

The Annual Cycle of Kiel Bight Plankton: A Long-term Analysis

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ABSTRACT: Over the past decade, the annual cycle of the major pelagic processes in relation to environmental factors and species composition of the plankton has been studied intensively at a fixed station in Kiel Bight. A series of sequential phases, differentiated according to characteristic properties, succeed each other in a recurring pattern each year. The following phases have been differentiated: the spring diatom bloom, the late spring copepod maximum, the summer stratification, the fall blooms and the winter dormancy. Each phase represents a particular pattern of biogenous element cycling, both within the pelagic system and between the pelagic and benthic systems. Each phase is also characterized by a spectrum of dominant species, many of which do not recur each year. Greatest variation is found amongst bloom diatoms, whereas large, slow-growing species such as the *Ceratia* and most metazooplankton are highly recurrent. Variation in species composition is not related to long-term trends since the past century, in spite of the considerable increase in anthropogenic nutrient input to the Bight. Short-term events appear to determine occurrence of fast-growing species, many of which have benthic resting stages in their life histories. It is concluded that more attention should be paid to life history strategies of species if the mechanisms of seasonal succession are to be elucidated. Long-term observations on appearance or absence of the various species in relation to environmental properties can provide clues as to the nature of these life history strategies.

Introduction

The history of quantitative plankton research goes back a century to Hensen's (1887) pioneering study of plankton standing stock and production conducted in Kiel Bight (Bay is a synonym) from 1882 to 1885. His intention was to develop a standardized methodology for estimating the potential food supply of fish in the sea in order to establish a scientific basis for fisheries regulation. Since then, numerous investigations have been carried out in the Bight that can be grouped into periods according to the methods chiefly employed.

Up to the twenties, microscopic counting of net samples was the usual method (Hensen 1887; Lohmann 1908; Büse 1915; Busch 1920). Chemical analyses supplementing microscopy were introduced by Brandt (1899, 1902, 1920a, 1920b), who believed in nutrient control of plankton biomass. Lohmann's monumental work, which included live counting of centrifuged plank-

ton, seemed to refute Brandt's hypotheses. This period is characterized by the controversy between Lohmann and Brandt (Brandt 1920a, 1920b) as to the true nature of the annual plankton cycle in the Bight and its controlling mechanisms.

From the thirties onwards, accent was shifted to physico-chemical analyses (Wattenberg and Meyer 1936; Krey 1942) and in the fifties and sixties, numerous studies of environmental properties and pelagic processes based on measurements of seston, organic matter, chlorophyll, protein, etc., were carried out in the Bight (Krey 1952, 1961; Lenz 1963, 1974; Hickel 1967; Zeitzschel 1965; Devulder 1968; Schinkowski 1969; Horstmann 1971). Microscopy was of secondary importance in these studies. Krey (1956) initiated a monthly survey of physical and chemical properties of the water column at two stations in western Kiel Bight from 1957 to 1975 that has been evaluated by Babenerd (1980).

Since 1972, intensive studies of plankton ecology and dynamics in relation to cycling of matter between the pelagic and benthic systems have been carried out at a fixed station—the “Hausgarten” by the planktologist team of the Joint Research Project (SFB 95) of Kiel University. The weekly to bi-monthly sampling intervals and the detailed investigation of environmental features as well as production and fate of plankton in relation to its species composition have provided new insight into some functional aspects of the Kiel Bight pelagic system. On the basis of these data, Smetacek et al. (1984) have distinguished five seasonal stages of the annual cycle. Each stage represents a particular pattern of the cycling of matter between the pelagic and benthic systems as reflected at the compartmental—phytoplankton, bacterioplankton, protozooplankton and metazooplankton—level of resolution of the pelagic community.

A rigorous comparison with data on earlier annual cycles is hampered by differences in choice of stations, methodology, sampling frequency and degree of pelagic system coverage. Thus, only observations of seasonality in composition and occurrence of phyto- and zooplankton will be compared here within the framework of the five stages differentiated by Smetacek et al. (1984). The salient features of these five stages have been presented below following a brief introductory account of the Bight. Thereafter, the implications of such a long-term analysis are discussed with a two-fold aim: a) to determine whether a long-term trend reflected in species composition of the Bight plankton can be ascertained; b) to gain insight into survival strategies of the dominant species and genera by comparing year-to-year recurrence and variability in relation to the physico-chemical environment.

GENERAL FEATURES OF KIEL BIGHT

Kiel Bight is part of the Belt Sea, one of a series of basins and swells connecting the brackish Baltic with the North Sea. Babenerd (1980) has reviewed the hydrography of the Bight. Its average salinity range of 14–24, $\bar{x} = 18.7$ p.p.t., indicates an approximately equal mixture of Baltic and North Sea water.

The Bight, with an average depth of 17

m, is enclosed on three sides and connected in the north-east to the main channel of the Belt Sea—the Great and Fehmarn belts (Fig. 1). Land run-off into the Bight is negligible. Sewage from the city of Kiel (230,000 inhabitants) is pumped into the open Bight after mechanical and biological treatment. Hydrography of the Bight is characterized by influx of low salinity surface water (maximum in May) from the Fehmarn Belt and high salinity bottom water (maximum in fall and winter) through a system of channels from the Great Belt. This channel system ends in the western corner where residence time of water in the Bight is longest. This is the site of a routine station since 1955 and also of the “Hausgarten.”

Surface and bottom salinity in the Bight invariably differ, the discrepancy being greatest in summer and least in winter. Vertical temperature distribution is homogeneous till about May/June at 6–8 °C. Thereafter, a thermocline develops at 10–14 m depth in conjunction with a halocline. The temperature of the surface layer reaches a peak of 17–18 °C by mid-August when bottom temperatures are approximately 10 °C. Vertical temperature homogeneity is achieved by late September, although salinity differences—no longer in the form of a distinct halocline—can be present until strong storms in winter homogenize the entire water column.

The plankton of the Bight is typically marine. Characteristic Baltic organisms such as cyanophytes, rotifers and the cladoceran *Bosmina* are of minor importance. Many of the marine species are at the end of their salinity tether in the Bight and some, e.g., *Sagitta*, *Pleurobrachia*, are common only in some years.

The annual cycle of the pelagic system is basically similar to that of other temperate enclosed water bodies and special features are a result of peculiarities of hydrography and topography. Annual primary production, measured in 1973, was found to be 158 g C per m² (Bodungen 1975), which is a typical coastal temperate value (Parsons et al. 1977). To my knowledge, the earliest estimate of marine primary production was that of Hensen (1887), who extrapolated from the biomass of the fall *Ceratium* bloom and obtained a figure of 137 g C per m² per

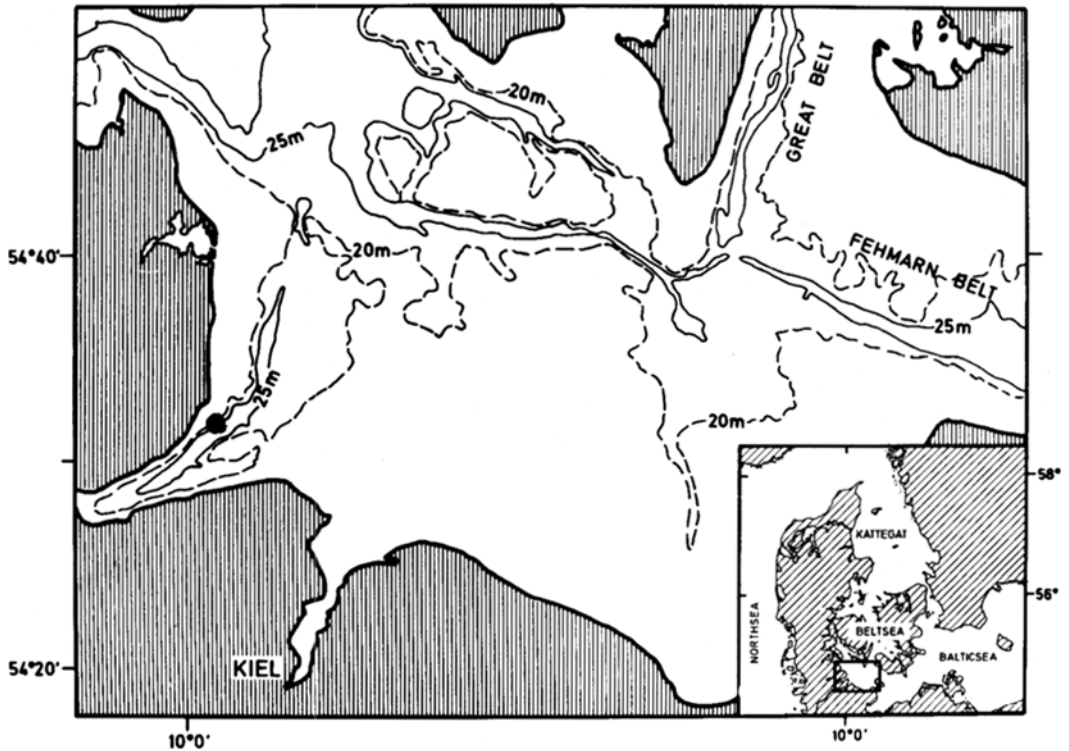


Fig. 1. Kiel Bight and its location between the Baltic and North seas. The "Hausgarten" site is indicated with a dot.

yr for Kiel Bight. He regarded this value as a minimum, however, and felt that actual production was much higher.

THE FIVE STAGES OF THE ANNUAL CYCLE

Winter

The winter (December to mid-February) water column is characterized by low biomass ($<50 \text{ mg C per m}^3$) and high nutrient concentrations. Phosphate and nitrogen levels are similar each year (1.1 ± 0.1 and $12.1 \pm 0.6 \text{ mmol per m}^3$, respectively) and remain fairly constant throughout the period. The Baltic proper has lower winter nutrient levels than the Belt Sea (Bodungen 1975); therefore, incursions of Baltic water, signalled by low salinity, reduce nutrient levels. Vertical mixing of this surface layer results in eventual restoration of typical Kiel Bight values, indicating that these winter levels are equilibrium values. They are regulated, in all likelihood, by interaction between dissolved and particulate phases at the sediment interface (Balzer 1978; Pollehne 1980).

The phytoplankton population is sparse and small numbers of copepods, comprising all the important species, overwinter in the Bight. As nauplii are always present, albeit in small numbers (Lohmann 1908; Fahlteich 1981), this overwintering population apparently remains active throughout, feeding primarily on detritus supplemented by phytoplankton (Lenz 1977). Biomass of the latter decreases through the winter, with lowest values in February, immediately prior to the spring bloom (Lohmann 1908; Smetacek 1975).

Spring

Four spring blooms have been depicted in Fig. 2. The spring bloom of 1973 was atypical due to large-scale advection of both surface and bottom water which disrupted the normal pattern evident in the other years, where the bloom developed and declined within the same water mass. The timing of the bloom is dependent on weather; in calm sunny springs, culmination can occur before mid-March whereas in windy, cloudy

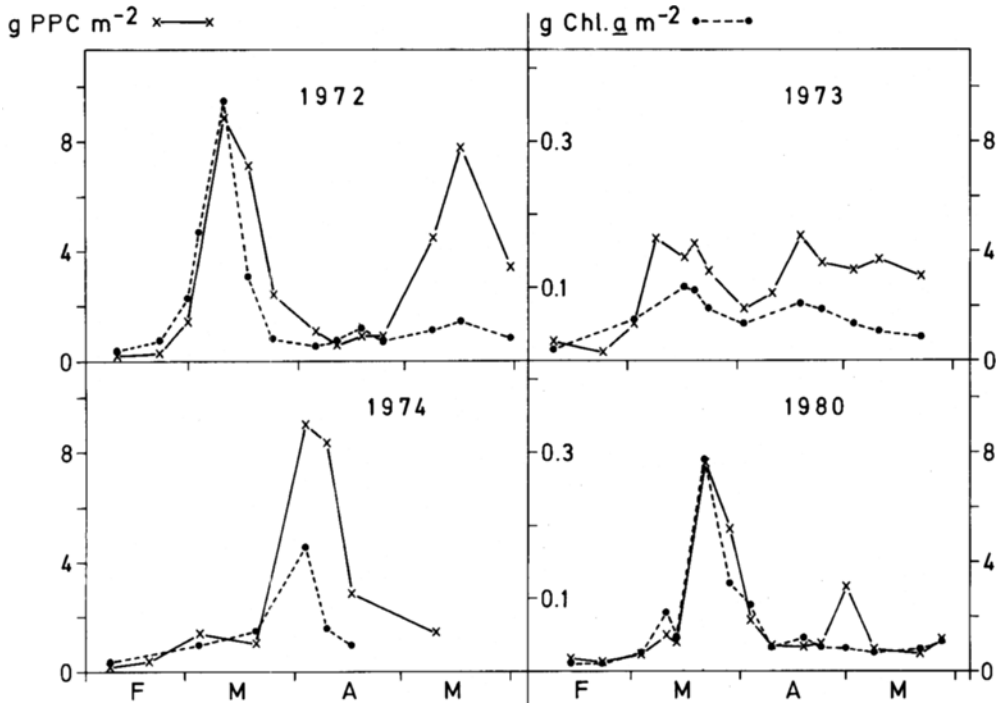


Fig. 2. Development of the spring phytoplankton bloom in the "Hausgarten" from four years integrated for the 20 m water column. PPC = phytoplankton carbon calculated from cell counts and volume estimations, Chl. a = chlorophyll a (1972/73/74 from Smetacek 1975; 1980 from Peinert et al. 1982).

springs, the bloom can be delayed to early April.

The decline of the spring bloom is brought about by nutrient depletion and rapid sedimentation of diatom cells, resting spores and phytodetritus. Calculations based on winter nutrient levels, using Redfield ratios, and direct ^{14}C -measurement of primary production indicate that approximately 1 g C per m^3 is produced by this bloom, and results from sediment traps show that more than half the total production sediments out of the water column. Sedimentation of the bloom was also reported by Lohmann (1908).

Except for timing, the pattern of spring bloom growth and the biomass yield to pelagic and benthic heterotrophs is basically similar each year (Schulz 1983). Further, except for 1973 where flagellates were also important, the spring bloom is always dominated by diatoms, although the species composition varies considerably from year to year (Table 1). The protozooplankton, as defined by Sieburth et al. (1978) also exhibit great interannual variability in species com-

position, although, as a group, they attain biomass peaks of similar size ($\sim 50 \text{ mg C per m}^3$) every year in the spring. Naked ciliates, tintinnids, gymnodinian dinoflagellates and *Ebria tripartita* can dominate biomass in different years (Lohmann 1908; Smetacek 1981; Stegmann and Peinert 1984).

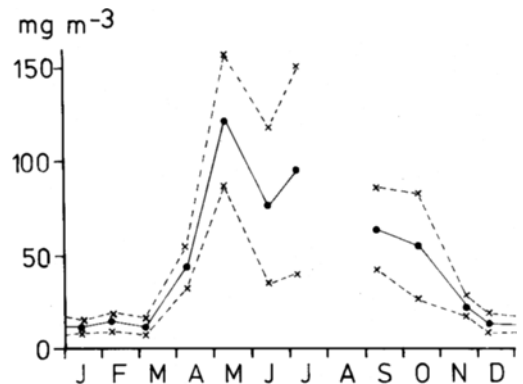


Fig. 3. Monthly averages of zooplankton biomass in Kiel Bight (dry weight per m^3) calculated from monthly data from 3 years and 9 stations. No samples were taken in August. The dotted line represents standard deviations (from Hillebrandt 1972).

TABLE 1. Species dominating spring bloom biomass in different years.

Year	Culmination Time	Dominant Species	Reference
1961	mid-March	<i>Thalassiosira</i> , <i>Skeletonema</i>	Hickel 1967
1962	end-March	<i>Thalassiosira</i> , <i>Skeletonema</i>	Hickel 1967
1966	mid-March	<i>Thalassiosira nordenskiöldii</i>	Schinkowski 1969
1967	early April	<i>Chaetoceros curvisetus</i>	Devulder 1968
1972	mid-March	<i>Detonula confervacea</i> , <i>Skeletonema</i>	Smetacek 1975
1973	March–April	<i>Nanoflagellates</i> , <i>Chaetoceros</i>	Smetacek 1975
1974	early April	<i>Chaetoceros</i> spp.	Smetacek 1975
1980	mid-March	<i>Detonula confervacea</i>	Peinert et al. 1982
1983	mid-March	<i>Thalassiosira polychorda</i>	Nöthig 1984

The copepods dominate metazooplankton biomass and are much more predictable in their appearance in spring than the protistan plankton. All the overwintering adults increase biomass during the bloom, although *Pseudocalanus* and *Eurytemora* appear to grow faster than the others (Hillebrandt 1972; Kraneis and Martens 1975; Schnack 1978; Stegmann and Peinert 1984). Because of the high phytoplankton/zoo-plankton biomass ratio in spring, grazing is of only minor importance (Fig. 3).

Late Spring

Small flagellates (10–20 μm) have always been observed to dominate phytoplankton biomass from mid-April to early June. In most years *Prorocentrum balticum* (formerly *Exuviaella baltica*) was the dominant species (Lohmann 1908; Lenz 1963; Smetacek 1975), although unidentified gymnodinians (Stegmann and Peinert 1984) and a chrysophyte (Nöthig 1984) have also dominated. The biomass in this period shows great interannual variation, due to variation in the nutrient supply. The two important sources of the latter are pelagic remineralization of the remains of the bloom and sedimentary input. This period is characterized by the first zooplankton maximum (Fig. 3), dominated by *Pseudocalanus elongatus*, which represents the first copepod generation spawned by overwintering adults feeding on the spring bloom. Copepod biomass build up is based primarily on production of the small flagellates, and yearly variation in peak height of zooplankton biomass is surprisingly small, in striking contrast to that of phytoplankton. The biomass peak is in the order of 40–50 mg C per m^3 (Lohmann 1908; Hillebrandt 1972; Martens 1976; Stegmann and Peinert 1984).

Species composition of protozooplankton is variable and their biomass declines concomitant with the copepod build up. The presence of this inverse relationship between protozoan and metazoan biomass indicates control of the former by grazing of the latter (Smetacek 1981; Stegmann and Peinert 1984). Because of the heavy grazing pressure exerted by the large copepod population, sedimentation rates are the year's lowest (Smetacek 1980a, 1980b).

Summer

The invariable decline of the *Pseudocalanus* peak in June, brought about perhaps by grazing of the rapidly growing *Aurelia* population (Möller 1979), is followed by a period of lower plankton biomass levels. Thereafter, phytoplankton biomass starts increasing and attains a maximum in August or early September, which is approximately two-thirds that of the spring and fall maxima. The steady build up of pelagic biomass is invariably due to dinoflagellates and is interspersed by subsidiary blooms of diatoms, the number, duration and size of which vary widely from year to year. Smetacek (1984) has attributed these blooms to sporadic storm-induced injections of nutrient-rich bottom water to the upper layer. Nutrient depletion by these blooms is followed by a short period of heavy sedimentation (Smetacek 1980a; Pollehne 1980). Apart from such bloom events, sedimentation rates over the summer months are generally low. Stagnation of bottom water over the summer results in oxygen depletion and nutrient accumulation; this process has been observed every year, although there is interannual variation in the extent and severity of oxygen depletion (Krey and Zeitzschel 1971; Babenerd 1980).

Increasing biomass over the summer is accompanied by diversification of the pelagic food web, which attains its greatest level of complexity in August. Many species are present each year, albeit contributing varying proportions to total biomass. The characteristic dinoflagellates are *Prorocentrum micans*, *Ceratium tripos* and *C. longipes*. The diatom composition varies considerably: *Cerataulina bergoni*, *Chaetoceros* spp., *Guinardia flaccida*, *Rhizosolenia alata*, *R. hebetata* f. *semispina*, *R. fragilissima* and *Skeletonema costatum* are invariably present and contribute to the sporadic blooms although these can also be almost monospecific. Nanoflagellates are also represented in significant numbers, as are cyanophytes, but the latter are not nearly as important in the Bight as they are in the open Baltic (Jansson 1978). Species composition of the early summer period is more variable between years than the late summer population.

The metazooplankton attains a biomass peak similar to that of the May peak (but not included in Fig. 3), in August/early September each year. All the major feeding types are represented: *Oikopleura*, mussel larvae, *Pseudocalanus*, *Paracalanus*, *Acartia*, *Centropages*, *Oithona*, *Aurelia* and in some years, *Sagitta* (Hensen 1887; Lohmann 1908; Martens 1976). Many of these species attain their annual biomass peak in this month. Apart from the sporadic blooms, the phytoplankton/zooplankton biomass ratio is low, indicating that this is primarily a recycling system. New nutrient input events from the sediments or bottom water result in temporary phytoplankton biomass increase; a part of this input is retained within the system—presumably depending on the rate of heterotrophic response—but the excess material sediments out. Primary production levels and assimilation ratios are high, and nitrogen concentrations very low in the upper 15 m. As phosphate starts accumulating within the entire water column (Bodungen 1975; Babenerd 1980), nitrogen is considered to be the controlling element (Bodungen et al. 1976); this is due to the low N/P ratio of nutrients mobilized from anoxic sediments (Pollehne 1980; Balzer et al. 1983).

The zooplankton population starts de-

clining in September for unknown reasons. There is no concomitant increase in carnivores (Hillebrandt 1972; Martens 1976), although the phytoplankton composition changes significantly, leading to the fall bloom.

Fall

The fall bloom is initiated in September by break-down of summer stratification resulting in upward mixing of nutrients from stagnating bottom layers. This nutrient input is accompanied by biomass build up of the late summer ceratia, particularly *Ceratium fusus*, and generally to a lesser extent, *C. tripos*. The growing *C. fusus* population culminates in October and peak biomass attained is comparable to that of the spring bloom. The *Ceratium* fall bloom is the most recurrent feature of phytoplankton succession in the Bight as it is mentioned in all relevant studies to date, i.e., since about the middle of the last century. This degree of recurrence would be surprising if the causative factors were solely related to physical and chemical features of the immediate environment. The critical period when the *C. fusus* population starts increasing its biomass relative to the various other late summer species shows considerable interannual variation with regard to vertical mixing and nutrient input. Weather thus appears to have little influence on development of this bloom, although the size of the peak and the relative proportions of the dominant species might well be controlled by depth and intensity of vertical mixing.

The fate of this bloom is similar to that of the spring, and the bulk of the population rapidly sediments out. The decline of the dinoflagellates is generally followed by rapid growth of a mixed diatom population comprising various species. In some years, biomass of this bloom can attain sizable proportions—in the same range as that of the spring—and in other years, it is only a minor feature of the annual cycle. Apparently, the size of this bloom is dependent on prevailing weather conditions as light is the critical factor in this period. There is considerable interannual variation in the composition of this bloom. In some years up to six species contributed significantly to biomass, whereas in others, a single species dominated. All

the summer diatoms can be of importance including forms such as *Chaetoceros curvisetus*, *C. radians*, *Nitzschia* spp. and *Thalassiosira* spp. Sedimentation of this bloom, although not as thoroughly studied as in the case of the spring bloom, also appears to be its primary fate (Graf et al. 1983); however nutrient depletion is not the factor triggering sedimentation of the fall diatoms. During fall the phytoplankton/zooplankton biomass ratio is high, and the protozoan biomass exceeds that of metazoans, similar to the spring situation. Many fall protozoans (*Protoperidinium*, *Polykrikos*, *Tiarina*, *Strombidium*) are characteristic of this period and recur each year (Lohmann 1908; Smetacek 1981).

Discussion

Anthropogenic nutrient input to the Baltic and North seas has increased considerably over the last decades, although reliable figures on input rates and fate of these nutrients are scarce. Evidence for eutrophication of the Baltic proper has come from enhanced oxygen depletion below the halocline (Fonselius 1972) and increased benthic biomass above it (Cederwall and Elmgren 1980). However, no obvious changes have been noticed in the pelagic system of the open Baltic in contrast to the situation in the coastal regions and particularly enclosed bays (Melvasalo 1981). Considering that Kiel Bight is such a coastal enclosed system, one would expect eutrophication to be proceeding here as well. The evidence for presence or absence of such a trend is ambiguous. In August of the past few years, but particularly in 1981, the zone of oxygen depleted water in the Bight spread out to an exceptional extent (Gerlach 1983). Concomitant data on plankton biomass and sedimentation are unfortunately not available. However, these years were also characterized by unusually stable summers and the severity and extent of anoxia might have been more a result of prolonged bottom water stagnation rather than increased organic input (Gerlach 1983). Indeed, vertical instability in summer not only replenishes oxygen in bottom water but also, by initiating blooms in the surface, increases organic input to the sediments. Allochthonous nutrient input will aggravate such a "nat-

ural" eutrophication following prolonged bottom water stagnation as described for the Baltic by Gargas et al. (1978).

Kiel Bight is estimated to receive a total of 1,000 tons of sewage phosphorus a year (Gerlach 1983); this would increase the phosphate content of Kiel Bight water by 0.03 mmol per m³ per month, equivalent to approximately 0.7 g C per m², assuming a C:P ratio of 106:1 by atoms (Redfield ratio). This monthly rate is in the same range as daily primary production peaks in summer and can be considered as negligible from this viewpoint. However, monthly sedimentation rates during the critical summer period range between 1.5 (June) and 6 (August) g C per m² (Smetacek 1980a), and if the extent of oxygen depletion is indeed directly proportional to the rate of organic input to bottom water and sediments, the summer allochthonous input, constituting 20% of the total summer sedimentation, might well have some effect. Since labile organic substances such as proteins accumulate in the sediments under oxygen depletion (Graf et al. 1983; Meyer-Reil 1983), it is likely that a 20% increase in input will not unduly aggravate the situation. This excess material could easily be broken down during the prolonged oxygenated period of fall and winter, thus not necessarily affecting the winter nutrient equilibrium. The seasonal relationship between organic input and benthic metabolism in the Bight has been discussed by Pollehne (1980), Graf et al. (1983) and Meyer-Reil (1983) and is the subject of ongoing investigations.

With regard to the pelagic system there is little indication of a significant trend in either plankton biomass or production over the past. Thus, winter nutrient concentrations have not changed since the last three decades (Gerlach 1983) and are typical levels found in the non-growing season of similar coastal waters (Pomeroy et al. 1965). Further, Babenerd (1980) could not discern a trend in the data from the monthly survey of 1957–1975, the period when the greatest increase in anthropogenic nutrient input must have occurred. However, because of the low degree of temporal resolution of this data, subtle trends would not be obvious. The most sensitive indication of anthropogenically induced eutrophication would

be sustained high phytoplankton biomass levels during the nutrient impoverished late spring and summer seasons. As this is just what Lohmann (1908) found, the Brandt/Lohmann controversy can finally be resolved in this context.

Brandt (1920a, 1920b), who based his conclusions on net-plankton distribution in the open Bight, maintained that there were two maxima—the spring and fall blooms—separated by a prolonged period of low biomass. Lohmann (1908) collected his samples at weekly intervals and also examined the nanoplankton, which he concentrated with a centrifuge. He found highest plankton biomass in August, a finding which Brandt (1920a, 1920b) rejected outright.

Since then, both men have been vindicated with regard to their respective underlying hypotheses: Brandt's belief that nutrients control biomass under stratified conditions and Lohmann's assertion of the importance of nanoplankton in the sea. It now appears that the choice of study sites was largely responsible for the controversy. Lohmann's station was located in the outer Kiel Fjord which is more eutrophied than the open Bight, both in terms of nutrients and chlorophyll (Krey 1942). It must have been even more eutrophied in Lohmann's time because the raw sewage load to the Fjord from the city of Kiel and from anchored ships was greater until the twenties when sewage from the city of Kiel was diverted to the open Bight. Further, Lohmann (1908) found that *Skeletonema costatum* was the most important contributor to plankton biomass and *Heterocapsa triquetra* was important in summer. Both these species are far more common in the Kiel Fjord than in the open Bight (Schinkowski 1969; Horstmann 1971).

However, on a general level the Brandt/Lohmann controversy is essentially still unresolved; witness the current discussions on the productivity of the mid-oceanic gyres (Kerr 1983). The controversy revolves around the size of the relevant organisms (today's equivalent of Lohmann's nanoplankton is picoplankton) and the relative role of factors such as nutrient input rates in controlling plankton growth. The difficulties are related not only to the limitations of methods (Omori and Hamner 1982),

which give rise to conceptual confusion, but also to the wide-spread tendency to generalize from individual observations prevalent since Hensen's days. Pomeroy (1981) has stated: "The study of ecosystems as such, rather than simply of component species, is still in a formative stage in which investigators are exploring in many directions with no generally agreed-upon approach." The approach for analyzing the Kiel Bight annual cycle adopted here differentiates stages of the system in terms of light or nutrient control of plankton standing stock and the source of the nutrients fueling pelagic primary production. Thus, changing spatial features of the environment (depth of light penetration and mixing) give rise to a temporal sequence of various patterns of energy flow and cycling of matter. Such sequential patterns can be found spatially in estuarine systems (Kemp et al. 1982) or along transects away from an upwelling site in the ocean (Margalef 1978). Eppley et al. (1983) and Smetacek (1984) have discussed the relationship between input of "new" nutrients to pelagic systems and loss due to sedimentation. They point out that heaviest sedimentation occurs immediately following "new" production and decreases under conditions of "regenerated" production.

Whereas the physico-chemical forcing functions of the pelagic ecosystem are now well recognized, much less is known about the factors selecting plankton species composition (Smayda 1980). Attempts at explaining patterns of occurrence based on single features such as phylogeny, size or growth rate of an organism have not proved very successful in the past. It now appears that more attention will have to be paid to the life history strategies of individual plankton species if one is to explain their distribution in time and space (Garrison 1981; Davis 1982). Long-term data can give valuable clues as to the possible nature of these strategies by showing the degree of variability or recurrence in species appearance in relation to environmental features. Both Lohmann (1908) and Smetacek (1975) showed that seasonal appearance and rapid growth of the dominant species was generally not a result of horizontal advection. Thus, we are dealing primarily with a true species succession rather than a sequence in

the Bight (see Smayda 1980 for a discussion of these terms).

Hensen (1887) was struck by the comings and goings of the various plankton species in the course of the year and he suggested that many of these organisms had benthic resting stages in their life cycles. He pointed out the prevalence of this strategy in diatoms, dinoflagellates and tintinnids and speculated that the difference between neritic and oceanic species might well lie in the presence or absence of such benthic stages. This view of plankton succession was lost from sight until quite recently, when the role of such life cycle strategies in determining the appearance of particular species of diatoms (Garrison 1981), red-tide dinoflagellates (Provasoli 1979), and chrysophytes (Sandgren 1983) was confirmed. Hensen (1887) thought that marine ceratia could also have such a life cycle, which is, however, not the case (Margalef 1978). Hensen had evoked the sediments as a spatial anchor for the drifting plankton because he assumed that the annual cycle observed by him was a recurrent pattern. Long-term data from the Bight show that only some species are recurrent and the majority variable in their appearance; ironically, it is the species with known benthic resting stages—many neritic diatoms, red-tide dinoflagellates, tintinnids—that show greatest year-to-year variability in appearance and those without such stages—the ceratia, most copepods—that are the most predictable in the Bight.

Long-term data from the North Sea and Atlantic (Colebrook 1982) have shown that shifts in the dominance patterns of species occur over time scales of many years in wide areas with greatly differing physical environments (Gieskes and Kraay 1977). The presence of such long-scale temporal shifts indicate that the small time scales of the immediate growth environment cannot sufficiently account for the success of a species. Harris (1980) has stressed that more attention should be paid to the various time scales of phytoplankton response to its environment. He suggested that smaller time scales would be of greater importance. However, the build up of dominant species generally occurs over weeks, apparently independent of day-to-day changes of weather.

The long-term observations of the Kiel Bight plankton cycle raise two important questions: Why are the ceratia in particular and the late summer/early autumn populations in general so predictable and the others—particularly those with benthic stages—so variable in their appearance in the Bight? One possible solution would be to search for species-specific differences in the time scales of response to the environment. Thus, ceratia grow slowly over the summer months and, being relatively unpalatable and long-lived, build up a large population by the end of the summer. Storm-induced input of new nutrients during the summer is utilized by diatoms as they respond more rapidly to such events. However, nutrient input following fall mixing is taken up by ceratia, particularly *C. fusus*, rather than diatoms. Presumably, this is due to the *Ceratum* population having attained a “critical mass” at the time of fall mixing. A few cell divisions of the entire population in the 2–3 weeks following mixing would suffice to account for their large fall biomass. Further, the nutrient-rich bottom water is less than a third of the total volume of water in the Bight, and dilution of the population by vertical mixing is accordingly small. The large “seeding” stock of ceratia can thus outcompete faster-growing species present in smaller quantities. The size of the biomass peak attained in any one year is probably not of survival value to the species, as death is the fate of most individuals of a large bloom (Walsh 1983). Thus, the ceratia are widely present during summer and fall in the temperate zone, but the biomass peak typical for Kiel Bight is by no means the usual pattern (Smayda 1980).

When nutrient input exceeds the *Ceratum* growth rate, as invariably occurs in October, diatoms take up the excess nutrients, particularly ammonia, and form the late diatom bloom of varying composition. These are again mostly opportunistic species with benthic resting stages, although recurrent species such as *Guinardia flaccida* are also important contributors to biomass.

Sanders (1968) has classified ecosystems along an axis ranging from physically governed to biologically accommodated systems. Species characteristic of former systems would be geared to respond rapidly to

physically induced environmental change in contrast to species characteristic of biologically accommodated systems. Thus, one might regard bloom diatoms as belonging to the former category and summer forms, particularly ceratia, to the latter, with of course, many intermediate types. Species with fast response rates grow rapidly, and by stripping their environment of nutrients, change their growth conditions. Prolonged residence in an environment no longer favorable for growth would have no survival value and these species tend to be those that form resting stages en masse and sediment out. This strategy, in contrast to persistence in the surface layer of other species, particularly the slower growing ones, would ensure that the reproductive success of one year is carried over to the next. Davis (1982) distinguished four functional groups of phytoplankton: bloom diatoms, large slow-growing diatoms, microflagellates and large dinoflagellates. He suggests that particular combinations of light, mixing and nutrient supply will favor dominance of the phytoplankton assemblage by one of these functional groups. This explanation satisfactorily accounts for the general pattern of phytoplankton species succession in the Bight.

The survival strategy of a pelagic reproducing and a benthic resting stage is widespread in lake diatoms (Lund 1971; Jewson et al. 1981; Reynolds and Wiseman 1982) where the degree of recurrence is also much greater than in Kiel Bight. This also applies to other marine inshore systems such as Long Island Sound and Narragansett Bay (Smayda 1980). Why then is there so much variability in the Kiel Bight diatoms? The answer, I believe, lies in the topographical heterogeneity of the Belt Sea and the extreme influence of weather on hydrography and timing of the diatom blooms. Banse (1955) found that meroplanktonic larvae in the Belt Sea were concentrated in patches of a few hundred meters' extent. The frequency of resuspension and resedimentation of surface sediments in the bight, particularly in winter, is likely to disrupt the seed beds of a previous year's bloom. Further, Davis et al. (1980) have shown that resting spores of some diatoms are not resistant to anoxic conditions, whereas others

are susceptible to light (Hargraves and French 1983). Thus, it is likely that distribution of diatom resting spores in the Bight is also patchy and species dominance of a bloom can well be determined by chance. Under these conditions, rapid growth rates in the water column would be more important than the success of a previous year's population. Because of the shorter residence time of such species in the water column, their distribution, like those of meroplankton, is apt to be more patchy than that of slower growing species and also more susceptible to the turbulence regime as suggested by Kemp and Mitsch (1979) for phytoplankton in general.

The high degree of recurrence in biomass and species composition of the Bight's metazooplankton indicates biological rather than physical control of this group. In spite of a well developed cycle of species succession, year-to-year fluctuation in biomass levels and timing of appearance are much more predictable than in the majority of the protists. Because of their long response time metazooplankton are less susceptible to vagaries of the weather; further, the reproductive success of small herbivorous copepods is independent of the composition of its food (Harris et al. 1982). The Kiel Bight observations show that ctenophore predators, often observed to regulate copepod populations in shallow enclosed seas (Greve 1981; Harris et al. 1982), are also not necessarily of importance. Rather, it appears that internal control such as predation of nauplii by adult copepods or some unknown intrinsic features of the life cycle are more important in regulating their biomass than environmental factors such as food availability or predation pressure—of course within certain limits.

Summing up, long-term data can provide clues about functional aspects of pelagic systems and survival strategies of component species but more detailed observations of the actual relationships are called for before a better understanding of the factors regulating the annual cycle of plankton will emerge.

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