A review of Russian plankton research in the Gulf of Mexico and the Caribbean Sea in the 1960-1980s

Una revisión de investigaciones rusas de plancton en el Golfo de México y Mar Caribe en los 1960-1980's

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ABSTRACT

A book, 28 articles and two technical reports were published as results of the Soviet-Cuban and Soviet expeditions in 1962-1984, involving plankton samples collected at about 2,070 stations in the Gulf of Mexico and the Caribbean Sea. The results of those studies remained virtually unknown to the international community because they were published mainly in Russian. Two main types of water circulation in the Gulf resulting from the intensity of the Yucatan Current were distinguished. It was concluded that offshore regions of the Gulf of Mexico and the Caribbean Sea were oligotrophic, the deep-sea regions of the latter being richer in phytoplankton compared to deep-sea areas of the Gulf. Due to the upwellings and runoff from the Mississippi river, the Bank of Campeche, the northwestern Gulf, and the west Florida shelf were characterized by a relatively higher plankton production and by more pronounced seasonal changes in plankton biomass. Cyclonic and anticyclonic horizontal circulations were found to be the main reason for spatial changes in productivity of the Gulf. In various regions, the highest productivity was reported in different seasons, principally in winter on the northern shelf and in summer-autumn on the southern shelf of the Gulf. The annual dynamics of plankton biomass were traced in the Bank of Campeche. In the Caribbean Sea, both the Venezuela shelf and the Honduras continental slope were characterized by their higher productivity. The large amount of data obtained can be used to evaluate long-term changes in biological productivity in the region, species composition, and plankton communities.

Key words: Plankton, primary production, upwelling, Gulf of Mexico, Caribbean Sea.

RESUMEN

Un libro, 28 artículos y dos reportes técnicos fueron el resultado de las expediciones soviético-cubanas y soviéticas entre 1962 y 1984 en las cuales se colectaron muestras de plancton en aproximadamente 2,070 estaciones en el Golfo de México y el Mar Caribe. Los resultados de los estudios permanecieron virtualmente desconocidos por la comunidad internacional ya que se publicaron principalmente en ruso. Se distinguieron dos tipos principales de circulación en el agua del Golfo de México como resultado de la intensidad de la Corriente de Yucatán. Se concluyó que las regiones oceánicas del Golfo de México y el Mar Caribe son oligotróficas mientras que las regiones profundas del Caribe son más ricas en fitoplancton en comparación con el Golfo. Debido a las surgencias y las descargas del río Mississippi, el Banco de Campeche, la parte noroccidental del Golfo y la plataforma continental oeste de Florida se caracterizaron por tener una producción relativamente alta de plancton y por tener los cambios más pronunciados en su biomasa. Se encontró que la razón principal de los cambios espaciales en la productividad del Golfo es la circulación horizontal ciclónica y anticiclónica. En varias regiones, altas productividades han sido reportadas en diferentes temporadas

climáticas, principalmente en el invierno sobre la plataforma norte y en verano-otoño en la plataforma sur del Golfo de México. La dinámica anual de la biomasa del plancton fue investigada en el Banco de Campeche. En el Mar Caribe, tanto la plataforma continental de Venezuela como el talud continental de Honduras se caracterizaron por su productividad elevada. La gran cantidad de datos obtenidos en la región, puede ser usada para evaluar cambios a largo plazo en la productividad biológica, la composición de especies y las comunidades planctónicas.

Palabras clave: Plancton, producción primaria, surgencia, Golfo de México, Mar Caribe.

INTRODUCTION

Because of drastic political changes in the beginning of the 1960s in Cuba, a steep growth in oceanological studies in the Gulf of Mexico and the Caribbean Sea supported by the USSR was observed. In 1962, the program of Soviet-Cuban complex studies of the biological resources in the Gulf of Mexico and the Caribbean Sea was launched. Since 1964, the studies became regular and included oceanological surveys (hydrology, hydrochemistry and planktology) and fishery research. On Soviet fishing boats, issues such as physical and chemical oceanographic conditions, biology, and an abundance of selected groups of organisms (tuna fish, demersal fish of shelf regions and shrimps) were emphasized. Studies on oceanographic conditions and their variability in time, determination of high biological production regions, and revealing indicators for successful search for fish assemblages were the main aims. Sampling encompassed the 0-500 m layer, the 50-200 m layer being paid much attention because of the usual occurrence of fish there. In the period of 1962-1984, during Soviet-Cuban and Russian expeditions to these regions, about 2,070 plankton stations were carried out (Tables 1 and 2). Plankton was sampled with water bottles and nets, mesh size 70, 86, 138 or 168 mm. The results of those studies remained virtually unknown to the international community, since they were published mainly in the USSR in Russian (a book, 28 articles, two technical reports, and a synopsis of a PhD thesis, in total, over 550 pages). A high percentage (75%) of the publications were provided with English and/or Spanish summaries (Khromov, 1965a, b, c, 1967; Zernova & Mola, 1965; Kondratieva & Sosa, 1966; Ivanov, 1966; Anischenko, 1968; Kondratieva, 1968; Roujiyaynen et al., 1968, 1971; Zernova, 1969, 1970a, b, 1974a, b, 1975, 1976, 1982; Kabanova & López-Baluja, 1965, 1970; Bessonov & González, 1971; Bessonov et al., 1971; Krylov, 1974; Vinogradova, 1974, 1976; López-Baluja, 1976, 1983; Zernova & Krylov, 1974; Kabanova, 1981; Zernova & Zhitina, 1985; López-Baluja et al., 1992). Some articles on biological productivity and plankton were also published in Spanish. Publications in Spanish by López-Baluja written together with Russian co-authors (López-Baluja & Vinogradova, 1972, 1974; López-Baluja et al., 1985, 1986, 1987) are not considered here due to their availability for the Latin American and the U.S. scientific communities.

The chief purpose of the present article is to review mainly planktological research with a special emphasis on phytoplankton and to underline the most important results obtained and the overall conclusions. Despite much work that has been done in the last decades in the Gulf of Mexico marine ecosystem, especially within the Gulf of Mexico Program (Kumpf et al., 1999), results discussed herein remain an important historical background and deserve more attention. Although the analyzed publications contain numerous data on the physical and chemical characteristics of waters as well as on the commercial fisheries in the study region, they are beyond the scope of the present contribution. Similarly, to assess the historical data from the point of view of the present knowledge obtained mainly by the U.S., Mexican, Cuban and other Latin American oceanographers remained beyond the objectives of the study.

RESULTS AND DISCUSSION

Water movements and their influence on plankton development

1. Winds and horizontal water movements

Due to climate conditions, in October-April the high pressure dominates the North American region; therefore northern and northeastern winds blow across the Gulf of Mexico. In April-August, the Azores high-pressure center is responsible for the dominance of the southeastern winds. The interaction of air mass circulation with coastal line and bottom relief produce a complicated system of surface currents and cyclonic and anticyclonic water gyres, or eddies. In the Gulf of Mexico and the Caribbean Sea, wind regime and currents strongly influence the size and the position of gyres and the intensity of upwelling. In the southern Gulf of Mexico, the intensification of the Yucatan Current, which occurs mainly in summer and autumn, results in a more intensive upwelling above the shelf, which in turn is responsible for high biological production (Bessonov et al., 1971). The intensity of the Yucatan Current changes the character of horizontal circulation in the Bay of Campeche. In the Bank of Campeche, two types of circulation can be distinguished depending on the intensity of the Yucatan Current. Changes in the intensity of

Vessels	Years, months	Number of stations	Number of samples	Sampling gear	References
Vessels of AtlantNIRO (17 cruises)	1962- 1966	861	no data	net, mesh 168 µm	Khromov, 1965a, b, 1967; Bogdanov <i>et al.</i> , 1968
"Akademik A. Kovalevsky", cruises 1-3	1964, September- December	55	565	water bottle, net 3,042 openings/cm ² of gauze, hyponeuston net	Ivanov, 1966; Roujiyaynen <i>et al.</i> , 1968, 1971
"Akademik A. Kovalevsky", cruise 6	1965, March- April	57	265	water bottle	Kabanova and López-Baluja, 1970 Zernova, 1974a, 1982; Zernova and Zhitina, 1985
"Akademik A. Kovalevsky", cruises 6-8	1965	156	162	net, mesh 86 µm	Zernova and Mola, 1965; Zernova, 1969, 1970, 1975
	1965-1973	no data	no data	water bottle, nets mesh 70 mm, 168 μm	Zernova and Krylov, 1974
'Xiphias", 'Manchua", 'Cuba Mar", "Makaira", 'Cayo Largo", "Sardina"	1968- 1984	798	1151	water bottle, net	López-Baluja <i>et al.</i> , 1992
SRTR 9112, 9075, 8030	1969- 1970	124	no data	net 168 µm	Krylov, 1974
No data	1970, July	6	88	water bottle	Vinogradova, 1976
"Akademik Kurchatov", cruise 14	1973, February- April	6	36	net, mesh 70 µm	Zernova, 1975; Zernova and Zhitina, 1985
"Moscow University", cruise 5	1975, July- August	7	33	water bottle	Zernova, 1975; Zernova and Zhitina, 1985 López-Baluja <i>et al.</i> , 1992

Table 1. Data on Soviet and Soviet-Cuban planktological studies in the Gulf of Mexico and the Caribbean Sea in the 1960-1980s.

the current have a seasonal character. In summer it increases, and in winter it pronouncedly diminishes. In spring and autumn, both types of circulation are observed. However, the character of circulation in the Bank of Campeche seems to depend largely on interannual fluctuations of the intensity of the Yucatan Current (Bessonov *et al.*, 1971).

2. Vertical water movements (upwellings and downwellings)

Based on the data on the position of thermocline, distribution of temperature, salinity, phosphates and oxygen, the vertical water movements in the upper 200 m layer were mapped. It was found that upwellings take place during the greater part of the year in the following regions (Fig. 1): (1) the southern Caribbean Sea, especially near the shelf of Trinidad, Tobago, and Venezuela; (2) the Bank of Campeche; (3) along the northern shelf of the Gulf of Mexico; (4) the continental slope and offshore of the southern Florida shelf; (5) the western Bay of Campeche. Downwellings prevail in (1) the middle and northern parts of the Caribbean Sea including the Cayman basin, (2) the middle part of the eastern Gulf of

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Mexico, and (3) north of the Bay of Campeche. In summer, upwellings occur in (1) the Mona Passage area, (2) near the western margin of the Bank of Campeche and in the middle of the Bay of Campeche, the northwestern Gulf of Mexico, and the northern Florida shelf. All mentioned upwelling zones are located near the left margin of currents. In other regions, especially in the Caribbean Sea, water stratification is stable, and nutrients cannot reach the photic zone. The main reason for vertical water movements was suggested to be a transverse circulation in currents (Bogdanov et al., 1968). In the narrow Yucatan Channel, the strong Yucatan Current is characterized by intensive transverse circulation resulting in intensive upwelling along the eastern margin of the Bank of Campeche. Based on data on temperature and salinity, zones of upwellings and downwellings in the Bank of Campeche were distinguished (Bogdanov, 1965, 1967). Especially strong upwellings occur above the continental slope and at the external margin of the shelf, which can be clearly seen by more pronounced changes in temperature and phosphate distribution both in deeper waters and at surface layers.

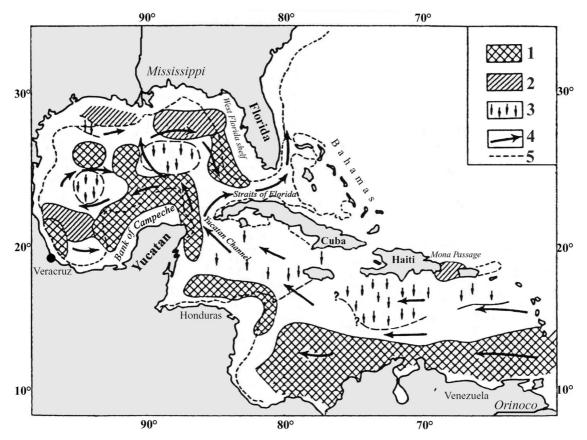


Figure 1. Regions of upwellings and downwellings in the Gulf of Mexico and the Caribbean Sea: 1 – upwelling through most of the year; 2 – upwelling in summer; 3 – predominance of downwelling; 4 – main surface currents in summer; 5 – shelf margin (after Bogdanov *et al.*, 1968, with changes).

Upwellings provide the surface waters with phosphates and other nutrients and are related to the high biological production and plankton biomass in some areas of the Gulf of Mexico and the Caribbean Sea (Fig. 2). The reasons for changes in the biological production were thoroughly studied in 1962-1968 (Bogdanov *et al.*, 1968; Bessonov *et al.*, 1971; Bessonov & González, 1971).

3. Influence of water movements on plankton development

A. Influence of water movements and stratification on plankton biomass. Stability of water layers was used to characterize the intensity of vertical water movements (Bessonov *et al.*, 1971). This characteristic is especially important in the formation of biological productivity. It was found that the value of stability of water layers can characterize the conditions of formation of productivity. The value of stability in the Bank of Campeche was found to be high, unlike most regions in the Gulf of Mexico. It increases with the intensity of the Yucatan Current. Besides, the mean depth of the layer with the maximal stability also increases.

Upwelling influences not only the quantitative characteristics of phytoplankton development but also the species composition, which was shown for the Bank of Campeche in July 1970 (Vinogradova, 1976), Before upwelling, the wet biomass of phytoplankton did not exceed 500-700 mg/m² and the amount of detritus 100-300 g/m². When the upwelling started, the biomass of phytoplankton reached 2,000 mg/m² and the amount of detritus 700 g/m². At the peak of upwelling, the wet biomass of phytoplankton reached 31 g/m², which is comparable to the values known from the North Atlantic during spring bloom (Vinogradova, 1976). Upwelling destroys the thermocline, thus providing the surface layer with nutrients. Diatoms proliferate more actively, and at the same time benthic diatoms and abundant detritus can be found in the water column. At the later stage, cold waters rich in nutrients spread into the shelf. When upwelling finishes, the thermocline develops again. In this period, cold water remains only in the near-bottom layer in the shape of a dome. In the Bank of Campeche area, the influence of upwelling on the phytoplankton development is guite noticeable only in the neritic zone and almost unnoticeable in the oceanic zone (Vinogradova, 1976). The high content of detritus in the Bank of Campeche region can be due to bottom vegetation and wind. In some cases, a high amount of detritus in the surface and near-bottom layers can be related to phytoplankton developed during the most active phase of upwelling. In the Bank of Campeche, speed of upwelling varies between 0.8 and 1.2 knots, increasing in summer (Vasiliev & Torin, 1965). The position of the main (not seasonal) pycnocline was determined to study the biotope of phytoplankton (Zernova, 1982). In a larger part of the Gulf of Mexico, the density gradient was small and usually increased noticeably in the upwelling zones where the main pycnocline lay higher.

Unlike the Gulf of Mexico, the hydrological regime in the Caribbean Sea is relatively homogenous. North-Atlantic waters, primarily transported with the North-Equatorial Current to the Caribbean Sea, are very warm, poor in both nutrients and plankton (Kanayeva, 1963). Seasonal changes in water temperature are not pronounced. The eddies produced along the westward Caribbean Current differ slightly in their characteristics. The northeastern Caribbean Sea is influenced by the northeastern trade wind, which in summer moves a little to the north. It is suggested that the wind pushes the water from the Atlantic Ocean through the Greater Antilles, which produces a local upwelling. For example, in June 1964, in the area south of Mona Passage, the wet biomass of plankton reached 350 mg/m³ (Khromov, 1965b). The Caribbean Sea can be characterized as an oligotrophic basin with wet plankton (in fact, zooplankton) biomass less than 100 mg/m³. This value is probably underestimated due to the usage of large mesh plankton nets (Table 1).

It is known that in the tropical waters of the Pacific, Indian, and Atlantic oceans, phytoplankton is more abundant only in the zones where the thermocline (or, in general, pycnocline) is relatively close to the sea surface (Vinogradov & Voronina, 1962, 1964; Kanayeva, 1963). In the downwelling zones, the thermocline is located very deep, which takes place in the extensive zones of the Gulf of Mexico and the Caribbean Sea. Therefore, on the whole, the wet plankton biomass in these regions is not high. In the upper 100 m, it usually does not exceed 100-150 mg/m³ (Bogdanov *et al.*, 1968). The photic layer in the Caribbean Sea is especially poor in nutrients, which is the main factor limiting phytoplankton development. In 90% of the area of the Caribbean Sea, the wet biomass of plankton varies between 30 mg/m3 and 100 mg/m³. Minimal values of the biomass of plankton are known from the northwestern Caribbean Sea, where it does not exceed 70

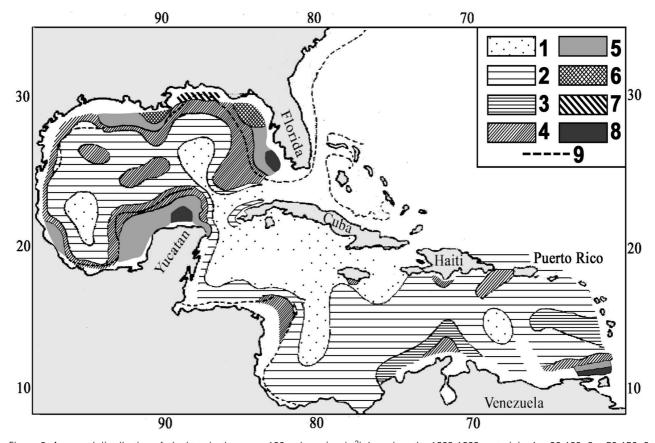


Figure 2. Averaged distribution of plankton in the upper 100-m layer (mg/m³), based on the 1962-1966 materials: 1 - 30-100; 2 - 50-150; 3 - 100-200; 4 - 100-300; 5 - 200-600; 6 - 200-1,000; 7 - 100-3,000; 8 - 300-1,000; 9 - shelf margin (after Bogdanov*et al.*, 1968, with changes).

mg/m3. The region near the shelf of Trinidad, Tobago, and Venezuela is the most productive in the Caribbean Sea due to upwelling and the Orinoco River runoff (Khromov, 1965b; Bogdanov *et al.*, 1968). In this area, plankton intensively develops during the most part of the year, and its biomass reaches 800-900 mg/m³. Since upwellings related to the Caribbean Current occur along its left margin (Ivanov, 1970), the near-shore areas of the South America are comparatively more productive, especially in autumn and winter.

Diminishing thickness of the photic zone and the position of the pycnocline closer to sea surface are indicators of upwelling in the center of a cyclonic gyre resulting from the divergence of currents. In the centers of anticyclonic currents, the photic layer becomes thicker, and stratification of the water column is less pronounced due to downwelling. Thus, water circulation is responsible to a greater extent for the level of biological productivity. However, due to spatial shifts in the position of the zones of maximal concentrations of phyto-, zooplankton and higher levels of food webs not always high production areas correspond to the centers of cyclonic avres (Vinogradov & Voronina, 1964). As a result, maximal concentrations of carnivorous tuna fishes can be found in the center of anticyclonic gyres (Bessonov & González, 1971). The more intensive the upwelling is, the more disjunctive in space are the maximal concentrations of different food levels. Bottom elevations in the Bank of Campeche result in cyclonic gyres, where deep waters enriched by nutrients raise to the upper photosynthetic layer, and are responsible for commercial fish assemblages in the central and eastern parts of the Bank of Campeche, the areas of maximal catches often being observed at the periphery of cyclonic gyres (Bessonov et al., 1971).

B. Correlation between phytoplankton development and abiotic factors. Zernova (1982) studied the dependence of phytoplankton development on abiotic factors (temperature, phosphates, pycnocline) in the Gulf of Mexico. In offshore areas, she found a positive correlation (0.57; p<0.05) between phosphate concentration and phytoplankton biomass in the open Gulf and low correlation (0.01; p>0.05) in the downwelling regions. These results correlate with the earlier published data: it is known that usually in oligotrophic areas of the open sea in the tropics correlation between the two variables is not traced (Semina & Tarkhova, 1970; Semina & Chyong, 1974). It was hypothesized that in the Bank of Campeche the development of phytoplankton was due to the local turnover of nutrients above the shelf, both regenerated at sea bottom and by mineralization in the water column, which can result in high abundance and biomass of phytoplankton even beyond the upwelling zones (Zernova, 1969, 1982).

The vertical distribution of biomass of plankton or abundance and biomass of phytoplankton in relation to abiotic and biotic factors are discussed in several publications (Khromov, 1965a, c; Roujiyaynen *et al.*, 1968; Vinogradova, 1976; López-Baluja *et al.*, 1992). Many details regarding phytoplankton vertical distribution are omitted in the present article. It is interesting to note that deep maxima of phytoplankton biomass were found in the Gulf of Mexico (López-Baluja *et al.*, 1992). Usually, they were bound with increased nutrient concentrations and the position of the main pycnocline. Sometimes, phytoplankton was more abundant near the bottom in shallow waters.

C. Circadian variability in phytoplankton abundance and biomass. Of special interest are 24-hour observations via 4-hour intervals at two stations in the Bank of Campeche in April 1965 (Zernova, 1970). It was found that dinoflagellates had maxima of abundance and biomass at noon (up to 12.5 mg/m³). Diatoms had maxima at 4-8 a.m. (up to 0.765 mg/m³) and minima between 5 p.m. and midnight (0.018-0.313 mg/m³) and at one station also at noon (0.002 mg/m³). Cyanophytes had slightly pronounced maximum between midnight and 4 a.m. (23.9-43.1 mg/m³). Thus, maxima and minima of total phytoplankton abundance and biomass during a 24-hour cycle depended on the dominant major taxonomic groups.

II. Seasonal changes in plankton biomass, temporal successions

1. Seasonal changes in plankton biomass

The main zones of upwellings and downwellings are stable in both time (within a year) and space (Fig. 1), resulting in a small variability of quantitative characteristics of plankton in such regions as the north part of the west Florida shelf and the Bank of Campeche area (Khromov, 1965a, 1967; Bogdanov et al., 1968). In both regions, the maximal biomass was found in summer in relation to the intensification of the Yucatan Current, which enhances upwellings in these areas. However, during a year, the fluctuations in biomass did not exceed 2-3 times (Fig. 3). In the northern Gulf of Mexico, they are less pronounced than in the Bank of Campeche. In the region north of Veracruz, plankton was found to be more abundant in winter. Sometimes, pelagic coelenterates and tunicates are responsible for relatively high values of wet plankton biomass (up to 300 mg/m³), as it occurs in the middle part of the Bay of Campeche and above the shelf of Honduras (Bogdanov et al., 1968). Minimal values of plankton biomass (up to 70 mg/m³) were registered across the northwestern Caribbean Sea.

Seasonal changes in plankton biomass were traced in the Rada Bight near Habana, the northeastern Gulf of Mexico, in 1970-1971 (Vinogradova, 1974; López-Baluja *et al.*, 1992).

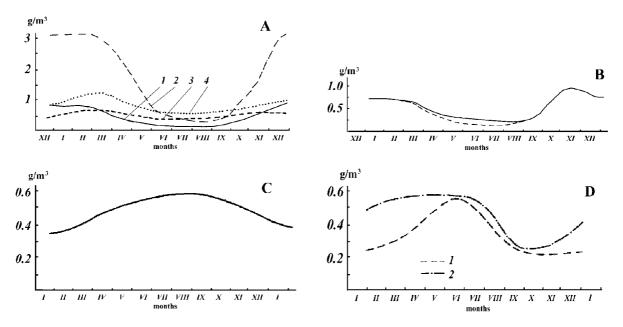


Figure 3. Annual dynamics of plankton biomass in the Gulf of Mexico: A – northern shelf of the Gulf, November 1962 – October 1964 (1 – east of the Mississippi estuary, mean values; 2 - east of the Mississippi estuary, maximal values; 3 - west of the Mississippi estuary, mean values; 4 - west of the Mississippi estuary, maximal values); B – northwestern Florida shelf, mean values, November 1962 – October 1964: the period March-August is given with a dotted line as possible variation due to non-standard materials obtained in June; C – southwestern Florida shelf; D – the Bank of Campeche, mean values, November 1964 – February 1966 (1 – eastern transect along 87°20'W; 2 – western transect along 91°W) (A and B – after Khromov, 1965a; C and D – after Khromov, 1967, and Bogdanov *et al.*, 1968, with changes).

Three maxima of phytoplankton abundance and biomass were observed: abundance maxima – in October $(12x10^6 \text{ cells/m}^3)$, June and April, and the highest biomass maximum – in June (23 mg/m³). Minimal values of abundance and biomass were estimated in May $(1.7x10^6 \text{ cells/m}^3)$ and in January (1.8 mg/m^3) , respectively.

A. Influence by river runoff and precipitation. In some seasons, river runoff significantly influences biological production in bringing nutrients. It especially occurs in the Mississippi and Orinoco estuaries. In the area east of the Mississippi estuary, the highest for the Gulf of Mexico wet biomass of plankton was found – over 3,000 mg/m³ (Bogdanov et al., 1968). River runoff value and distribution change considerably in time and are influenced by local winds, coastal currents, and precipitation, which results in great seasonal variation of plankton biomass. It is also responsible for significant spatial variation near estuaries. Along transects, wet plankton biomass varied in the area east of the Mississippi River from 200 mg/m³ to 3,000 mg/m³ and in the northwestern Florida shelf from 180 mg/m³ to 1,100 mg/m³ (Bogdanov et al., 1968). Maximal wet plankton biomass values in these areas were usually observed in cold season (October-March), especially in spring and autumn, in the periods of increased river runoff. In winter, plankton is also usually abundant. In very cold winter, when river runoff is much decreased, plankton

biomass near the Mississippi estuary can be low. For example, in the very cold winter of 1965-1966, in the area east of the Mississippi estuary the wet plankton biomass was as low as 130 mg/m³ (Bogdanov *et al.*, 1968).

Based on the studies on species composition and seasonal groups of species, in Cuban waters, two seasons are clearly distinguished (López-Baluja et al., 1992): winter – the dry season (January-April) and summer - the rainy season (May-August). Autumn and spring are transitional periods. The division of the year into the two floristic seasons corresponds with physical and chemical oceanographic conditions. Near the southwestern coast of Cuba, in summer, both the phytoplankton abundance and biomass slightly increase due to river runoff. After hurricanes resulting in mixing waters, they increase significantly. After one of the hurricanes, the abundance of phytoplankton reached 7.84x10⁹ cells/m³ and its biomass 70 g/m³. Near the northwestern coast of Cuba, seasonal changes in phytoplankton are hardly distinguished. It was noted that the sharpest changes occur in the vicinity of cities and settlements, which is due to seasonal differences in river runoff and anthropogenic eutrophication related to it (López-Baluja et al., 1992). In the open sea around Cuba and, in particular, in the Gulf of Mexico, alteration of the dry and rainy seasons results in different vertical distribution of phytoplankton. In summer, phytoplankton is concentrated in the surface layer due to shallow halocline. In winter, two maxima are observed, at the 25 m depth and at the 75 m depth above the main pycnocline. In the Campeche Gulf, two types of vertical distribution of phytoplankton, heterogenous and homogenous, are related to intensifying (in spring) and weakening (in autumn) upwelling in the western part of the Gulf.

B. Influence by upwellings. In the zones greatly influenced by upwellings, seasonal fluctuations of plankton biomass strongly depend on them. It is known that in the Bank of Campeche the area enriched by nutrients is twice as large in summer as in winter (Bessonov et al., 1971). The intensity of the Yucatan Current, which determines horizontal circulation pattern, is of seasonal character.

Based on five surveys and 292 stations in 1962-1964, Khromov (1965a) mapped the horizontal distribution of plankton biomass in the upper 200-m layer, presented graphics of the vertical distribution of plankton biomass along several transects, and traced the seasonal dynamics of plankton biomass in different parts of the Gulf of Mexico. He concluded that while in the northern Gulf of Mexico seasonal changes in hydrological conditions, the composition, and abundance of plankton are well distinguished, in its southern part they are noticeably smoothened. At least, as regards seasonal fluctuations in plankton biomass, this conclusion is contradictory to the results published by the same author later (Khromov, 1967; Bogdanov et al., 1968; see Fig. 3). According to Khromov (1965a), in the northwestern shelf of the Gulf of Mexico, three regions are rich in plankton in the cold period: (November-January) the northwestern Florida shelf (up to 1,200 mg/m³) and the regions east and west of the Mississippi estuary (700 and 3,100 mg/m³, respectively). For the west Florida shelf, this is in contrast to the data of Bogdanov et al. (1968) mentioned above.

C. Mean phytoplankton biomass values. Despite seasonal variability of phytoplankton biomass, based on the data obtained during one to three and more surveys of different regions of the Gulf of Mexico, López-Baluja et al. (1992) found it possible to calculate the mean annual values of wet phytoplankton biomass: 143 mg/m³ near Cuba, the eastern and western regions differing greatly in biomass (40 mg/m³ in the southwestern region, 86 mg/m³ in the northwestern, 412 mg/m³ in the northeastern and 250 mg/m³ in the southeastern region); 47 mg/m³ in the Gulf of Mexico (96 mg/m³ in the neritic zone and 10.4 mg/m^3 in the oceanic zone).

2. Temporal successions and size of phytoplankters

It is known that the distribution of algal cells attributed to different size classes can give a clue to temporal successions of phytoplankton. Based on the samples taken by net, mesh size 70 mm, algal cell size was studied in February-April 1973 (Zernova, 1975). It was found that in the upwelling zones in the southern Gulf of Mexico, small-sized cells (less than 20 µm) constituted over 90% of the total number of cells. In the downwelling zones, their share diminished down to 60-70%. The studies on cell size allowed Zernova to trace a temporary succession in the direction from the upwelling zone down the stream to the downwelling zone. The minimal size (11 μ m) was noted for the southern deep-sea basins, the maximal (28 µm) near the Cuban coast, and the intermediate in the area of the Puerto-Rico Trough (22 μ m) and the Yucatan and Columbian deep-sea basins (18 µm). The positive reliable correlation was found between the mean cell diameter and phosphate concentration at the 100 m (0.76; p<0.05) and 200 m depths (0.90; p<0.01) as well as between the mean cell diameter and temperature at the 200 m depth (0.61; p<0.05). Succession of smaller-sized species followed by larger-sized ones with aging waters of the Yucatan Current was also noted by Zernova and Zhitina (1985). The data obtained confirm the classical scheme of successions in phytoplankton communities (Margalef, 1967a, b; Sournia, 1982). It was suggested that the low concentration of silicates in the Gulf of Mexico results in a smaller-sized phytoplankton in comparison to temperate regions (Roujiyaynen et al., 1968). In the Gulf of Mexico, phytoplankton in the upwelling zones is at the initial stage of its succession and in oligotrophic areas in its final stage (Zernova, 1974a). Differences in size composition of phytoplankton communities are responsible for not matching the peaks of abundance and biomass (López-Baluja et al., 1992).

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III. Phytoplankton species composition and communities

1. Inventory of major phytoplankton groups

In the Gulf of Mexico and the Caribbean Sea, some 1,580 microalgal species dominated by diatoms and dinoflagellates were recorded, about 1000 being purely planktonic, up to 174 species per station being found (Zernova & Krylov, 1974). However, the most comprehensive list of planktonic algal taxa is given by Roujiyaynen et al. (1971). They listed about 700 species and varieties, presented brief data on their geographic distribution in the world ocean, and presented a comparative taxonomic analysis at the level of genus and species found in three major regions: the Gulf of Mexico, the Caribbean Sea and the Straits of Florida. The list includes unpublished data by Kondratieva. It was found that planktonic flora is more diverse in the Gulf. In total, in these three regions, the list included 299 diatoms, 235 dinoflagellates, 90 chrysophytes and prymnesiophytes (mainly coccolithophorids), 52 cyanophytes and 13 chlorophycean, euglenophycean and prasinophycean species and varieties. Most of the cyanophytes were freshwater species. Based on the samples collected in the period of 1965-1985 in the Gulf of Mexico, the Caribbean Sea, and Cuban waters, López-Baluja et al. (1992) presented a list of 529 algal

species, which comprises 264 dinoflagellates, 230 diatoms, 21 prymnesiophyceans, 8 cyanophytes, 3 chrysophyceans and 3 cryptophyte, chlorophycean and prasinophycean species. The authors also presented the data on the mean cell volume of many species compiled from literature as well as brief biogeographic and ecological characteristics. A list of 131 algal species and intraspecific taxa found in the Gulf of Mexico and the Straits of Florida was given by Ivanov (1966).

The studies carried out in March-April 1965 in the southern Gulf of Mexico have shown that in offshore areas, the role of dinoflagellates increases and the importance of isolated species in the community decreases, which results in high values of diversity index (Zernova, 1974a).

The number of species in the Caribbean Sea seems to be less than in the Gulf of Mexico; however, this can be related to the fact that the former has been studied to a smaller extent (López-Baluja et al., 1992). Compared to the Gulf of Mexico, the flora of the coastal Cuban waters is characterized by more numerous benthic and tychopelagic diatoms of the genera Amphora, Licmophora, Navicula and Nitzschia, freshwater diatoms of the family Naviculaceae, cyanophytes of the genera Anabaena, Nostoc, Oscillatoria and Spirulina and chlorophycean genus Chlorella. Unlike Cuban waters, the Gulf of Mexico is inhabited by a wider variety of dinoflagellate genera, which characterizes the planktonic flora of the Gulf as oceanic. In Cuban waters, the number of taxa per station was 4 to 35 and in the Gulf from 25 to 175. Diatom species were more diverse in the coastal zone and dinoflagellates in offshore regions. The highest number of phytoplankton species was found in the Yucatan Channel and in the southwestern Gulf of Mexico.

2. Phytoplankton communities

A. Neritic, oceanic and transitional biocoenoses. To study phytoplankton communities (or, more exactly, the phytocene of plankton communities), statistical methods were used (Fager, 1957; Krylov, 1971). Based on water-bottle samples, the phytoplankton community of the southern Gulf of Mexico was studied from the point of view of associations between stations, the mean number of species per station being about 100 (Zernova & Zhitina, 1985). The stations situated in the area of mixed coastal and offshore waters were the most similar between them in terms of algal species composition. Based on Fager's method (1957), groups of species were distinguished. The authors concluded that in the study area, the distribution of phytoplankton community is mosaic, and there are no essential differences in its structure. Based on the samples taken at the Campeche Bank by net, mesh 168 mm, two primary (neritic and oceanic) and a secondary (transitional) biocoenoses were distinguished (Krylov, 1974). The

On the basis of comparative analysis of species composition and the composition of dominant species, quantitative distribution of phytoplankton, and the diversity index, five regions were distinguished in the Gulf of Mexico: (1) the upwelling zone in the Yucatan Channel near Yucatan Peninsula; (2) the western Bank of Campeche; (3) the offshore area north of the Gulf of Campeche beyond upwelling zones, (4) the cyclonic upwelling zone in the Bay of Campeche, and (5) the Yucatan Channel and the Straits of Florida (Zernova, 1974a). It was concluded that their boundaries corresponded to the boundaries of the regions distinguished on the basis of physical and chemical oceanographic characteristics. The diversity index was low in the zones of intensive upwelling and increased more than fourfold to the zones where upwelling was not observed due to lower abundance of diatom species and the increased number of dinoflagellate species. In addition, the species structure of the phytocene of Cuban waters and the Gulf of Mexico was analyzed using Jaccard's similarity index (López-Baluja et al., 1992).

It is obvious that the communities distinguished with the use of statistical methods differ in structure; however, smaller-sized species, especially delicate flagellates, were not considered, since in most cases the taxonomic observations on living cells were not carried out. Also, it is clear that underestimation of small-sized flagellate species implies underestimation of the number of species as well as their abundance, which must influence the diversity index values.

In the Bank of Campeche, strong positive correlation between abundance of phytoplankton and temperature was found only for dinoflagellates in both the neritic (0.43; p>0.05) and oceanic zones (0.59; p<0.01) and for coccolithophorids in the offshore area (0.65; p<0.01), and reliable negative correlation (-0.50; p<0.01) only for diatoms in offshore area (Zernova, 1982).

B. Red-tide and bloom events. The red tide in the Gulf of Mexico was observed by Russian authors in the Bank of Campeche in July 1965 (Zernova, 1970b, 1982). Water coloring was produced by the dinoflagellate *Scrippsiella trochoidea*

(Stein) Loeblich III (referred to as Gonyaulax minima Matzenauer) (1.4x10⁶ cells/m³) and ciliates (106 cells/m³). The red tide supposedly caused by Karenia brevis (Davis) G. Hansen et Moestrup (referred to as Gymnodinium breve Davis) was observed in the surface 10-cm layer above the Bank of Campeche (Roujiyaynen et al., 1968). Red tides produced by dinoflagellates are often in the Gulf of Mexico and Cuban waters (López-Baluja et al., 1992). Non-toxic red tides caused by Akashiwo sanguinea (Hirasaka) G. Hansen et Moestrup (referred to as G. splendens Lebour), G. variabile Herdman, and Peridinium aciculiferum Lemmermann, often occur in the area north of Habana. In eutrophic coastal waters the diatom species of the genus Thalassiosira can also produce blooms. Mass development of T. subtilis (Ostenfeld) Gran was observed in the upwelling zone in the Bay of Campeche (Zernova, 1969, 1970). Among the mentioned species, only *P. aciculiferum* is freshwater-brackishwater, the rest being marine species. As seen, despite a long period of planktological studies in the Gulf of Mexico, only a few records of red tides are known, which can be due to the offshore large-scale character of oceanological surveys.

IV. Primary production

1. Data obtained by oxygen method. Until the 1960s, the only known data on primary production measured by oxygen method were by Riley (1939). In the period of 1962-1966, seven oceanographic surveys of about 70 stations each were carried out, four in the Gulf of Mexico and three in the Caribbean Sea. Since 1966, the Bank of Campeche became an object of detailed studies on biological productivity (Bessonov *et al.*, 1971). Unfortunately, the results obtained at 24-hour stations, including data on primary production measured by the oxygen method, have not been published.

2. Data obtained by radiocarbon method. In September 1964 -January 1965, primary production was measured by the radiocarbon method (Steeman-Nielsen, 1952) modified by Sorokin (1960) near the northwestern coast of Cuba (Kondratieva, 1968). It was shown that changes in primary production were related to the anticyclonic water circulation system, wind conditions, and water inflow of the Yucatan Channel. In winter, in shallow waters, 84.5% of potential production was due to small-sized diatoms. Calculated effective production in the surface 0-6 m layer made up 12% from potential production and 330% of biomass, i.e. the P/B coefficient was 3.3, which is a very high value. Calculated mean annual primary production in the study area was 90 gC/m². On the basis of the results obtained in the experiment, the mean rate of cell division of the dominant algal species was calculated. The cell division rate in diatoms (2.18-8 div./day for 15 species, with one exception 1.6 div./day) was higher than in dinoflagellates (2-4 div./day for 5 species). The generation time of unidentified small flagellates was 4 div./day.

In April, May, and June 1965, primary production was measured at 18 stations in the southern Gulf of Mexico and near the northwestern coast of Cuba (Kabanova & López-Baluja, 1970). The radiocarbon method modified by Sorokin was used. Also, experiments on measuring primary production in the waters enriched by nutrients (N, P, Fe and Si contained compounds) were carried out. It was concluded that the southern Gulf of Mexico is a high-productive area. The highest values of primary production were found in the Bank of Campeche – 50-100 mgC/m³/day at the sea surface and 500-1,450 mgC/m²/day in the layer of photosynthesis. Similar values were registered at the southwestern Florida shelf. High values (over 10 mgC/m³/day and 500 mgC/m²/day) were measured in the upwelling zone near Veracruz. In the area north of the Bank of Campeche, primary production varied between 5 and 20 mgC/m³/day at the sea surface and between 200 and 400 mgC/m²/day. Low-productive waters were in the central part of the Yucatan Channel, near the southwestern coast of Cuba and the Straits of Florida (0.1-2.8 mgC/m³/day and 50-200 mgC/m²/day). Coastal waters near northwestern Cuba were less productive than the southern Gulf of Mexico but more productive than the tropical waters of the open ocean. The distribution of primary production was found to be related to nutrients. Measurements of primary production in the waters of the southern Gulf artificially enriched with nutrients have shown deficiency in nutrients not only at deep-sea stations characterized with deep pycnocline but also in shallow highproductive areas, which decreased the photosynthetic rate. Near northwestern Cuba, deficiency in nutrients was observed only in low-productive areas.

It seems that there is strong positive correlation between the biomass of phytoplankton and the intensity of photosynthesis (Kabanova & López-Baluja, 1970). The correlation between these two characteristics was 0.80 (p=0.01) for the neritic zone and 0.72 (p=0.01) for the oceanic zone (López-Baluja et al., 1992). Seasonal studies on primary production in relation to nutrients near the northwestern coast of Cuba in 1967-1968 have shown that all nutrients (phosphates, nitrates, and silicates) seem to limit phytoplankton development (Kabanova, 1981). Primary production was higher in June-September. Peaks of primary production coincided with peaks of abundance of phytoplankton only in April-May, slightly shifted concerning each other in June, but in other cases there are no coincidences. On average, primary production increased in the rainy season (June-October) and decreased from January to June.

3. Data obtained by epifluorescence microscopy. Fluorescence microscopy was once used to distinguish dead and live phytoplankton cells (Ivanov, 1966). At two stations, studies were concentrated on the most abundant species, the cyanophyte *Oscillatoria thiebautii*, radiolarians and foraminiferans, which

were abundant sometimes. It was found that in the 100-200 m layer the number of live trichomes of *Oscillatoria* was about twice less than in the surface 0-100 m layer. Based on the materials of one station, all radiolarians and foraminiferans in the 0-100 m layer were found to contain endosymbionts, which implies their important role in primary production in the sea.

V. Grazing

Herbivorous zooplankton is primarily dependent on phytoplankton. In the Gulf of Mexico and the Caribbean Sea, strong positive correlation between phytoplankton and zooplankton biomass was found for both the neritic (0.54) and oceanic (0.67) zones (Shuvalov et al., 1970). Similar values were obtained by López-Baluja et al. (1992) for different regions of the Gulf of Mexico: 0.54 (p=0.01) for the neritic zone and 0.64 (p=0.01) for the oceanic zone. Vinogradova (1976) calculated utilization of phytoplankton by herbivorous zooplankton (tunicates, copepods and amphipod and decapod larvae) separately for the neritic and oceanic zones in the Bank of Campeche. In the oceanic zone, where upwelling did not influence noticeably phytoplankton development, utilization of phytoplankton varies slightly and reached 83-90% of the total biomass. In the neritic zone without upwelling, utilization reached 81%, then it dropped to 66% and 47%, while upwelling became more intensive. Kondratieva (1968) calculated that near the northwestern coast of Cuba 90% of the daily phytoplankton production was consumed by herbivorous zooplankton. In the surface 0-6 m layer, grazing constituted 282 mg/m² of wet weight, or 6.7 mgC/m². Thus, both the Gulf of Mexico and the Caribbean Sea are characterized with a well-balanced annual cycle of plankton communities (with no or low underexploitation of phytoplankton by herbivorous zooplankton). A non-balanced annual cycle should be expected only in the zones of powerful upwelling, where phytoplankton is underexploited.

VI. Concluding remarks

1. Critical review of methods. The use of different methods of sampling and calculation of plankton or phytoplankton biomass and primary production during the cruises to the Gulf of Mexico and the Caribbean Sea make comparisons difficult. Minimal mesh size used to sample plankton was 70 mm (Zernova & Krylov, 1974; Zernova & Zhitina, 1985), while most of net hauls was performed with a Juday's net, mesh size 168 mm, widely used in zooplankton research (Table 1). In some cases, mesh size is not indicated (Ivanov, 1966; Roujiyaynen et al., 1968, 1971). Some authors used various types of net. For example, the article by Khromov (1965a) is based on the material taken by a Juday's net, mesh size 168 mm, and a "nonstandard net" with unknown mesh size. López-Baluja et al. (1992) used nets with different mesh size (90, 175 and 180 μ m) in various regions of the Gulf of Mexico and the Caribbean Sea. The use of a Zaitsev's hyponeuston net during three

cruises to the Gulf of Mexico (Ivanov, 1966) was useful, since it obviously allowed the author to filtrate a greater amount of water and thus to catch rare species. Sampling with water bottles accompanied net sampling only occasionally (Ivanov, 1966; Roujiyaynen *et al.*, 1968, 1971; Zernova & Krylov, 1974). In phytoplankton studies, a wide range of sampling methods should be applied simultaneously.

In some cruises, the total plankton biomass was calculated (Khromov, 1965a, b, c, 1967; Bogdanov et al., 1968), which made it impossible to evaluate the partial contribution of phytoplankton and zooplankton. The so-called wet biomass of plankton was calculated using the device called Jaschnov's volumenometer (Jaschnov, 1959). During this procedure, large organisms, which were considered non-edible, were not taken into account. It should be noted that Jaschnov's method is rapid; however, it implies a different content of water contained in organisms, which are left drying on a filter paper for a while. Besides, this method, in fact, permits us to measure the volume of seston, including detritus, which is obviously more abundant in coastal areas. Moreover, it is questionable if hydromedusae, siphonophores and tunicates should be considered non-edible. The biomass of bacteria and phytoplankton was usually estimated by the calculation of species cell volumes (Anischenko, 1968; Kondratieva, 1968; Zernova, 1969; Vinogradova, 1976; López-Baluja et al., 1992); few details of this procedure, which is not so simple in the case of phytoplankton due to diverse and complicated cell shapes as commonly believed, were indicated.

The methods used to calculate the abundance and biomass of phytoplankton were also diverse. Usually, the settling technique with subsequent decantation of excessive water and sometimes with centrifugation was applied to concentrate phytoplankton (Ivanov, 1966; Zernova, 1974a; Vinogradova, 1976; Zernova & Zhitina, 1985). Biomass calculations related to a square meter by Kondratieva (1968) and Vinogradova (1976) make comparisons with the relevant data by other authors, who estimated biomass in mg/m³, difficult.

Formaldehyde solution (usually 2%) was used as a fixing agent where indicated (Zernova, 1969; Vinogradova, 1976; López-Baluja *et al.*, 1992). It is unknown if formaldehyde solution was neutralized, which is important to prevent elimination of coccolithophorids with time, which are diverse and abundant in tropical seas and for which neutralized formaldehyde is appropriate. It is known that formaldehyde fixation distorts cell shape of naked species and causes flagella to be thrown off in many flagellates (Throndsen, 1978). Only in one case (Zernova & Zhitina, 1985), phytoplankton was fixed with the weakly alkaline Lugol solution (designated in the article as Utermöhl solution), which is a more adequate fixative for flagellates. Acid Lugol solution was sometimes used in the Rada Bight near Habana (López-Baluja *et al.*, 1992), which

Year	Characteristics measured	Number of stations	References
1962-1967	Salinity, oxygen, phosphates, plankton biomass, fish concentrations	about 500	Bogdanov <i>et al.</i> , 1968 Bessonov, González, 1971
	Abundance and biomass of bacterioplankton	16	Anischenko, 1968
	Primary production (by radiocarbon method)	18	Kabanova, López-Baluja, 1970
	Salinity, oxygen, phosphates, pH, permanganate oxidation, biochemical oxygen demand, primary production (by oxygen method)	300	Bessonov <i>et al.</i> , 1971
1967-1968	Primary production, phosphates, nitrates, silicates	no data	Kabanova, 1981
1968-1979	Salinity, density, oxygen, phosphates, nitrates, nitrites, silicates	no data	López-Baluja <i>et al</i> ., 1992

Table 2. Data on Soviet and Soviet-Cuban chemical oceanographic, microbiological and biological production studies in the Gulf of Mexico and the Caribbean Sea in the 1960-1980s.

allowed the authors to count abundant nanoplankton. It should be noted that the taxonomy of many flagellate groups and the methods of studies of the non-preservable fraction of the phytoplankton in the 1960-1970s were not so developed and used as at present. No doubt, there are at least dozens of flagellate species, especially naked prymnesiophytes and dinoflagellates, which have not been recorded yet from the study region.

Application of the epifluorescence technique to distinguish dead and living phytoplankton cells and to study the color of light emitted by photosynthetic, dying and dead algal cells and symbionts of some protists bore an experimental character (Ivanov, 1966; only in this article the type of microscope and illumination device are indicated – a standard compound microscope MBI-3 together with the luminescence device OI-19, both made in the USSR). However, its application to marine phytoplankton research as early as in 1964 was a very progressive feature even considering that the first studies on microalgae to distinguish living and dead cells using the epifluorescence microscopy date back to the early 1950s (Gorjunova, 1951).

Only in a few works is the counting procedure described. Zernova (1969, 1970a, 1975) and López-Baluja *et al.* (1992) used Naumann's chamber of volume 1.0 cm³, the type of microscope not being indicated. The aliquots of samples taken in the areas, where algal blooms were, were diluted before counting. Similarly, small-sized diatoms were counted after significant dilution. Otherwise, algae were counted in a temporary water mount in 0.05 cm³ or 0.1 cm³. All plankton studies discussed herein, excepting the work by Ivanov (1966) mentioned above, were most likely performed using a standard compound microscope. This makes difficult further comparisons with the quantitative data obtained or to be obtained applying the Utermöhl method (a combination of an inverted microscope, sedimentation cylinders and combined plate chambers), which is widely accepted nowadays.

Calculations of primary production were performed only in several cruises (Table 2). Application of the oxygen (Winkler's) and radiocarbon methods would make the comparisons between them difficult, but the results of the study with the use of the oxygen method have not been published (Bessonov *et al.*, 1971). It goes without saying that the data on primary production obtained in isolated areas in certain time are neither indicative for the Gulf of Mexico and the Caribbean Sea, nor representative of the whole annual cycle of different phytoplankton communities.

"Temperature, salinity, oxygen, phosphates and pH and oxidation in neutral medium were determined according to the standard methods of hydrological and hydrochemical research accepted in the USSR" (Bessonov *et al.*, 1971: 15). Unfortunately, such a brief description of applied methods leaves much room for guesses. Much criticism and skepticism arises when the so-called standard methods are referred to. Probably, the most important is that in the 1960s, in the USSR salinity was estimated by argentimetry. Determination of salinity by conductivity became widely used only in the 1980s. Definitely, the use of the two methods of determination of salinity may be a source of difficulties when comparing sets of old and new data obtained by different methods.

2. What is a healthy approach? "During the past 30 years, human intervention has resulted in unprecedented changes in the Gulf ecosystem" (Kumpf *et al.*, 1999). Why not consider the large amount of data obtained in the earlier period to understand the present state of the ecosystem and probably to figure out the trends in the area around which about 50 million people live? No doubt, the book by Kumpf *et al.* (1999) is a great effort of the U.S., Mexican, Canadian, British and Philippine scientists. However, the contributors seem to be absolutely unaware of Russian and Cuban literature on physical, chemical, and biological oceanography published in Russian and Spanish, often containing summaries in Spanish

or English, disregarding the articles by Bogdanov *et al.* (1968) and Zernova (1969) cited by Lohrenz *et al.* (1999). Application of modern technology will not replace historical data, which sometimes is hard to compare with; however, they are a must for anyone who pretends to assess and to manage the Gulf of Mexico ecosystem.

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