DISTRIBUTION OF PLANKTONIC PRIMARY PRODUCTION IN THE BLACK SEA

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Abstract

Planktonic primary production data from the entire Black Sea are reviewed for the last two decades. Surface and vertical profile of data are spatially and seasonally compared for different significant areas (north-western shelf, western and southern coast, eastearn and western halistatic zones). High production rates, especially in the coastal waters of the NW and W Black Sea exhibit large inter- and intraseasonal variations. Such values clearly reflect meso- and eutrophic feature of these waters. There are major annual spring (diatoms) and autumn (coccolithophorids) blooms, followed in recent years by additional summer (dinoflagellates, coccolithophorids) blooms. The major primary producers are usually *Skeletonema costatum, Chaetoceros curvisetus, Peridinium trochoideum, Exuviaella cordata and Prorocentrum micans*. Factorial analyses reveal very high correlation coefficients between chlorophyll *a* concentration and salinity, primary production and salinity, and between chlorophyll *a* concentration and primary production. The annual cycle of plankton dynamics in the central Black Sea is being studied by means of an one-dimensional vertically resolved physical-biological upper ocean model, involving interactions between inorganic N (NO_3, NH_4), phytoplankton and herbivorous zooplankton, and detritus.

1. Introduction

Historically, before the last decade maxima in primary production of the Black Sea occurred twice a year, with a major bloom, mainly diatoms, in early spring, followed by a secondary bloom, mainly coccolithophorids, in autumn [26]. Such blooms occurred mainly in coastal areas. Recently, additional summer blooms composed predominantly of dinoflagellates and coccolithophorids (*Emiliana huxleyi*) have increasingly been observed

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[1, 7, 15, 16, 17, 26, 32]. Massive red tides along the Romanian [2, 3, 4, 5, 6] and Bulgarian [19, 20, 21, 24, 25] coasts have been reported. Intense blooms of certain plankton species, have also been cited during winter along the western Anatolian coast [29].

2. Methodology

Primary production (PP) was measured using two varieties of the ^{14}C technique [27]. The first modification was an *in situ* determination which was used during Russian and Romanian cruises [8, 9, 10, 33, 34]. According to this method two light and one dark (275 ml (Russia) or 250 ml (Romania)) bottles containing phytoplankton from different depths were each inoculated with 3-12 (Russia) or 5-25 (Romania) µCi aqueuos $NaH^{14}CO_3$ solution and incubated *in situ* (at the depths from where they were collected) during half of the light day (usually from noon to sunset). After recovery the bottles ware filtered under vacuum through 0.3-0.6 µm membrane filters. After filtration the filters were rinsed five times with 30 ml of filtered seawater. Then they were dried in open Petri dishes overnight at room temperature and placed into dark vials with 10 ml of liquid scintillator per vial. Activity of the filters was counted with a radiometer RZhS-05 (Russia) and Nuclear Enterprises LSCI manual scintillation counter or a Packard Tri-Carb 3385 automatic scintillation spectrometer (Romania).

The production in the sample per period of day light (12hrs) was calculated using the common formula with correction for dark fixation of carbon dioxide. The value for total carbon content in these samples were given by the hydrochemists or were set equal to 36000 mg C m^{-3}. Results were expressed as mg C m^{-3} d^{-1} for each investigated depth or as mg C m^{-2} d^{-1} for integrated primary production in the water column (PPI).

The detection limit for ^{14}C determination of PP at a given depth was approximately 0.5 mg C m^{-3} d^{-1}. Relative errors are very much dependent on the value determined and usually extended from 5 to 30% for most depths in the euphotic zone.

The second technique was a simulated *in situ* measurement of PP using a flow-through incubation box in which light conditions were simulated to be like those in the natural marine environment [29, 30, 38]. Two light and one dark glass or plastic bottles (50-250 ml, Ukrainian cruises and 25-50 ml, Turkish cruises) containing samples from different depths were inoculated with 5-20 µCi aqueuos $NaH^{14}CO_3$ solution and exposed to light for 4-8 hrs. After exposure the filtering and counting procedures were the same as in the first modification.

Absolute values of primary production obtained by these ^{14}C techniques should be compared only with much caution. The comparison is fraught with difficulties as intercalibration was not performed between the two techniques. Nevertheless, the estimates obtained are applicable for description of the distribution and seasonal dynamics of primary production.

3. Results and discussion

3.1. NORTHERN AND WESTERN SHELF: SURFACE, VERTICAL AND SEASONAL DISTRIBUTION

Surface primary production (PPS) in Sevastopol Bay is subject to great variation, both within each season and from season to season [28]. Usually, in such bays as Sevastopol and Gelendzhik, the annual cycle of PPS is characterized by three maxima in spring, late summer and autumn [29]. In the early months of spring (February-March) PPS ranged from 11-35 mg C m^{-3} d^{-1}. Toward the end of this period (April-May) one could observe intensive blooms of *Skeletonema costatum* and *Chaetoceros curvisetus* which were accompanied by PPS of 240-400 mg C m^{-3} d^{-1}. In summer (June-August), when phytoplankton was dominated by the pyrrhophyte algae *Peridinium trochoideum, Exuviaella cordata and Prorocentrum micans*, PPS varied from 14 to 280 mg C m^{-3} d^{-1}. In autumn (October-November), when plankton was again dominated by diatoms, PPS varied from 20 to 80 mg C m^{-3} d^{-1}. In winter (December-January) the potential PPS constituted only 7-8 mg C m^{-3} d^{-1}. According to these results this part of the Black Sea can be regarded as an eutrophic region.

Maximum productivity during spring - autumn was found on the NW shelf. High productive areas were also observed on the NE shelf. The next highest values were reported along the Romanian (western) and the Anatolian (south - western) coasts, and extended into the central region separating the eastern and western gyres [7, 32]. Limited observations suggest that the western Anatolian coast is also a region of relatively high productivity [31].

Eutrophication started in the NW shelf area influenced by high nutrient outflow from the Danube and Dnestr rivers, and progressed southward along the western shelf [7, 13].

Early results obtained off Constanta during summer 1977 gave PP values ranging between 297-825 mg C m^{-3} d^{-1} in the upper water layer (0 m) and between 238-243 at 5 to 10 m.

Other results obtained in the same shelf zone off Constanta (0 m) during 1978 ranged between 4.7 to 67 mg C m^{-3} d^{-1} in December and 71.3 to 1,162.8 in July [8]. Thus, the development of photosynthetic assimilation and primary productivity, which is maximum in summer (July) and minimum in winter (December), closely follows the evolution of environmental factors (e.g. light and temperature: July = 62,163 lx, 24^0 C; December = 2,123 lx, 11^0 C). Monthly data for primary production in surface (0m) waters were obtained in the nearshore and offshore up to 30 nautical miles zones of Constanta during 1979 [9]. Microscopic analysis (taxonomic composition, weight of the major groups) of phytoplankton was performed at the same time. The results gave mean PPS values that ranged from 47.2 (January) to 475.4 (March) mg C m^{-3} d^{-1} and a mean annual PPS of 54.8 g C m^{-3} y^{-1}. The variability in these values was usually correlated with phytoplankton density and biomass. The highest PPS values in March were correlated with maximum phytoplankton biomass reaching 13.9 to 32.2 g m^{-3}. This production was primarily due to the diatoms *Skeletonema costatum, Thalassiosira subsalina and Detonula confervacea*. In April, diatoms (almost exclusively *Skeletonema costatum*) had a density of 33,180 cells l^{-1} and a biomass of 9,978 mg m^{-3}. In May, maximum densities and biomasses were also recorded nearshore and decreased seaward. These data indicate the spatial and seasonal variability of PPS in Constanta shelf waters. Maximum level during spring was due to abundant development of diatoms, whereas high values during early summer were a consequence of the massive occurrence of dinoflagellates. In this area higher values were found nearshore compared with those in the offshore zone. The results in the offshore zone of Constanta ranged between 1.7 to 1,938 mg C m^{-3} d^{-1} in the surface layer and the integrated values (0-50m) ranged between 0.2 to 27.4 g C m^{-2} d^{-1} [10]. Total annual PP was estimated to be 7,625,000 t C y^{-1} in this sector of the Romanian coast. The highest PP occurred in the 0-10 m layer (except for June, when the maximum value was found at 25 m).

Other results were obtained in 1982 at a distance of 1.2 n.m. off Constanta from depths of 0,5 and 10 m [11]; analyses of chlorophyll *a* and microscopic counting of phytoplankton (density and biomass) were performed simultaneously. Mean annual PP values at these depths were 5.2, 1.4 and 1.0 mg C m^{-3} h^{-1} , respectively. The annual average integrated primary productivity was 2.3 mg C m^{-2} h^{-1} . Maximum productive rates occurred in late spring and summer during this particularly year (Fig.1). The vertical distribution of PP showed higher values at 0 m (except in May at 5 and 10 m, respectively). The maximum annual mean value also occurred at 0 m. The higher PP level in the surface layers (Fig.1), was consistent with 1980 data from the same sector collected down to 50 m depth [10, 11].
The maximum PP in July was due to an intense bloom of the dinoflagellate *Exuviella cordata*.

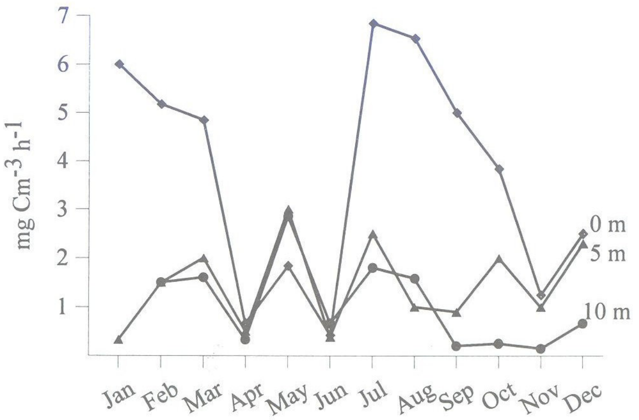


Figure 1. Annual cycle of planktonic primary productivity at 0, 5 and 10 m in the Constanta nearshore sector in 1982 (cf. [11])

Comparisons between primary productivities in different areas along the whole western Black Sea coast from the region north of the Danube to north of the Bosporus can be made with the 1982 data set [12]. The very high values offshore north of the Danube (much higher than those during the last two decades) were due to the intense eutrophication of the north-western part of the Black Sea as a consequence of the

nutrients carried by the Danube and implicitly by the frequent occurrence of intense phytoplankton blooms.

The highest PP values compared to the other sectors occurred offshore of the Danube in May and reached 1,530 mg C m^{-3} d^{-1} and 1.6 g C m^{-2} d^{-1} . In this sector, in contrast to the two southern ones, maximum PP was determined in the upper layer between 0 to 5 m (Fig.2). Factorial analysis gave very high correlation coefficients between chlorophyll *a* concentration and salinity (-0.91), between primary production and salinity (-0.94) and between chlorophyll *a* and primary production (0.91), suggesting that the waters with the most river influence had the most biological activities.

All PP data collected in the offshore zone of Constanta between 1977 and 1982 by means of the ^{14}C method showed evidence of the highly eutrophic feature of the Romanian Black Sea coastal waters [7]. Estimates of primary production and phytoplankton biomass along the Romanian coast in the 1980's were much higher than in the previous two decades.This was due to a general increase of eutrophication and more frequent and intense blooms.

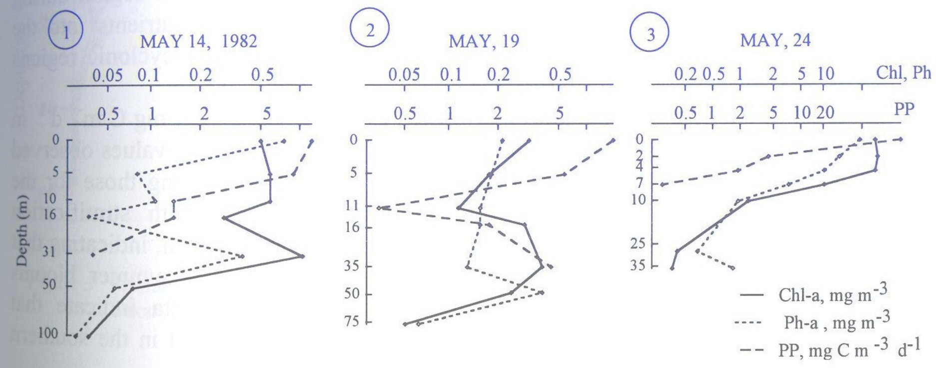


Figure 2. Vertical distribution of primary production (PP), chlorophyll-a (Chl-a) and phaeopigments-a (Ph-a) off the Bosporus (Turkey) (1), off Caliacra (Bulgaria) (2) and off the Danube (Romania) (3) in May, 1982 (cf. [12])

3.2. SOUTHERN OFFSHORE WATERS

The spring-time surface productivity in the southern Black Sea is modulated by transient dynamics [32]. Species differentiation and competition are evident along the boundary current systems. Early summer blooms coincide with peak flood discharges from major rivers, and influence the spread of eutrophication in the basin.

Until recently, data on optical transparency, phytoplankton biomass and PP were very limited for the southern Black Sea [36]. Light penetration is generally limited to upper 15-40 m, with the downward attenuation coefficient varying between 0.1 and 0.3 m^{-1} . Coastal waters of the region are fed by the riverine input whereas the cyclonically dominated open ecosystem is mainly controlled by influx from the oxygenated lower layers by vertical mixing that is much more effective in winter. However, the input from the anoxic layer is limited due to the presence of a strong permanent halocline in the basin. Halocline coincides with the suboxic zone which is in between the oxic and anoxic waters, where intense denitrification and redox-dependent processes also limit nitrogen and phosphorus input to the productive layer [22]. Thus, surface waters are always poor in inorganic nutrients during the stratified seasons because the photosynthetic uptake rate exceeds the nutrient input rate in the spring.

The photosynthetic carbon production rate range from 247-1,925 and 405-687 mg C m^{-2} d^{-1} in the spring and summer-autumn periods, respectively.

Relatively high PP rates were observed in the upper euphotic zone to 10-20 m and these values always showed similar vertical profiles (Fig.3). Below this layer, PP decreased markedly due to light limitation. This was confirmed by the maximum production P(M) rates, which are the production rates when deep samples are exposed to full light conditions. P(M) rates were similar to the near surface production rates down to the base of the euphotic zone.

Production rates P (during true noon) and daily production rates P(D) ranged between 1-10 mg C m^{-3} h^{-1} and 2-200, respectively, for the top 10 to 20 m. The highest rates were observed at a frontal station (off Sinop) in the RIM current region during April, 1996. At this location the latteral and vertical transport of nutrients into the euphotic zone was much more effective than in the cyclonic and anticyclonic regions (Fig.3).

The depth-integrated production rate was as high as 1,925 mg C m^{-2} d^{-1} in April, 1996 in the RIM current frontal zone near Sinop, similar to those values observed on the NW shelf and off the Romanian coast [7] and greatly exceeding those for the central Black Sea [36]. The results obtained for the seasons with stratification (September-October, 1995 and June-July, 1996) were also relatively high, indicating that in addition to characteristic spring and autumn blooms, short-term summer blooms occurred in the Black Sea [7, 15, 16, 17]. These preliminary data indicate that considerable spatial and temporal variation of primary production exist in the southern Black Sea as well as the northern and western shelf.

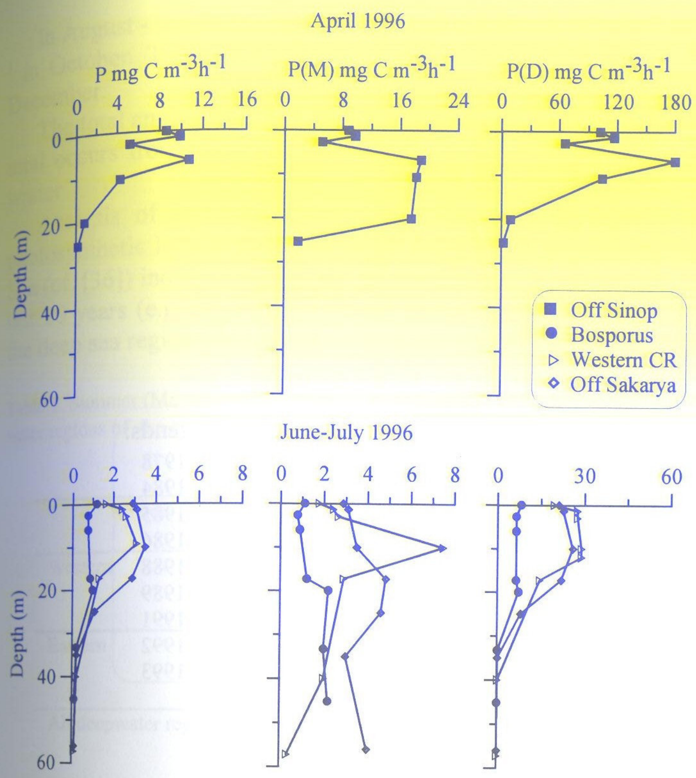


Figure 3. Primary production (P), maximum rates (M) and daily rates (D) off Bosporus, Sinop, Sakarya and in the western cyclonic region during April and June-July 1996 ([36])

3.3. OPEN REGIONS (EASTERN AND WESTERN HALISTATIC ZONES)

Despite the deficiency of year-long seasonal data for the open sea, it is possible to use the historical data sets [28, 34] to draw conclusion about seasonal changes of PPI within the western and eastern cyclonic gyres.

Enhanced mixing of the cyclonic gyres in winter was responsible for estimates of PPI that amounted to 300-700 mg C m^{-2} d^{-1} with a maximum in the centre of the gyre (Fig. 4).

PPI reached a maximum in March with an average of 640 mg C m^{-2} d^{-1}. Production was also the largest (1200 mg C m^{-2} d^{-1}) in the centre of the gyres, decreasing to 200 mg C m^{-2} d^{-1} towards the periphery. The community *Nitzschia delicatissima* and *Rhizosolenia calcar-avis* reached maximum population during this period. In different years the winter-spring peak of phytoplankton growth in the central area took place either in February or March.

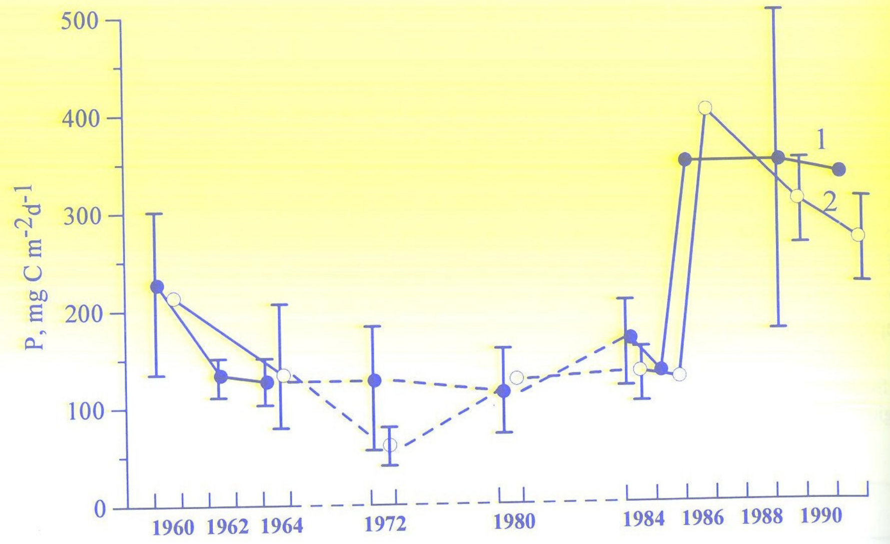


Figure 5. Historical change of summer (May-September) mean primary production in the western (1) and eastern (2) deep water (>1000 m) regions of the Black Sea (cf. [36])

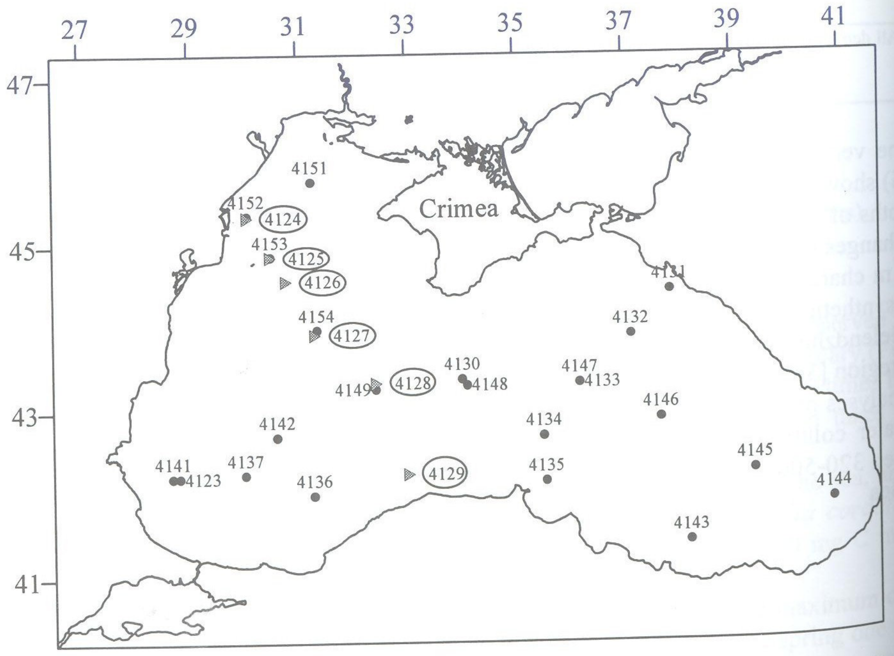


Figure 6. Location of primary production sampling stations during the 44th cruise of R/V "Dmitri Mendeleev" between July-September 1989 (Data from the NATO TU-Black Sea joint data bank (METU IMS, Erdemli-Icel, Turkey)

regions [37]. The autumn changes in the distribution of vertical phytoplankton started in the western parts of the sea and gradually extended to the east.

3.4. MODELLING

The annual cycle of plankton dynamics in the central Black Sea was recently studied using an one-dimensional vertically resolved coupled physical - biological upper ocean model [23]. This model involved interactions between inorganic N (NO_3 , NH_4), phyto-plankton and herbivorous zooplankton biomasses, and detritus. It simulated

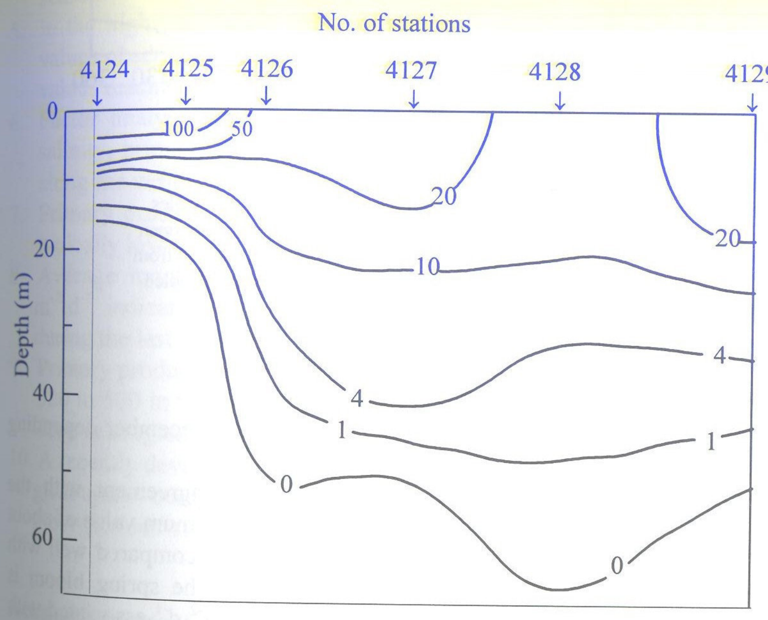
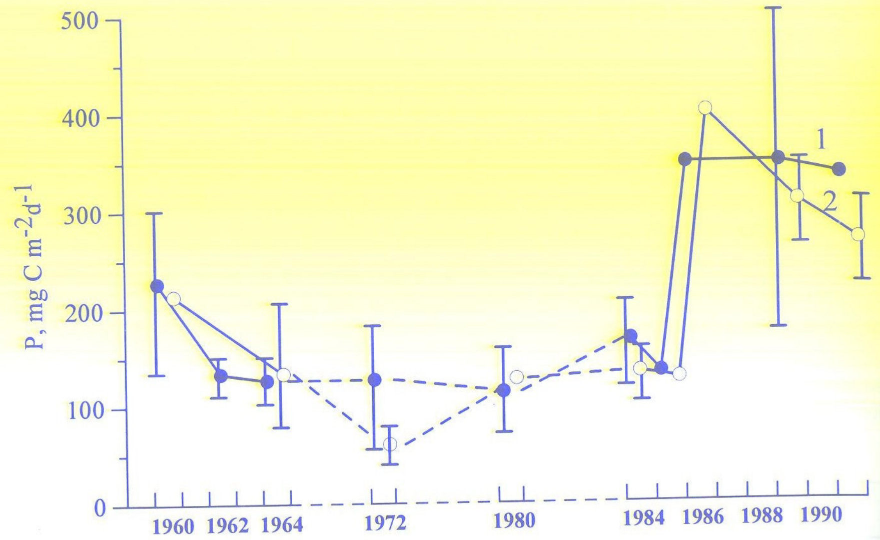


Figure 7. Vertical distribution of primary production (mg C m^{-3} d^{-1}) along the western transect shown in Fig. 6 (cf. [34]): the section was constructed using the stations circled in Fig. 6

seasonal and vertical characteristic features, in particular, formation of the cold intermediate water mass and yearly evolution of the upper layer stratification, annual cycle of production with the spring and fall blooms, and the subsurface phytoplankton maximum layer in summer. The computed seasonal cycles of the PPI distribution compared reasonably well with the data. The annual cycle of PP distribution was constructed by combining the field observations within the central basin during the last decade [36].The continuous line gives the corresponding model predictions (Fig.8). Year-to-year variability in the productive cycle was observed. Initiation of the spring bloom was shown to be critically dependent on the stability of the water column. It was followed by lower PP at the time of establishment of the seasonal thermocline in April.



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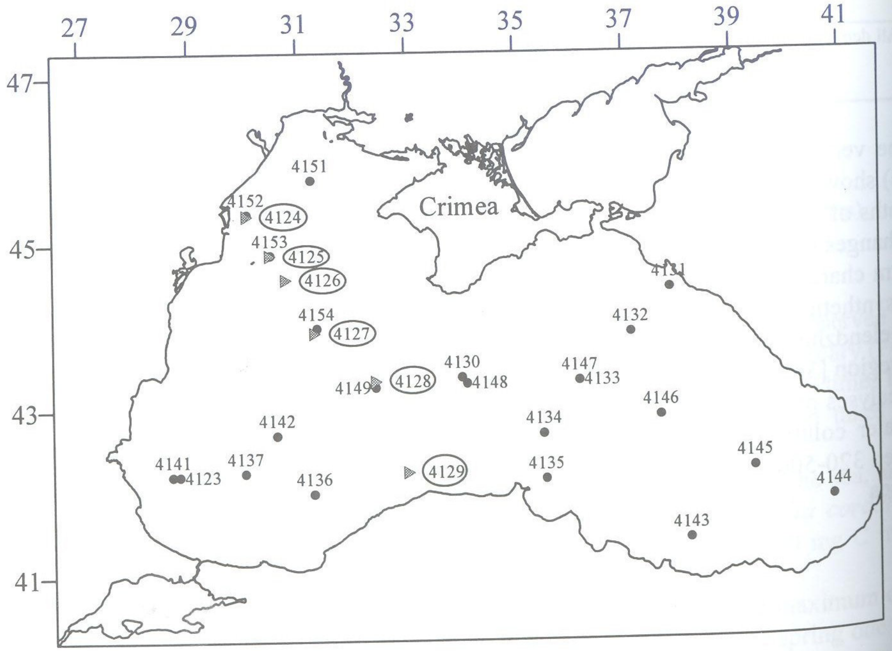

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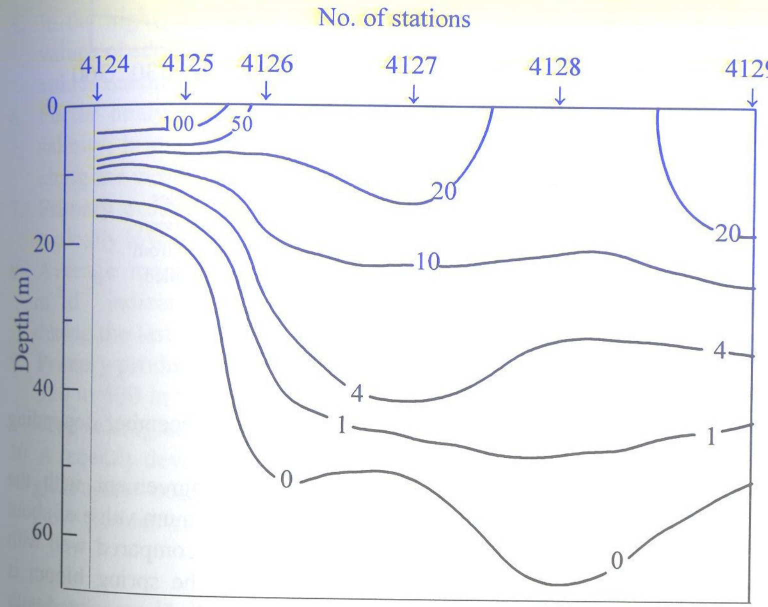

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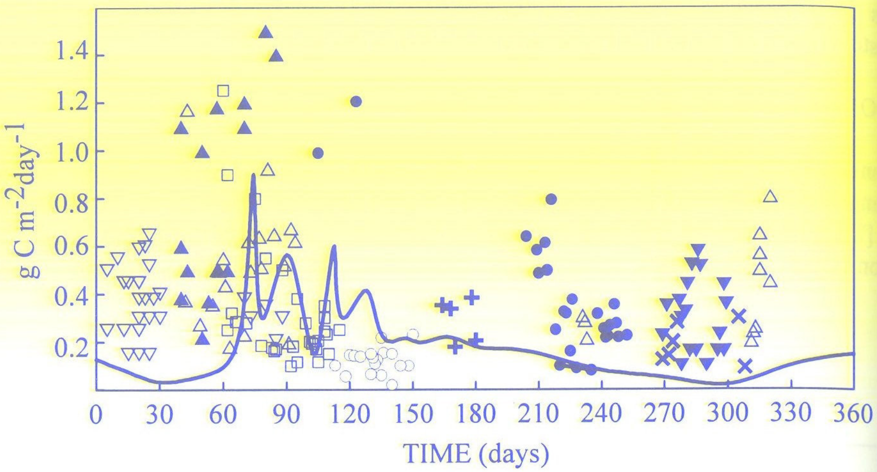

Figure 8. A composite picture of the distribution of integrated primary production (PPI) during the year compiled from different data sources (open and solid triangles, 1991; solid circles, 1989; open squares, 1988; plusses 1986; crosses, 1985; open circles,1984; solid and open reverse triangles, 1978). The data are redrawn from [36].The continuous line shows the primary production predicted by the coupled physical-biological model (cf. [23].

The autumn bloom took place sometime between October and December depending on environmental conditions.

The integrated PPI computed by the model yielded better agreement with the composite data (Fig.8). The integrated model PPI attained its maximum value of about 900 mg C m^{-2} d^{-1} during the period of the March bloom [23]. This compared well with the measured bloom productivity of 400-1,300 mg C m^{-2} d^{-1} . The spring bloom is followed by the three smaller peaks of about 500-600 mg C m^{-2} d^{-1} associated with the regenerated PPI in the spring. PPI estimates of about 300-500 mg C m^{-2} d^{-1} during May were also comparable with the May, 1988 measurements of 339 and 573 mg C m^{-2} d^{-1} at two stations within the Central Black Sea [17]. August to October was shown to be the least productive period characterized by model values of less than 200 mg C m^{-2} d^{-1}, whereas observed values varied from 200 to 500 mg C m^{-2} d^{-1} in the same period.

This model predicts PPI values reasonably well for most parts of the year except during the autumn bloom season. The maximum model estimate of autumn PP of 200 mg C m^{-3} d^{-1} was somewhat less than the observations.

4. Conclusions:

1. A general increase of eutrophication is reflected by more intense and frequent phytoplankton blooms that have characterized the Black Sea during the last two decades.
2. In addition to the usual early spring and autumn blooms, additional summer and sometimes even winter blooms have occurred in more recent times.
3. High primary production rates have been registered especially in the north-western and western coastal waters.
4. In the NW area, primary production varies greatly seasonally as well as within each season.
5. In the highly eutrophic western coast, e.g. off Constanta, the highest production values observed in shallow waters reached up to 1,162 mg C m^{-3} d^{-1} in July; offshore values reached up to 1,938 mg C m^{-3} d^{-1} or 27.4 g C m^{-2} d^{-1} in August.
6. Factor analysis revealed high correlation coefficients between chlorophyll *a* and salinity, primary production and salinity, and chlorophyll *a* and primary production along the western coast.
7. Primary production in the centers of the eastern and western halistatic zones were typically low during late spring, summer and autumn.
8. Average monthly production values in both gyres varied from 200 to 745 mg C m^{-2} d^{-1} indicating an increase in this parameter by approximately a factor of two during the last 20 years.
9. Primary production ranged from 570 to 1,200 mg C m^{-2} d^{-1} on the NW shelf, between 320 to 500 in the regions of continental slope, and between 100 to 370 in the central deep sea regions.
10. A recently developed one-dimensional vertically resolved coupled physical - biological upper ocean model predicted primary production values reasonably well for most periods of the year.

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