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An overview of the plankton communities of the Gulf of Maine

by

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Introduction

This paper was written in response to the request for an overview of the biological system of the Gulf of Maine, by the ICNAF Environmental Working Group (Circ. Letter 75/5). It summarizes the knowledge of the phytoplankton and zooplankton, including a description of dominant species as well as biomass and productivity data for these components in the Gulf of Maine. The paper does not cover planktonic bacteria, fungi, or protozoans nor does it include the benthos or fishes. It was felt that with the short period of time available for preparation of this paper, a synopsis of the phytoplankton and zooplankton would prove most useful in providing a basis for an understanding of the biological system in the Gulf of Maine particularly with reference to factors controlling survival of larval fish.

This document is not intended to be a history of oceanography in the Gulf of Maine. Most of the biological oceanographic studies in the Gulf were made in the first half of this century, and Colton (1963) has provided a thorough history of oceanography in the Gulf of Maine prior to 1963.

Only a generalized view of the plankton communities in the Gulf of Maine is possible because only a few broad-scale studies have been done, and these were conducted at different times and with disparate methods, some of which were qualitative. This is particularly true in the case of production and biomass estimates, where much of the early data is more qualitative than quantitative. Nevertheless increased knowledge about the lower trophic levels is fundamental to better understanding of fish production, and even qualitative studies will point out areas where additional research is necessary.

The area covered in this paper is shown in Figure 1. The Gulf of Maine includes the oceanic bight from Nantucket on the west to Cape Sable on the east, including Nantucket Shoals, Georges Bank and Browns Bank, extending out to the 200 meter depth contour. The flora and fauna of the Gulf of Maine is primarily a boreal assemblage of species, with subtropical, tropical, temperate and arctic immigrants at various times of the year. The general non-tidal surface circulation in the deep basin of the Gulf of Maine consists of a counter-clockwise gyre most of the year, with a clockwise gyre on Georges Bank in the spring and summer (Bumpus 1973). The bottom circulation in the Gulf and on Georges Bank appears to be in the same direction as the surface flow but at lower velocities.

This paper is divided into two major sections, one on phytoplankton, and one on zooplankton. The phytoplankton section contains information on the seasonal and geographic changes in species composition, standing stock and primary production, as well as material on the factors limiting phytoplankton growth in the Gulf of Maine. The zooplankton section contains a synopsis of the reproductive cycles of dominant species and of variations of biomass and abundance of zooplankton throughout the year.

Phytoplankton

Phytoplankton studies in the Gulf of Maine were carried out as early as 1912 (Bigelow, 1914). Further work by Bigelow resulted in his classic work on the plankton of the offshore waters of the Gulf of Maine (1926). These studies employed plankton nets and therefore present only a qualitative picture of the larger phytoplankton. Ryther and Yentsch (1959) found that phytoplankton nets do not sample the nannoplankton (those phytoplankton that will pass through the pores of a fine plankton net) and that due to clogging, the abundance of larger forms may also be underestimates. Studies carried out by Gran and Braarud (1935), Bigelow, Lillick and Sears (1940), Lillick (1940), Sears (1941), Riley (1941, 1946), and Hulburt and Corwin (1970), provide a more quantitative picture of the phytoplankton community in the Gulf of Maine.

With the exception of the study by Hulburt and Corwin (1970) all of the studies mentioned above were carried out in the early 1930's. Although I have generalized the seasonal phytoplankton cycle based on these studies it should be pointed out that a complete time series, of sampling throughout any one year does not exist.

Dominant species

The dominant phytoplankton of the Gulf of Maine are the diatoms, with approximately 130 species present in the plankton during the course of a year. The diatoms are followed in importance by the dinoflagellates and coccolithophorids. Silicoflagellates are often widespread in the Gulf of Maine but rarely are they the dominant phytoplankter.

Another type, *Phaeocystis*, is never widespread but may be abundant locally. Lillick reported a bloom in Massachusetts Bay for a short period of time, although Parker and Mulligan (TRIGOM - PARC,1974) found no *Phaeocystis* in their study of Massachusetts Bay in 1972-1973. There are large numbers of small green flagellated nannoplankton (called muflagellates by Lillick, 1940) which were otherwise unidentifiable, but possibly of great importance in terms of their contribution to the annual primary production of the area. Ryther and Yentsch (1959) have observed that the nannoplankton in southern New England waters contribute about 92% of the total photosynthesis. This figure is in accord with values determined by Malone (1971) who found that the nannoplankton contributed about 90% on the average to primary production. The nannoplankton become relatively more important as the nutrient concentration decreases (Malone,1971) and so they can be expected to be particularly important during the summer months in the Gulf of Maine.

Seasonal and geographic variations in species composition

Most of the following discussion on species composition is based on the work of Lillick (1940). The species composition of the phytoplankton varies with the season, and it varies geographically within a season. Figures 2-7 illustrate some of these changes. The smallest number of species are present in the Gulf of Maine during the winter. At the time of the spring phytoplankton bloom the number of species increases, and remains at a fairly high level through the summer and early autumn, and then decreases in late autumn. The following discussion will pertain to the Gulf of Maine in general, unless an area within this region is specifically mentioned.

1. Winter flora. The winter flora is characterized by a paucity of both species and individuals (Bigelow, Lillick and Sears,1940; Lillick,1940; Sears,1941). Generally the dominant species at this time of year are *Chaetoceros excentricus*, *C. centralis*, *Thalassionema nitzschoides*, *Ceratium longipes*, *C. tripos* and *Prorocentrum micans*, although the importance of the various species will vary from place to place within the Gulf (Figures 2, 3). For example, *Cosinodiscus* and *Ceratium* are the dominant forms in the western and northern coastal areas, while on the eastern side of the Gulf *Peridinium*, *Exuviaella* and the neritic diatoms, *Melosira sulcata* and *Thalassionema nitzschoides*, are the most important. On Georges Bank there is still another assemblage of species; *Ceratium*, other dinoflagellates, *Cosinodiscus* and other neritic forms occur in about equal numbers.

In general as winter progresses *Cosinodiscus* becomes the dominant phytoplankter in the Gulf of Maine, and boreal species which are rare at the beginning of winter, such as *Biddulphia*, *Chaetoceros*, *Rhizosolenia alata*, *Thalasseonema nitzschoides*, and *Skeletonema costatum* (in coastal areas) increase in numbers. It is at this time, too, that some arctic forms appear, *e.g. Navicula van hoeffeni*, and that the dinoflagellates reach their nadir. The dinoflagellates are at a disadvantage at this time (and into the spring) because the lower temperatures mean an increased solubility of carbonate (Harvey,1966).

2. Spring flora. The spring phytoplankton bloom starts sometime between early February and early April in the Gulf of Maine. The species composition at several places within the Gulf of Maine is given in Figures 2, 4. The first species to bloom in the major portion of the Gulf are *Thalassiosira decipiens* and *T. nordenskoeldi*, while *Chaetoceros socialis* initiates the bloom on Georges Bank (Lillick,1940; Sears,1940). The most abundant organism in the Gulf of Maine at this time is *T. nordenskoeldi* followed by *T. decipiens*, *T. gravida*, and *Porosira glacialis*. Other less abundant but important species are *Chaetoceros borealis*, *C. convulutus*, *c. debilis*, *C. decipiens*, *C. compressus*, *C. laciniosis*, *C. furcellitus*, some arctic forms, *Fragilaria oceanica*, *Navicula van hoeffeni*, *Achnanthes taeniata* and a cold water

dinoflagellate *Ceratium arctic* in the eastern Gulf of Maine. Although *Thalassiosira* is the usual dominant phytoplankter, *Chaetoceros debilis*, and other species of *Chaetoceros* are sometimes the most abundant phytoplankton.

3. Summer and autumn flora. The species composition at various locations in the Gulf of Maine during the summer is represented in Figures 2, 5. By early summer, the most important species in the Gulf of Maine will include the following diatoms: *Chaetoceros* spp., *Coscinodiscus centralis, Guinardia flaccida, Leptocylindrus danicus, Rhizosolenia, Thalassionema nitzschoides, Thalassiosira decipiens, T. nordenskoeldi* and *Thalassiothrix longisseme*. However, in some years in the deep basin there will be virtually no diatoms in the early summer but instead a dinoflagellate community. This assemblage will include *Ceratium longipes* (maximum abundance in July), *Ceratium tripos* (maximum abundance in August), *C. bercephalum, C. fusus, Peridinium depressum, P. conecum, P. crassipes, Dinophysis* sp., *Exiviella* sp. and occasionally *Coccolithus huxleyi*.

By midsummer in the deep basin of the Gulf, the dinoflagellates *Ceratium* and *Peridinium* become the dominant forms even in years when the early summer flora was predominantly diatoms (Figures 2, 6). This may be due to the increased water temperature and the fact that some dinoflagellates can vertically migrate 10-20 m into nutrient rich waters below the thermocline (Epply, *et al.*, 1969). On Georges Bank the diatoms continue to dominate the phytoplankton, probably because the wind and tidal mixing of the water column ensure a supply of nutrients regenerated on the bottom. The species found on Georges Bank in the summer include *Chaetoceros* spp., *Rhizosolenia, Leptocylindrus minimus, Coccolithus huxleyi* and a small form of *Thalassiosira* (Sears, 1941).

The late summer flora (August-September) (Figures 2, 7) is characterized by a second less intense diatom bloom in shoaler waters of the Gulf of Maine. In the coastal regions of the Gulf, *Chaetoceros debilis, C. decipiens, C. compressus, C. lacineosis, Skeletonema costatum* and *Rhizosolenia alata* are the most important species. On Georges Bank *Rhizosolenia alata* is the most abundant species, although *R. setigera, R. imbricata* and *R. lebatata* are also important. The phytoplankton of the deep portions of the Gulf of Maine consists of predominantly dinoflagellates, although silicoflagellates are at their seasonal peak, and occasionally *Coccolithus huxleyi* will bloom. After the autumn bloom a mixed flora of dinoflagellates and diatoms persists on Georges Bank (Sears, 1941) and in the coastal regions of the Gulf of Maine. The species present include *Guinardia flaccida, Thalassionema gravida, Coscinodiscus concinnus*, several species of *Chaetoceros, Rhizosolenea, Melosira sulcata*, and *Ceratium*, together with a large variety of neritic and tychopelagic diatoms. In the whole region, late September is the end of active growth of the phytoplankton and the beginning of the transition to the winter minimum, *Chaetoceros* dominated flora.

Seasonal cycles of biomass and primary productivity

The phytoplankton standing stock in the Gulf of Maine is characterized by a winter minimum, a heavy spring bloom, a sharp decrease during the summer almost to winter levels, and a moderate autumn bloom followed by a decline in standing stock to the winter minimum values (Figures 8, 9). The standing stock of phytoplankton on Georges Bank is much greater at all seasons of the year than in other parts of the Gulf of Maine. Primary productivity measurements are available only for Georges Bank and Massachusetts Bay. The seasonal changes in primary productivity are similar to those of the biomass except that following the spring bloom primary production does not decline as rapidly as the biomass.

The information on biomass and productivity summarized in Figures 8-10 represents a composite of information given in Bigelow *et al.* (1940), Riley (1941), Sears (1941) and Parker and Mulligan (TRIGOM - PARC 1974). The values for chlorophyll in Figure 9 are derived from Riley's (1941) plant pigment analysis, which employed Harvey Plant Pigment Units (HPPU), using a conversion factor of mg chlorophyll = $(3 \pm 1 \times 10^{-4})$ (# of HPPU) (Strickland, 1960). These rough estimates of the chlorophyll content/m^2 are subject to additional error, because the methods employed to concentrate the phytoplankton for pigment analysis did not adequately sample the nannoplankton; however, they should be adequate for an indication of gross changes in the standing stock.

During the winter the lowest values of biomass (2×10^6 cells/0.1 m^2, 40 mg Chl/m^2) and primary production (0 g C/m^2/day) are observed, although the exact time may vary from year to year. Besides the yearly variations there are also differences from place to place within the Gulf of Maine (Bigelow, *et al.*, 1940). The phytoplankton minimum occurs in December in the deep basin, western coastal region and on Georges Bank, while on the eastern side of the Gulf the phytoplankton minimum occurs in January (Bigelow, *et al.*, 1940).

The spring bloom begins in late February to mid-March in the coastal waters and on Georges Bank. At this time the biomass may be as high as 11,000 x 10^6 cells/0.1 m^2, and the primary production may reach values of 1.4 g C/m^2/day. The bloom does not begin in the deep basin of the Gulf until April or even May (Bigelow, *et al.*, 1940).

During the summer there is a decrease in the standing stock on Georges Bank (100 mg Chl/m^2 and 100 x 10^6 cells/0.1 m^2) as well as for the Gulf of Maine as a whole (10 x 10^6 cells /0.1 m^2). The data (Figure 9) for Georges Bank do not cover the whole summer, but in the Gulf (Figure 8) there is an increase in standing crop from June through September. Although the biomass on Georges Bank decreases drastically in the summer, the change in the primary production is less severe, decreasing to approximately 0.2 g C/m^2/day in September. Riley (1941) did not continue his investigation past September. Parker and Mulligan's data (TRIGOM - PARC, 1974) from Massachusetts Bay indicated two moderate autumn blooms in 1973 (Figure 10).

Following the period of autumn activity the standing stock and primary production reach their winter values.

Factors limiting primary productivity and biomass.

During the winter there is a plentiful supply of nutrients in the water (Bigelow, *et al.*, 1940) but the depth of the mixed layer, due to wind and tidal mixing, greatly exceeds the critical depth (the critical depth is the depth at which the total community photosynthesis equals the total community respiration) (Sverdrup, 1953). On Georges Bank the mixed depth extends to the bottom but the critical depth lies above the bottom due to the low level of solar insulation. As the season progresses the water column becomes more stable with increased solar radiation (and in coastal areas, increased runoff); at the same time the depth of the photic zone extends until the critical depth exceeds the depth of the mixed layer. Once this occurs the spring bloom will commence (Sverdrup, 1953). This does not happen until late February to mid-March in the coastal region and not until late April or even May in the deep basin of the Gulf (Bigelow, *et al.*, 1940). The situation on Georges Bank is different. During the spring the water on Georges Bank is not stratified (Clarke, *et al.*, 1943) but it is shallow enough for the mixed depth and critical depth to both be at the bottom; this usually takes place in late February to March.

During the summer, in the shallow areas and particularly on Georges Bank the mixed layer extends to the bottom, insuring a steady supply of nutrients regenerated by bacterial action on the bottom. The existence of a pycnocline in the waters of the central basin, a condition necessary for the start of the bloom, restricts the flow of nutrients to the depleted surface waters from the nutrient rich waters at depth. Riley (1946) in his model of primary production for Georges Bank, used phosphate as the limiting nutrient, although phosphate is not usually considered as limiting phytoplankton growth in the marine environment (Roels, 1971; Yentsch, 1975). Karaulovsky (1975) demonstrated that phosphate and nitrate were present in Georges Bank water during the summer. Bigelow, *et al.* (1940) postulated that nitrate was the limiting nutrient for the phytoplankton of the deep basin of the Gulf of Maine. However, Vaccaro (1964) has shown that in August when nitrate concentration was lowest, ammonia was available in biologically significant quantities. There are probably additional sources of nitrogen that may also be important to phytoplankton in the Gulf of Maine. It has been demonstrated that urea (McCarthy, 1972; Carpenter, 1972) and dissolved amino acids (Schell, 1974; Wheeler, *et al.*, 1974) can be used by phytoplankton for growth. These sources of regenerated nitrogen (ammonium, urea, and amino acids) are strong possibilities in the Gulf of Maine due to the large number of zooplankton grazing on the phytoplankton. Ketchum (1968) has observed that approximately half of the phosphorus requirements of the phytoplankton are met through the regeneration of nutrients. Nitrogen regeneration was not measured but in other areas it was found to be significant (Jawed, 1973; LeBorgne, 1975). The large numbers of fish may also contribute regnerated nutrients (Whiteledge, 1975).

In view of the observations of Bigelow (1926) and Fish and Johnson (1936) on the enormous numbers of herbivorous zooplankton, in particular, *Calanus finmarchicus*, it is likely that zooplankton grazing limits the phytoplankton populations in the Gulf of Maine. Steele (1974) has postulated that herbivores limit phytoplankton growth in the marine environment. Cushing (1968) has shown this to be the case in a similar area where *Calanus finmarchicus* is the dominant zooplankton organism. The proposed mechanism for a grazing limited bloom is as follows: in response to the spring phytoplankton bloom, *Calanus finmarchicus* lays its eggs, after the eggs hatch the nauplii start to feed, as the nauplii grow to adults they consume enough phytoplankton to decrease the standing stock. At present we do not have enough data for a test of this hypothesis for the central basin Gulf of Maine, *i.e.*, if grazing is limiting the biomass of the phytoplankton, the primary production should remain fairly high. If, on the other hand, nutrients are limiting phytoplankton growth, both the biomass and the primary production should decrease.

From the data in Figure 10 it appears that for Georges Bank grazing is limiting the magnitude of the bloom. In Massachusetts Bay it appears that after a brief bloom in April nutrient limitation (nitrate concentration decreased to 0 mg-at/l, Frankel and Pearce, TRIGOM - PARC, 1974) causes a swift decline in primary production, followed by regeneration of nutrients, leading to another bloom in June which is limited by grazing. With the approach of autumn the stability of the water column decreases and mixing breaks down the pycnocline resulting in an influx of nutrients into the surface waters. If several days of calm weather ensue, thus allowing the depth of the mixed layer to rise above the critical depth, a fall phytoplankton bloom is likely. The fall bloom will be smaller than the spring bloom (Riley, 1946; Parker and Mulligan, 1974) and more variable as to the time of occurrence. After the autumn bloom, the depth of the mixed layer becomes greater than the critical depth and winter conditions prevail.

Average levels of primary production.

Based on Riley's (1941) paper the yearly primary production of Georges Bank is approximately 120 g C/m^2/year. Riley's (1941) determinations were made using the oxygen production technique and are not as accurate an estimate as can be obtained with the ^{14}C technique (Steeman-Nielsen, 1965). Nevertheless this value of primary production is in reasonable agreement with observations made by Parker and Mulligan (1974) of about 200 g C/m^2/year in Massachusetts Bay (another highly productive area in the Gulf of Maine). Values from similar coastal environments by Steele (1974) working in the North Sea of 90 g C/m^2/year and Ryther and Yentsch (Ryther, 1963) in the New York Bight area, of 120 g C/m^2/year at deep stations and 160 g C/m^2/year in shoaler waters as well as the work of Emery and Uchupi (1974), suggest that the primary production in the Gulf of Maine is in the range of 100-200 g C/m^2/year.

Zooplankton

Major surveys of the zooplankton of the Gulf of Maine have been carried out by Bigelow (1926) and Fish and Johnson (1937). Since then there have been numerous investigations, though usually on a smaller geographic scale, of the zooplankton in the Gulf (Clarke, 1933, 1934a, b; Clarke and Zinn, 1937; Redfield, 1939, 1941; Redfield and Beale, 1940; Clarke, *et al.*, 1943; Riley and Bumpus, 1947; Whitely, 1948; Colton, *et al.*, 1962; Mullen, 1963; Pavshtics, 1963; Pavshtics and Gogoleva, 1964; Sherman, 1966, 1968, 1970; Sherman and Perkins, 1971; Mauchline and Fisher, 1969; Grice and Hart, 1962 in the area south of Cape Cod and others). The following discussion of the zooplankton populations will be an attempt to summarize from the sources listed above, and others, the annual zooplankton cycle in the Gulf of Maine.

Dominant species

The zooplankton of the deep basin of the Gulf of Maine has been characterized by Bigelow (1926) as a "*Calanus* community" This includes *Calanus finmarchicus*, *Pseudocalanus minutus*, *Metridia lucens*, *Sagitta elegans*, *Euthemisto*, *Thysonoessa*, *Meganyctiphanes norvegica*, *Pleurobrachia pileus* and *Euchaeta norvegica*. The copepods *Calanus finmarchicus*, *Pseudocalanus minutus*, *Oithona similis* and *Metridia lucens* are the most abundant species in the Gulf of Maine (Fish and Johnson, 1937). *Calanus* may contribute up to 70% of the total zooplankton biomass (dry wgt) and *Metridia* may be almost as important (Mullin, 1963). Other species that are numerically important members of the zooplankton during the year are *Centropages typicus*, *Anomalocera patersonii*, *Euthemisto compressa* and *Temora longicornis* (Fish and Johnson, 1937). Bigelow (1926) and Fish and Johnson (1937) considered *Limacina retroversa* as an endemic species but Redfield (1939) showed this to be an immigrant form that does not reproduce in the Gulf of Maine. The fauna on Georges Bank consists of a similar assemblage of species with the exception that *Calanus finmarchicus* does not occur and *Pseudocalanus* is the most abundant copepod. This is perhaps because of the predation by the chaetognath, *Sagitta elegans*, that are present (Clarke, *et al.*, 1943). *Sagitta elegans* is the only endemic chaetognath in the Gulf of Maine; *Eukrohnia lamata*, *Sagitta maxima* and *S. lyra*, species that occur in abundance in the Gulf are all carried in by deep currents and do not reproduce (Redfield and Beale, 1940). *Sagitta serratodentata* is an immigrant from the oceanic surface waters off the shelf (Redfield and Beale, 1940). The abundance of the deep-water chaetognaths is related to their abundance offshore and to their longevity. *S. serratodentata* fluctuates in abundance in response to parcels of water entering the Gulf, probably in a manner similar to that observed for populations of *Limacina retroversa* (Redfield, 1939).

Reproduction cycles

Fish and Johnson (1937) found that reproduction of *Calanus finmarchicus*, *Pseudocalanus minutus*, *Thysanoessa* sp. and *Meganyctiphanes norvegica* starts in April in the western Gulf of Maine. For species such as *Calanus finmarchicus* (Fish, 1936a) and *Meganyctiphanes norvegica* (Fish and Johnson, 1937) the western coastal region is the principal source of the population.

Pseudocalanus minutus and *Oithona similis* have their main area of reproduction in the outer Gulf and eastern basin (Fish, 1936b,c and Fish and Johnson, 1937). *Sagitta elegans* spawns on Georges Bank (Clarke, *et al.*, 1940) and in the coastal waters of the western Gulf of Maine (Sherman and Schaner, 1968). *Sagitta* has an extended spawning period, spring through autumn, and produces one generation a year (Sherman and Schaner, 1968). Bigelow (1926) reports that the ctenophore, *Pleurobrachia pileus*, spawns in the shoal areas of the Gulf of Maine. This species is thought to spawn in late summer and autumn with the overwintering eggs that mature the following spring (TRIGOM - PARC, 1974). *Metridia lucens* does not appear to reproduce in the Gulf of Maine (Fish and Johnson, 1937). Bigelow (1926) proposed that *Metridia* was carried into the Gulf via Great South and Northeast Channels, and across Browns Bank. At various times of the year benthic larvae become important components of the zooplankton. For example, barnacle larvae (Fish and Johnson, 1937; Pavshtics and Gogoleva, 1964), *Mytilus* larvae (Fish and Johnson, 1937), and sea scallop larvae (Damkaer and Au, 1974) sometimes reach high localized densities.

Seasonal variations in species composition and biomass

Calanus is the first of the three most abundant species to reach its peak abundance (May) followed by *Pseudocalanus* (June) and then *Oithona* (August). During the summer, warm water forms such as salps, ctenophores and coelenterates appear in the Gulf of Maine (Bigelow, 1926; Pavshtics, 1965). Pavshtics (1965) observed that with this change in the composition the quantity of food suitable for herring decreases. Bigelow (1926) noted that these organisms are predators on zooplankton, fish eggs and larvae. *Centropages typicus*, which in some years reaches great abundance in the fall, appears to be confined to the inner Gulf, Bay of Fundy and Georges Bank. Fish and Johnson (1937) regard the Georges Bank population as separate from the population in the rest of the Gulf. The area of maximum zooplankton abundance shifts position with the season. From late summer to December zooplankton are most abundant in the northern portion of the Gulf, during the winter the center of abundance shifts to off the Massachusetts coast and in late spring and early summer it is found on the southern margin of the Gulf, Georges Bank and the western coastal region (Redfield, 1941).

The annual cycle of zooplankton biomass is represented in Figure 11. Some of the variations observed between years is due in part to the sampling methods and gear used by the different investigators. The data should, however, present a gross picture of the seasonal cycle. Although all three investigators found an increase in zooplankton abundance in May, Bigelow (1926) and Fish and Johnson (1937) observed a decline during the rest of the summer. This pattern was also observed by Sherman (1970) for the coastal waters of the Gulf of Maine. This contrasts sharply with the picture presented by Redfield (1941) for the two years he sampled. He observed an increase during the course of the summer until September, although the levels reached in each year were markedly different. In order to get an idea of the probable cause of this increase, the circulation pattern in the Gulf of Maine and its effects on the zooplankton should be examined.

Zooplankton cycles in relation to circulation

Redfield (1941) has hypothesized that the surface waters flow in a great cyclonic eddy, augmented by inflow on the eastern side over the Scotian Shelf. Water is lost from the system to the southeast over Georges Bank. Colton and Temple (1961) found this loss of water over Georges Bank to be of such significance that they termed spawning and retention of larval fish on Georges Bank as an enigma. In the winter and early spring inflow replaces a considerable portion of the Gulf water with new water. Redfield (1941) feels that at least one-half of the zooplankton population of the Gulf of Maine is lost through this mechanism. Populations do not develop in this "new" water until spring, by which time this water extends over the northern half of the Gulf. The water in the southern region of the Gulf contains a rich flora from the previous summer, which has only been partially reduced during the winter. In spring and summer, inflow and outflow diminish and the water in the southern half of the Gulf is carried northeasterly. This results in the water starting its second trip around the Gulf carrying a rich fauna. This is an idealized picture of course and neglects lateral mixing, but the general pattern appears supported by Redfield (1939, 1941) and the physical oceanographic work of Bumpus and Lauzier (1965).

The volume of water entering and leaving the Gulf probably varies year to year, due to changes in meteorological and oceanographic conditions. For example, Colton *et al.* (1962), Pavshtics and Gogoleva (1964), and Sherman (1966) using oceanic copepods as indicators reported on intrusions of slope water into the Gulf of Maine. It appears that most of the 'zooplankton poor water' enters the Gulf across the Scotian Shelf (Redfield, 1941). Redfield (1941) proposed that the population of the Gulf is impoverished in proportion to the amount of this water entering the area, since the inflow is proportional to the amount of zooplankton rich water leaving the Gulf of Maine. Sherman (1970) suggests that changes in the amount of water entering the Gulf from river discharge may be the cause of changes in the coastal zooplankton abundance from year to year. River discharge from the St. Lawrence may play a large role in the amount of water entering across the Scotian Shelf (Sutcliffe, *et al.*, 1975). In years in which small amounts of low salinity water enters the Gulf, either across the Scotian Shelf, or by direct river discharge, the surface salinity should be high. Redfield (1934) found that during the summer of 1934 the surface salinity in the Gulf of Maine was exceptionally high, and so was the zooplankton biomass as compared with 1933 (Figure 11).

The circulation of water is not only an important factor in the deep basin of the Gulf of Maine but on Georges Bank as well. Clarke, *et al.* (1943) observed that the distribution of *Sagitta elegans* on Georges Bank was restricted to the "mixed area". The "mixed area" was an area where "turbulence produced by tidal currents and by the wind in the relatively shallow water . . . causes a vertical mixing of the water which results in a nearly uniform distribution of temperatures and salinity from top to bottom. . . particularly in the central portion of the Bank" (Clarke, *et al.*, 1943). *Sagitta serratodentata* and S. enflata were abundant outside this zone but never within it. A similar distribution was observed for *Calanus* and *Pseudocalanus*, the latter occurring within the "mixed area", the former only in the stratified waters surrounding the "mixed area" (Clarke, *et al.*, 1943).

Sherman (personal communication) has proposed that the seasonal changes in zooplankton abundance are the result of local fluctuations in water temperature and stability, rather than large scale circulation. Lasker (1974) has shown that the stability of the water column plays an important role in the survival of anchovy larvae. He (Lasker, 1974) found that the first feeding larvae are dependent on chlorophyll maximum layers, which are only present when the water column is stable. Not only must there be a dense enough aggregation of phytoplankton in the chlorophyll maximum but the size and species composition are also critical. For example, if the organisms present were too small (optimum food size is approximately 50μ) or of a species such as *Chaetoceros* (with numerous spines) the larvae did not feed.

A similar mechanism with respect to zooplankton may exist in the Gulf of Maine. Copepod fauna in the Gulf of Maine is characterized by swarms of nauplii and copepodites after the spring phytoplankton bloom (Bigelow, 1926; Sherman, 1970). If the stability of the water column is destroyed and the dense patches of phytoplankton bloom are dispersed (*e.g.* by a series of storms) the young copepods may not be able to obtain enough food to survive.

Future research

There is a need for further quantitative studies of primary and secondary productivity to provide a better basis for relating these phases of organic production to potential fish production.

From the standpoint of gaining insight into the factors controlling the survival of larval fish, a better understanding of zooplankton dynamics, especially predator-prey-interactions between larval fish and zooplankton, must be achieved. Pavshtics (1963) has reported that when the species composition of the zooplankton changed from the copepods to salps and ctenophores this food was less suitable to herring. Several investigators have shown that copepods are the predominant food organism of young herring (Sherman and Honey, 1971; Sherman and Perkins, 1971; Damkaer and Au, 1974), young cod, haddock, coalfish (Marak, 1960) and young redfish (Marak, 1974). An area that may be of great importance to larval fish survival is the predation on them by zooplankton (Lillelund and Lasker, 1971; Theilacker and Lasker, 1974) especially by *Sagitta*, ctenophores and coelenterates (Bigelow, 1926). *Sagitta* and ctenophores such as *Pleurobrachia pileus* may be of special importance to larval herring since they are both abundant in the Gulf of Maine at the time herring spawning occurs.

A useful first step in the investigation of zooplankton populations in relation to the growth and survival of herring larvae would be to fully sort and analyze the invertebrate components of the larval herring survey samples, in conjunction with an examination of the herring gut contents. This analysis should include a look at the abundance of smaller zooplankton, as well as nauplii and copepodites of larger forms, collected with the fine mesh nets. This will provide an estimate of the abundance of potential predators on the larvae as well as quantifying the abundance of food organisms for the larvae. In addition, comparing the gut contents with the abundance of food types available will yield insight into possible selectivity of preferred prey. The area of larval fish mortality studies, including recommendations for future research has recently been discussed in a colloquium on Larval Fish Mortality and Fishery Research, held in January, 1975 at LaJolla, California.

In order to understand the role that the zooplankton play in the transfer of energy to higher trophic levels, an investigation of the effects of zooplankton on the phytoplankton community (including regeneration of nutrients and grazing) is needed. The effect that various physical factors, such as the loss of water from the Gulf of Maine gyre over Georges Bank, and biological factors, *e.g.* the timing and species composition of the phytoplankton blooms, have on the abundance and life cycles of the zooplankton need to be delineated.

Although zooplankton dynamics is the more immediate and difficult area of concern, we also need better information on the primary productivity of the Gulf of Maine, including the effects of biotic and abiotic factors on primary production. Primary production studies in various parts of the Gulf, such as Georges Bank the coastal region and the deep basin are necessary to refine the range 100-200 g C/m^2/year so that estimates of the production at higher trophic levels (similar to those of Steele, 1974) can be refined. For example, if the average value of 150 g C/m^2/year is used for primary production on Georges Bank, and a conversion efficiency of 15% is used between trophic levels, then .51 g C/m^2/year will be the production at the fourth trophic level (fish). This is well above the minimum finfish production of .19 g C/m^2/year based on fish catch.(Clark and Brown, 1975) for Georges Bank. This calculation represents only a rough estimate for several reasons: 1) a straight food chain has been assumed rather than a food web which would reduce the yield to a given trophic level (Steele, 1974), 2) the food chain consists of only phytoplankton → zooplankton → carnivores → fish, however, if the nannoplankton play an important role in the primary production of the Gulf an additional level of microzooplankton is necessary (Parsons and Lebrasseur, 1970), 3) a conversion efficiency of 15% has been assumed and this might not be the actual value.

In order to gain a better understanding of the fish production that can be supported by a given amount of primary production the structure of the food web must be elucidated, and improved knowledge on the contributions of bacteria, dissolved organic carbon and particulate organic material (detritus).

It is possible to use knowledge about the productivity of the lower trophic levels to estimate fish production (for a comprehensive discussion of the need and problems involved in obtaining estimates of this type, see Dickie, 1971). Au (1973) has attempted to estimate the maximum finfish yield from ICNAF Subareas 5 and 6 using primary productivity data. An increased knowledge of the energy pathways at the lower trophic levels of the food web will lead to a theoretical basis for deriving a limit of fish catch such as that used in the second tier TAC.

The areas of investigation outlined in this section are not meant to be a definitive list of the biological oceanographic studies needed in the Gulf of Maine. They should be viewed only as a place to start in obtaining information on the plankton communities that will be useful in fisheries management.

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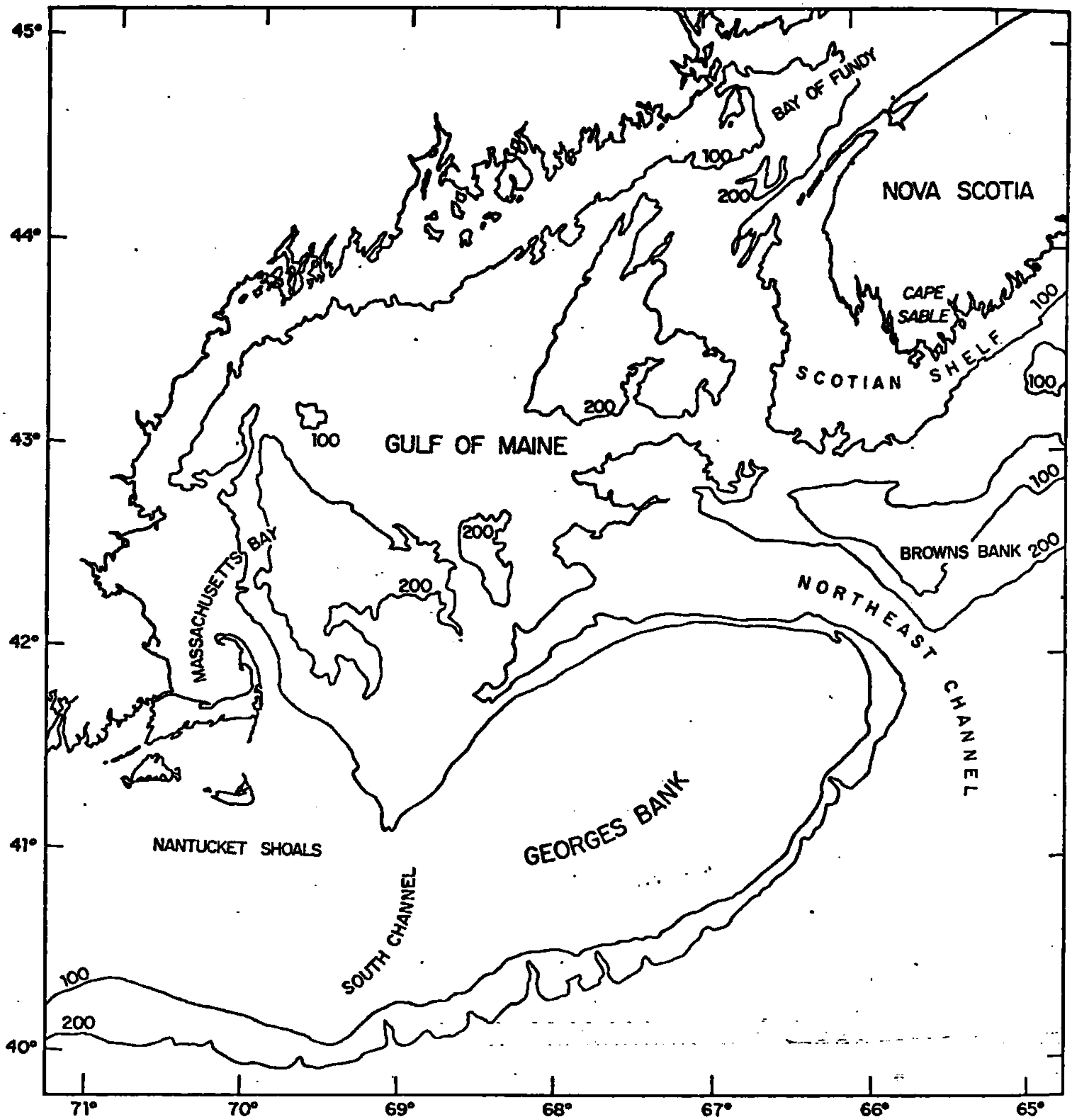

Fig. 1. The Gulf of Maine. (Depths are in meters).

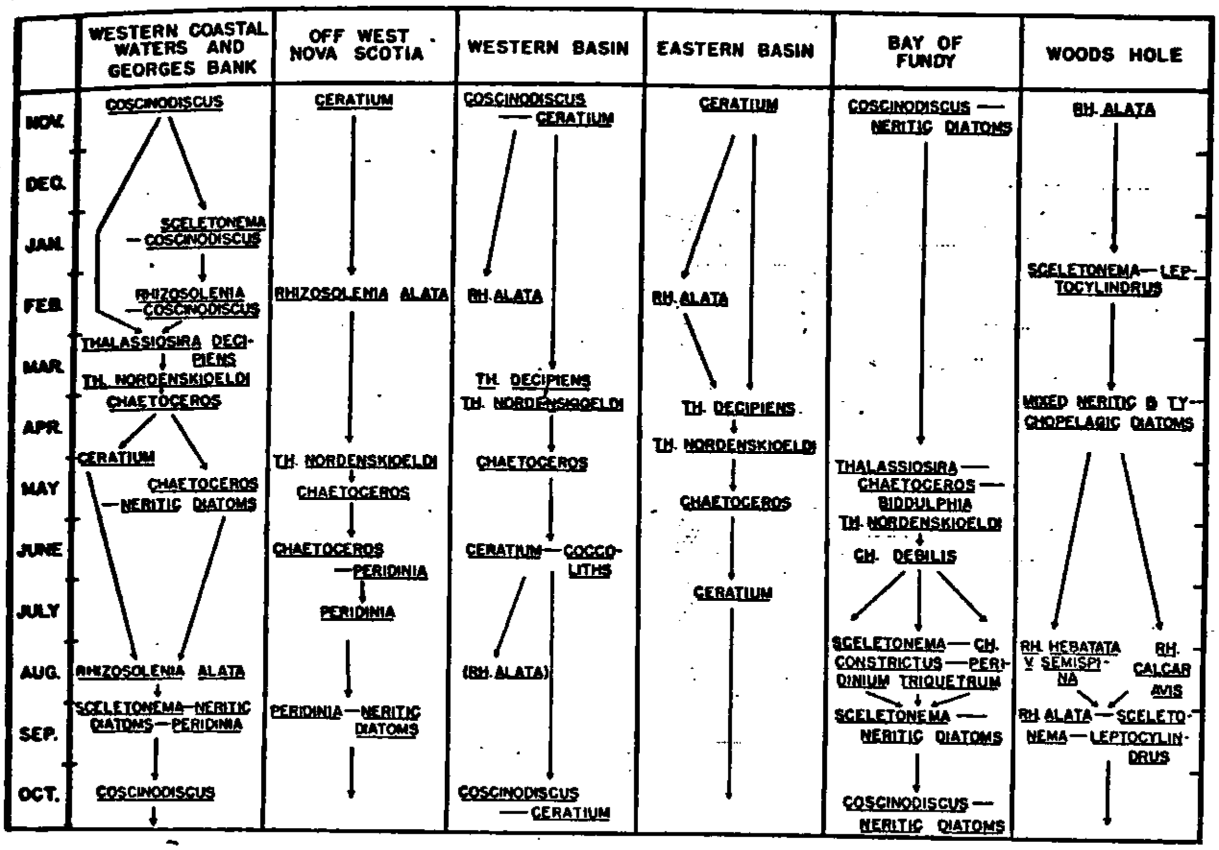

Fig. 2. Seasonal succession of dominants in representative parts of the Gulf of Maine (derived from all sources). From Lillick (1940).

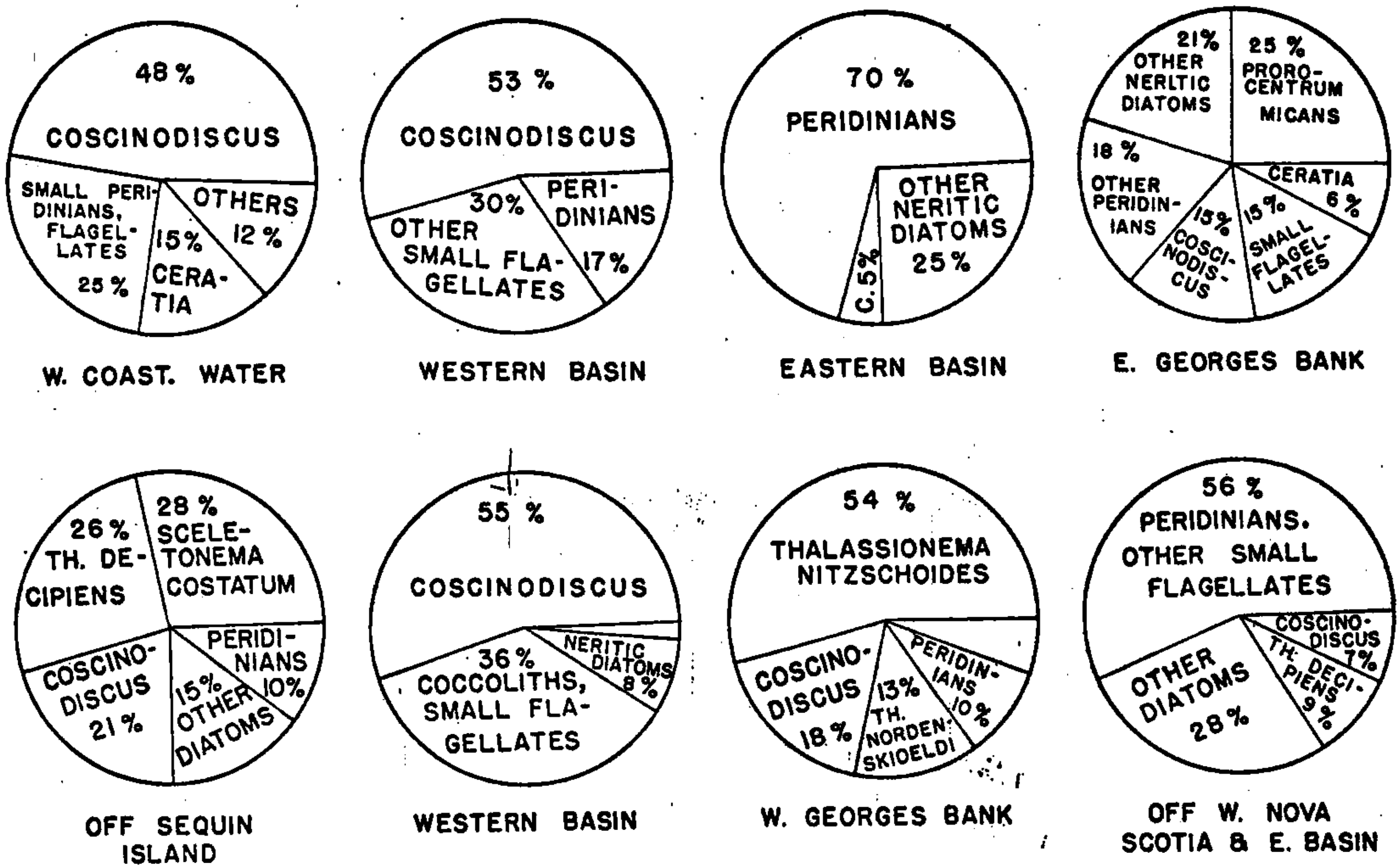

Fig. 3. Percentage composition of the phytoplankton at representative localities in the Gulf of Maine; above, December 1933 (C. = Coscinodiscus); below, January 1934. From Lillick (1940).

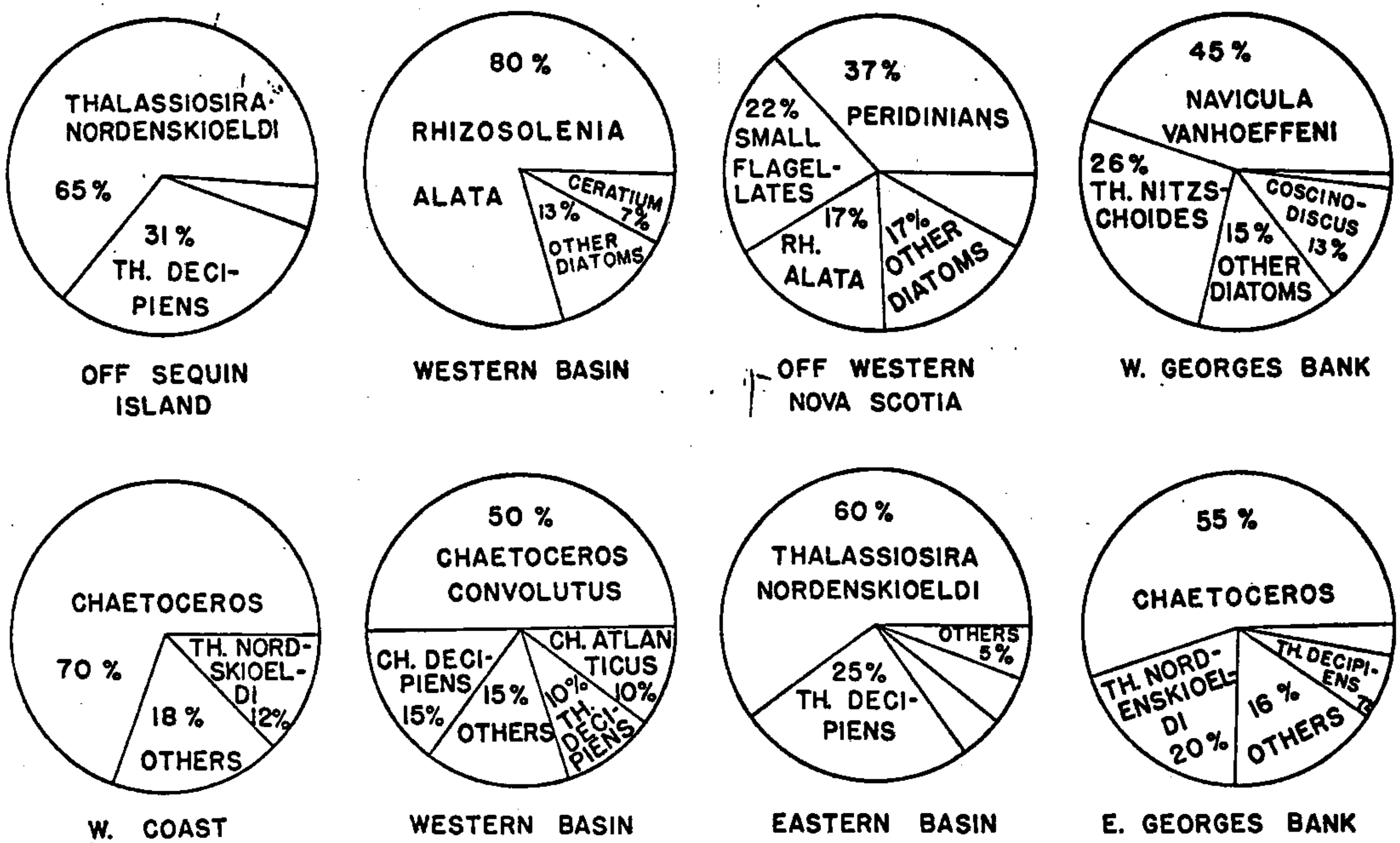

Fig. 4. Percentage composition of the phytoplankton at representative localities in the Gulf of Maine in 1934; -- March (above) and late April-early May (below). From Lillick (1940).

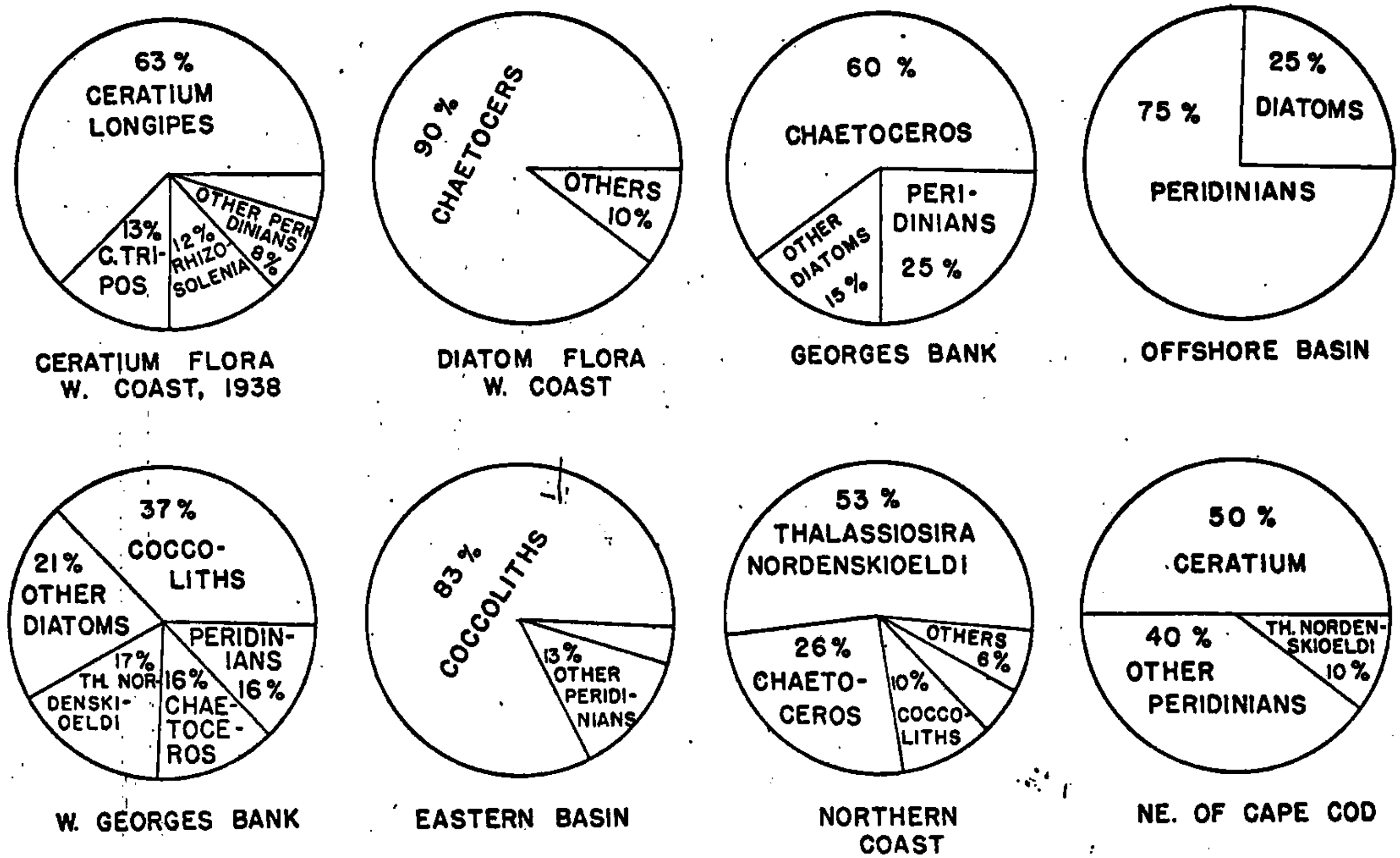

Fig. 5. Percentage composition of the phytoplankton at representative localities in the Gulf of Maine, late May-early June 1934 (above), and late June-early July 1933 and 1934 (below). From Lillick (1940).

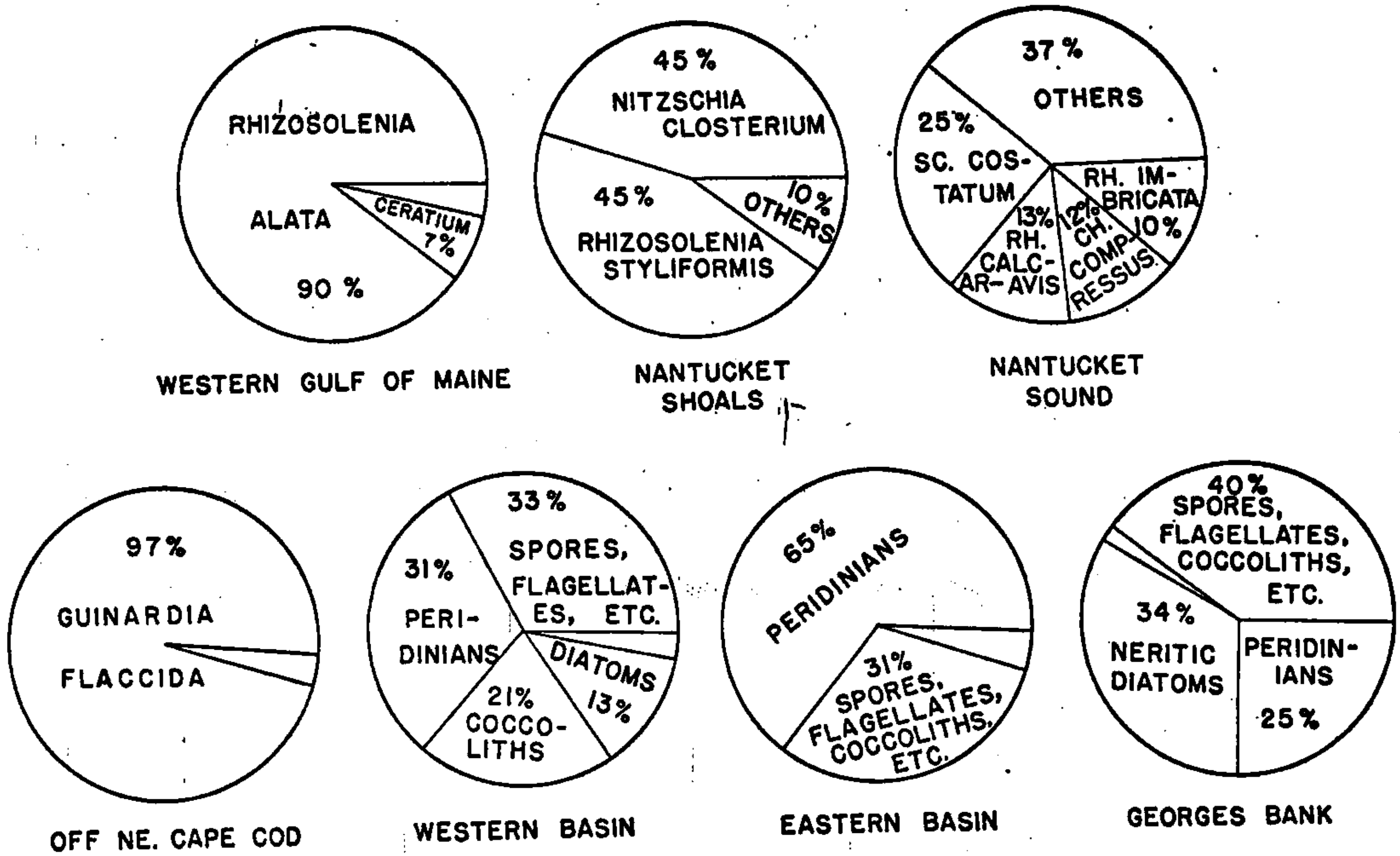

Fig. 6. Percentage composition of the phytoplankton at representative localities in the Gulf of Maine, August 1936 (above) and September 1933 (below). From Lillick (1940).

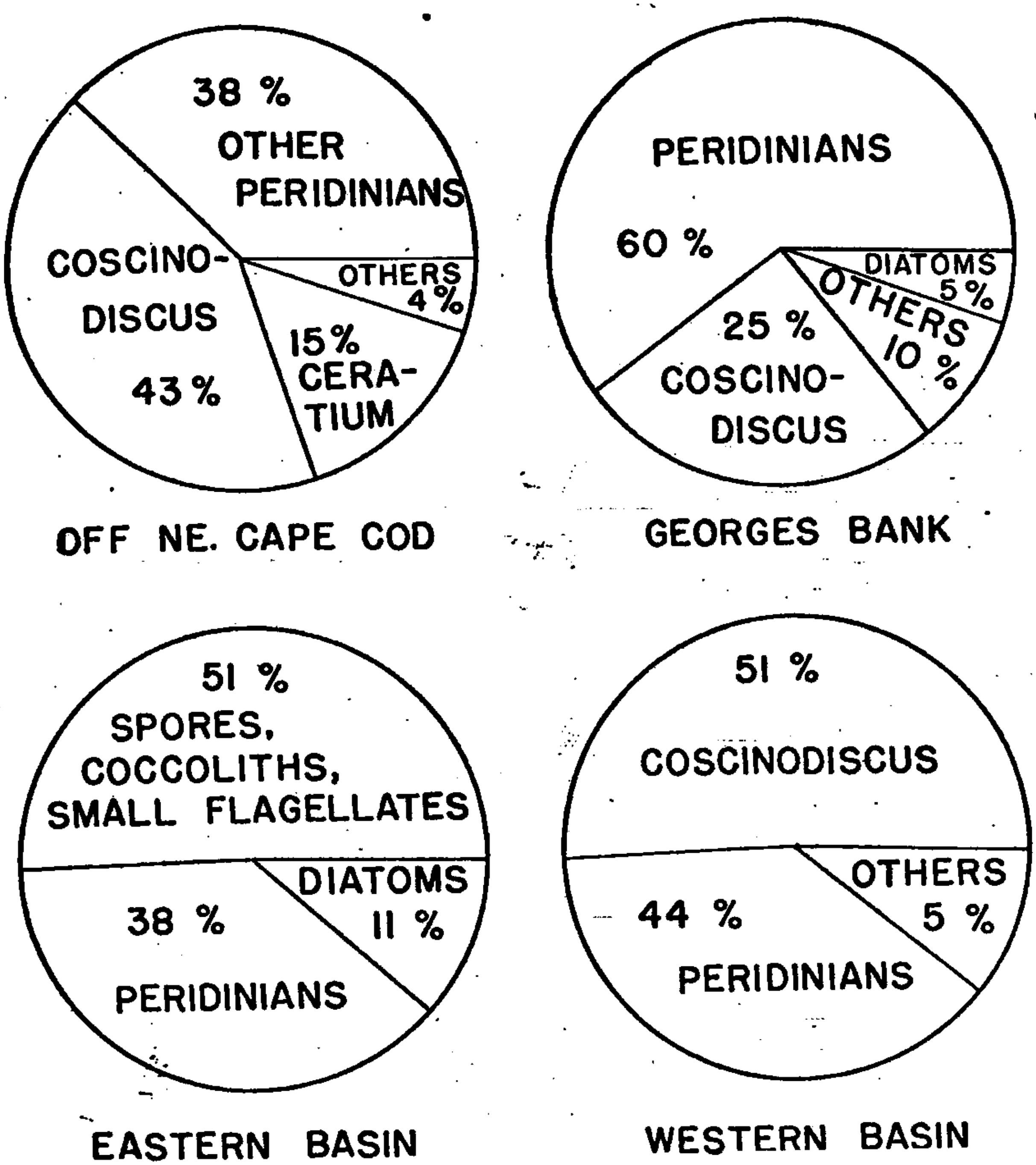

Fig. 7. Percentage composition of representative localities in the Gulf of Maine, October 1933. From Lillick (1940).

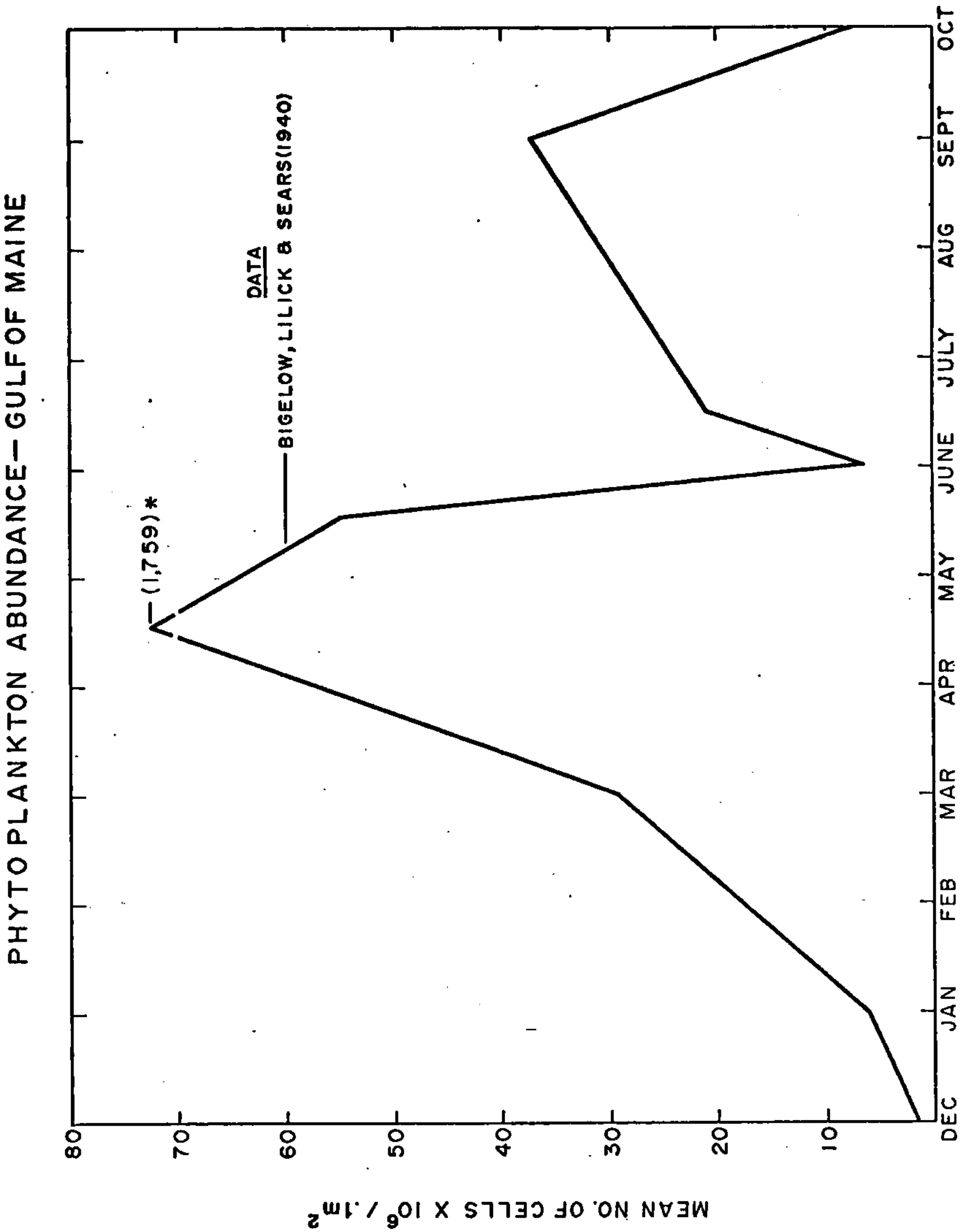

FIG.8

* NO.S IN ( ) = VALUES EXCEEDING THE GRAPHS SCALE

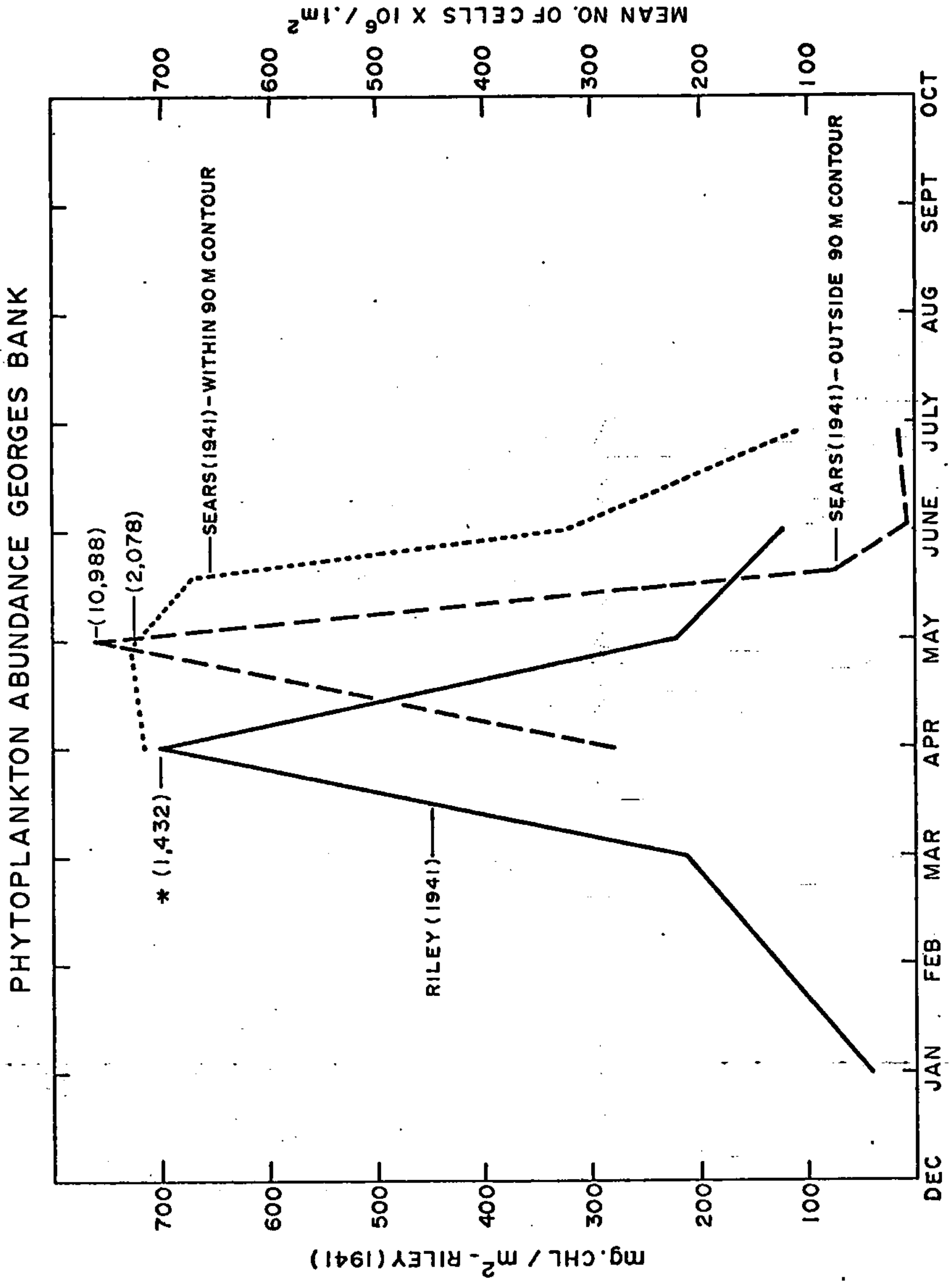

FIG.9

* NO.S IN ( ) = VALUES EXCEEDING THE GRAPHS SCALE

PRIMARY PRODUCTION IN THE GULF OF MAINE

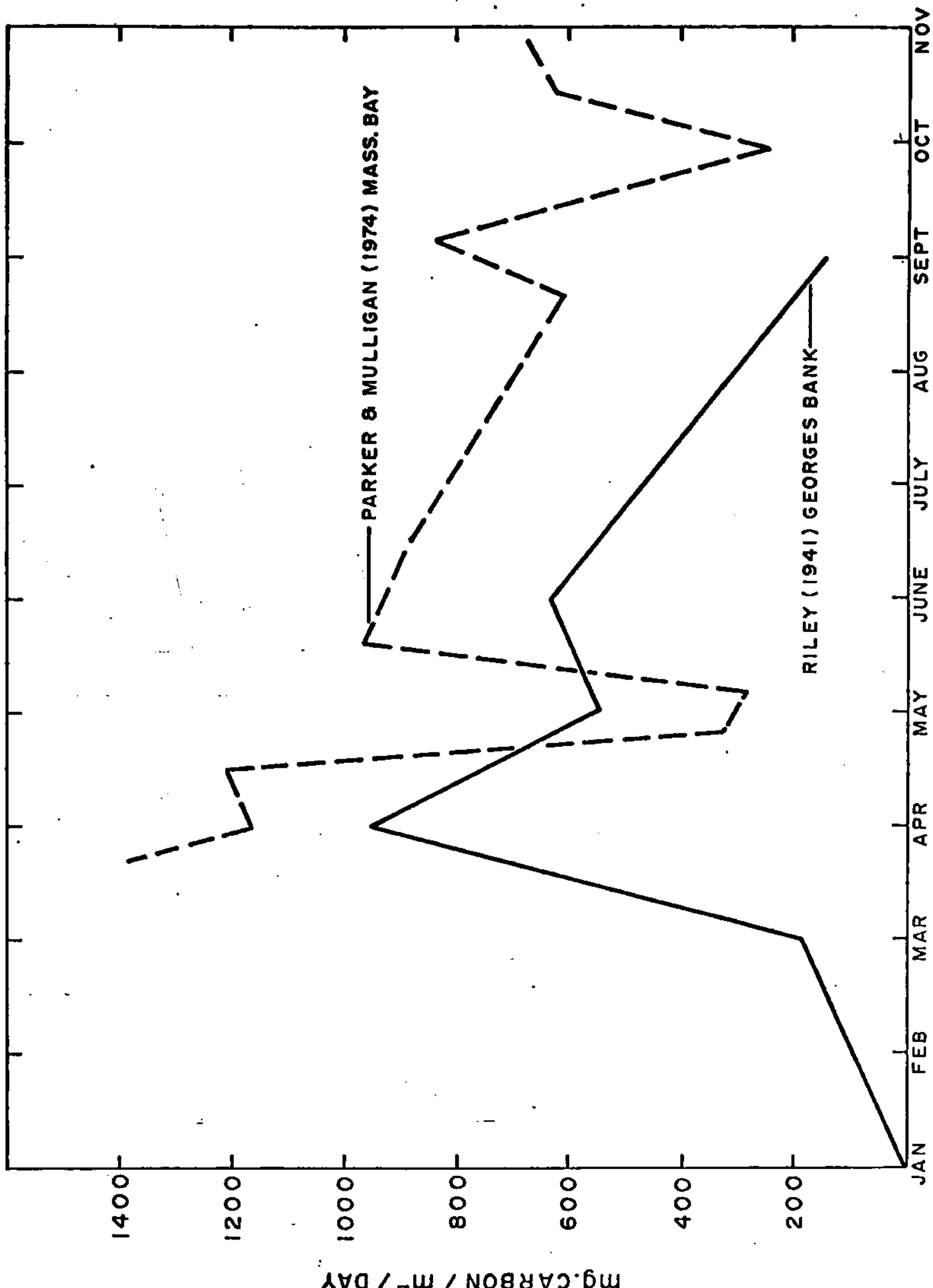

FIG. 10

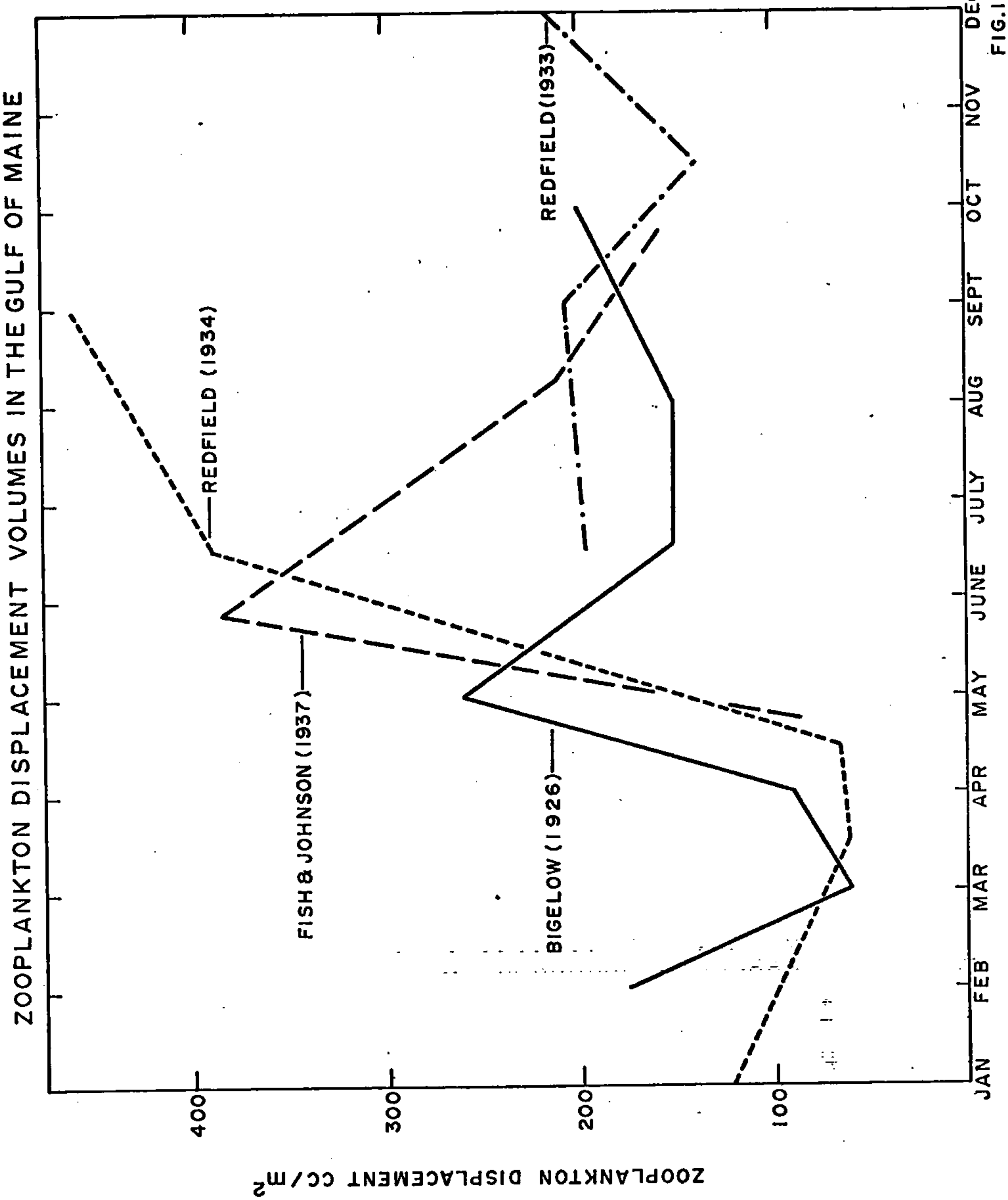
ZOOPLANKTON DISPLACEMENT VOLUMES IN THE GULF OF MAINE
REDFIELD (1934)
REDFIELD (1933)
FISH & JOHNSON (1937)
BIGELOW (1926)
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
400
300
200
100
ZOOPLANKTON DISPLACEMENT CC/M²

FIG. 11