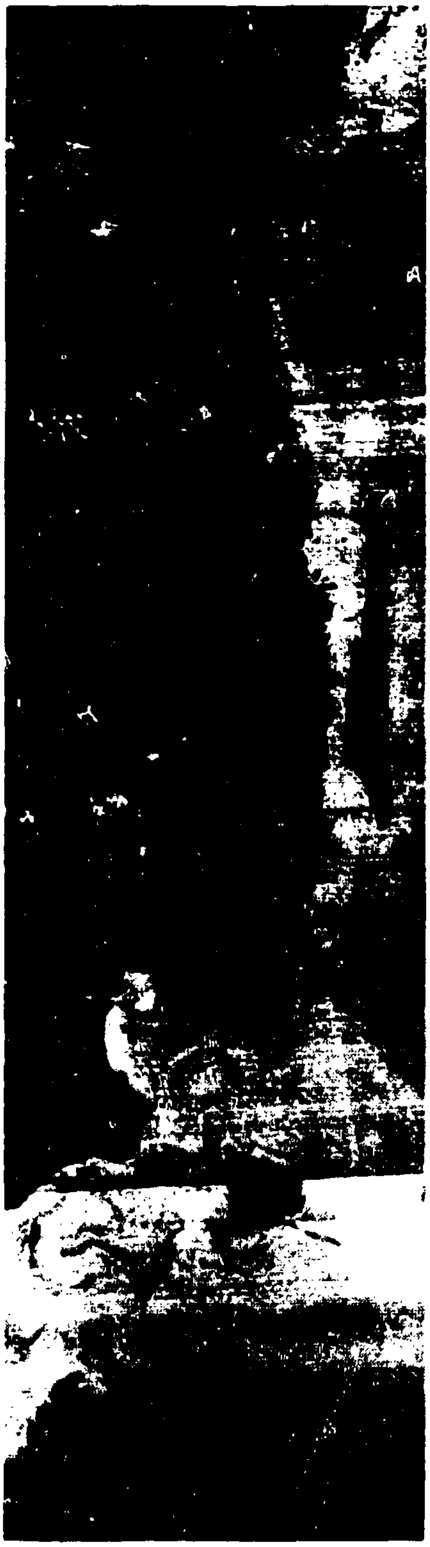


Fig. 12. Satellite picture from an ERTS-1 passage over the Baltic

at 90 km height on July 3, 1973 at 09.30-09.36 hours. The dark streaks in the water are blooms of the blue-green alga *Nodularia spumigena*, able to fix atmospheric nitrogen. A rough calculation of the bloom shown in the picture amounts to 1300-1700 tons of C (Nyqvist, 1974). Note the high concentrations in the northern part of the area and in the wide bay of southern Sweden, which are upwelling areas.

This injection might stimulate the autumn bloom of dinoflagellates, green algae and diatoms. The autumn is the period for accumulating energy reserves for the winter. The big zooplankton are now at a maximum and herring and sprat feed intensively, storing large fat reserves (Aneer, 1975).

During winter the total plankton biomass is scarce. Herring and sprat having problems with pelagic food, switch to bottom feeding (Fig. 5). In later years the herring migrate to the inner archipelagos where it stands in dense and large schools which might reach the size of 12 000 tons (Aneer *et al.*, 1978). As the herring does not feed during the period before spawning, this might be a way of saving energy, standing in the less turbulent water where predation pressure is small. After spawning in May the young feed in shallow water for a couple of weeks before returning to the pelagic zone.

The described dynamics is typical for the Central and Northern Baltic proper. In the south, the intermittent water flowing from the North Sea may cause up to nine different blooms during the year (von Bodungen, 1975; Smetacek, 1975). In the Bothnian Sea and Bothnian Bay the polar pulse of light causes one dominating phytoplankton maximum (Lassig and Niemi, 1975).

Gross calculations of production

The total annual primary production measured as ^{14}C-fixation amounts to at least 100 g C m^{-2}. This is of the same order of magnitude as in the shallow areas of the ocean. The secondary production of zooplankton has been estimated to 5 g C m^{-2} yr^{-1} (Ackefors, 1975). There are losses other than sinking of phytoplankton from the trophic layer. A considerable amount of dissolved organic carbon is being released from the phytoplankton-zooplankton-bacteria interactions (Hobro *et al.*, in print). Using ^{14}C-technique and fractioned filtering, Larsson and Hagström (in print) have shown the stimulating effect of phytoplankton exudate on bacteria. Of a total primary production of 93 g C m^{-2} yr^{-1}, 61 g C is incorporated in phytoplankton, 25 g in bacteria and 7 g as exudates. The annual average sedimentation of particulate matter amounts to 40 g C m^{-2} in the Northern Baltic proper (Larsson, pers. comm.).

The production of fish is difficult to calculate both due to absence of good quantitative methods and too meager fishery statistics. Table 1 shows the official catches of the main species. Of pelagic fish, herring is by far the most important followed by sprat. In the far north the fresh water species whitefish Coregonus spp. and cisco (C. albula) are locally important. A rough calculation of the total amount of fish in the Baltic proper has been made by Ackefors and Hernroth (1972). The biomass was estimated at 1.0-1.8 x 10^6 tons and the production at 0.8-1.2 x 10^6 tons yr^{-1}. The pelagic fish has probably increased since that time (See Eutrophication processes).

The soft bottom subsystem

Dominating species and biomasses

Sand and silt from land run off, decaying algae from the phytal zone and organic matter from the pelagic system settling in three or four pulses during the year fuels the soft bottom system. The deposited material is broken down successively by different types of bacteria which form "chemical food-chains" in the soft substrate. In bottoms within the photic zone they show a vertical zonation. Desulphovibrio breaks down the organic material to hydrogen sulphide which is oxidized by Beggiatoa in the presence of oxygen to pure sulphur. This bacteria is therefore a gradient organism living close to the sediment surface receiving oxygen from above and hydrogen sulphide from below. The pure sulphur is taken care of by the purple sulphur bacteria Chromatium which oxidize it to sulphate. These and other bacterial processes and their couplings with the ciliated Protozoa have been thoroughly investigated by Fenchel (1969).

The whole series of carbohydrate hydrolysers, nitrifiers and sulphate reducers would not function without the preparation of the organic material by the meio- and macrofauna. Elmgren (in print) has classified the vertical distribution of these faunal elements into three zones:

1. An upper well oxygenated zone down to ca. 50 m depth with a rich and diverse meio- and macrofauna.

2. A transition area around the primary halocline where oxygen greatly fluctuates, the fauna gradually disappears, leaving at the lower border the macrofaunal species Harmothoe sarsi and a few meiofaunal taxa, mostly nematodes.

3. A lower, continuously oxygen-poor zone without macrofauna and only a few thousand nematodes per m^2.

Compared to other marine areas the soft bottoms are extremely simple systems. The diversity decreases from south to north

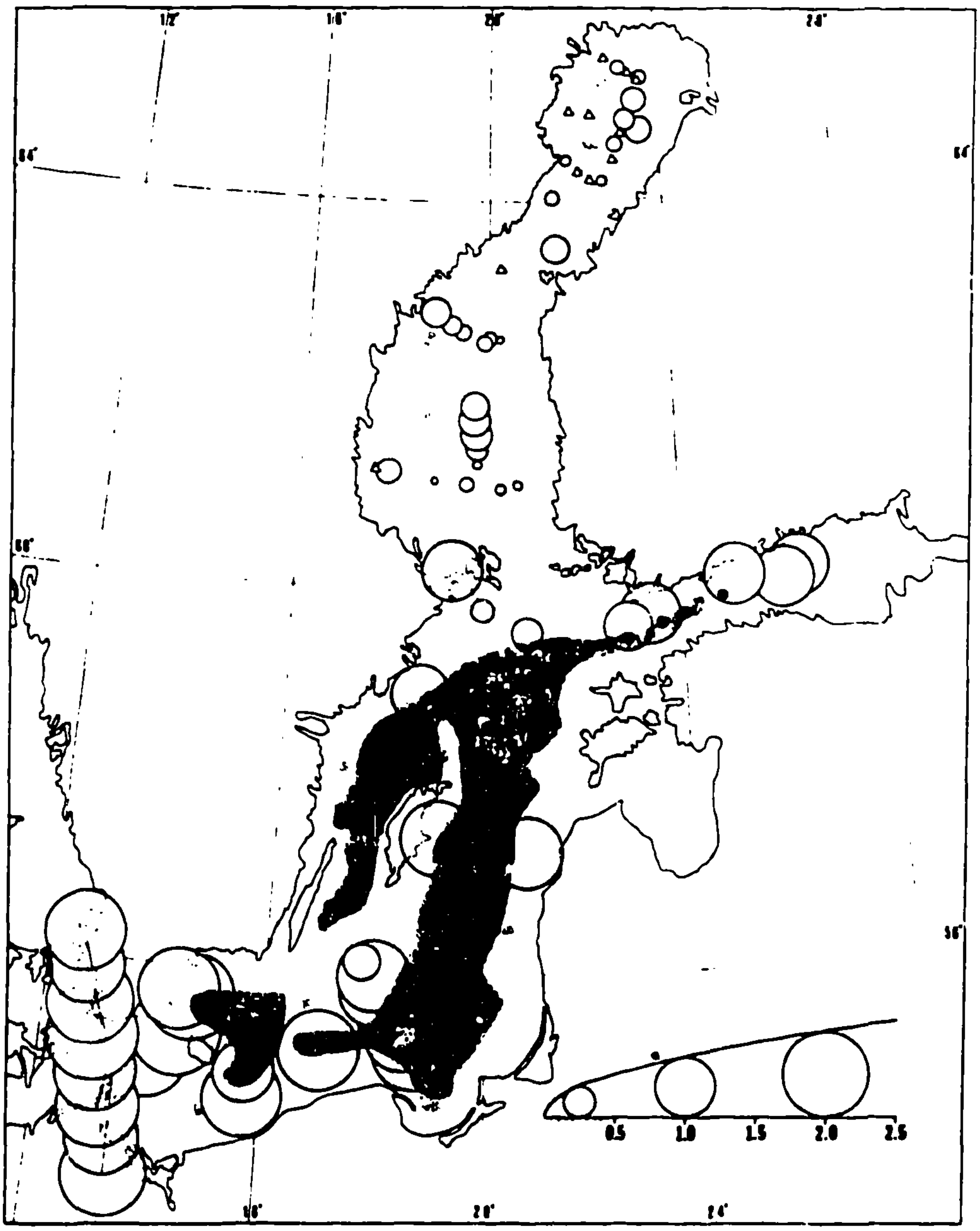


Fig. 13. Species diversity of macrofauna in the Baltic Sea in June and July 1967. Triangles indicate stations where only one species was recorded. Black areas show hydrogen sulphide, grey areas oxygen values below 2 ml litre $^{-1}$. Filled circles indicate station without macrofauna. (Andersin et al., 1977).

(Fig. 13). In the South polychaetes like *Scoloplos armiger* and *Harmothoe sarsi* and crustaceans like *Diastylis rathkei* and *Pontoporeia femorata* are very common, though the bivalves *Astarte borealis* and *Macoma baltica* dominate by biomass (Andersin *et al*., 1977). In the central Baltic the crustaceans are very common with *Pontoporeia affinis*, *P. femorata* and *Mesidothea entomon* as dominating species and *Macoma baltica* as the only bivalve. In the Gulf of Bothnia the community is nearly entirely made up by *P. affinis* with *Mesidothea entomon* next in order.

The meiofauna can be classified as a *Cyprideis-Manayunkia* community (Remane, 1940) as far up as to the Aland Sea.

Based on results from the international "Joint macro- and meiofauna sampling programme for the whole Baltic", Elmgren (in print) computed an increase of macrofauna biomass from ca. 1 g m^{-2} in the Bothnian Bay to over 100 g m^{-2} (wet weight, including shell) in the northern Baltic proper. Further increase was reported through the Arkona Basin (Andersin *et al*., 1977) and in the Kiel Bay, where values as high as 600 g m^{-2} have been reported (Arntz, 1971). Meiofauna shows less increase from values of close to 2 g m^{-2} in the Bothnian Bay (Elmgren *et al*., in print) to a 3 or 4 fold biomass in Northern Baltic proper. No increase further south has been reported so far.

This could be explained by the parallel increase of primary production from north to south which to a great extent fuels the benthos. The changing ratio between macro- and meiofauna might be caused by the better utilization of limiting food resources of the meiofauna (Elmgren, in print).

Production of benthos

The dynamics of the soft bottom benthos is probably best described as the Odum energy flow model of Ankar and Elmgren (1976) valid in first hand for the same 160 km^2 investigation area as for the phytal quantification (Fig. 14). The values at the "heat sinks" represent respiration losses, the number within the hexagons standing crops and the values at the outflows to the right of the hexagons represent the net production. The important role of the bacteria (III) and the detritivores (IV, VI) is obvious. The total meiofauna production is about half that of the macrofauna. The total calculated benthos production is ca. 340 kJ m^{-2} yr^{-1} (ca. 7 g C m^{-2} yr^{-1}), half of which is left for the bottom fish when respiration, mortality and consumption within the system have taken their share.

Using respiration to production values from literature, the annual amount organic material needed for running this system was estimated as 40 g C m^{-2} yr^{-1}. In a more recent paper, Ankar (1977) using respiration per biomass values arrived at

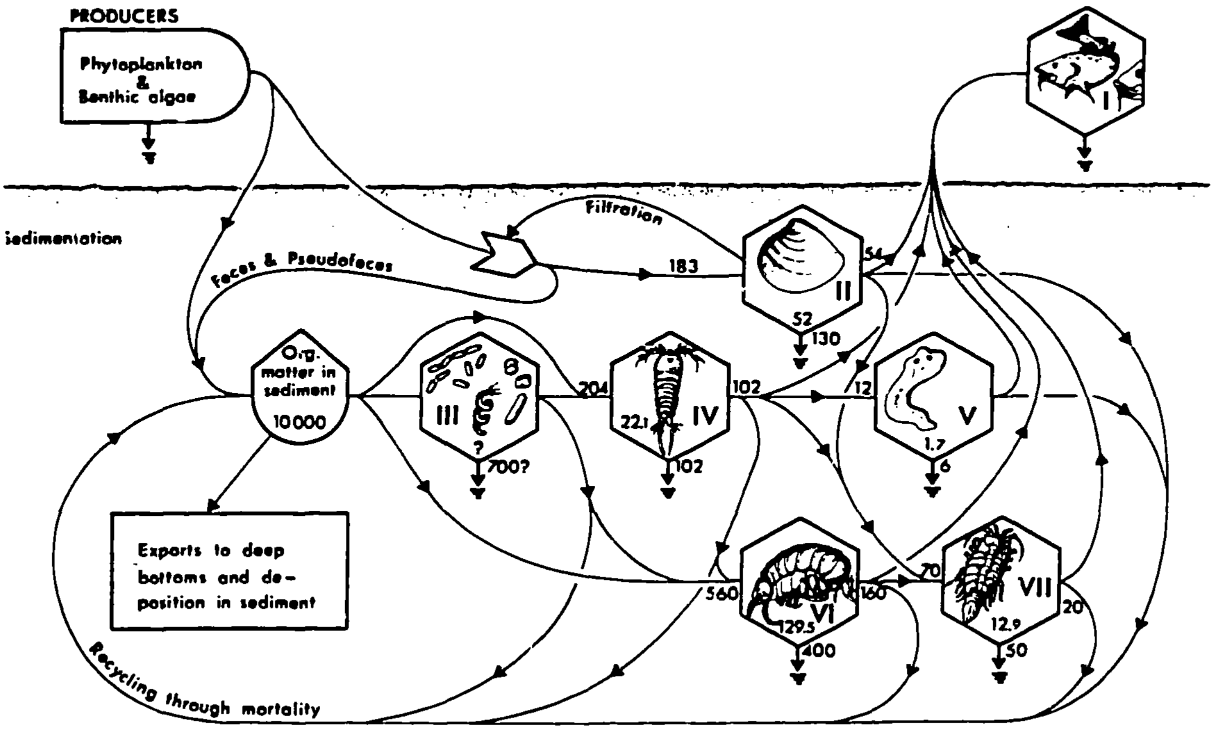


Fig. 14. Rough energy flow model of the benthic ecosystem of the Askö-Landsort area. I. fish, II .Planktivores, III. Bacteria and ciliates, IV. Meiofauna, detritovores, V. Meiofauna, carnivores, VI. Macrofauna, detritovores, VII. Macrofauna, carnivores. Biomass measured, production estimated, respiration guessed at. Storages in KJ m^{-2} yr^{-1}. Figures to the left of the hexagons indicate assimilation (R + P). Faeces and organic excretion are considered never to have left the organic pool in the sediment (from Ankar & Elmgren, 1976).

60 g C m^{-2} yr^{-1}. In any case, this seems to match the calculated sedimentation from the pelagic system of 40 g C m^{-2} yr^{-1} quite well.

Even regardless of the severe oxygen conditions at depths greater than 50 m the Baltic offers meagre conditions for bottom fish (Hempel and Nellen, 1974). Both cod and flounder grow less, and the 1 part per thousand salinity necessary for the successful hatching of the cod roe is restricted to the deeper parts of the southern Baltic, often present with low oxygen concentrations. Along the margins of the continent, the viviparous blenny (*Zoarces viviparus*) and the fourhorned sculpin feed on *Harmothoe* and *Pontoporeia*, the former also on *Mytilus* and *Macoma* (Aneer, 1975).

Table 1

Catch of different fishes and invertebrates in The Baltic including The Sound and The Belt Sea 1975. The figures have been calculated from the statistical data published by Conseil International pour l'Exploration de la Mer.

Species	Catch in metric tons
Herring (*Clupea harengus*)	414,757
Sprat (*Sprattus sprattus*)	201,434
Cod (*Gadus morhua*)	234,156
Various gadiiforms	2,471
Salmon (*Salmo salar*)	2,943
Various salmonids	11,294
River eels (*Anguilla spp*)	4,180
Flounder (*Platichtys flesus*)	11,988
Plaice (*Pleuronectes platessa*)	9,944
Various pleuronectiforms	1,786
Various freshwater fishes	20,421
Various marine fishes	25,853
Fishes unsorted, unidentified	27,646
Total catch of fishes	968,873
Blue mussels (*Mytilus edulis*)	4,664
Various molluscs	10
Lobsters (*Homarus* spp, *Nephrops norvegicus*)	11
Shrimps (*Palaemonidae*, *Pandalidae*)	195
Total catch of invertebrates	4,880

Commercially, cod is next to herring in importance (Table 1) whereas flounder shows much smaller catches, far from matching the North Sea flatfish on the market.

CHANGES IN PRODUCTION DUE TO POLLUTION

Eutrophication processes.

For 1976, Andersin *et al.* (1977) calculated the area with unfavourable oxygen conditions as 10 000 km^2 or 25% of the total Baltic area. Although the main reason for this is the persistent stratification of the water due to hydrographic conditions, man's increasing waste flows certainly play an important role. According to Ahl & Odén (1972) for river discharge and Engvall (1972) for urban and industrial outflow, as much as 80% of the discharge of phosphorus and 50% of the nitrogen in Sweden is caused by man's activities. Fonselius (1972) has calculated that as little as an extra 10% of the carbon annually produced in or discharged to the Baltic is sufficient to deplete all oxygen present below the halocline in one year. The normal stratification of the phytal zone has changed in polluted areas (Lindgren, 1975). There has been a general shift from perennial algae (*Fucus*, *Furcellaria*) to annual filamentous species (*Cladophora*, *Pilayella*). This will most certainly affect the total productivity of the coastal systems in the long run. But there are some positive changes also. Herring (gechlin, 1968) and sprat (Schultz, 1970) have increased their stocks due to increased phyto- and zooplankton populations. The benthic fauna above the halocline in the central Baltic have increased their biomass by at least 17% during the last 50 years (Cederwall, pers. comm.). The populations of *Mytilus* feeding eider ducks have also increased substantially over the last thirty years (L. Jansson, pers. comm.).

Accumulations of hazardous substances, long turnover time, stable stratification and low temperatures make the Baltic an effective sink both of organic material and chemical substances. This is clearly shown by the classical example of DDT and PCB concentrations in Baltic organisms in comparison with corresponding populations on the Swedish west coast. The fauna contain around 10 times as much of these hazardous substances (Jensen *et al.*, 1969), (Fig. 15). Due to the high PCB concentrations, only ca. 30% of the females of the Baltic seal population are fertile each year, pointing to near extinction of this species (Kihlström, pers. comm.).

On the other hand, the situation has improved, e.g., concerning the accumulation of mercury in Baltic organisms. The previous high levels of mercury in the feathers of guillemots are now down to concentrations of the previous century thanks to the Swedish mercury ban in 1966 (Olsson, pers. comm.).

Oil pollution

The frequent use of the Baltic as a transportation area also causes a high frequency of oil spillage. Chronic effects of oil pollution resulting in changes of bottom communities around urban areas have been shown by Leppakoski (1978). The serious effects of wrecked oiltankers on the sea bird population are well known. In the archipelago it is disastrous. One investigated oil spill in the Archipelago Sea (Fig. 1) in 1969 was found to have visible effects in the phytal and soft bottom systems but 30% of the eider

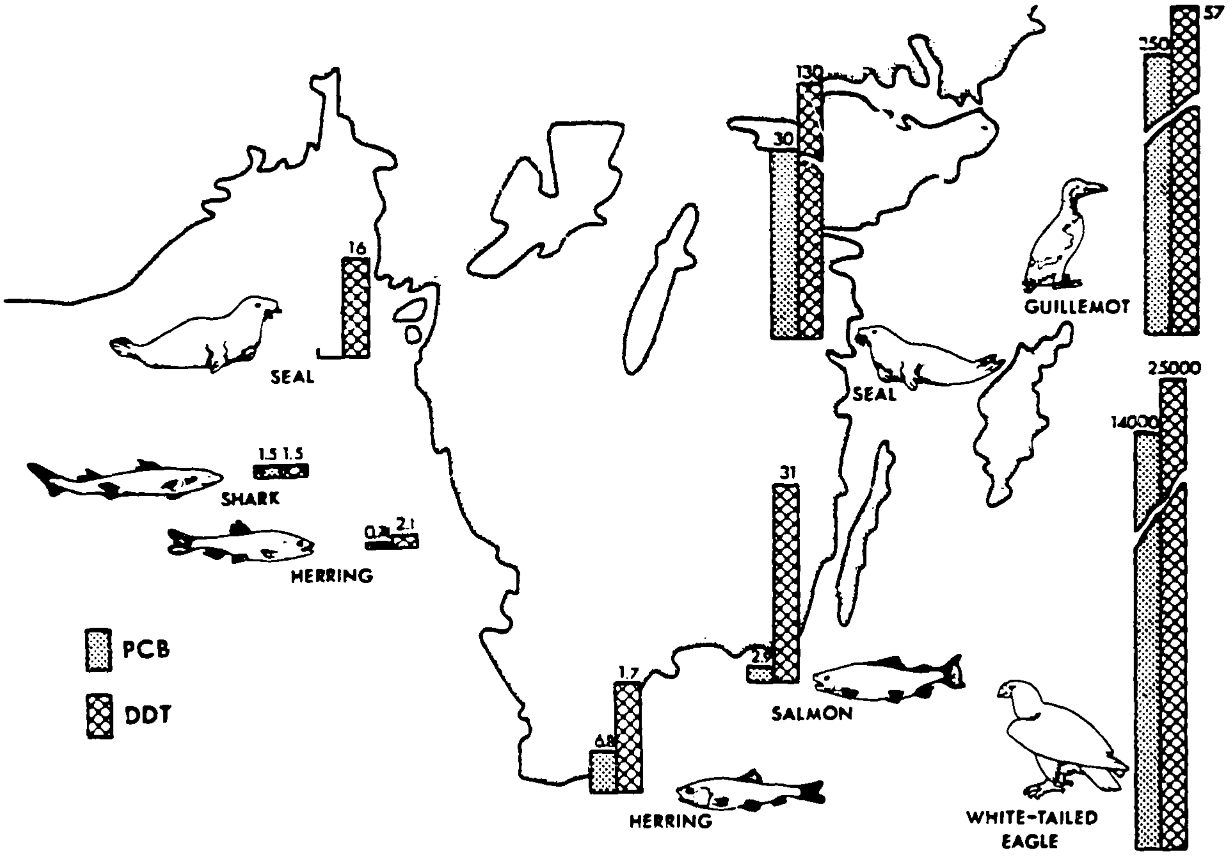


Fig. 15. Amounts of DDT (sum of all DDT derivatives) and PCB in organisms from the Baltic and the Atlantic. The concentrations are expressed as mg per kg fat (from Jensen, Johnels, Olsson & Otterlind, 1969).

duck populations were wiped out (Leppakoski, 1973). Laboratory tests have shown negative effects of even highly diluted mixtures of oil and emulsifiers on herring larvae and populations of the ecologically important amphipod _Gammarus oceanicus_ (Lindén 1974, 1976). The larvae showed increased mortality and deformation of the spine and the amphipod decreased in fecundity and growth.

SYSTEMS ANALYSIS

The most advanced dynamic model of a Baltic ecosystem up to now is probably that of Sjoberg & Wilmot (1977). It was used to explore the forcing processes of a spring bloom based on the results of Hobro _et al._ (in print). It showed how insolation was responsible for starting the bloom, but also how it could be checked by sustained deep mixing. The total uptake of nutrients was determined primarily by vertical mixing.

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GUIDE LINES FOR ECOSYSTEM RESEARCH IN COASTAL LAGOONS

by

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INTRODUCTION

One stated objective of this seminar is "to provide guide lines for future research in coastal lagoons". I heve translated this to mean "problems concerned with identifying the core problem and continuing research towards its eventual solution". To this end I propose to briefly sketch the development of the Commonwealth Scientific and Industrial Research Organization (CSIRO) Estuarine Project and share the experiences and lessons we have learned in its execution. My particular bias will be recognized as a belief that today's ecological problems should be attacked by interdisciplinary teams using a systems analysis approach rather than by an unstructured multidisciplinary bombardment.

EXAMPLE

The CSIRO Estuarine Project was initiated in 1973 from a point of view that the impact of developing technology on the estuarine ecosystem could not be predicted with the knowledge then available. By "ecosystem" I mean a complex of physical, chemical and biological properties which interact according to underlying laws. By predict I mean to foresee changes of major consequence to human use or acceptability. Such simple questions as "How will the estuarine ecosystem respond if a major portion of the fresh water runoff is diverted to another basin?", "What ecological changes are likely to result from dredging a channel through a shallow entrance sill?", or "How will the dissolved oxygen levels respond to the waste discharges of a proposed industry?" could not be answered without stringent qualification. A common thread to all such questions is "How will the ecosystem respond?" This question is married to the obligate correlate "How does the ecosystem work?" It is this latter question to which we addressed ourselves.

Interested staff came together in a series of meetings and began to develop the project in detail. The first step was to recognize the parts of the system and how they fit together as we then understood them. Choosing carbon as a common unit of measurement, a box-and-arrow schematic was constructed to describe the total system in an abstract and qualitative way. A basic list of five compartments was defined as shown in the matrix of Table 1.

Table 1. Carbon compartments used in abstract model. The matrix designates fluxes from donor to recipient compartments. The rates of flux are shown as determined either by the donor (D) or the recipient (R) or both (J) compartment sizes.

Donor	Recipient					Carbon compartment
	DIC	AUT	HET	DOC	DET	
DIC		R				Dissolved inorganic
AUT	D		J	D	D	Autotrophs
HET	D		J	D	D	Heterotrophs
DOC		R	R		D	Dissolved organic
DET			R	D		Detritus

A study site was selected (Port Hacking, Sydney, N.S.W.) for its convenience and boundaries of the target ecosystem were defined. Gains and losses across these boundaries and exchanges between sediment and water column subsystems were considered. The study site had a shallow entrance sill leading to a deeper basin known to periodically go anoxic at depth. A distinction was made between aerobic and anaerobic heterotrophic compartments in the sediment subsystem. The conceptual model defining the flow of carbon to, from and within the ecosystem is shown in Fig. 1. Together with controlling factors such as light, temperature, nutrient, salinity, oxygen and transport, this compartment and flux diagram became a statement of the broad goals of the study.

The second step was to translate the abstract concept into a real parameter programme. From an early reconnaissance the compartments of the model were equated with familar and common names, for example, AUT became phytoplankton, benthic micro- and macroalgae, seagrass and mangrove. HET became bacteria, zooplankton, nekton, invertebrates, epibenthos, etc. It was obvious that neither expertise nor support were available to study all compartments and fluxes in detail. The studies which did proceed were a

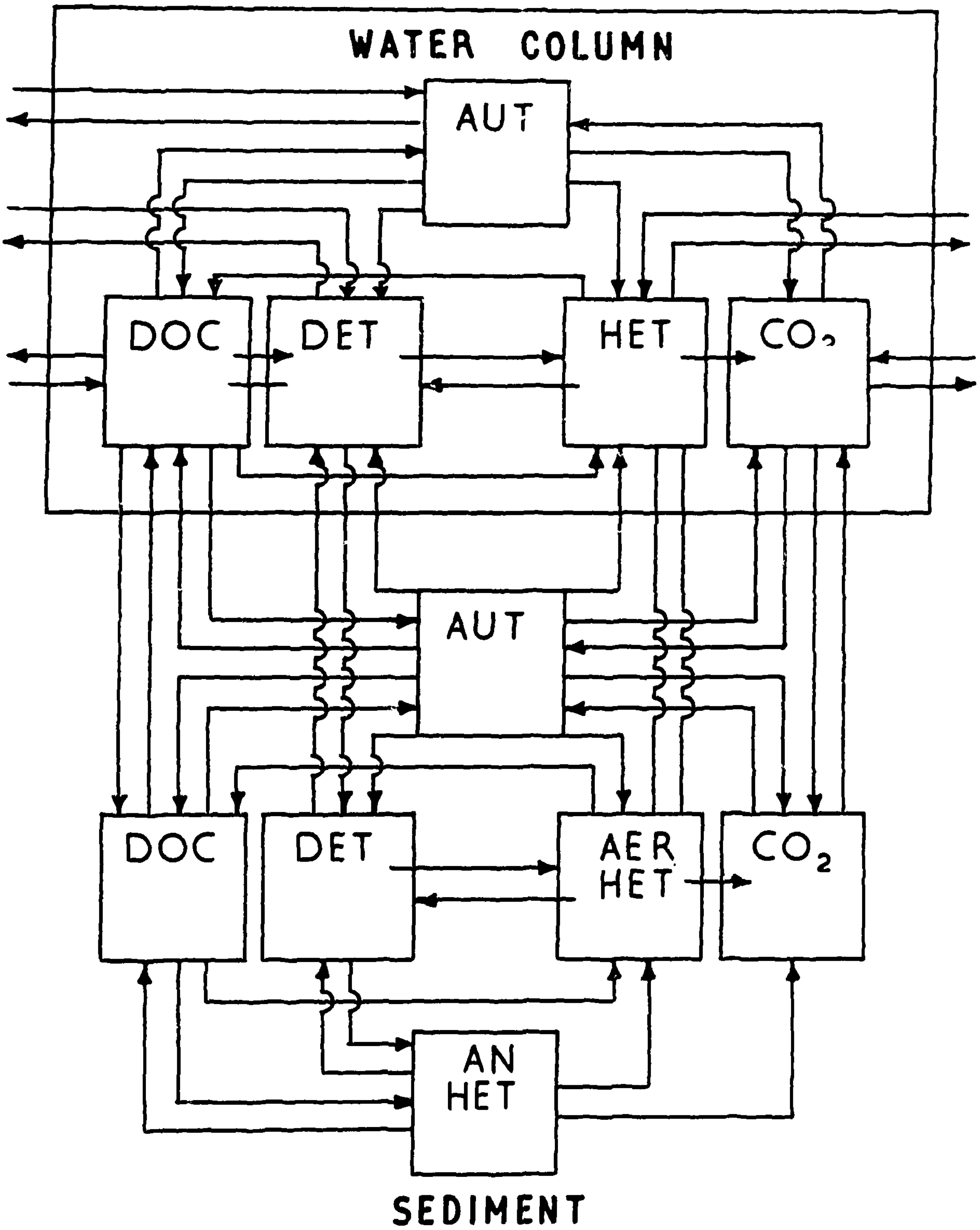

Fig. 1 Carbon Model showing the main compartments in which carbon

is found in the ecosystem and the inter-compartmental fluxes. Compartments are labelled as follows : AUT = autotrophic carbon; DOC = dissolved organic carbon; DET = detritus; HET = heterotrophic carbon; CO_2 = dissolved inorganic carbon; AER HET = aerobic heterotrophs; AN HET = anaerobic heterotrophs.

compromise between resources, interest and priority. These decided, a central programme of monitoring for temporal changes in compartment sizes and forcing factors was initiated to provide continuity and tie in. Individual scientists attacked selected problems identified as contributing to the stated goals.

A few scientists from outside the Division were attracted to the project, enlarging the scope of expertise available.

Without providing detail (available elsewhere), the results of the work of three investigators working with the AUT compartment are summarized in Table 2. Mr. B. Scott found production by phytoplankton to be both light and nutrient limited and upon occasion production was enhanced by increasing the biomass with exogenous plants brought in with tidal water. Mr. M. Giles found that pro-

Table 2. Primary production, South West Arm, Port Hacking, 1975-1976.

Taxon	Average rate ($mg\ C\ m^{-2}\ day^{-1}$)	Area ha	Estuary total ($tonnes\ C\ yr^{-1}$)
Phytoplankton[1]	40 [2]	110.	16 000
Benthic microalgae[3]	180	0.28	184
Seagrass[4]	356	2.25	2 924
Benthic algae	no estimate	= 0.03	
Mangrove	no estimate	= 0.03	

[1] Work of Mr. B. Scott, CSIRO Division of Fisheries and Oceanography.

[2] Integrated for whole estuary using P/area/depth and then dividing by surface area to obtain average.

[3] Work of Mr. M. Giles, Australian Atomic Energy Commission, Sydney.

[4] Work of Mr. H. Kirkman, CSIRO Division of Fisheries and Oceanography. Data are for *Posidonia australis* only. There are some 0.7 ha of *Zostera capricorni* for which production data are not yet available.

duction by benthic microalgae was limited by light. Mr. H. Kirkman found a seasonal cycle of growth of seagrass (*Posidonia australis*) leaves which suggests a light or temperature limitation. These attributes must be monitored to provide forcing functions for a primary production model.

Computer simulation was an ongoing process. It was assumed at first that a resultant model would be predictive and this came to be seen as essential. Later it became clear to all that this was beyond our available resources. However, there was still a need for an ecosystem model to collate and summarise the knowledge that had been gained. Such a model could be used to test the completeness of this knowledge by comparing its output to the known behaviour of the studied system. Based on the findings of Dr S. Godfrey (CSIRO Division of Fisheries and Oceanography), a model simulating the changing conditions during the marine-estuarine-marine cycle dictated by rainfall pattern was evolved by Mr. R. Sinclair (CSIRO Division of Computing Research). This model (output in Fig. 2) provides discrete strata in which biological processes proceed in tidal time steps. A biological model gradually evolved

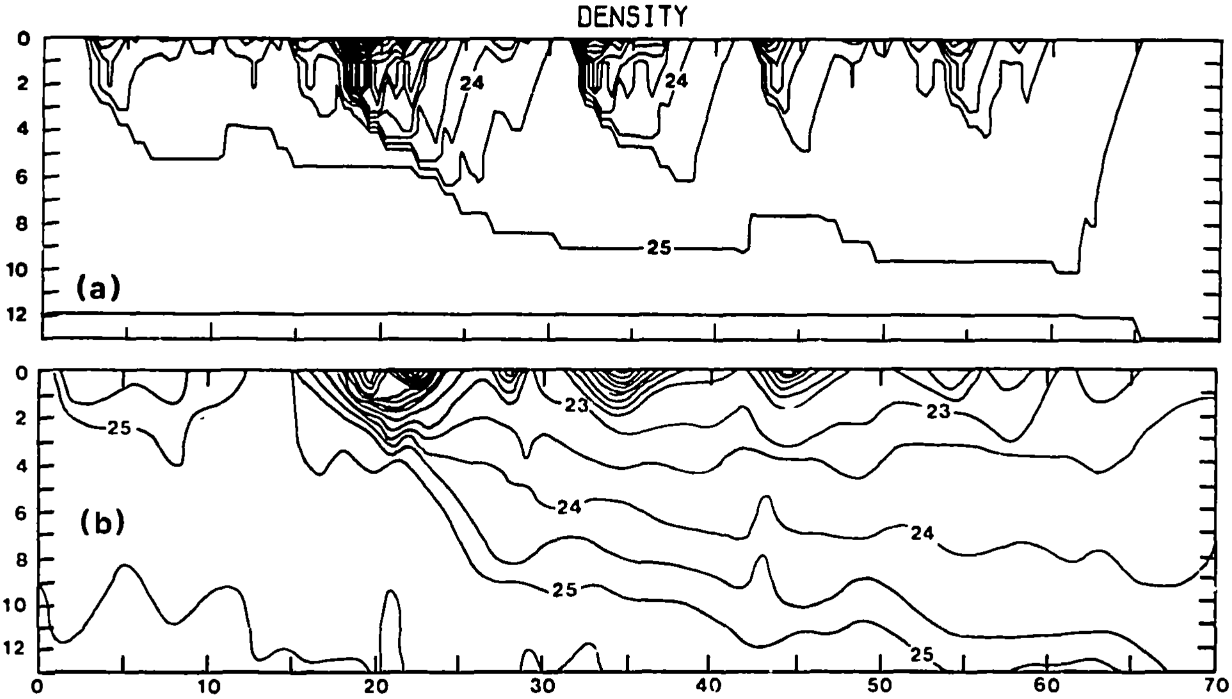

Fig. 2 Development of an Ecosystem Model of South West Arm (Port Hacking, N.S.W.) (a) Results of a computer simulation using daily rainfall as driving force. Rain pulses may be identified by surface isopleths of low . (b) Observed distribution during same time period as (a).

from Dr. D. Smith (CSIRO Division of Fisheries and Oceanography) through Mr. R. Sinclair and Dr. W. Cuff (CSIRO Division of Computing Research). The carbon flow of this model, based on measured compartment sizes and a variety of fluxes, some measured, some from the literature and some guessed at, is shown in Table 3. A synthesis of these physical and biological models is now being attempted and early trials are encouraging.

These results underline the need for a detailed description of the hydrodynamics of a study area as a prerequisite to further work and planning. In many cases this will be known. In our case it was not and the hydrodynamics proved basic to our understanding the changes taking place in the ecosystem. The development of an ecosystem model with a multidisciplinary framework is not a task for the faint-hearted. Our main impediments were related to clarifying what the model could and could not do for us and and to finding sufficient knowledge of the system to develop it. We found the model tended to run away with the study. Its danger lay in the inadequacy of its description of the real world. Once it became clear that a predictive model was not the goal, the simulation became helpful in focusing attention of participants with dissimilar disciplines onto a common problem and provided a common language.

CRITIQUE

The CSIRO Estuarine Project was conceived in 1973. Planning, equipment gathering and methodological development took until 1975. Field observation began in 1974 and continued to 1977 (a little is still continuing). Writing up is in progress and should finish in 1979. This is a total of six years and the involvement of some 12 full time core scientific staff plus support, with guidance and part-time participation of an additional 12 people. What of the objective, "How does the ecosystem work?" We can only give a partial answer, but it is more complete than the one we formerly gave. We can answer the questions posed in the introduction with less equivocation. We have underlined the basic truth that the ecosystem is incredibly complicated and a complete understanding is beyond our means and perhaps our ability. The real gains that have been made are interdisciplinary (interrelated efforts among several disciplines), and would not have been made had the project been merely multidisciplinary (work not necessarily related). The joint enterprise of physicists, chemists and biologists working towards mutually identified goals has provided an insight into the interactions of component parts of this ecosystem. While the relative importance of components (see example of Table 2) may be site-specific, the weights (coefficients of relative importance) necessary to relate these results to a similar ecosystem can be acquired more easily than a completely new set.

Table 3. Matrix of annual average compartment fluxes and biomass for Port Hacking study area. HET1 denotes aerobic heterotrophs, HET2 denotes anaerobic heterotrophs.

DONOR	RECIPIENT (mg c m^{-3} day^{-1}) Water column DIC	AUT	HET	DOC	DET
DIC		100			
AUT	8.0		76	8.3	8.3
W.C. HET	20			22	57
DOC	0.1		1.6		
DET			16		
DIC	82	0.2			
AUT	< 0.1		7.9	< 0.1	
SED. HET1			3.9		
HET2					
DOC				4.8	
DET					8.0

Table 3 continued

DONOR	RECIPIENT (mg c m^{-3} day^{-1}) Sediment DIC	AUT	HET1	HET2	DOC	DET	BIOMASS (g C m^{-3})
DIC	0.2	9.8					20.
AUT							0.18
W.C. HET			6.1				.25
DOC		< 0.1			34		1.
DET						57	.09
DIC		0.2					5.6
AUT	< 0.1		2.0		0.2		.01
SED. HET1					130	21	7.5
HET2			2.2		54	5.4	1.
DOC			180		45		5.
DET			42		45		137

RECOMMENDATIONS

With this experience it is possible, in retrospect, to say what we should and should not have done. This is probably best done as a set of general guidelines for setting up and executing an interdisciplinary project. These are set out as a time sequence in Table 4.

Table 4. General guidelines for ecosystem research in coastal lagoons

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1. Identification of broad problems and funds available.
2. Obtain the blessing of all concerned political bodies.
3. Appoint a project director with clear terms of reference, responsibility and delegated authority.
4. Identify the particular problem(s) to be studied, an acceptable level of solution, the projected time frame and predicted costs.
5. Commitment by sponsoring body for completion of project within a specified time frame.
6. Appointment of committed scientific staff and supporting personnel. Criteria are scientific experience, attitudes to interdisciplinary team research, and willingness to complete project.
7. Initiate a core programme of monitoring attributes identified as forcing or limiting functions.

It will be noticed that specific research projects and instructions on how to conduct them are not included. The former will be identified by the systems analysis approach starting with identification of the problem and the choice of staff. The conduct of the research is largely for the individual participants to determine.

Prior to commencing an ecosystem study, it will be well to recognise that these problems are incredibly complex, particularly in estuaries and shallow water lagoons where such features as substrate, runoff and adjacent land use become particularly important. Agencies initiating such projects should be thinking in terms of decades rather than years of study and have a clear idea of the specific problems to be studied and level of funds likely to be available.

These areas are usually under the jurisdiction of several political bodies, ranging from local to international in scope. The project may be sorely harassed, even to a point of collapse, unless jurisdictional problems are sorted out and blessings acquired in the initial planning stages.

A project director should be appointed at this time. He should have the responsibility for the appointment of further staff, control the project funds, and be directly responsible to the sponsoring body. Without this line authority, it may become unlikely, except by accident, that a mutually desirable goal will be achieved. There is a tendency for interdisciplinary programmes to evolve into multidisciplinary ones, through the "prima donna" attitudes of scientists. You might be left, in metaphor, with an orchestra of soloists, a frustrated conductor, and a bewildered audience.

The project director should further define the basic task, using a systems analysis approach (he may need the help of a modeller), and identify an acceptable level of solution. This will allow him to decide on the staff and support needed to solve the stated problem and to arrive at a compromise between the project and available funds acceptable to the sponsors. In this way the sponsors will have a clear idea of what they can expect for their investment, and the director will not be expected to work miracles. This calls for a term commitment by the sponsors that once the project is started it will be completed. It also calls for a commitment by the technical participants that they will see the project through.

Ecosystem problems embrace several disciplines, but are not likely to be solved by simply assembling a group of individuals, each expert in an appropriate field. The key word here is interdisciplinary rather than multidisciplinary. Our tertiary formal education institutions tend to train people to act as soloists rathern than members of a team (who has heard of a multiple authorship Ph.D. thesis?). Ecosystem problems, however, demand a team approach for their solution, hence the ability and willingness to work as a team member is an important criterion when selecting staff.

Windfall funds tend to enlarge the scope of the project rather than increase its efficiency, and are therefore a mixed blessing. A reduction in funds below the anticipated level calls for a rescheduling of time frames at best and a complete redefinition of goals at worst. It is usually disastrous to the project.

In summary, I advocate a goal-oriented interdisciplinary structure in solving ecosystem problems in estuaries and shallow water lagoons. An open-doored project with ill-defined goals may fund research which is exciting, worthwhile, brilliantly thought out and executed, but has little connection with the problem specified by the sponsors.

Biological Approach to Coastal Lagoons: Metabolism and Physiological Ecology

by

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INTRODUCTION

Many countries consider or reconsider the possibility of improving their current knowledge on coastal lagoons. Biologists who have been concerned with lagoons previously were interested in determining the identity and, to some extent, the abundance of species, and how this information related to environmental variables. More recent investigations have been concerned with subjects such as chlorophyll, photosynthesis and net respiration.

Having acquired this basic knowledge, many questions of particular interest for the increase of our understanding of the functioning lagoon systems now need to be answered. This is especially true for the critical problems of energy relationships, notably at the sediment/water interface. Coastal lagoons are very dynamic systems having a productivity high turnover. However, the large and often drastic changes, e.g., in temperature and salinity, result in dynamic spatial and temporal distribution patterns of transient and resident organisms. These complex natural patterns of variation must be understood or at least recognized, before an attempt can be made to exploit rationally these biota and to relate any alterations to abnormal environmental changes (pollution) which may evenutally occur.

A coastal lagoon is often the site of valuable fisheries but is also a region primarily affected by man's dumping of a wide range of substances. Our limited knowledge suggests that there are highly adapted communities of organisms with great ecological, fundamental and economical interest.

Most of the living communities exhibit great numerical changes in the course of time, and their ability to survive these changes is one of their most remarkable features. This has been revealed, particularly during recent years, in ecological studies based on metabolism measurements, including work in physiological ecology. These research topics are becoming increasingly important. For these reasons, research programmes centered on the following aspects are highly desirable:

1. Knowledge of metabolic processes of communities,

2. Studies of the physiological and biochemical strategies of adaptation being developed by significant species and populations,

3. Incorporation of this information in a suitable simulation language as a means of modelling these complex systems.

These three aspects are closely related and they are highly correlated with other aspects such as population dynamics and biogeochemistry.

METABOLISM AND PRODUCTIVITY

The metabolism in coastal lagoons depends largely on the supply of biologically utilizable material produced by primary production and decomposition processes. An understanding of the metabolism will thus depend on: (1) an accurate quantitative estimate of the material input, its nature, and relative utilizability, (2) appreciation of the communities' use of the material (implying a knowledge of interactions of the various community components), and (3) an analysis of how material is lost from the system.

Furthermore, a better understanding of the energy flow at the water/sediment interface, and of the benthic productivity, which is known to be important in coastal lagoons, depends upon the evaluated importance of microflora, bacteria, micro- and meiobenthos, in connection with macrobenthos. Recent improvements have resulted from measurements of total in situ community metabolism. The metabolic studies of single taxon are necessary complements of the in situ studies, and during recent years this approach has become increasingly important.

SUBJECTS FOR RESEARCH

Particulate organic matter (detritus, bacteria)

Quantitative sampling

- Collectors fixed at various depths above the bottom

- Coarse (sup. 240 microns), fine (64 microns) and nanno (inf. 64 microns) can be collected with nets of different mesh sizes.

Chemical composition

- Composition of detrital input to the sediment by direct microscopic examination (fecal pellets, plant cells, diatoms)

- Enumeration of bacteria associated with particles: fluorescence microscopy

- Measurements of particle organic carbon and ATP: allows calculations of living versus dead organic carbon

- Classical analysis for pigments, carbon, nitrogen and ash weight.

Utilization as food

- Very little is known about which food items are actually assimilated and support the animal's metabolism: it is therefore important to evaluate the input of food and to have a clear idea on the partition of energy among coexisting species

- Plant debris and benthic microflora (green, blue algae, diatoms, and fungi) are often very important but their role as food items should be evaluated by labelling techniques

- Bacteria are metabolically very active and their importance in the enery flow must be studied using fluorescence and radio-tracer techniques

- Bacterial flora, present both in sediments and water mass, are involved in many chemical cycling and recycling processes. There is an urgent need for increased understanding of their role in coastal lagoons.

Dissolved organic matter

Quantitative sampling

- Samples of water and of sediment (can be taken without great difficulty by sampling bottles and sediment corers)

- Separation of particulate and dissolved organic matter by filtration (material passing a 0.20 micron or 0.45 micron nucleopore filter is generally taken as the dissolved fraction).

Chemical composition

- Total organic carbon
- Dissolved organic nitrogen
- Free amino acids
- Sugars (single and polymerized)
- Fatty acids

Degradation and utilization as food

- Degradation of specific organic compound is followed most easily as $^{14}CO_2$ production after the addition of a labelled compound to the intact sediment

- There is some evidence that protozoans and metazoans, and certainly bacteria can take up dissolved organics.

Metabolic activities

An understanding of the production potential of lagoons requires a quantitative measurement of energy consumed by living communities in relation to the total energy available.

In situ respiration

The respiration measurements, when correctly interpreted, offer the possibility of estimating interrelationships in living populations. A large portion of organic input is lost through respiration, but the fraction may change with conditions related to the oxidizability of organic matter (water salinity, temperature, oxygen tension, nature and source of organic matter).

Oxygen uptake

The community metabolism is a measure of the total respiration of all organisms present in the sediment and underlying water. Community respiration is commonly estimated by oxygen uptake rates in undisturbed sediment. Two techniques are currently in use:

- Bell jars or other enclosures in situ

- Sediment core brought to the laboratory

With both methods, measurements of sediment oxygen demand are monitored continuously by means of an oxygen electrode or analyzed before and after incubation. Oxygen uptake measured after poisoning the water represents a rate of inorganic chemical oxidation. The difference between rates of total uptake and inorganic chemical oxidation is aerobic respiration. Annual oxygen uptake by the sediment surface is probably a good way of estimating the oxidative loss of organic input during the year.

CO_2 production

For the purpose of relating sediment surface metabolism to the cycle of organic carbon in the ecosystem, it is desirable to measure CO_2 production at least over an annual cycle.

Anaerobic metabolism

Inorganic chemical oxidation is often taken as a measure of anaerobic metabolism, but it gives an underestimate of the true value. Therefore, anaerobic metabolism must be measured independently. This may be done using direct calorimetry but such a technique is very difficult.

Respiration of group organisms

Partition of community metabolism

Many of the measurments of *in situ* benthic respiration seem to underestimate the importance of *meiofaunal* and *microfaunal* components. Community metabolism is ideally partitioned into all the component population species. An accurate estimation of the relative magnitude of total community respiration contributed by *macrofauna*, *meiofauna*, *microfauna*, *microflora* and *bacteria* should be based on more ecophysiological investigations (See section - Physiological Ecology), and a better understanding of the aerobic and anaerobic fractions of metabolism.

Metabolic role of meiobenthos and microbenthos

It has become increasingly accepted from recent studies made on shallow estuarine sediments that a relatively high percentage of the total community respiration (up to 60%) may be attributed to the meiofauna, microfauna and microflora components. Respiration rates calculated from individual measurements on microfauna and meiofauna species, using different techniques of microrespirometry (Cartesian diver, polarographic electrodes), give values of oxygen uptake approximately 20 times greater than tnat of equal biomass in macrofauna. These values are 200 and 5000 microliters O_2 h^{-1} g^{-1} for meio- and microfauna (ciliates), and 10 to 300 microliters O_2 h^{-1} g^{-1} for macrofauna. Therefore, meiobenthos and microbenthos would consume much more energy in the form of organic matter, microflora, and bacteria, than the respective macrofauna does. A discussion of the ecological and metabolic relevances of these differences is complicated by the fact that the rate of oxygen consumption varies with the size of the animals. The methods based on experimental values may tend to overestimate respiration rates. Nevertheless, oxygen uptake, determined by conducting experiments with animals in their natural living conditions, have given results with very good concordance. Estimates of the meiofaunal contribution to total community respiration in lagoonal fish ponds at Arcachon have shown that meiofauna (mainly composed of nematodes and copepods) contributed from 9% to 58% of the total community respiration.

Consequences of *in situ* respiration, respiration of group organisms and energy flow relationships

In coastal lagoons, as in other shallow sheltered areas, deposit feeding micro- and meiofauna use the primary production, and are preyed upon by carnivorous meiofauna (such as turbellarains) and larger metazoans (such as polychaetes or crustaceans). However, this predatory activity seems to be comparatively small. Very high densities of microfauna and meiofauna have been found in estuarine sediments: 10,000 to 10,000,000 m^{-2}, and corresponding to biomass of 1 to more than 20 g m^{-2} (wet weight). It seems, then, that in such areas a significant part of the primary sources of organic matter which are converted to meiofauna tissue are NOT passed upwards to higher trophic levels. As there is strong evidence the estuarine macrofauna can use directly organic matter (e.g., fish of the family Mugilidae), the amount left for these larger consumers would not be optimal.

While further work in this area is required, it does appear that the role of *meiobenthos* and *microbenthos* (Protozoans) in coastal lagoons is very important in terms of energy flow as well as in bacterial populations.

The meiofauna generally defined as those matazoans which pass through a 500u sieve and are retained on a sieve with mesh widths smaller than 60 are an important component of detrital systems that have been largely overlooked in previous attempts to partititon benthic systems, notably in coastal lagoons.

It is quite difficult to obtain a realistic view of trophic efficiency of detritus use. This is due to the difficulty in partitioning the flow of energy or matter through different trophic levels within the sediments, and to measure the resultant or concomitant energetic or respiratory losses at each transfer.

Before we attempt to establish flux rates between compartments we must first realistically separate those compartments in benthic studies.

Meiofauna can compete with macrofauna under certain conditions in terms of utilization of microbial and detrital food. A significant part of the benthic primary production which is converted to meiofaunal tissue might not be passed upwards to higher trophic levels.

PHYSIOLOGICAL ECOLOGY

Physiological ecology is the part of ecology which deals with physiological and biochemical mechanisms developed by an organism to succeed in its habitat.

Research has now entered a stage where we are beginning to understand the competitive interactions of multi-species in terms of different modes of adaptation. The biochemical properties of adaptation of individuals and populations are very important for a true understanding of stressed lagoon systems, and emphasis is placed on the evolution of these adaptations in the formation of communities.

The very existence of any organism will depend on its capacity to adjust to daily and seasonal changes. Each organism does not regulate by any single pattern but is resourceful in utilizing a wide range of regulatory mechanisms, e.g., the euryhaline homeosmotic species are able to regulate the composition of their body fluids by passive or active mechanisms which maintain a steady state of ionic and water flux between external and internal media. All these adaptive properties imply different specializations. A considerable amount of work has been done during the last decade on the biochemistry and physiology of species living in estuaries and lagoon systems. However, most of the attention has been directed towards physiological or biochemical end points. There is, at present, widespread interest in rearing and harvesting organisms of nutritional value in the coastal lagoons, salt marshes and mangroves that are extremely productive and are, nevertheless, in a state close to an excess of eutrophication. Coastal lagoons receive temporary immigration from the sea and, to a lesser extent, from the land-based waters. While some species may actively seek the most favourable environment by migration, others with limited locomotive ability or which are trapped in lagoonal enclosures, must cope with the environment.

Stress is an inescapable part of life in coastal lagoons, e.g., the salinity effects are complicated by the interaction of other environmental factors and are mediated eventually, through an osmotic behaviour which is highly adaptive in nature. Conversely, isolation of temporary immigrants in lagoon enclosures can alter the ad libitum migratory tendencies and trigger osmoregulatory disfunctions. It is very probable that periods of prolonged neuronal and hormonal activity, often related to prolonged environmental stress, may produce some shortage of energy demands for growth or maturity, which is reinforced at a certain moment by some generalized reduction of metabolic energy (reduction of ATP production) as in the case of low temperature in winter, accidental anoxia due to high eutrophication in summer, hypoglycerinia due to starvation or to some unbalanced condition of nutrient availability. It is noteworthy that apart from the naturally occurring stress, many polluting substances can alter osmoregulatory as well as other metabolic mechanisms. Osmotic balances as derived from a study of blood chemistry and tissue composition can indicate a "healthy" or "unhealthy" state relative to given environmental conditions. Modification in the gill ATPase activity of amphihaline fish can give some significant indication of their migratory tendencies.

Microfaunal and meiofaunal communities are very successful in reproducing and growing in coastal lagoons. These opportunistic species have short generation times and their production/biomass tend to be considerably higher than that of macrofauna. They therefore require a high level of metabolic energy and food consumption to complete their life cycle and it may be assumed that their protein metabolism is elevated.

Little systematic work has been done, for example, in comparing the osmotic adjustments of laboratory adapted organisms with field populations from contrasting habitats. It is necessary therefore to increase our knowledge on the DYNAMIC ASPECTS of adaptive adjustments, with ECOLOGICAL BIAS, of species that have been shown to exhibit differential penetration in lagoons.

The key variables such as salinity, temperature, oxygen tension and other major environmental factors influence greatly differential penetration, colonization, and establishment of animal and vegetal communities. Such approaches, however, are beset by methodological and interpretive difficulties, and therefore it is necessary to standardize the methods of sampling, capture, handling and laboratory techniques. Physiological periodicities, temporal shifts due to localized abiotic effects and variations due to reproductive conditions, should all be taken into consideration in the future.

Ecophysiological strategies of meiobenthos

A high degree of tolerance to many environmental factors has been shown in many meiobenthic species. Recent studies using sophisticated methodology have shown the independence of metabolic activities over large environmental temperature, salinity, and oxygen ranges, suggesting the existence of metabolic compensations.

Furthermore, increased evidence of many original features of ecophysiological adaptation presented by meiobenthic organisms and the general importance of meiobenthos in coastal lagoons tends to encourage future studies which try to define the complex picture of all the acquired adaptive features of meiofauna in their habitats.

Ecophysiological strategies of macrobenthos

Sampling evidence and the examination of fishing and collecting records from coastal lagoons and other embayment systems indicate that fish and many macrobenthic economic species, such as crustaceans and molluscs, invade periodically these estuarine habitats. The key variables of salinity, temperature, and to a lesser extent oxygen are important and probably influence greatly the differential penetration and movements of animal populations. Osmotic balances derived from the study of blood chemistry and tissue composition can indicate a "healthy" or "unhealthy" state relative to given environmental conditions.

SUBJECTS FOR RESEARCH

Survey of the principal environmental parameters and their apparent effects on the distribution of the species

- Salinity
- Ions (mainly Na^+, Cl^-, Ca^{2+}, Mg^{2+} and their ratios in natural waters of varying salinity)
- Oxygen tension
- Eutrophication process and organic pollution.

Multiple factors effects and survival tests

Patterns of osmoregulation

- Chemical determinations on plasma samples:

  total plasma osmolality

  plasma electrolytes, Na^+, Cl^-, K^+, Ca^{2+}

- Field sampling and seasonal variations
- Experimental adaptation to different salinities and temperetures: short-term and long-term adaptation
- Effect of light and food

Participation of physiological and biochemical mechanisms in osmoregulatory responses of the species

- Measurement of sodium-potassium ATPase activity in different effector organs of teleost euryhaline fish (gill, intestine, kidney). In euryhaline fish, this enzyme stimulation is involved in a sodium regulating cellular pump
- Changes in the free amino acid content, notably in the parietal muscle, and its relation to an isosmotic intracellular regulatory mechanism, present in several crustaceans and some fishes
- Histometrical profiles of hypophysis and interrenal organs in fish. Levels of circulating hormones (prolactin, cortisol and other steroids). The pituitary-interrenal system is probably of importance in the control of salt and water balances.

THE FLUX OF CARBON, NITROGEN AND PHOSPHORUS BETWEEN COASTAL LAGOONS AND OFFSHORE WATERS

by
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INTRODUCTION

Like other estuarine systems, the ecology of coastal lagoons reflects the interaction of influences from land, freshwater, and the sea. It is tempting to develop a simple conceptual model of these relationships in which the lagoon receives inputs from land and freshwater, carries out various transformations of these inputs, and then passes on certain outputs to the offshore waters. This view has characterized much of our thinking about salt marshes for the past twenty years and has influenced many concepts of estuarine geochemistry. While we are beginning to realize that the situation is considerably more complicated (eg., Nixon et al., 1977; Woodwell et al., 1977; Haines, 1978), such a simple model does not encourage us to examine the input of material from offshore, a major term that should be a part of any estuarine ecosystem analysis. Even if there is a net flow of material seaward over a long time, there may be periods during the annual cycle when the sea is an important source of nutrients, trace elements, or organic matter for the estuary or lagoon.

Although the more obvious flux of material from estuaries to the offshore waters is usually included in conceptual models, it is seldom measured. This is understandable because of the formidable problems involved in making onshore-offshore flux measurements regardless of the substance of interest or the direction in which the net flux is taking place. The major difficulty lies in obtaining accurate measurements of water transport over a long enough period so that small differences in concentrations can be integrated over time with confidence (Kjerfve et al., 1978). However, the coupling of estuarine and offshore systems is gaining increasing recognition as a major problem for study (NSF-IDOE, 1977; COMS, 1978) and exciting data are beginning to become available, especially for specialized systems such as salt marshes (Heinle and Flemer, 1976; Day et al., 1977 Haines, 1977; Moll, 1977).

The interaction of coastal lagoons and offshore waters may be particularly important since lagoons generally have relatively minor freshwater inputs compared with river mouth estuaries or riverine salt marshes.

The southern coast of Rhode Island is characterized by a series of lagoons and salt ponds stretching from Watch Hill to Pt. Judith (Fig. 1) which fit the classical description of a lagoon in that they are shallow bodies of high salinity water lying behind a barrier spit with their long axis parallel to the coast and have a regular connection with the sea. With the exception of Pt. Judith Pond, which was breached permanently in 1910, all of the major systems along this coast were periodically isolated from the sea until permanent breachways were constructed between 1950-1960. Until that time, these systems were connected with the offshore water of Block Island Sound by narrow, winding, shallow channels that were often closed entirely by longshore sand transport. This

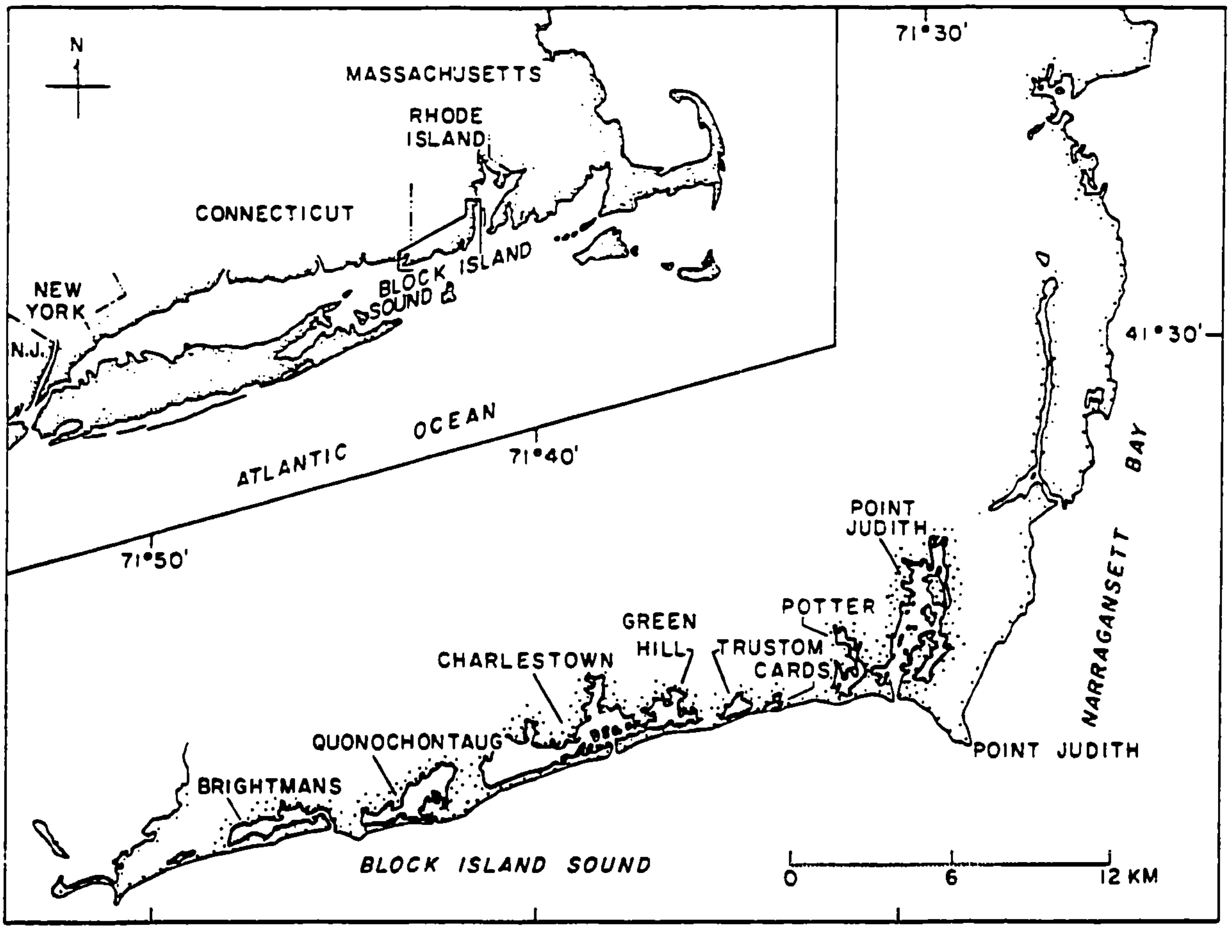

Fig. 1 Location of the Charlestown-Green Hill Pond lagoon complex on the south shore of Rhode Island with the waters of Block Island Sound offshore.

type of connection produced coastal ponds in which salinites varied from near zero to that approaching coastal sea water. There was little regular flow between the ponds and the Sound and the onshore-offshore transport of material occurred in large pulses when storms caused overwash of the beach by sea water or when enough fresh water had accumulated in a pond to overflow the barrier beach and cut a breachway. It was also customary for local farmers and fishermen to dig breachways during spring and fall each year to maintain the migration passage and brackish salinity necessary for the large oyster, white perch and alewife fisheries that used to characterize the ponds.

The construction of stabilized breachways some 25 years ago converted the salt ponds into coastal lagoons having an open connection with Block Island Sound and produced dramatic changes in the ecology of the lagoons (Lee, 1980). While it is difficult to know if the ecology of the lagoons has stabilized since the major perturbation of breachway construction, there do not appear to have been any dramatic changes in the chemistry or biology of Charlestown - Green Hill Pond, the largest lagoon complex in the area, since it was last studied intensively in 1956-57 (Conover, 1961). In this paper we have tried to take advantage of an extensive set of data recently collected on the concentrations of a variety of different materials of ecological importance in the lagoon and offshore to make a preliminary estimate of the magnitude and direction of the flux between this lagoon complex and Block Island Sound. While the absolute amount of material transported cannot really be well known without more detailed studies of water transport and mixing, the nature, importance and general pattern of the coupling between the lagoon complex and offshore seems clear.

Description of the Study Area

Charlestown - Green Hill Ponds are the largest of the lagoons that lie behind barrier spits along the south shore of Rhode Island (Fig. 1). Together they are about 8.3 km long and vary in width from narrow, winding channels up to 1.5 km wide. Their total area is about 866 hectares (2140 acres) with a volume of 9.24×10^6 m^3, a mean depth of just over 1 m and a maximum depth of 2.5 m (Stolgitis *et al.*, 1976). These shallow basins rest on glacial outwash sediments of poorly sorted gravel which have been overlain on the northern side by fine silty lagoon sediments and, along the southern side, by sand that has washed over the barrier beaches during storms or been transported in through the breachway (Dillon, 1970). Charlestown Pond is connected with the sea via a permanent 30 m wide rip-rapped breachway that was constructed in 1952. Green Hill Pond is not connected directly to the Sound, but is open to Charlestown Pond and the sea through a narrow breach and a channel which was dredged through marsh flats in the 1960's (Fig. 2). The ponds have a semi-diurnal tide with an average

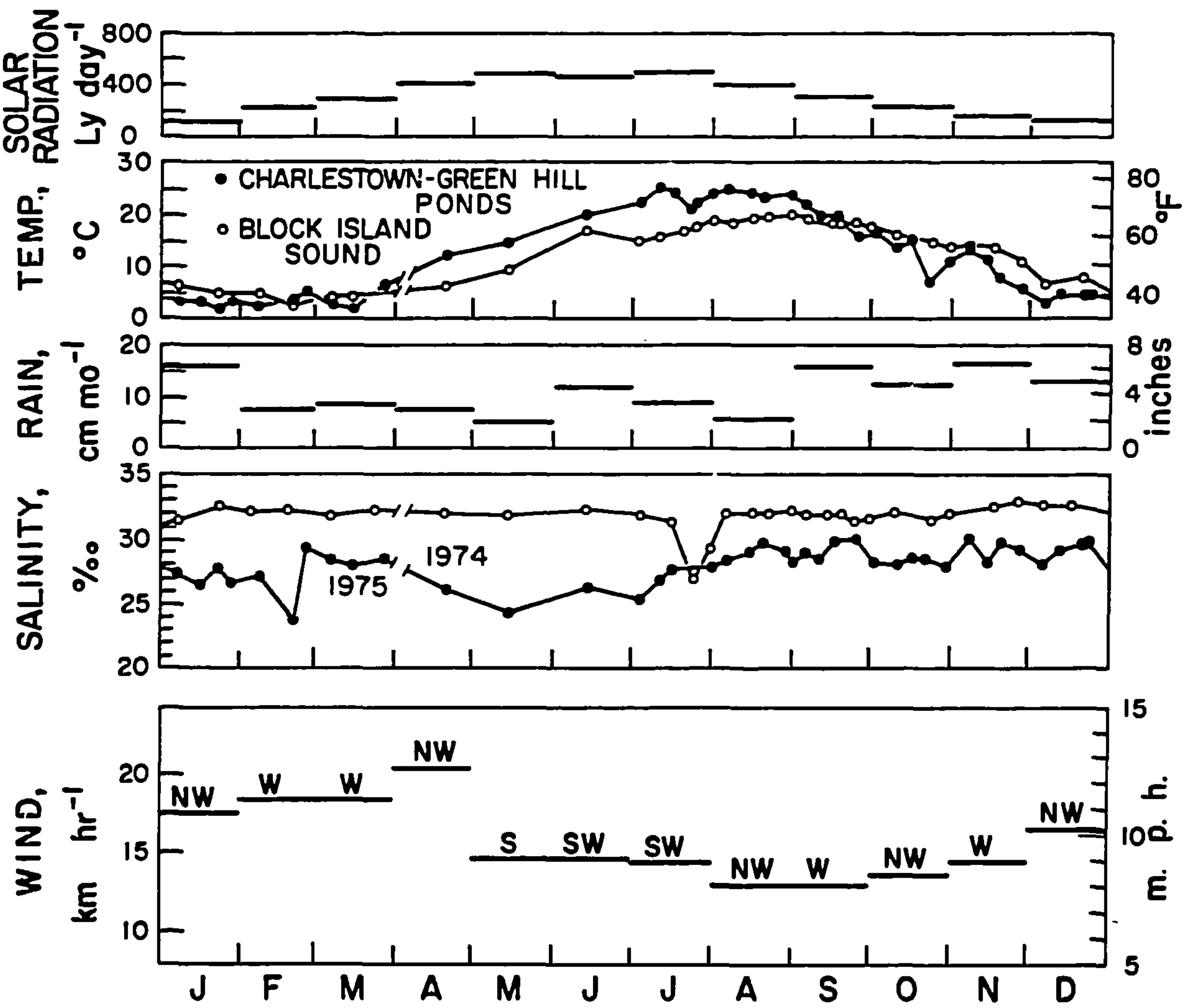

Fig. 2 Location of sampling stations in the lagoon complex and offshore used by Marine Research during 1974-1975.

10 cm range that varies from 0 to 0.6 m, depending on location in the ponds (Conover, 1961). Fresh water input via stream flow is limited by the recessional moraine north of the lagoons. Only one stream of consequence flows into each pond along the northern or landward edge, but there is probably also some subsurface groundwater seepage to the lagoon (Fisher, personal communication). As a result of the low freshwater input, salinities in the lagoon complex are only a few parts per thousand lower than found offshore and there is little seasonal variation in the freshwater content (Fig. 3).

There is, however, a marked seasonal cycle in solar radiation and temperature that influences the timing of primary production

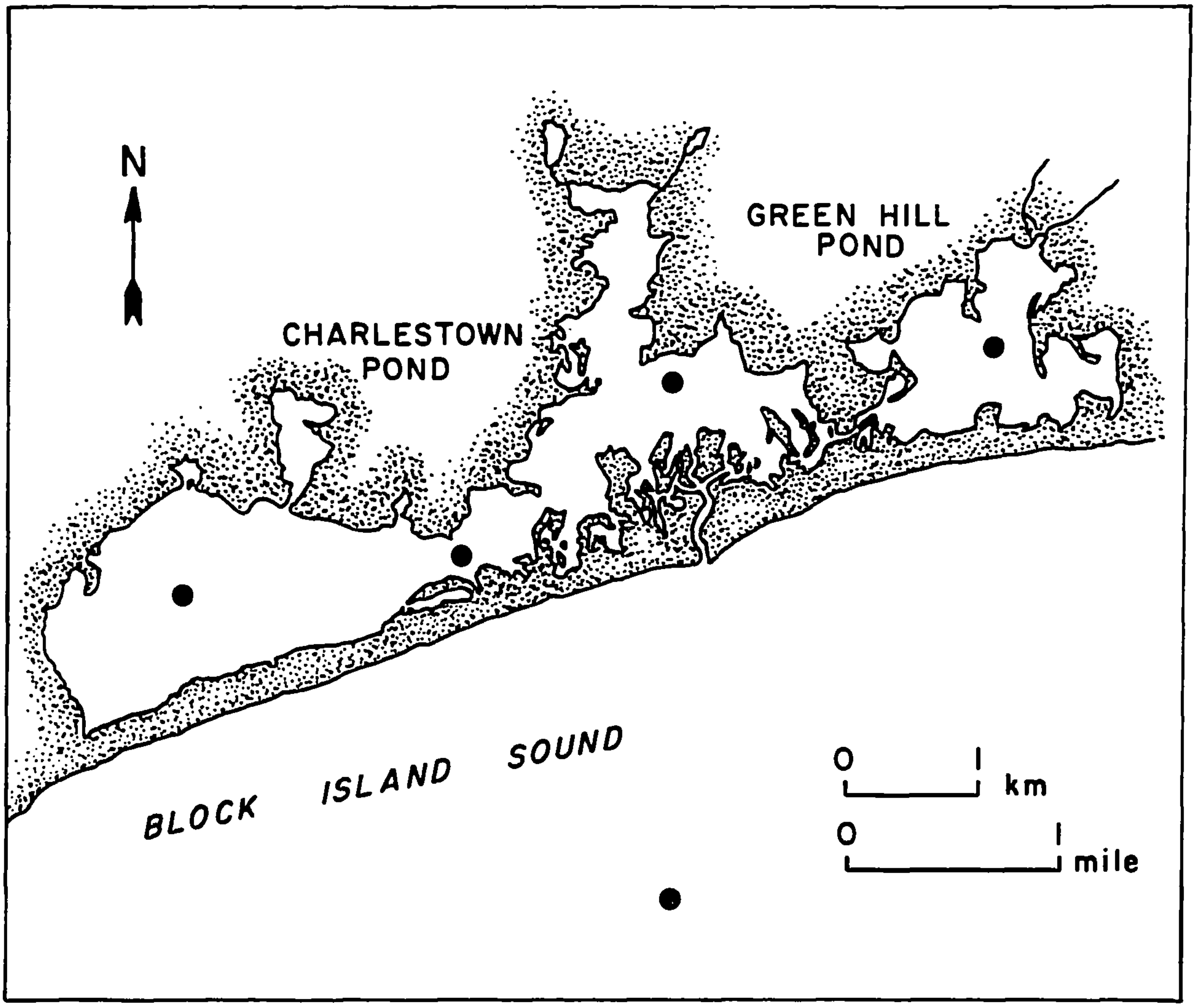

Fig. 3 Seasonal patterns of physical forcing functions in the lagoon and offshore in Block Island Sound.

and nutrient regeneration (Fig. 3; Conover, 1961; Short, 1975; Nixon *et al.*, 1975). While the lagoon cools and warms more rapidly than the offshore waters, tidal exchanges help to keep the temperature differential between the two systems to less than 5°C (Fig. 3). Circulation in the shallow lagoon is probably also influenced by the seasonal wind pattern in which there is a shift from strong west-northwest winds in winter to mild southwest winds in early summer (Fig. 3). Wind driven currents interact with dense beds of eelgrass, *Zostera marina*, to produce gyre currents in the open Western Basin of the lagoon that retard the flushing rate and help to conserve materials in the lagoon (Short *et al.*, 1974).

Aside from the eelgrass, which has a high biomass in certain areas but produces only a modest standing crop when averaged over the whole lagoon (Short, 1975), primary production is carried out by phytoplankton, seaweeds and epibenthic diatoms. The lagoon has been characterized in the past by abundant shellfish, finfish and waterfowl populations, but there are indications that all of these may be declining as a result of over harvesting (Lee, 1980). The lagoon is also a productive nursery area for a number of fish species, especially the winter flounder, *Pseudopleuronectes americanus*.

Development pressures have increased dramatically around the lagoon in the last 25 years, and there are now over 2000 houses in the watershed. All of these depend on individual leach fields for sewage disposal, but it is difficult to know if they represent any significant input of nutrients to the lagoon. In the past, much of the land around the lagoon was used for farming and pasture and it is possible that nutrient inputs from the land may have been greater under those conditions (Lee, 1980).

METHODS

Data Collection

The data discussed in this study were collected by consulting firms under contract to the New England Power Company for an environmental impact report pertaining to their proposal to construct a nuclear power plant on the north shore of Charlestown Pond. Marine Research Inc. of Falmouth, Mass. did most of the biological and chemical work and Raytheon Corp. of Portsmouth, R.I. measured the physical parameters. The raw data were compiled in a series of reports and appendices published by NEPCO (1978). Bimonthly samples were collected near the surface and bottom at five stations in Charlestown and Green Hill Ponds, and from surface, mid-depth and bottom water at an offshore station located about 3.5 km south of the lagoon in Block Island Sound in about 20 m of water (Fig. 2). Samples were taken over a year, beginning April 1974 and continuing through March 1975.

Analytical Methods

Temperature and salinity were measured twice a week in the pond and weekly in Block Island Sound using a Hydrolab Model 2A salinometer. The ponds were covered with ice during a two week period between February 20 and March 4, 1974, and this was the only time that sampling was impossible.

Phytoplankton standing crops and production rates were estimated using standard analysis of chlorophyll *a* and *in situ* ^{14}C incubations

Zooplankton populations were sampled concurrently with the phytoplankton populations. Triplicate samples of 250 liters each were pumped through a #20 (80u) mesh net. Subsamples were taken for identification and then filtered, dried at 20^0C to constant weight and reported as biomass (± 0.1 mg).

Nutrient concentrations were measured at monthly intervals from surface, mid-depth and bottom in Block Island Sound and at bimonthly intervals from surface and bottom depths at all five stations in the ponds. Samples were filtered through GFA glass fiber filters and analyzed according to Strickland and Parsons (1968). The nutrients sampled and analytical precisions were reported as follows: NH_3 (± 0.1 ug-atom $litre^{-1}$); NO_3 (± 0.05 ug-atom $litre^{-1}$); NO_2 (± 0.01 ug-atom $litre^{-1}$); DON (not reported); PO_4 (± 0.03 ug-atom $litre^{-1}$); DOP (± 0.03 ug-atom $litre^{-1}$); particulate carbon (not reported). Dissolved organic phosphorus and nitrogen were analyzed by U.V. oxidation. Particulate carbon was measured by filtering all suspended matter onto precombusted GFC 2.4 cm glass fiber filters before combustion in a Hewlett Packard Model 185 13 CHN analyzer (Marine Research Inc., 1975).

Estimating the Flushing Rate for the Charlestown-Green Hill Pond Complex

It is extremely difficult to make a precise determination of the flushing rate for a shallow, morphologically complex system like the Charlestown -Green Hill Pond region. Moreover, the rate varies in different areas of the lagoon and from day-to-day as the tidal range, wind, and freshwater input change. Preliminary simulations using a numerical hydrodynamic model of circulation in the lagoon also suggest that the flushing rate may vary seasonally depending on the extent of eelgrass, Zostera marina, growth (Short n et al., 1974). Nevertheless, we have attempted to derive an average flushing rate for the overall lagoon complex by following the rate of loss of various materials from the lagoon. While freshwater is often used as such a tracer in estuarine systems, the freshwater input here is too small and erratic to be used effectively, especially since the salinity measurements were taken two weeks apart and are only good to 0.1 parts per thousand. Occasionally, however, large pulses of larvae were released in the lagoon. The numbers of larvae in the pond were orders of magnitude higher than offshore, so that a strong gradient was present, and the numbers declined exponentially over time as expected for a first order linear flushing model. The slopes (-k, base e) and coefficients of determination (r^2) for the flushing estimates using this method are summarized in Table 1 and compared with estimates obtained from freshwater budgets and tidal current fluxes. Studies of the offshore circulation using dye, drift bottles, and computer simulation models have shown that only 5-10% of the water leaving the lagoon on an ebb tide re-enters on the next flood (NEPCO, 1978; M. Spaulding, personal communication). There

Table 1. Flushing estimates for Charlestown - Green Hill Pond

Method	Date	r^2	$-k$ day^{-1}	% day^{-1}
Particulate Organic Carbon Loss	7/8-9/10	0.93	0.120	11.3
Bivalve Larvae Loss	6/10-7/1	0.91	0.117	11.0
Gastropod Larvae Loss	18/9-6/11	0.99	0.121	11.4
Polychaete Larvae Loss	28/5-28/6	0.86	0.120	11.3
Polychaete Larvae Loss	23/10-26/11	0.71	0.074	7.1
Fresh Water Budget [1]	Dec.	-	-	9.4
Breachway Water Flux [2]	May, June, Oct., Nov.	-	-	18.0

[1] Conover, 1961
[2] NEPCO, 1978

are difficulties with all of the methods used, but in general they suggested that an estimate of 10% day^{-1} would not be unreasonable, and we have used this value in the flux calculations.

Calculation of Fluxes

Estimates of the net flux of materials between the lagoon and Block Island Sound were calculated by averaging the concentration measurements from surface and bottom samples at the five stations in the lagoon (Fig. 2) and comparing the result with the average of surface, mid-depth and bottom samples from the offshore station (Fig. 2). The difference between the average lagoon and offshore concentration of each material at each sampling time was multiplied by the flushing rate (10% day^{-1}) to produce a daily flux. The daily flux estimates (one for each material for each sampling day) were then integrated over the annual cycle to estimate the yearly flux into and out of the lagoon for a variety of nutrients and organic matter.

RESULTS AND DISCUSSION

Carbon Flux

The concentration of particulate organic carbon was virtually always higher in the lagoon than offshore, with the maximum difference occurring during summer (Fig. 4). While it might be assumed that the higher concentrations in the lagoon were the result of a greater rate of primary production, it is not clear that this is the case. If ^{14}C estimates of phytoplankton net production in the lagoon are combined with estimates of eelgrass pro-

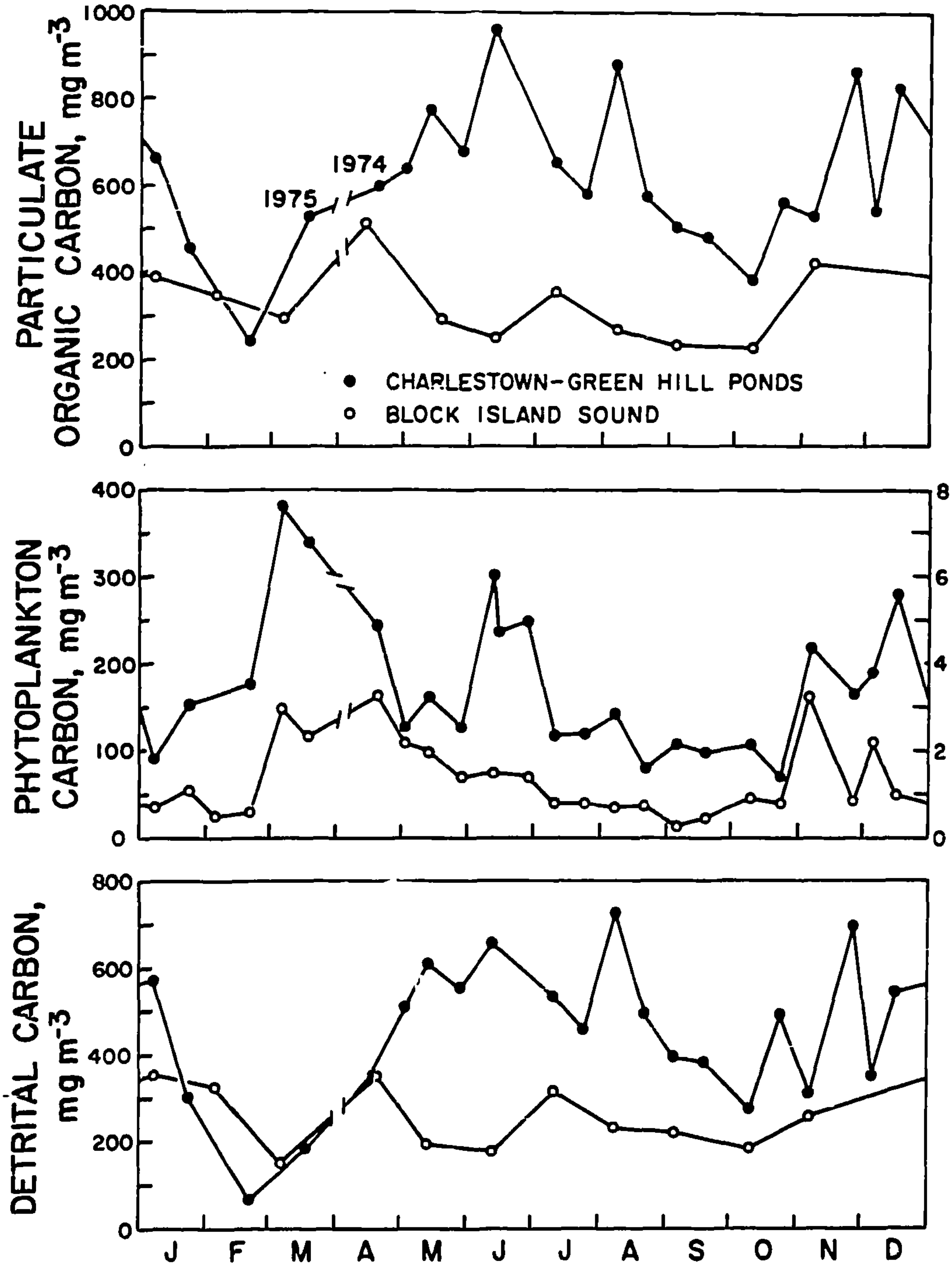

Fig. 4 Mean concentration of particulate organic carbon over an annual cycle in the lagoon and offshore.

duction in the system (Short et al., 1974; Short, 1975) and ^{14}C measurements of epibenthic diatom production from nearby lagoons and estuaries (Marshall et al., 1971), it appears that there may be an annual primary production of about 150 g C m^{-2} within the lagoon. This is only slightly more than recent ^{14}C measurements suggest for Block Island Sound and less than reported earlier for the Sound by Riley (1952). Given the uncertainty in all of these numbers, it does not appear that primary production within the lagoon is appreciably greater than found offshore. However, measurements have not yet been made of seaweed production in the lagoon nor have any estimates been made of the input of detrital carbon from surrounding wetlands. Whatever the source, the concentration gradient results in a flux from the lagoon to the offshore waters of some 158 x 10^6 g C yr^{-1}, or about 13% of the primary production (Table 2).

It is difficult to evaluate the importance of this organic carbon supplement to the ecology of Block Island Sound, but some perspective may be gained by realizing that the carbon flux from the lagoon is approximately equivalent to the carbon fixed in only 10^6 m^2 (approximately 250 acres) of the Sound. Pictured another way, the export from the lagoon to the Sound is roughly equivalent to the production of an area of the Sound that is about 10% of the

Table 2. Annual Carbon Budget for Charlestown - Green Hill Pond

	ug-atom C litre $^{-1}$ yr^{-1}	g C m^{-2} yr^{-1}	10^6 g yr^{-1}
Phytoplankton production	1335	32	265
Eelgrass production [1]	917	22	182
Benthic epiflora production [2]	3751	90	745
Total production	6003	144	1192
Phytoplankton export	328	7.8	65
Zooplankton export	174	4.1	34
Detrital export	301	7.1	59
Total export	803	19.0	158

[1] Short, 1974
[2] Marshall, 1971

size of the lagoon. Even if all of the lagoons along the coast export an equivalent amount of carbon, it is unlikely that it could be a very important term in the energy budget of the offshore waters.

Since the measurements of particulate organic matter included phytoplankton as well as suspended detrital organic matter, we felt that it might be useful to make some attempt to separate the two kinds of material. The concentration of phytoplankton carbon was estimated by converting measurements of Chl a to carbon using a ration of 1:50 by weight (Kremer and Nixon, 1978). Again, the levels of phytoplankton carbon were consistently higher in the lagoon than offshore (Fig. 4). This was true even during fall and spring blooms which may be initiated offshore but produce larger standing crops in the lagoon. Summer blooms in the lagoon appear to be driven entirely by events within the system and do not spread offshore (Fig. 4). The export of phytoplankton carbon appears to be about 65 x 10^6 g yr^{-1}, or 25% of the phytoplankton production (Table 2).

Determination of detrital carbon export was obtained from the difference between particulate carbon and the estimate of phytoplankton carbon. As expected, concentrations were higher in the lagoon so that there was an export on the order of 59 x 10^6 g C yr^{-1}. Thus, the export of detrital carbon was approximately equal to the flux of phytoplankton carbon over the annual cycle.

Because their abundance is so much lower, zooplankton were not really included in the particulate organic carbon measurements. However, it was possible to evaluate their contributions (including meroplankton and ichthyoplankton) to the fluxes of various materials by using independent measurements of zooplankton biomass. It was assumed that 35% of the zooplankton dry weight was carbon. Since the biomass of zooplankton was virtually always higher in the lagoon, there was once again a marked export of carbon from the lagoon (Fig. 5). While the larger standing crop in the lagoon during summer may be due to greater numbers of copepods, the peak in February appears to result from a strong pulse of winter flounder larvae (*Pseudopleuronectes americanus*). The peak in November is due to larvae from the blue mussel, *Mytilus edulis*. The flux of zooplankton carbon is about half of that for phytoplankton and makes up about 20% of the total carbon export (Table 2).

Nitrogen Flux

In general, the oxidized forms of inorganic nitrogen are present in higher concentrations offshore than in the lagoon, so that Block Island Sound acts as a source of nitrate and nitrite. This fertilization from offshore is particularly striking during winter

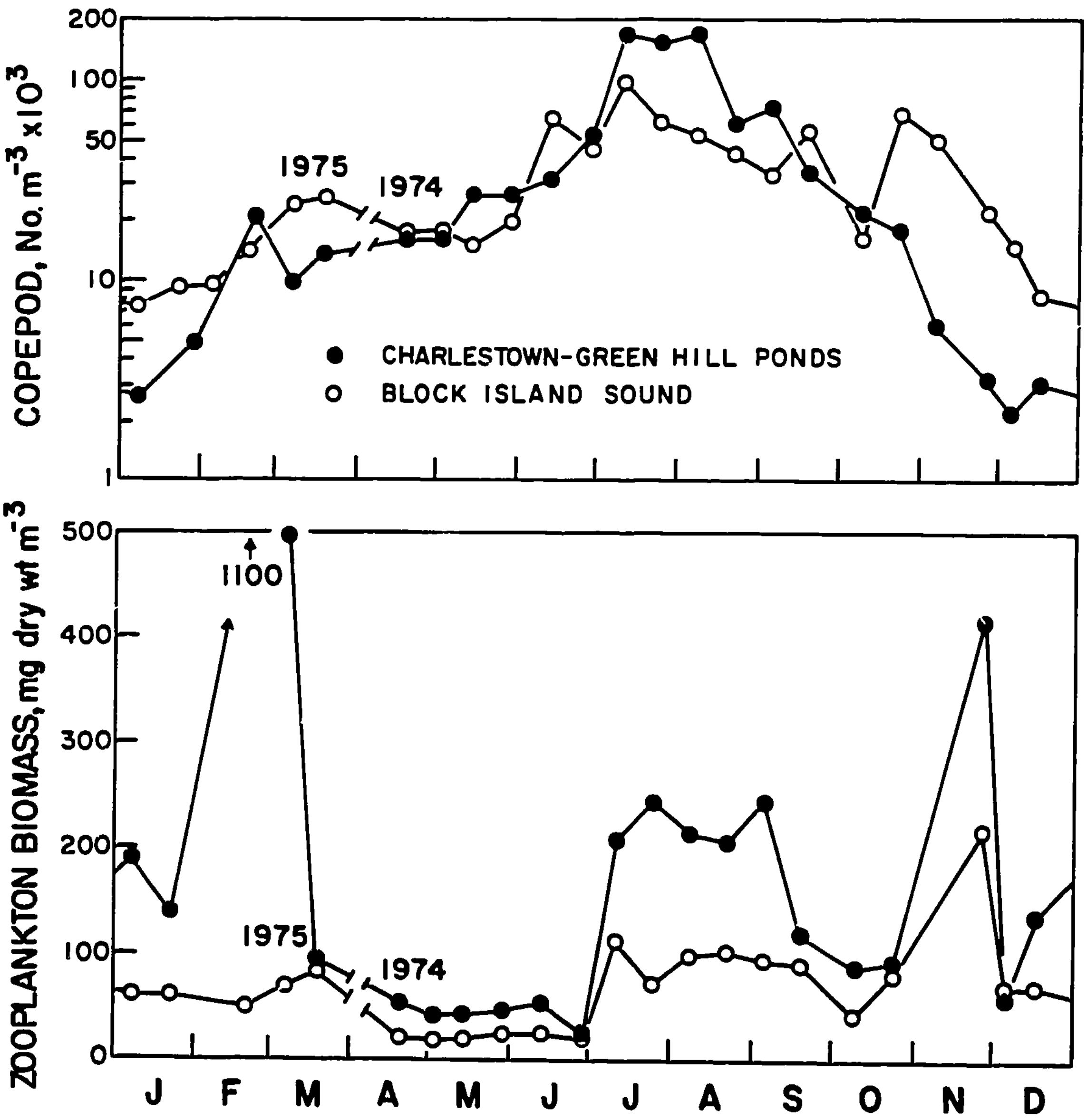

Fig. 5 Mean numbers of copepods and zooplankton biomass (>80u) over an annual cycle in the lagoon and offshore.

and early spring (Fig. 6). It seems remarkable at first that the lagoon should have been able to maintain a concentration gradient of some 2-3 ug-atom litre^{-1} for months at a time when phytoplankton standing crops and productivity were relatively low, there were no obvious algal blooms, and there was virutally no eelgrass growth (Short, 1975). However, a comparison of phytoplankton growth rates as measured by ^{14}C uptake show that even during winter, the productivity of phytoplankton per unit volume in the

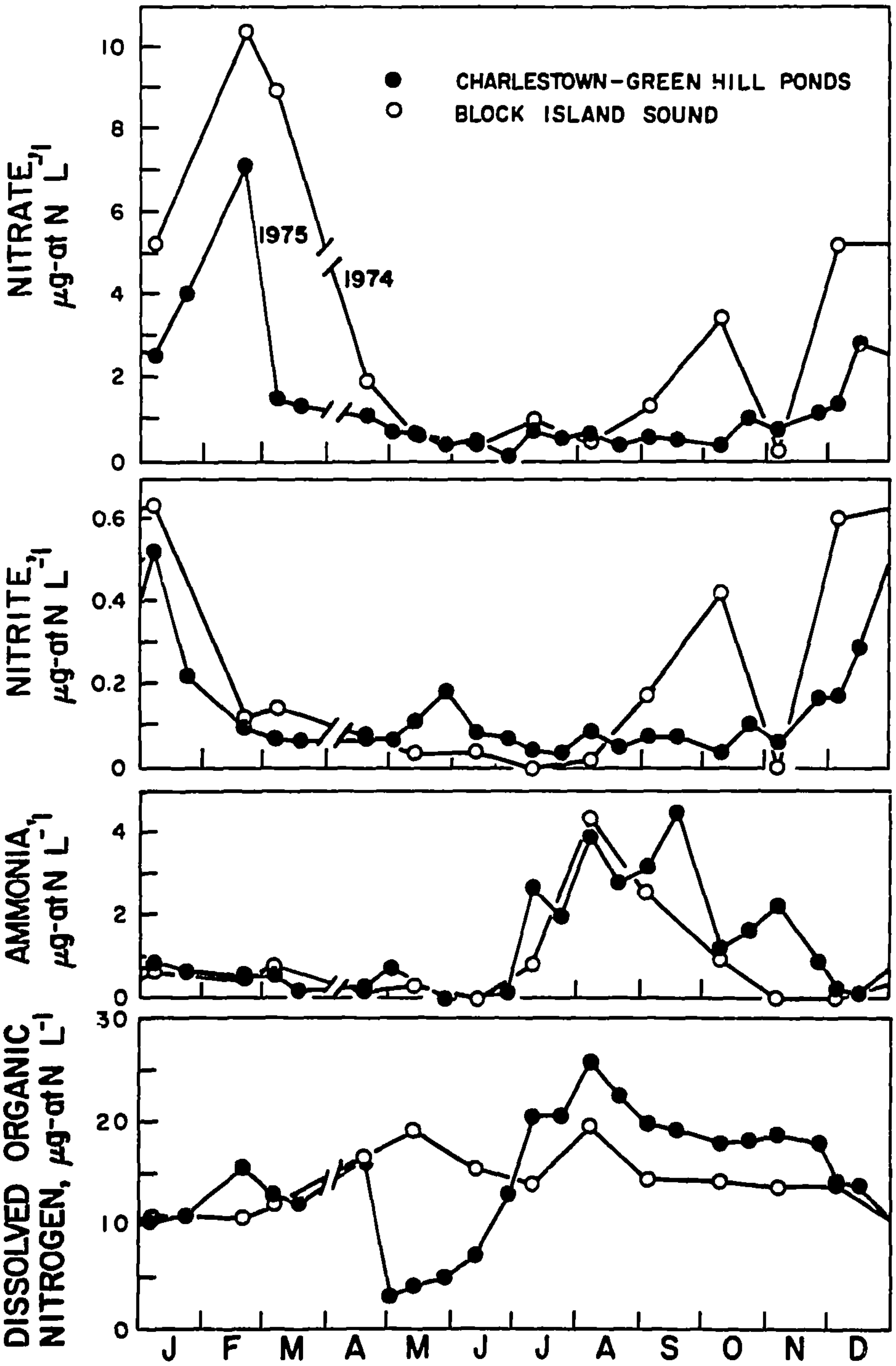

Fig. 6 Mean concentration of nitrogen in various forms over an annual cycle in the lagoon and offshore.

lagoon exceeds that of the Sound by 30-40 mg C m^{-3} day^{-1} (Fig. 7). Assuming that the phytoplankton have a composition approaching that of Redfield organic matter (C:N:P ratio of 106:16:1), this enhanced production would result in an excess nitrogen uptake of about 0.4 ug-atom day^{-1}, or more than enough to maintain the observed concentration gradient in spite of a substantial flux from offshore. When integrated over the entire year, the flux of oxidized forms of nitrogen into the lagoon amounts to about 735 x 10^9 ug-atom $litre^{-1}$ or enough nitrogen to support than 40% of the annual phytoplankton production (Table 3).

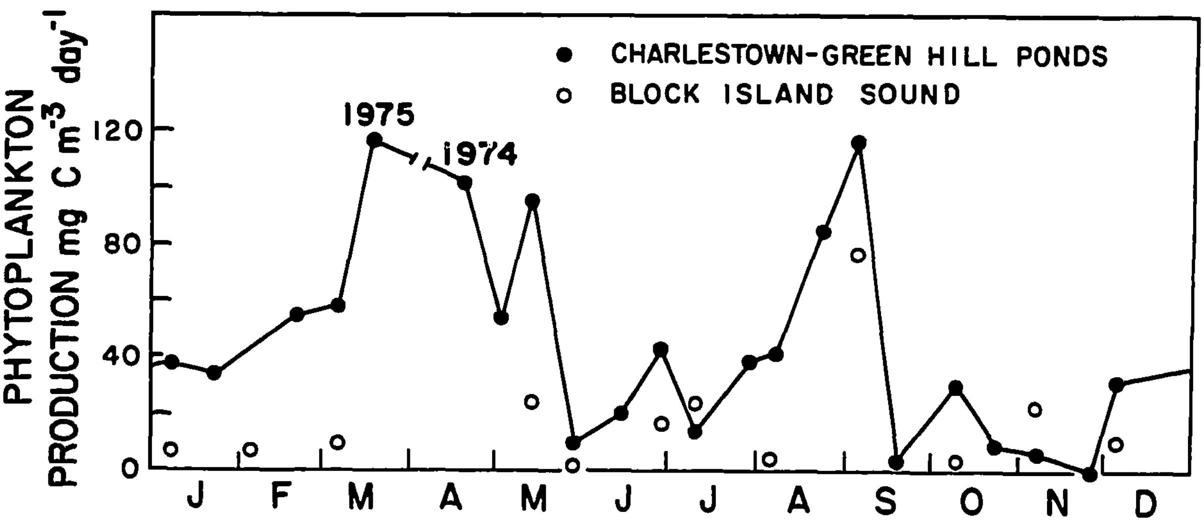

Fig. 7 Mean phytoplankton net production from ^{14}C uptake measurements in the lagoon and offshore. While the production per unit volume is generally lower offshore, the greater depth (20 m vs. 1-2 m) results in a much higher production per unit area.

Ammonia concentrations were highest in summer and fall when values are also higher in the lagoon than offshore (Fig. 6). The timing of the ammonia pulse is probably a result of the lower rate of phytoplankton growth during July and August (Figs. 4 and 7), though it is unclear why the values are not higher in the lagoon. In spite of the fact that phytoplankton growth, and presumably nitrogen uptake rates per unit volume are similar in both areas during this period (Fig. 7), the flux of ammonia per unit volume from sediments to the overlying water should be much greater in the lagoons where the average depth is an order of magnitude less than offshore. The sediments are a major source of ammonia in coastal marine systems during this time of year (Nixon <u>et al.</u>, 1975). It is possible that a large fraction of the nitrogen incorporated into organic matter in the lagoon is exported and not rem-

Table 3. Annual offshore nitrogen exchanges for Charlestown - Green Hill Pond and Block Island Sound.

	ug-atom litre^{-1} yr^{-1}	10^9 ug-atom yr^{-1}
Nitrate		
Imported	85.3	732
Exported	0.4	3
Net Import	84.9	729
Nitrite		
Imported	1.0	9
Exported	0.4	3
Net Import	0.6	6
Ammonia		
Imported	0.9	8
Exported	15.2	130
Net export	14.3	122
Dissolved organic nitrogen		
Imported	56.9	488
Exported	91.7	787
Net export	34.8	299
Particulate phytoplankton Nitrogen		
Imported	0	0
Exported	49	420
Net export	49	420
Particulate zooplankton nitrogen		
Imported	0	0
Exported	26	223
Net export	26	223
Particulate detrital nitrogen		
Imported	0	0
Exported	45	386
Net export	45	386

ineralized in the sediments, thus resulting in an abnormally low ammonia release. The same result may also be due to vigorous eelgrass growth earlier in the summer (Short, 1975) which has depleted the sediment pore water ammonia (Okuda, 1960). Of course, it may be that the ammonia flux from the sediments in the lagoon is high, but that the nitrogen is rapidly taken up by very productive epibenthic diatoms and algae in the lagoon (Marshall et al., 1971). In any case the similarity of ammonia concentrations results in a relatively small summer export of ammonia nitrogen from the lagoon compared with an import of nitrate during the winter that is more than five times greater (Table 3).

While there is a net flux of inorganic nitrogen into the lagoon from offshore over the year, there is a much larger export of organic nitrogen (Table 4). About 20% of this organic nitrogen leaves the lagoon as dissolved organic nitrogen (Fig. 6), while the rest is in particulate form (Table 3). There is considerable uncertainty about the exact values of particulate nitrogen, of course, since they have been inferred from carbon values rather than measured directly as the dissolved forms were. Nevertheless it seems clear that the lagoon acts as a nitrogen transformer, importing oxidized inorganic nitrogen from offshore and exporting

Table 4. Annual nitrogen balance for Charlestown - Green Hill Pond and Block Island Sound.

	ug-atom litre^{-1} yr^{-1}	10^{12} ug-atom yr^{-1}
Total nitrogen		
Imported	144	1.24
Exported	228	1.96
Net export	84	0.72
Inorganic nitrogen		
Imported	87	0.75
Exported	16	0.14
Net import	71	0.61
Organic nitrogen		
Imported	57	0.49
Exported	212	1.82
Net export	155	1.33

reduced and particulate nitrogen (Table 4). While the offshore exchange budget suggests that nitrogen input from land and freshwater are important in maintaining the production of the lagoon, it appears that the major nitrogen input to the system comes from offshore.

Phosphorus Flux

There are two striking differences between the seasonal cycle of phosphate abundance in the lagoon and offshore (Fig. 8). First, as might be expected, the cycle offshore shows a typical open ocean pattern with a winter maximum and summer minimum, while the lagoon shows a typical estuarine cycle with a summer maximum. Second, and quite surprisingly, the levels of phosphate in the lagoon are much lower than found offshore. This is the opposite of the usual estuarine concentration gradient such as that found in nearby Narragansett Bay (Kremer and Nixon, 1978). These two features result in a large flux of phosphate from offshore into the lagoon (Table 5). As with nitrate (Fig. 6), the phosphate flux into the lagoon is particularly strong during winter when biological activity is minimal. However, while the excess of phytoplankton carbon fixation per unit volume in the lagoon compared with offshore during this period (Fig. 7) could account for the lower nitrate levels observed, it does not appear large enough to maintain the phosphate concentration gradient. For example, if Redfield organic matter is being produced, the excess of lagoon primary production over that of the Sound is about 30 mg C m^{-3} day^{-1} (2.5 ug-atom $litre^{-1}$ day^{-1}) which would require a phosphorus uptake of about 0.02 ug-atom P $litre^{-1}$ day^{-1}. The estimated flux into the lagoon at this time is about four times greater. It is quite possible that much of the phosphate being brought into the lagoon is being taken up by the sediments (Stirling and Wormald, 1977) or being removed by reactions with iron.

As with nitrogen, there is a net export of both dissolved and particulate organic phosphorus over the year (Table 5). The net result is a marked imbalance in the phosphorus exchange between the lagoon and the Sound, with exports exceeding imports by more than 50% (Table 6).

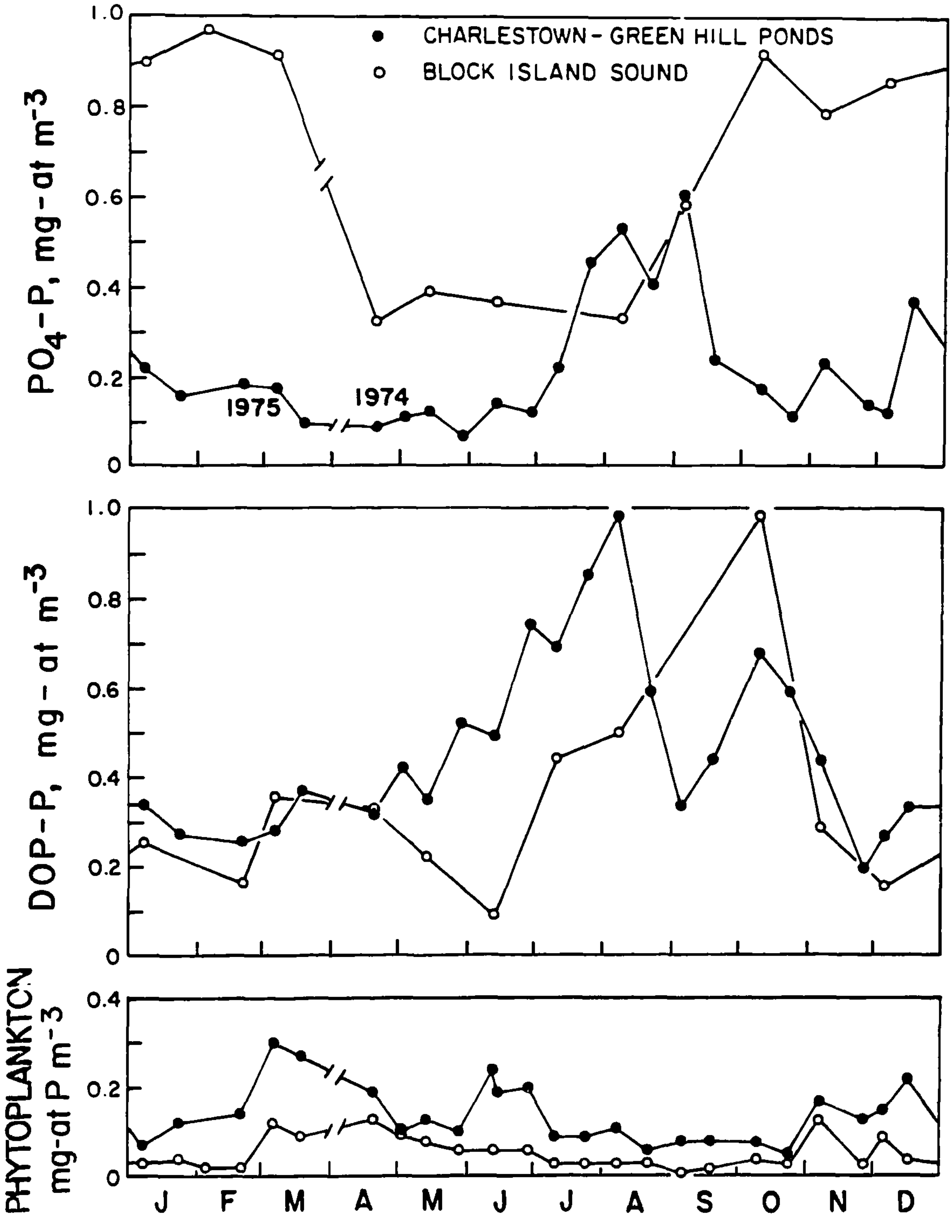

Fig. 8 Mean concentration of phosphorus in various forms over an annual cycle in the lagoon and offshore.

Table 5. Annual offshore phosphorus exchanges for Charlestown - Green Hill Pond and Block Island Sound.

	ug-atom litre $^{-1}$ yr^{-1}	10^{9} ug-atom yr^{-1}
Phosphate		
Imported	5.86	50.3
Exported	0.47	4.0
Net import	5.39	46.3
Dissolved organic phosphorus		
Imported	1.87	16.0
Exported	3.98	34.0
Net export	2.11	18.0
Particulate phytoplankton phosphorus		
Imported	0	0
Exported	3.06	26.3
Net export	3.06	26.3
Particulate zooplankton phosphorus		
Imported	0	0
Exported	1.64	14.1
Net export	1.64	14.1
Particulate detrital phosphorus		
Imported	0	0
Exported	2.84	24.4
Net export	2.84	24.4

Table 6. Annual phosphorus balance for Charlestown - Green Hill Pond and Block Island Sound

	ug-atom $litre^{-1}$ yr^{-1}	10^9 ug-atom yr^{-1}
Total phosphorus		
Imported	7.73	66.3
Exported	11.99	102.9
Net export	4.26	36.6
Inorganic phosphorus		
Imported	5.86	50.3
Exported	0.47	4.0
Net import	5.39	46.3
Organic phosphorus		
Imported	1.87	16.0
Exported	11.52	98.8
Net export	9.65	82.8

If the lagoon is in approximate long term steady-state with regard to phosphorus, the supposition is that this excess is being met by inputs from land and freshwater. Even if this is true, the role of the offshore waters as a source of phosphorus is appreciably greater.

Again, the lagoon and offshore waters are tightly coupled systems in which the lagoon imports oxidized inorganic phosphorus and exports the material in reduced organic form. While the flux from offshore is clearly of major importance in maintaining the productivity of the lagoon, it is more difficult to establish the importance of the reciprocal organic export from the lagoon to the ecology of the offshore waters. It may be that the importance of the organic export lies more in its quality and form then in its bulk quantity. Fish eggs, larvae and plankton may have a much greater impact on the offshore waters than their contribution to the mass of carbon exchanged suggests.

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Management Council and the Office of Sea Grant Programs, U.S. Dept. of Commerce, NOAA.

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