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Course on Oceanography of Semi-Enclosed Seas
15 April - 3 May 1991

"Selected Topics in Marine Biology"

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Selected topics in marine biology[1]

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1. PLANKTON AND PRODUCTIVITY IN THE OCEANS

1.1. Terminology

Plankton consists of the group of organisms unable to move against horizontal or vertical transport of the water. Plankton may be floating or may live at the air-seawater interface. It can be divided into ***bacterioplankton, phytoplankton and zooplankton.*** In the contrary to plankton, members of the ***nekton*** (adult fishes, some crustacea, cephalopods and marine mammals) are capable of counteracting currents. ***Neritic plankton*** occurs in waters above the continental shelf. ***Oceanic plankton*** (=***pelagic plankton***) is found oceanward from the continental shelf - continental slope break. ***Holoplankton*** are organisms that spend essentially all their active life stages in the open waters. ***Meroplankton*** consists of organisms having alternate pelagic and bottom

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dwelling phases in their life cycles. ***Plankton productivity*** refers to the amount of living tissue produced per unit time. It is often estimated as carbon contained in living material and generally expressed as grams of carbon produced daily in a column of water intersecting one square meter of sea surface (gC/m^2/day) or as a grams of carbon in a given cubic meter per day (gC/m^3/day). ***Primary production*** is that part of the productivity ascribed to photosynthetic plankton. ***Secondary production*** refers to the production of organisms that consume the growth products of primary production. Similarly, ***tertiary production*** refers to the consumption of the secondary producers. ***Food chain*** is a transfer scheme from primary to secondary and higher-level producers. Similarly, a ***food web*** describes an array of species with more complex food transfer patterns. ***Standing crop*** or ***biomass*** is measured as dry weight or wet weight in a given volume of seawater (mg/liter, g/m^3). In order to estimate biomass at the primary producer level, instead of dry weight we might measure a related parameter, such as chlorophyll. ***Grazing*** is general term for predation on smaller organisms, frequently used to describe feeding of the zooplankton.

1.2. Composition of the phytoplankton

Diatoms are dominant members of the phytoplankton, particularly in the temperate and boreal inshore waters. Diatom cells are enclosed in a siliceous frustules which give them characteristic rigid shapes. The cell size ranges from 10 to 500 μm. They may occur as single cells or as cell chains. Binary cell division is the dominant way of reproduction in diatoms. Interestingly, resting spores are produced by many neritic species during unfavorable conditions. Diatoms frequently build up large stocks because of their high growth rate; optimal cell doubling rate is in the range of 0.5 to 6 doublings per day.

The ***dinoflagellates*** are motile unicellular algae with two flagella, one of which is located in a girdle groove around the body. Because of their motility (some forms can swim up to 10 m per day) the dinoflagellates are generally not as uniformly distributed in the water column as are non-motile diatoms, but tend to congregate in layers of a few metres tick. This group often dominate the subtropical and the tropical phytoplankton and are important constituents of the phytoplankton of temperate and

boreal autumn assemblages. Dinoflagellates are particularly noteworthy as the cause of the harmful ***red tides***. Red tide is the name given to the dense phytoplankton population appearing suddenly and coloring the water red or red brown. Various algae may contribute to red tides but only species of the genera *Gonyaulax* and *Gymnodinium* are responsible for a toxic effects such as invertebrate and fish mass mortalities. When these plankters are filtered by oysters and other shellfish, the shellfish become highly poisonous and may prove fatal if consumed. Bioluminescence is common in dinoflagellates and the flickering of shallow waters at night can usually be attributed to *Noctiluca*.

The ***coccolithophores*** are unicellular golden brown algae which are important constituent of the pelagic phytoplankton, especially in tropical waters. The cells are approximately spherical and covered with a series of calcium carbonate buttons or plates known as coccoliths. Vast deposits of coccoliths occur in places at the ocean floor.

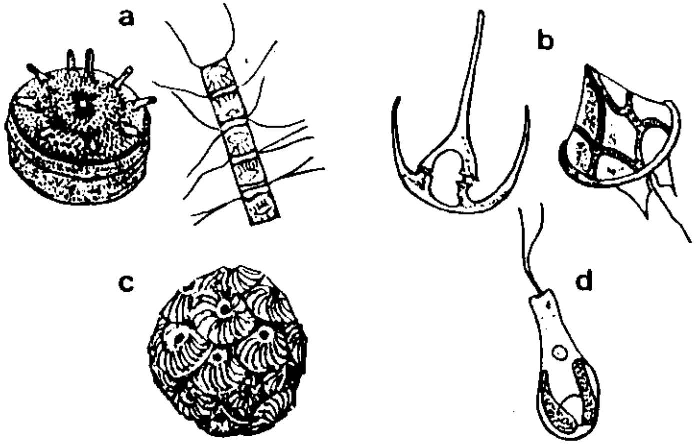

Figure 1. Some members of the phytoplankton: (a) Diatoms; (b) Dinoflagellates; (c) Coccolithophores; (d) Microflagellates (from Levinton, 1982).

1.3. Composition of the zooplankton

Copepods are the largest group of crustacea in the world zooplankton fauna. They range from less than 1 mm to several millimeters in length. Most species are free-living zooplankters, usually ingesting phytoplankton as their principal food source. The calanoid copepods dominate oceanic systems; *Calanus finmarchicus* is widespread in all temperate to Arctic seas. The calanoid copepods employ a filtering mechanism to obtain particles from the water. The female lays eggs in clutches with an interval of about half a month between each clutch. The clutch size is determined by the food availability for females. Copepods have large depth distribution and undergo vertical migrations involving active movement toward deeper water during the day with movement toward the surface at night.

Cladocera are important in inshore and particularly estuarine zooplankton communities. The genus *Podon*, for example, occurs in estuaries and preys on other zooplankton.

Euphausids are small shrimplike planktonic crustacea that are common in pelagic waters of high productivity throughout the world. They are the most important food of baleen whales in the Antarctic. Euphausids often occur in high concentrations and occasionally are dominant members of the deep scattering layers that reflect sonar. Many species are luminescent. The luminescent material is located within the light-producing organs called photophores.

Pteropods are highly modified holoplanktonic gastropods, swimming with lateral projections from the side of the foot (parapodia). Pteropods can occur in great numbers under appropriate conditions of tides and currents. The pteropod shells sink to the bottom in great abundance and form sediments known as pteropod oozes.

Larval forms - most groups of marine animals pass trough a larval stage that acts as the distributory phase in the life cycle. The eggs hatch not into a miniature adult but into a minute transparent larva as different from the adult as caterpillar from a butterfly. The larvae of several different groups share the same characteristics, because they face the common problems of keeping afloat in the plankton during the dispersal phase. They then need to select the site for settling and transformation into the adult. Larvae, therefore, are often ciliated, with cilia arranged in rings and bands around the surface. They usually have eyespots to help direct them into the rich grazing of the upper layers, and simple equilibrium sensors to keep them upright. To aid ciliary or muscular effort to maintain position, larvae often have long extensions of the body to slow the rate of sinking. Change to adult form may be remarkably radical and rapid, or it may be a long gradual process.

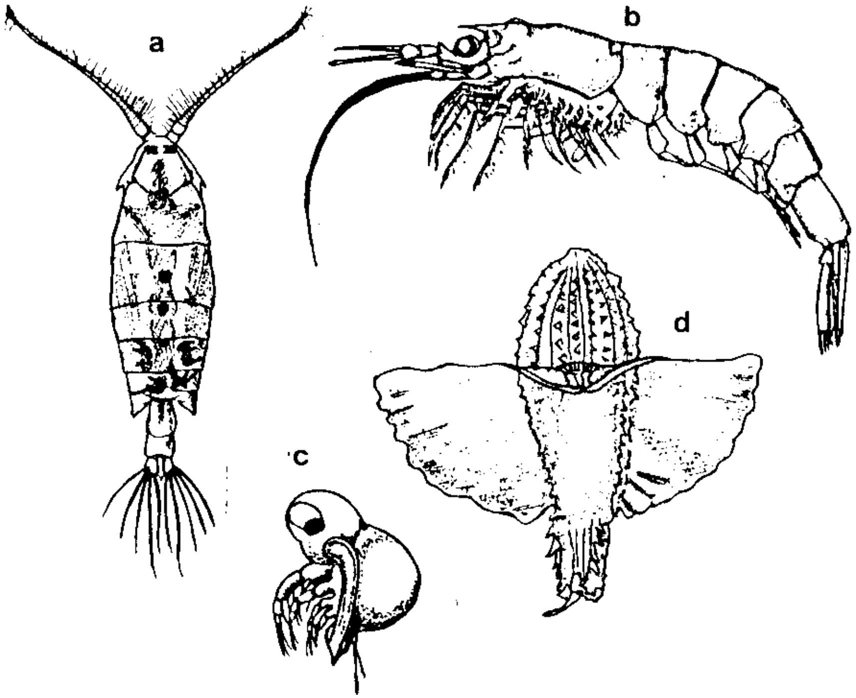

Figure 2. Some members of the zooplankton: (a) Copepods; (b) Euphausids; (c) Cladocerans; (d) Pteropods.

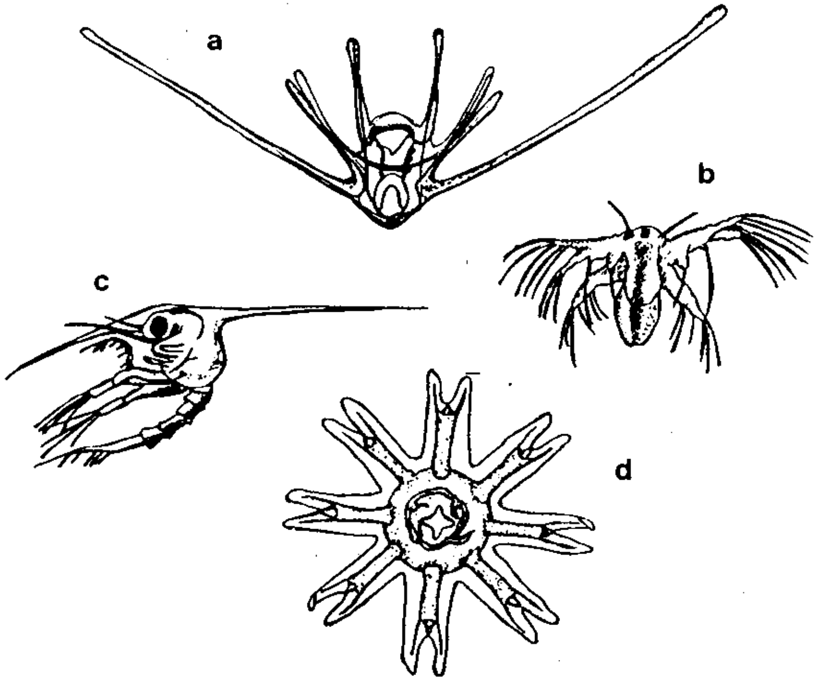

Figure 3. Some larval forms: (a) ophiopluteus (Brittle stars); (b) Nauplius (Copepods); (c) Zoea (Crustacea decapoda); (d) ephyra (Jellyfishes).

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Please note: These notes are intended for internal distribution only

2. PLANKTON DYNAMICS AND SPATIAL STRUCTURE

2.1. Terminology

Aggregated spatial distribution is the case where individuals in space occur in clusters too dense to be explained by chance. Similarly, ***patchiness*** is the condition where organisms occur in aggregations. A ***bloom*** is a population burst (usually phytoplankton) that remains within a defined part of the water column. A dense outburst of phytoplankton (usually dinoflagellates) coloring water red or brown is known as the ***red tide***. Consequently, the ***spring diatom increase*** is the major rapid population increase of diatoms occurring during spring in temperate-boreal latitudes. The ***euphotic layer*** is the depth zone extending from the surface to the depth permitting photosynthesis. The lower boundary of this zone is usually defined as the depth of the 1% daylight penetration. ***Compensation light intensity*** is that light intensity at which oxygen evolved from a photosynthesizing organism equals that consumed by its respiration. ***Compensation depth*** is the depth of the compensation light intensity. ***Critical depth*** is the depth above which total integrated photosynthetic rate in the water column equals total integrated respiration.

2.2. Plankton dynamics in a seasonal cycle

Plankton standing crop often shows a predictable seasonal dynamics that can be explained in terms of a few parameters. The pattern differs geographically as follows (Fig. 4). In the Arctic a single summer peak of phytoplankton abundance is followed by a peak of zooplankton abundance. In neritic temperate and boreal environments a spring phytoplankton increase is followed by a decrease, which coincides with a zooplankton increase. In the late spring and summer the zooplankton decline and a peak of phytoplankton follows in the fall. In the tropics no obvious alternate pattern of phytoplankton and zooplankton abundance occurs. Figure 5. shows an idealized diagram tracing changes in plankton, light, and nutrients during the year in a temperate-boreal inshore waters. Generally, the spring is dominated by a large increase in the diatom populations. The patterns of riverine inflow, upwelling and/or the accumulation of nutrients from winter may contribute to this spring diatom increase. Guillard and Kilham (1977) have summarized three main stages in this process. Stage I is initiated by a set of factors that permit sudden nutrient availability under favorable condition for diatom growth. A diatom increase is dominated by species with small cell size, high surface to volume ratio (1 in terms of $\mu m^2/\mu m^3$), high division rates (higher than one doubling per day), and high standing crop indicating bloom conditions (10^6 - 10^7 cells/l). Stage II is characterized by larger cells with reduced surface to volume ratio (0.2 - 0.5), an increased diatom species richness, and reduced standing crop (10^4 - 10^5 cells/l). Dissolved nutrients are now on the decline.

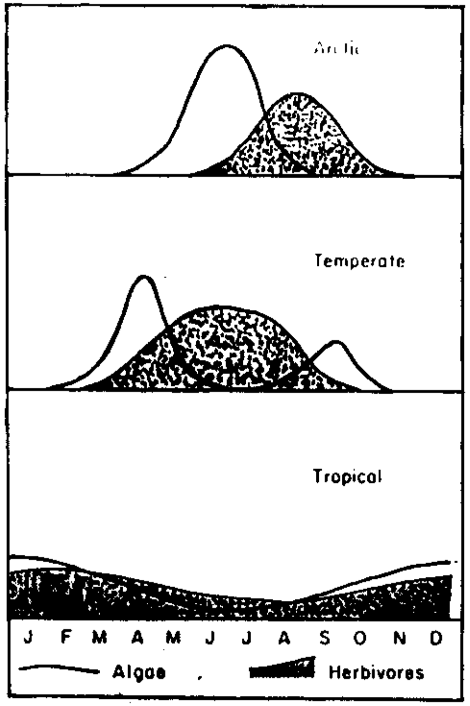

Figure 4. Phytoplankton and zooplankton seasonal cycles at different latitudes: (a) Arctic; (b) temperate-boreal neritic; (c) tropical (after Cushing, 1975).

Stage III is characterized by diatoms capable on doing well under conditions of low dissolved nutrients. Species in this stage are survivors of stage II. Standing crop decreases and diatoms that have dominated previous stages produce resting spores and sink out from the nutrient poor water column. The decline in diatoms is followed by phytoplankton flora that varies depending on locale. Very often, in summer and fall microflagellates and particularly dinoflagellates become abundant. Generally, the zooplankton become abundant and reach their yearly maximum after the spring diatom increase. The initial dominance is primarily by calanoid copepods, the major grazers of diatoms. Maximum copepod standing stock is reached in the summer months. Depending on varying conditions, the different groups may dominate the zooplankton. Often, in coastal and estuarine areas the cladocerans are very abundant during the summer months. Meroplanktonic larvae of benthic invertebrates are common in late spring and early summer months.

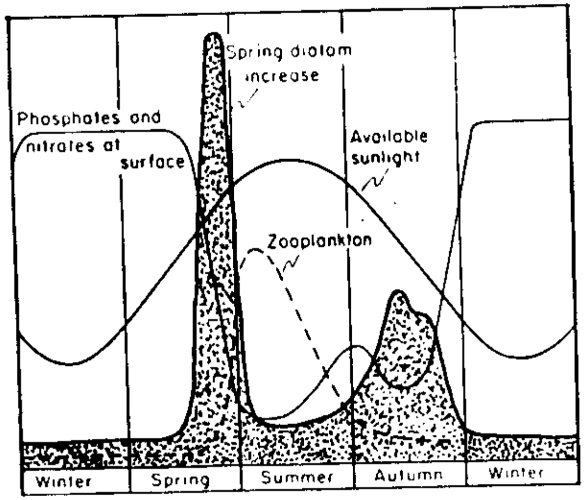

Figure 5. Idealized diagram tracing changes in plankton, light and nutrients during the year in a temperate-boreal inshore body of water (from Levinton, 1982).

Water column parameters are extremely important for the development of plankton blooms. Light intensity, for example, decreases exponentially with increasing depth and becomes a limiting factor for photosynthesis. At the compensation depth the photosynthetic rate equals the respiration rate. At the depths below the compensation depth the decay of organic matter will prevail the production. Therefore, it is unlikely that the phytoplankton bloom will start in that portion of the water column below the compensation depth. These relationships would hold if there is no vertical mixing in the water column. Figure 6. shows various stages of phytoplankton growth in a stratified water column. At time t_0, just after active vertical mixing of water, the plankton is uniformly distributed and hence the respiration must be constant as a function of depth. However, the photosynthesis per unit biomass at each depth is different, being inhibited at near surface by high light intensities and then decreasing from a subsurface maximum due to light attenuation. Therefore, the growth rate of phytoplankton will be different at each depth and the profiles of phytoplankton biomass and photosynthesis will change with time. As the phytoplankton biomass increase at the sub-surface photosynthetic maximum, the average extinction coefficient

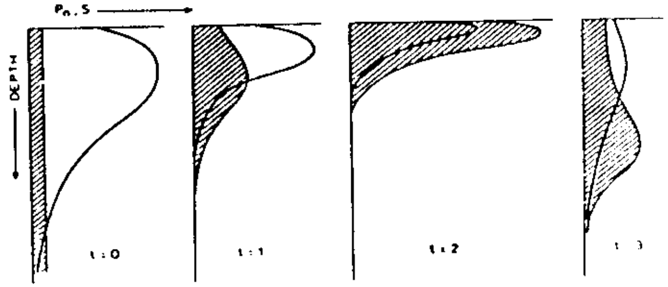

Figure 6. Schematic changes in phytoplankton biomass (S,▨) and photosynthetic activity (P_n,–) after three time intervals (t) in stratified water column (from Parsons et al., 1984).

of light will also increase, and self-shading will occur. Accordingly, the compensation depth and the maximum in phytoplankton growth becomes shallower. Providing there are sufficient nutrients, the pattern of photosynthesis and the standing stock of photosynthesis will finally maximize at the surface as a thin layer and the bloom will occur ($t=2$). As nutrients become exhausted in the surface layers, however, the depth of the maxima in the phytoplankton maxima and the primary productivity increases ($t=3$). If the water column is mixed (Fig. 7), plankton is uniformly distributed and hence respiration must be approximately constant as a function of depth. On the other side, the photosynthesis per unit biomass will decrease exponentially with depth. The phytoplankton bloom can occur only in the portion of the water column above the critical depth where the integrated total production exceeds consumption (respiration in this case). If the mixing depth is greater than the critical depth a phytoplankton bloom can not start because any potential profit in photosynthesis is lost through mixing to greater depths. Water column stability is thus an essential factor for the development of plankton blooms.

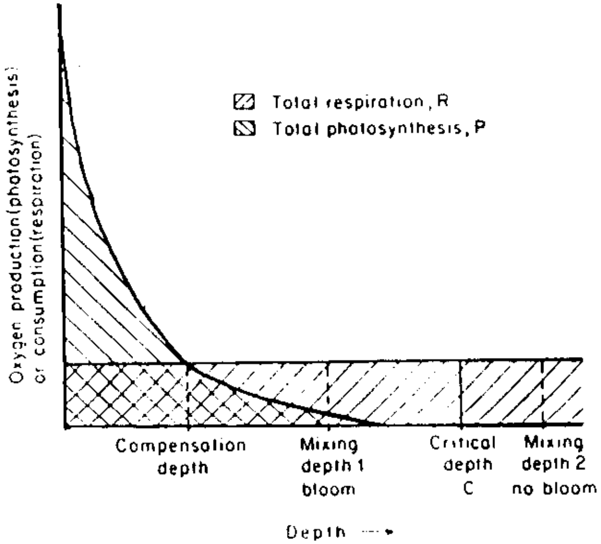

Figure 7. The relation of critical depth (C) and mixing depth (M) in the development of phytoplankton bloom (from Parsons et al., 1984).

2.3. Spatial structure of plankton: patchiness of plankton distributions

Figure 8. shows three basic patterns of spatial distribution. A sample of plankton rarely comes from a homogeneously distributed population. Both phytoplankton and zooplankton have aggregated spatial distributions at all scales of sampling. Parsons and Takahashi (1973) have summarized processes promoting formation of patchiness:

a) Physical-chemical boundary conditions, including light, temperature and salinity gradients.

b) Advective effects as in water transport, including small scale variations due to turbulence.

c) Grazing.

d) Reproduction rates within the population.

e) Social behaviour in populations of some species.

d) Intraspecific interactions resulting in either attraction or repulsion between species.

Wind moving over the surface generates spatial structure over a wide range of scales. Langmuir circulation results from the creation of vortices caused by wind-driven

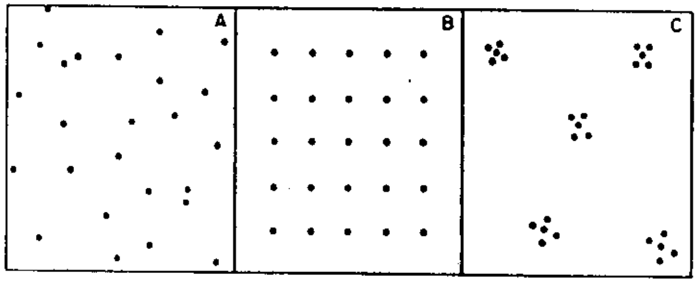

Figure 8. Patterns of spatial distribution: (a) random; (b) uniform; (c) aggregated.

water movement (Fig. 9). Phytoplankton cells may be sorted by small currents while zooplankton may be trapped in an upward current while attempting to swim downward to avoid surface light (Stavn, 1971). Wind-driven water motion often arranges Langmuir circulation along linear tracks. This can be observed in the Sargasso Sea, where *Sargassum* weed floats on the surface form wind rows. Consequently, plankton samples collected parallel with the wind direction will be more variable than those collected perpendicularly to the wind.

Patchiness on the scale of approximately 200 km occurs within the cyclonic rings occurring in the Gulf Stream (Fig. 10). The advection of colder and deeper water towards the surface brings with it a supply of nutrients which is the basis for the increased primary productivity and standing crop within the ring.

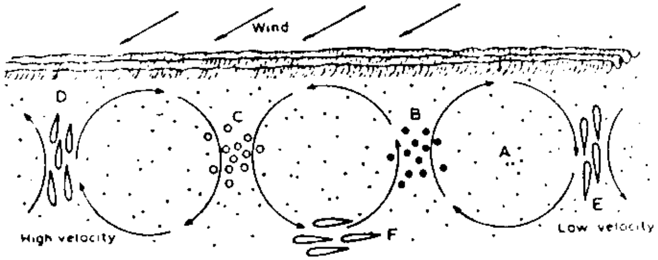

Figure 9. Langmuir vortices and plankton distribution (after Stavn, 1971): A - neutrally buoyant particles randomly distributed; B - particles tending to sink, aggregated in upwellings; C - particles tending to float, aggregated in downwellings; D - organisms aggregated in high velocity upwelling, swimming down; E - organisms aggregated in low-velocity downwelling, swimming up; F - organisms aggregated between downwellings and upwellings where there is less relative current velocity than within the vortices.

It has been observed many times that zooplankton patches tend to alternate with the phytoplankton patches. Active movement of zooplankters and overgrazing of phytoplankton patches may result in such alternations (Fig. 11).

The vertical component of plankton patchiness is determined by a variety of factors including light intensity, density gradients and the availability of nutrients (food) at the surface. The vertical migration of zooplankton and their aggregation at specific depths is also extremely important.

The simplest consideration in determining the smallest size scale of a plankton patch is to consider the growth rate versus the rate of diffusion of plankton away from the patch. Obviously, if diffusion exceeds the growth rate, the patch is destroyed. From theoretical considerations, Okubo (1977) has summarized various estimates of patch size and concludes that for a phytoplankton growth rate of 1 division per day the patch (if circular) could maintain the size of about 1-2 km. For the growth rate of 0.1 division per day the patch size has to be from 15 to 50 km.

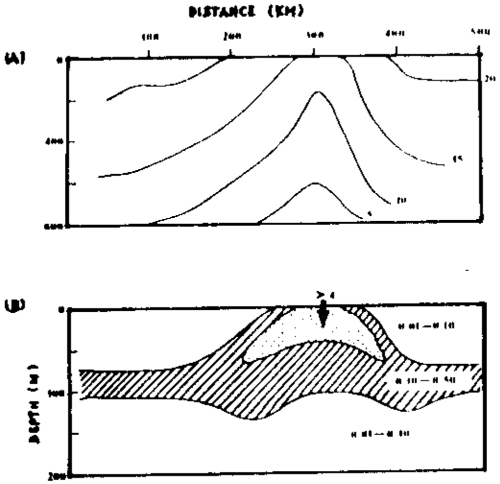

Figure 10. Approximate vertical section through a cyclonic ring in a subtropical ocean: (a) temperature; (b) phytoplankton biomass (µg Chl*a*/l) (from Parsons et al., 1984).

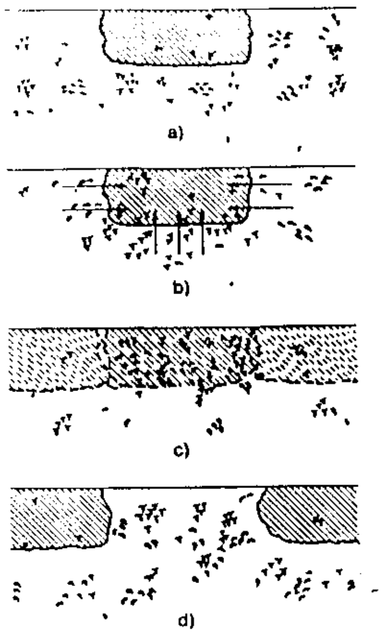

Figure 11. Schematic presentation explaining alternations of phytoplankton and zooplankton patches (after Bainbridge, 1953).

3. BIOLOGICAL CONSEQUENCES OF MARINE EUTROPHICATION: THE NORTHERN ADRIATIC SEA CASE

3.1. Terminology

Environmental stress may be defined as an environmental change to which an organism cannot acclimate. Consequently, ***disturbance*** is a rapid change in the environment that greatly alters previously persistent biological community. Water bodies or habitats with high concentrations of nutrients are ***eutrophic*** while those with low concentration of nutrients are ***oligotrophic***. Natural or anthropogenic introduction of nutrients and organic matter into the aquatic environments promotes various interrelated processes on the ecosystem level which are known as ***eutrophication***.

3.2. Eutrophication of the northern Adriatic Sea: origin and historical development

Twenty two years ago Piccinetti & Manfrin observed a mass mortality of benthic animals in the coastal waters near Rimini (Fig. 12). This phenomenon, apparently caused by hypoxia near the bottom, has become more frequent and more widespread in the ensuing years. In September 1974 a mass mortality of bottom macrofauna was recorded in the Bay of Trieste. During September and October 1975, oxygen depletion caused a wide-range benthic mortality along the coast south of the Po Delta while during autumn 1977 extensive areas of mass mortality were detected south of Venice. Similar events were observed in the Bay of Trieste during September 1980 and again during September 1983 when the affected area was estimated to cover between 50 and 150 km^2 (Stachowitsch, 1984). The most recent reports describe a wide-range hypoxia in connection with benthic mortality during the late summer 1988 and 1989. Several interrelated arguments support the hypothesis that the increasing occurrence of mass mortalities in the northern Adriatic Sea is a consequence of eutrophication. First, an analysis of the oxygen data collected during summers 1911-1984, demonstrated a trend towards higher values near the surface (Fig. 13a) and a trend towards lower values near the bottom (Fig. 13b). The changes appear to be substantial: during the last 75 years the oxygen concentration has increased for about 1.1 ml l^{-1} at the surface and decreased for about 2.2 ml l^{-1} at 2m above the bottom. In addition, the readings of

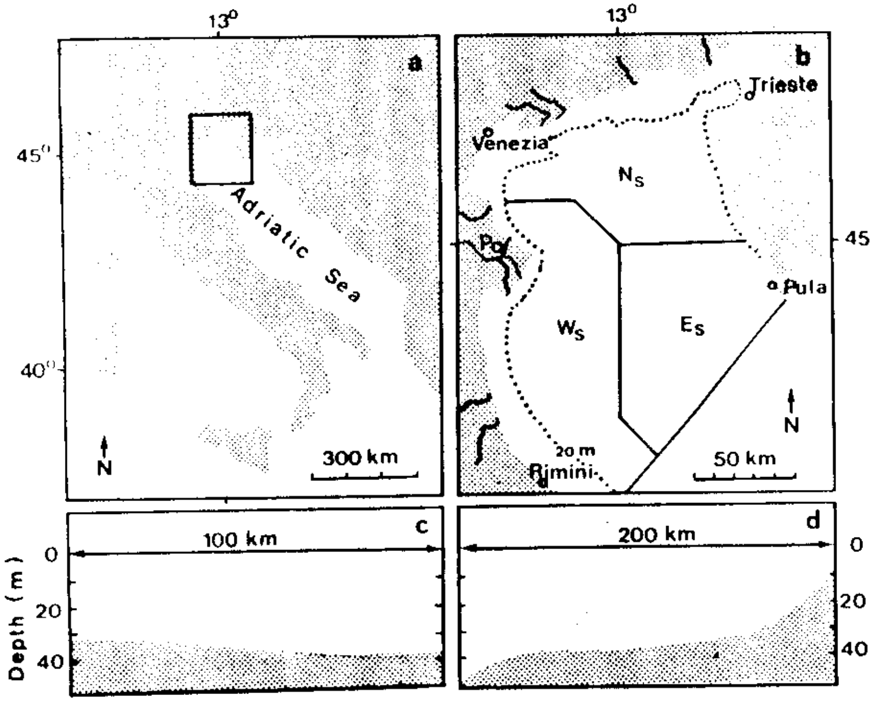

Figure 12. The area of the northern Adriatic Sea. E_s, N_s and W_s indicate eastern, northern and western subareas, respectively. The cross-sections along 45°N (c) and 13°E (d) are shown.

Secchi disk depth, during springs 1911-1981 show a clear decreasing trend (Fig. 13c). The data exhibit also additional features: the trends in oxygen content and Secchi disk depth become evident after 1965; before that date they are practically undetectable. In addition, the variability of the data begin to increase after 1965; the rate of change is the smallest in the southern subarea, increases in the northern subarea while being the most pronounced in the western subarea.

The identification of 1955-1965 as a start of a significant trend of increase in oxygen concentration at the surface and a decrease near the bottom may be explained

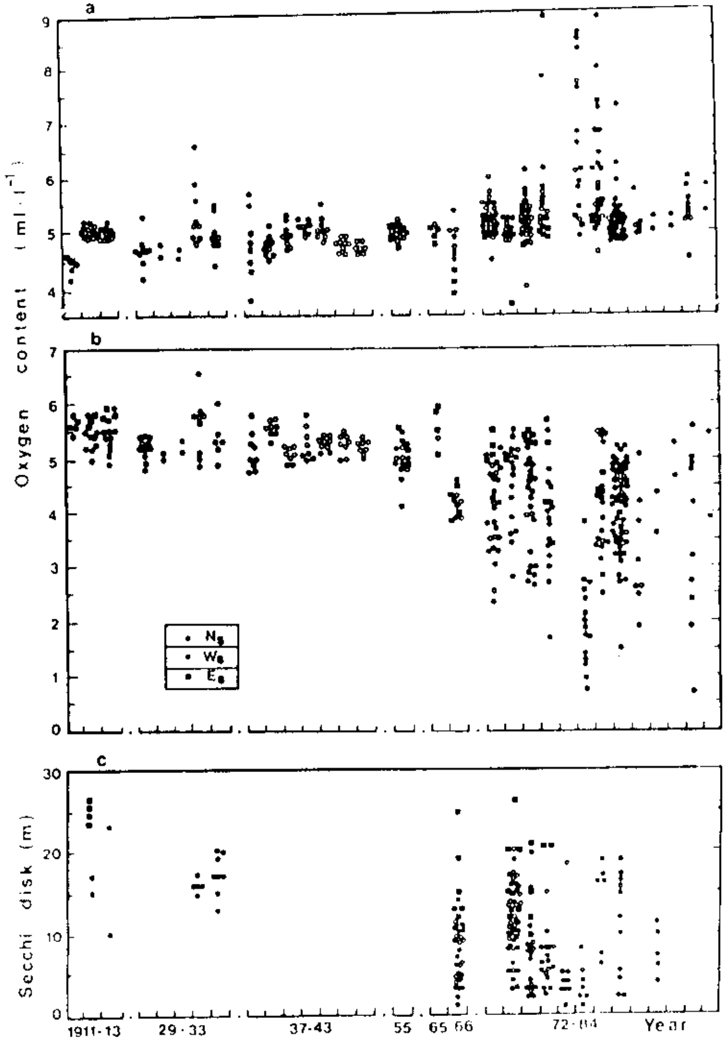

Figure 13. Oxygen content during August-September (a, b) and Secchi disk visibility during April-May (c), in the northern Adriatic Sea from 1911 to 1984; (a) - surface layer, (b) 2m above the bottom.

by the fact that in those years fertilization practices and usage of detergents containing phosphorus were started to increase rapidly. The consumption of nitrogen fertilizers and phosphorus fertilizers in northern Italy have increased five-fold and three-fold, respectively, during the last forty years (Fig. 14). Moreover, the production of phosphoric acid in Italy increased twelve-fold during the same period of time. This is important since the phosphoric acid is a precursor for the synthesis of polyphosphates which have been extensively used in the industry of detergents. As a whole, the consumption of phosphorus and nitrogen in the Po River drainage basin as well as in the drainage areas of other north Adriatic Rivers seems to has increased at least for a factor of five during the last forty years. In the Po River, the concentration of reactive phosphorus and the concentration of total inorganic nitrogen have increased two-fold and two and a half-fold, respectively, during the last twenty years. As a result, influx of nutrients to the sea started to increase rapidly some thirty years ago. This caused a trend towards higher primary production at the surface and, consequently, higher oxygen concentration resulted (Fig. 13a). At the bottom, the primary production started to decrease due to the decrease in light penetration (Fig. 13c). Moreover, due to the increased sedimentation of organic matter from the pelagic strata, oxygen demand at the bottom increased. Two important facts can further reinforce the hypothesis that the above sequence of events has indeed occurred. Firstly, the increasing difference between the oxygen content at the surface and the oxygen content near the bottom is the largest in the western subarea, which is under direct influence of Po River (Fig. 12). Recent assessment have shown that the Po River brings about 16000 tons of phosphorus per year which accounts for more than 50% of the total yearly inflow to the area. As much as a half of that quantity originates from detergents and synthetic fertilizers. This is extremely important, because it was demonstrated that in the northern Adriatic Sea phosphorus rather than nitrogen is the principal nutrient controlling phytoplankton productivity. Secondly, an interesting fact concerning historical changes in phosphorus loading was reported from the Venice Lagoon: in the radiodated sediment cores a significant increase in phosphorus concentration was measured in the upper 15-20cm, which had accumulated during the last 30-40 years.

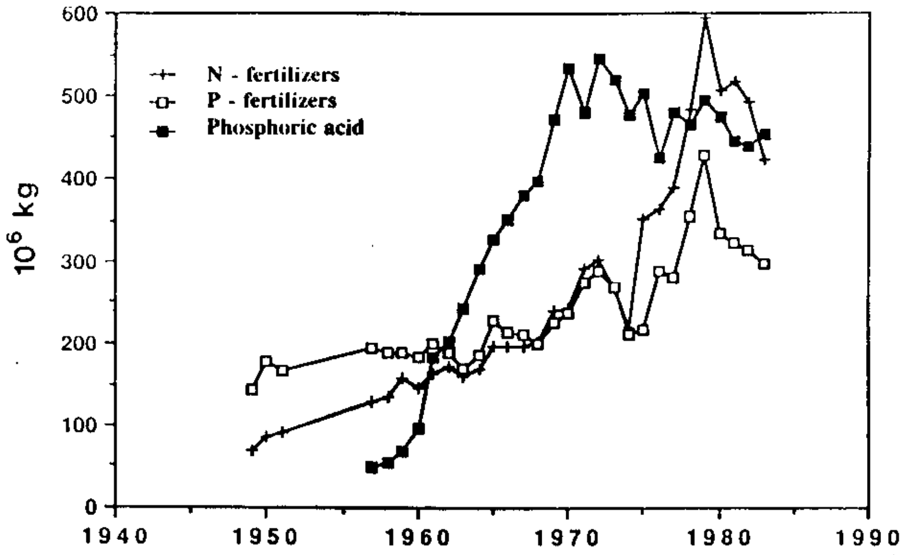

Figure 14. Consumption of nitrogen and phosphorus fertilizers (as N and P) in northern Italy and production of phosphoric acid of Italy during the period 1948-1983.

At present, the average oxygen saturation during August and September is lower than 50% only in the part of the western subarea approaching the Po Delta (Fig. 15). However, due to the variability of the data it is highly probable that the oxygen saturation lower than 20% occurs along the western coast and in the Bay of Trieste. Just from these areas have the reducing benthic mortalities been reported.

3.3. Eutrophication induced changes in the plankton and benthic communities

A wide-range benthic mortalities have been reported from western and northern subareas of the northern Adriatic Sea. As an example, we may consider the

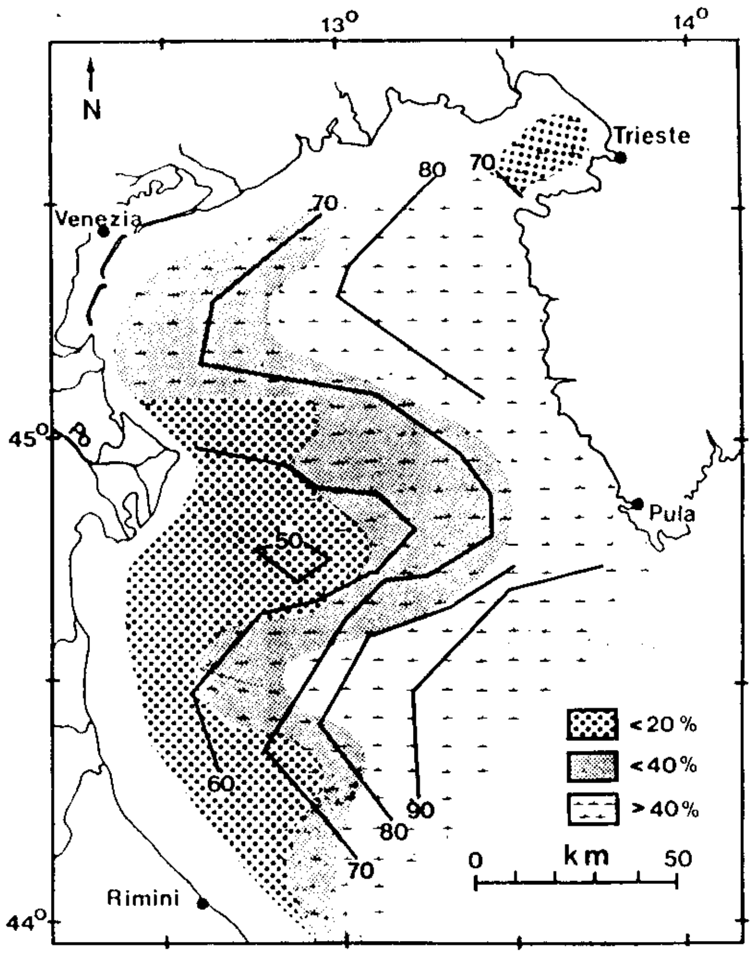

Figure 15. Distribution of oxygen saturation means in August and September, over the period 1972-1982. The minimum oxygen saturations at the 95% probability level are indicated.

mass mortality in the Bay of Trieste, during September 1983. The area affected by hypoxia was estimated to cover at least 50 km^2. Within two weeks, all macrofauna including infauna and some fishes was reported dead (Stachowitsch, 1984). Since the benthic macrofaunal biomass averaged 200-300 g m^{-2}, the total faunal loss could have been well over 10 000 tons. Since in the northern Adriatic Sea hypoxia has become a recurring event, the recolonization of large area which suffered from mass mortality is expected to be an infinitely slow process. As an example we may consider long-term decrease in the density of gastropod *Turritella communis which* has occurred over the past fifty years in the area approaching the Po Delta. Recent investigations reported a maximum of 40 specimens per square metre while, on the contrary, during the years 1934-1936, an average density of 165 specimens per square metre and a maximum of nearly 1500 specimens per square metre were reported. It is likely, that the increasing oxygen depletion at the bottom was one of the factors responsible for a decrease in population density of this snail.

Also, important changes have occurred in the plankton community. Assessment of the composition of the hydromedusan fauna over the period 1911-1984 revealed a substantial decline in the total number of species: as much as 30 species of meroplanktonic hydromedusans have completely disappeared from the northern Adriatic Sea (Fig. 16). The meroplanktonic hydromedusans have alternating pelagic (hydromedusa) and bottom-dwelling (hydroid) phases in their life cycles. On the contrary, no apparent trend is evident from the data on holoplanktonic hydromedusans and copepods. These species do not have a bottom attached phase in their life histories and, for this reason, they do not need bottom for their reproduction. The apparent correlation between the oxygen depletion at the bottom and disappearance of meroplanktonic hydromedusan species supports the hypothesis that these animals are extremely sensitive to low oxygen concentration. In the temperate latitudes, proliferation of the hydroids occurs predominantly during the warm period of the year. Most likely, the low oxygen content at the bottom which has occurred during recent summers, has affected proliferation of the hydroids. On the contrary, hypoxic conditions at the bottom could not have influenced the reproduction of exclusively pelagic species such as holoplanktonic hydromedusans and copepods. In this respect,

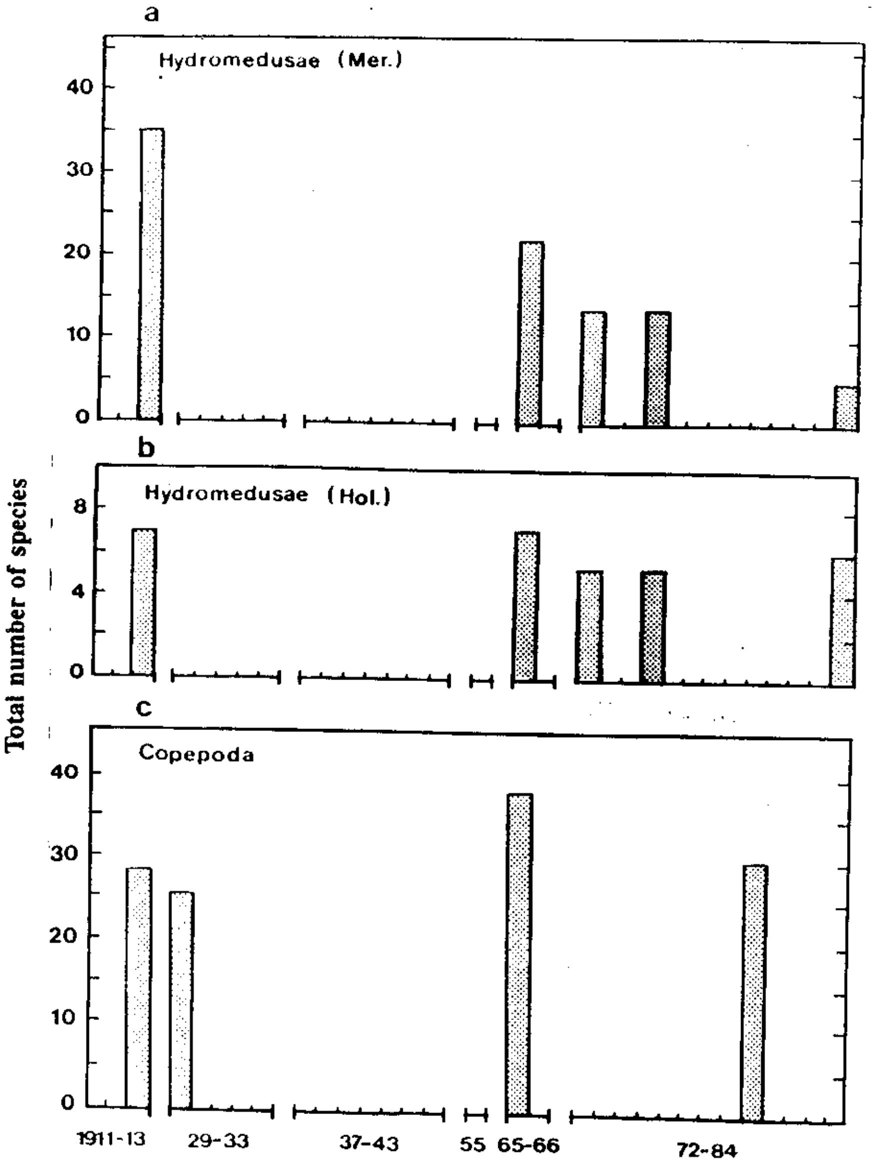

Figure 16. Total numbers of species of (a) - meroplanktonic hydromedusans, (b) - holoplanktonic hydromedusans and (c) - copepods in the northern Adriatic Sea from 1911 to 1984.

almost constant number of species within these groups over a long period of time, is reasonable.

Certain reproductive strategies enable species to alleviate the negative influence of a low oxygen content near the bottom. It is known that following sexual reproduction in cladocerans, the resting eggs produced sink to the bottom. In the northern Adriatic Sea, cladocerans are present in the plankton mostly during the warm period of the year. In August and September their abundance even exceeds those of the copepods and the region becomes a real Cladoceran sea. Among the northern Adriatic cladocerans, the most abundant species is *Penilia avirostris* which can alone account for about 80% of the zooplankton biomass. As a rule, this species disappears from the plankton by the end of November. The resting eggs overwinter at the bottom and hatch by the end of the following spring. Therefore, the summer bottom hypoxia does not interfere with the life cycle of species such as *Penilia avirostris*.

In the northern Adriatic Sea, phytoplankton blooms are known to have occurred from time to time for centuries. Recently, extensive bloom formation has been reported more frequently. It was observed that diatoms dominated blooms under isopycnal water column conditions while dinoflagellates, e.g. *Prorocentrum micans*, were primarily responsible for the summer blooms under stratified conditions. The summer dinoflagellate blooms are, perhaps, of recent origin although the paucity of historical data prevent any adequate conclusion regarding their antiquity. Nevertheless, it may be hypothesized that the occurrence of hypoxic conditions near the bottom is a disadvantage for diatoms rather than for dinoflagellates. Importantly, motile dinoflagellates may avoid the hypoxic waters while diatoms are unable to do that. Also, it was reported that exposure to low oxygen concentration may damage the diatom spores and thus prevent their germination.

3.4. Factors affecting oxygen depletion and benthic mortalities in the northern Adriatic Sea

In the northern Adriatic Sea, the development of hypoxia is directly associated with the decay of organic matter accumulated during the previous phytoplankton blooms. The seasonal cycle of primary production is characterized by three periods of bloom; January-April, June-August and September-November. The spring-summer and the fall maxima tend to coincide with the maximum of Po River discharge (Fig. 17a, b). The third maximum occurs during the period of winter overturn. The blooms occur in all three subareas of the northern Adriatic Sea although their amplitude decreases in the eastward direction. Accordingly, the integrated yearly primary production range from 55 gC m^{-2} in the easternmost section to 120 gC m^{-2} in the section approaching the Po Delta (Gilmartin & Revelante, 1983). The large portion of primary production sediments from the pelagic strata. At the depth of 15 metres, the sedimentation rates of particulate organic carbon ranged from 50 to 210 mgC m^{-2} day^{-1}. The latter value was recorded during late-spring bloom conditions in the area influenced by the Po River discharge. In the middle Adriatic Sea, the average sedimentation rate at the depth of 50 metres accounted for about 28% of the primary production. Since the northern Adriatic is shallower than 50m, the 0.3 is probably the lowest value of the sedimentation: primary production ratio that can be expected on a yearly basis. Therefore, assuming that the transfer coefficient is 0.3 and the respiratory quotient is 1, between 44 and 96 gO_2 m^{-2} $year^{-1}$ can be theoretically consumed by the benthic respiration processes. Towards summer, the oxygen demand at the bottom increases with increasing sedimentation and temperature (Fig. 17d). On the contrary, the reoxigenation through the pycnocline decreases with the increasing stability of the water column (Fig. 17c). As a consequence, the oxygen content at the bottom decreases. The oxygen content of the bottom "cold pool" decreases also due to the fact that the pycnocline gradually progresses towards the deeper parts of the water column (Fig. 18). During September, the pycnocline, which is at that time mostly thermocline, could approach the bottom on less than 10 metres. On occasion it may lie just few metres above the bottom. The phenomenon of near-bottom pycnocline seems to be important only in the shallower western and northern subareas. Interestingly, it is regularly associated with the occurrence of hypoxia in the Bay of Trieste.

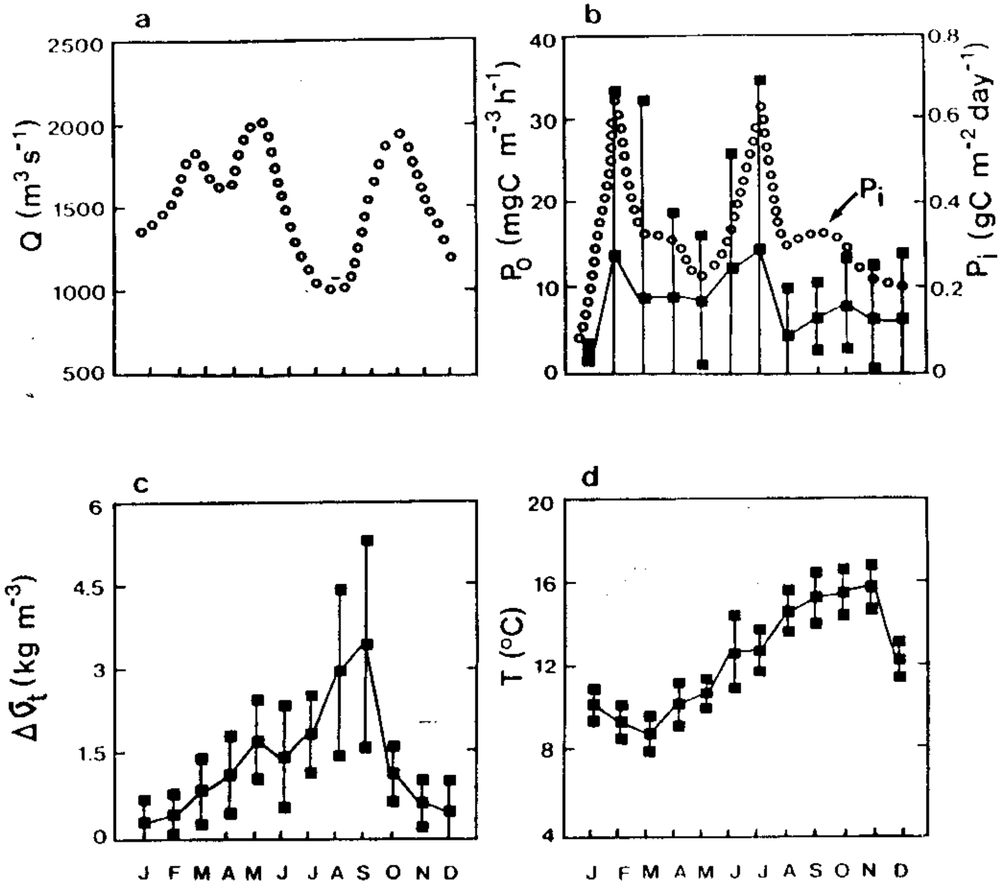

Figure 17. Monthly means of (a) - the Po River flow for the period 1966-1981, (b) - surface and integrated primary productivity, (c) -stability of the water column below 10m and (d) temperature at 2m above the bottom, western subarea. Vertical error bars indicate 1 standard deviation.

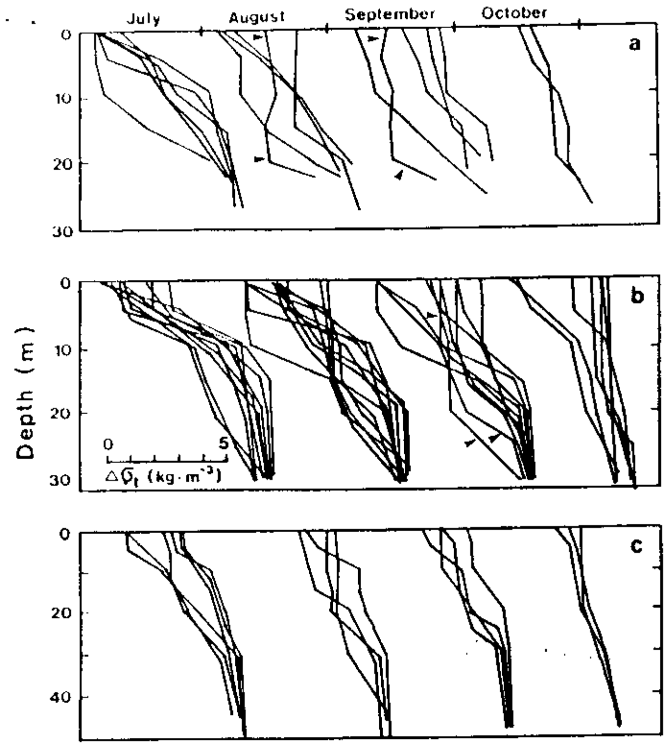

Figure 18. Plots of density anomaly (σ_t) versus depth during July-October, in the northern Adriatic Sea from 1972 to 1982; (a) - northern subarea, (b) - western subarea, (c) - eastern subarea. Arrows indicate near-bottom pycnoclines.

The development of hypoxic conditions at the bottom coincides with the periods of low wind frequency. Apparently, the pronounced hypoxia may develop only if the wind speed at the surface is lower than 4 m s^{-1} (Fig. 19). The stronger wind tend to destroy stratification and this process seems to progress linearly with the increasing wind speed. Accordingly, the wind faster than 8 m s^{-1} is able to mix the water column down to the depth of 30 metres, which is an average depth of the northern Adriatic Sea.

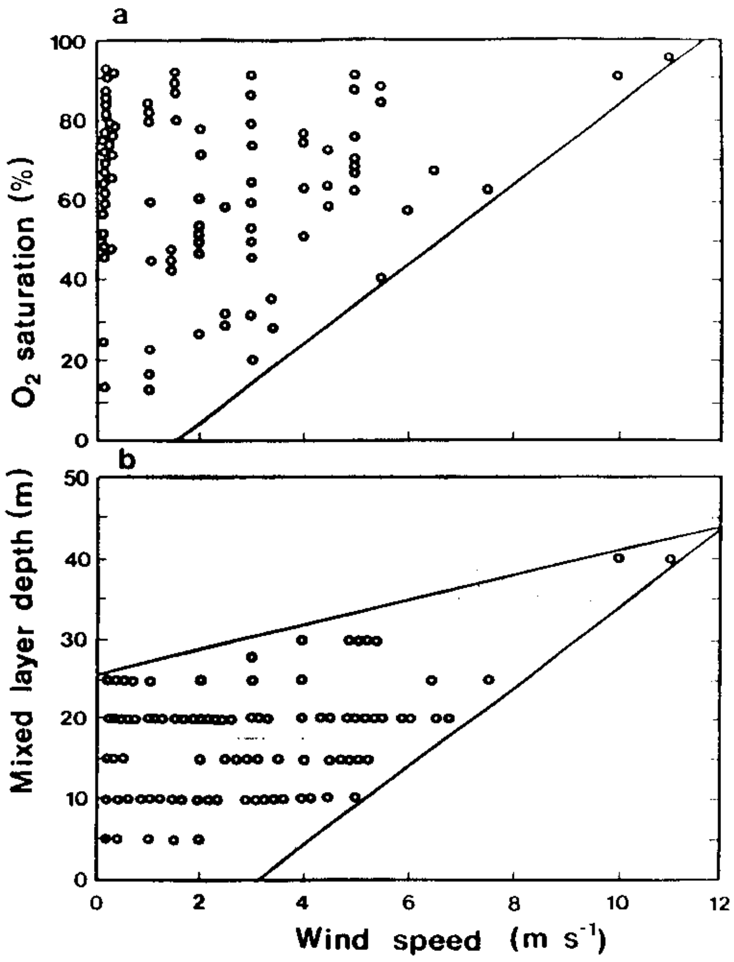

Figure 19. Oxygen saturation at 2m above the bottom (a) and mixed layer depth (b) versus wind-speed at the surface, in the northern Adriatic Sea during August and September. Mixed layer is considered to be that part of the water column saturated in oxygen more than 90%.

4. SELECTED LITERATURE

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