AMIT GULATI

BENTHIC PRIMARY PRODUCTION IN TWO DIFFERENT SEDIMENT TYPES OF THE KIEL FJORD (WESTERN BALTIC SEA)

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Dedicated to my loving Mother
who toiled with me at every stage of my life

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ZUSAMMENFASSUNG

ACKNOWLEDGEMENTS

ZUSAMMENFASSUNG

Ziel dieser Studie war es, die physikalischen, chemischen und biologischen Faktoren in bezug auf die benthische Primärproduktion von zwei verschiedenen Standorten, nämlich M: Mönkeberg (Grobsand, *Hoch-Energie-Fenster*) und T: Tirpitzmole (Feinsand, *Niedrig-Energie-Fenster*) in der Kieler Förde (westliche Ostsee) zu untersuchen. Sedimentproben wurden ein- bis zweimal pro Monat an demselben Tag von den beiden Stationen zwischen dem 30. Mai 1994 und dem 31. Juli 1995 genommen. Die benthische Primärproduktion wurde mittels der Mikroprofilmethode gemessen bei Benutzung einer Nadel-Elektrode statt der sonst üblichen Glas-Mikroelektrode. Dieses Verfahren wurde, der vorliegenden Literatur nach zu urteilen, hier zum ersten Male angewendet.

1) Das interstitielle Milieu der offenen Lokalität ist den hydrodynamischen Kräften stärker ausgesetzt als das geschützte Gebiet. In den Feinsand-Sedimenten wurde ein höherer Wassergehalt gefunden als in den Grobsand-Sedimenten. Der höhere Prozentsatz von suspendiertem Material in den beiden Sandstrand-Sedimenten ist überwiegend auf durch Wind hervorgerufene Wellen-Resuspension zurückzuführen.

2) Beide Sedimenttypen zeigten einen niedrigen organischen Kohlenstoffgehalt (< 1%), wobei die Feinsedimente einen höheren C_{org}-Gehalt von < 0,4% aufwiesen als die sandigen Grobsedimente (< 0,1%). Außerdem war ein höherer organischer Gehalt in den Sedimenten meistens verbunden mit einer Zunahme in der Porosität.

3) In der Regel wurde in den beiden Sandstrandsedimenten ein C:N Verhältnis von < 12 gefunden. Höhere Werte >12 wurden auf einen höheren Anteil an refraktorischem Material, z.B. von Makroalgen, aus Holzrückständen, Detritus sowie vaskulärem Pflanzenmaterial zurückgeführt.

4) Die Mikroflora bestand hauptsächlich aus pennaten Diatomeen (sowohl aus beweglichen als auch epipsammischen Arten). An den beiden Stationen wechselten die Mikrophytobenthos-Gemeinschaften von größeren zu kleineren Arten und umgekehrt, abhängig von verschiedenen Jahreszeiten und Umweltveränderungen. Die Anzahl lebender einzelliger Algen zeigte meistens einen steilen Anstieg im Frühjahr und Herbst, aber eine Abnahme im Sommer, die vermutlich durch starkes Grazing verursacht wird. Eine deutliche Schichtung der einzelnen Arten aufgrund unterschiedlicher physiologischer Bedingungen entlang des Tiefengradienten war ein typisches Merkmal. Die Mikrophytobenthos-Aktivität nahm in der Reihenfolge Frühjahr > Winter > Sommer > Herbst ab. Die Zellgröße ist ein wichtiger Faktor, da die Zellen kleiner Mikroalgenarten aktiver sind als die größeren Zellen.

5) Die Artenzusammensetzung der benthischen Diatomeen im Grobsand-Sediment (offen, *Hoch-Energie-Fenster)* bestand überwiegend aus kleinen epipsammischen an Sandkörnern

festhaftenden Arten mit einer Abundanz zwischen 17 und 1428 × 10^6 Zellen/cm^{-3}, während das Feinsand-Sediment (geschützt und *Niedrig-Energie-Fenster)* vorwiegend epipelische (oft größere Zellen), bewegliche Arten mit Abundanzen von 45 bis 4005× 10^6 Zellen/cm^{-3} aufwies. Die Besiedlungsdichte variierte an den beiden Stationen räumlich und zeitlich in den oberen Sedimentschichten bis 9 mm Tiefe, wies aber keine ausgesprochene Schichtung auf. Die 3-6 mm Sedimentschicht enthielt die reichste Mikroalgengemeinschaft. Vertreter aus der Familie Naviculaceae herrschten vor und spielten als sehr anpassungsfähige Arten eine entscheidende Rolle im Küstensediment der Kieler Förde. Die häufigste und am weitesten verbreitete Gattung, die offensichtlich allen Umweltbedingungen standhält, war *Navicula.*

6) Der Chlorophyll-a-Gehalt war höher in den Feinsand- (2,05-29,07 µg Chl-*a* cm^{-3}) als in den Grobsand-Sedimenten (0,95-13,17 µg Chl-*a* cm^{-3}). Die Hauptmenge von Chl-*a* an den beiden Stationen lag zwischen 3-6 mm. Die Chl-*a*-Konzentration war proportional zu der Gesamtzellzahl. Die benthischen Mikroalgen bilden mehr photosynthetische Pigmente bei bedecktem Himmel als bei Sonnenschein, um das reduzierte Lichtangebot auszugleichen.

7) Die durchschnittliche Dicke der oxischen Sedimentschicht betrug zwischen 4,5 und 17 mm an der Station M, während sie bei der Station T von 2,5 bis 23 mm reichte. Die oxische Zone im Sediment war abhängig von Wetterbedingungen, Sedimenttyp und der Mikrophytobenthos-Besiedlung. Daneben existierte eine schwach signifikante Korrelation zwischen der Dicke der oxischen Zone und der Sedimenttemperatur.

8) Die photische Zone betrug an den beiden Stationen meistens < 10 mm in Abhängigkeit von Sedimenttyp, Photonenfluß und der Absorption, bzw. der Streuung des Lichtes. Im Durchschnitt wurde eine tiefere photische Zone in den Grobsand-Sedimenten gemessen mit einer Variation von 4-16,5 mm als in den Feinsedimenten mit 2,5-21,5 mm.

9) Die Gesamtsauerstoffzehrung (TSOC) lag im Feinsand mit 29,6 bis 401,5 µmol O_2 m^{-2} h^{-1} höher als im Grobsand (19,2 bis 340,6 µmol O_2 m^{-2} h^{-1}). Die Sauerstoff-Flüsse waren am höchsten im Sommer und am niedrigsten im Winter. Der Bioirrigations-Fluß war aufgrund der Meiofauna (k_{Bio}) höher als der O_2-diffusive Fluß. Dieses war wahrscheinlich der Hauptfaktor, der für die Beschleunigung der O_2-Zehrungsraten verantwortlich war.

10) Die photosynthetische Aktivität, gemessen mit der Stahlelektrode, war doppelt so hoch wie mit der Glaselektrode, unabhängig von der existierenden Dunkelperiode, d.h. 3 bis 10 s. Je länger die Dunkelperiode, desto geringer ist die benthische Primärproduktion. Die Bruttoprimärproduktion gemessen mit der Stahlelektrode wird daher unterschätzt um den Faktor 0,35 ± 0,14 (n=7) bei einer Dunkelperiode von 10 s im Vergleich zur Glaselektrode mit 2 s. An der geschützten Lokalität (Feinsand, *Niedrig-Energie-Fenster)* lagen die photosynthetische Aktivität mit 0,06 bis 18,2 µmol O_2 cm^{-3} h^{-1} und die benthische

Primärproduktion mit 15,3 bis 454,3 mg C m^{-2} h^{-1} höher als an der offenen Station (Grobsand, *Hoch-Energie-Fenster*) mit 0,13 bis 16,7 µmol O_2 cm^{-3} h^{-1} beziehungsweise 38,6 bis 284,8 mg C m^{-2} h^{-1}. Die benthische Mikroalgen-Produktivität war 3,2 mal höher als die Phytoplankton-Produktivität.

Zusammengefaßt ergibt diese Studie, daß Mikrophytobenthosalgen zu den wichtigsten Primärproduktionskomponenten gehören, an der Sediment-Wasser-Grenzschicht wachsen und eine zentrale Rolle im Flachwasserökosystem der Kieler Förde spielen. Sie können auch dazu beitragen, das schwerwiegende Problem der Eutrophierung in diesem Gebiet zu überwinden.

1 INTRODUCTION

Benthic microalgal communities colonize in the upper few mms to few cms of the sediments in shallow marine and freshwater systems, where adequate light reaches the sediment surface to support the primary production. They grow in different habitats, showing heterogeneous patches, mosaic distributions with spatial and temporal variations in shallow intertidal areas, ranging from wave-swept beaches to detritus-laden brackwater lagoons (MACINTYRE et al. 1996), coarse sand to silt muds (PINCKNEY et al. 1994), non cohesive and cohesive marine sediments (YALLOP et al. 1994). The term microphytobenthos refers to benthic microalgae, autotrophic microbial consortia (PINCKNEY & ZINGMARK 1993C) including cyanobacteria. Microphytobenthos are attached to the stones, ice, salt marshes, submerged aquatic vegetation as well as on the illuminated sediments. On the basis of their attachment to the substratum in different habitats benthic diatoms have been classified as *epipelic*, *episammic*, *epiphytic*, *epilithic* (SNOEIJS 1993).

Microphytobenthos have shown to be most important autochthonous primary producers in a wide variety of shallow-water habitats (MILLER et al. 1996), constituting an important carbon source for the local benthic food web, where macroscopic vegetation is lacking (SUNDBÄCK et al. 1996). In addition to this, benthic microalgae releases oxygen, as a by-product of photosynthesis, which exhibits an important function in estuarine areas prone to hypoxia or anoxia, by relieving hypoxic conditions and serving as oxic refuges for estuarine fauna as observed in the estuarine shoal areas (RIZZO et al. 1996). Benthic microalgae and detritus may also be an important source of food for both macro- and microheterotrophs (WAINRIGHT 1990, de JONGE & van BEUSEKOM 1992). However, microphytobenthos being suitably sized are beneficial food items for meiofauna (SCHWINGHAMER 1983). They may provide as much as one third of the total primary production in some estuarine systems (VAN RAALTE et al. 1976, SULLIVAN & MONCREIFF 1988, PINCKNEY & ZINGMARK 1993b). Hence, they are an important component of the estuarine food webs (PETERSON & HOWARTH 1987, SULLIVAN & MONCREIFF 1990).

Most of the studies on benthic microalgal production have been done in estuaries and intertidal zones. Annual productivity values as high as 892 g C m^{-2} and hourly productivity rates up to 800 mg C m^{-2} have been reported by GRØNTVED (1962), HARGRAVE et al. (1983). The contribution and importance of microphytobenthos to the carbon budgets of shallow-water systems has widely been recognized from a range of estuarine ecosystems i.e. intertidal flats (CADÉE & HAGEMAN 1974, COLIJN & DIJKEMA 1981, LÄNGE 1983, COLIJN & DE JONGE 1984, DE JONGE & COLIJN 1994, BROTAS & CATARINO 1995), mud bottomed estuaries (HOPKINS 1963, ADMIRAAL et al. 1984) turbid estuaries (MACINTYRE & CULLEN accepted) to sandy tidal flats (PAMATMAT 1968, STEELE & BAIRD 1968, VARELA & PENAS 1985, ASMUS

& BAUERFEIND 1994, BRUNS 1994) or tidal currents (BALLIE & WELSH 1980, SHAFFER & SULLIVAN 1988), salt marshes (POMEROY 1959, SULLIVAN & MONCREIFF 1988), lagoons (FIELDING et al. 1988) and sandy beaches (MEYER-REIL et al. 1980).

Microphytobenthos are an indispensable component of the nutrient cycles (HÖPNER & WONNEBERGER 1985, RIZZO 1990), as they can alter the sediment water nutrient fluxes (RIZZO et al. 1992, REAY et al. 1995). The biofilms produced by the microbenthic algae at the sediment / water interface help in stabilizing sediments (HOLLAND et al. 1974, PATERSON at al. 1990, DELGADO et al. 1991a, MADSEN et al. 1993, YALLOP et al. 1994). They are the best indicators for recording the changes in the shallow water systems on account of their vertical migration in the sediment (PINCKNEY et al. 1994). Benthic microalgae can also stabilize sediments by producing biofilms, and thus reducing resuspension (HOLLAND et al. 1974, GRANT et al. 1986, PATERSON et al. 1990). Besides this, microphytobenthos plays a pivotal role in the ecosystem as it can ameliorate water quality (RIZZO et al. 1996) and act as indicator of eutrophication and pollution (ASMUS & BAUERFEIND 1994).

The Baltic Sea, is semi-enclosed, largest brackish Sea in the world (SEIBOLD 1970) having many features that determine its unique quasi-stationary properties (SCHULZ et al. 1992). From the geological point of view it is a young Sea (SEGERSTRÅLE 1957), or a big estuary (BRETTAR & RHEINHEIMER 1992), showing a high degree of variability in different temporal and spatial scales. It is characterized by a large net fresh water supply and a permanent halocline at 60-70 m which inhibits seasonal vertical mixing deeper than 70 m (SCHULZ et al. 1992, SAMUELSSON 1996). It is also a detritus-based system (JANSSON 1972), providing a unique habitat for its flora and fauna therefore, making it a very important ecosystem. From north to south, it extends over 12° of latitude from 66° N to 54° N and on the east-west axis from 30° E to 10° E. The average depth is 55 m and having total water volume of approximately 23.000 km^3. It lies in a humid climatic zone with a considerable surplus of rains.

The productive system of the Baltic Sea consists of trophogenic layers of pelagial and litoral systems, while the latter is of great importance in the northern part because of long and shallow coast (HÄLLFORS et al. 1981). The microphytobenthos production in the Baltic Sea varies from 0.3-103 mg C $m^{-2} h^{-1}$ (SUNDBÄCK 1983 in PEEKEN 1989) at the water depth >1m, respectively. The average phytoplanktonic production in the Baltic Sea is 100 g C m^{-2} yr^{-1} (LASSIG et al. 1978). The present status of the pelagic system in Baltic Sea reflects clear signs of eutrophication, which are more pronounced in the coastal areas than the open waters with the dramatic increase in chlorophyll-a (biomass) and primary production (WULFF et al. 1986, GERLACH 1990). Direct inputs of anthropogenic origin and remobilzed reserves from sediments as well as the effect of the long-lasting stagnation in the Baltic Sea are the main sources for the enhancement of the biological production (SCHULZ et al. 1992).

The western Baltic Sea includes a number of shallow water areas e.g. Kiel Bight and Kiel Fjord, with the most prominent hydrographical features. The Kiel Bight, being a separate region between the Little Belt, Great Belt and Fehmarn Belt, forms the south western part of the Belt Sea. It has a mean depth of about 20 m (BABENERD & GERLACH 1987). Besides this, areas shallower than 8 m are covered either by sand, or by "Lag sediment", while muddy sediments start at about 12 m water depth in sheltered regions. However, their contribution is significant only at water depths exceeding 18 m (BABENERD & GERLACH 1987). In such a system, the close proximity of the sediment-water interface, to the productive surface layer exerts a profound influence on the structure and the functioning of the entire system (SMETACEK et al. 1987, GRAF 1992). The remineralization processes in the bottom layers of particularly shallow areas of the western Baltic have an immediate influence on the algal production in the upper water layers. Furthermore, in comparison to the open areas of the Baltic, where long term remineralization processes are less significant as compared to the short-term turnovers (PROBST 1977).

Shallow water sediments of the western Baltic Sea may represent a self-supporting system governed by benthic primary production, especially during the periods with sufficient light available (MEYER-REIL 1987). The strong diurnal rhythms of benthic primary production (JØRGENSEN et al. 1979, KARG 1979, REVSBECH et al. 1981) imply a coupling between autotrophic and hetrotrophic processes in shallow water sediments. This has also been well observed in sandy sediments of the Kiel Bight (MEYER-REIL and GRAF unpublished data). The benthic primary production of Kiel Fjord has not been studied extensively. However, SCHULZ (1983) has illustrated the importance of microphytobenthos in the food chain as well as in the trophic interrelationships of the western Baltic Sea. However, studies carried out in the laboratory demonstrated that the production of the microalgae could be stimulated through the feeding of mussel (*Macoma baltica*) on it (JASCHINSKI 1989).

Nonetheless, to date the studies on microphytobenthos and eutrophication in regard to western Baltic Sea have been insufficiently investigated (GERLACH 1990). Moreover, anthropogenic impact not only imply eutrophication and contamination, but also the physical disturbances as a result of human activity on shallow coastal areas which might lead to the modification or loss of productive habitats (SUNDBÄCK et al. 1996). The dearth of information on the benthic primary production has largely been due to lack of suitable and modern techniques. As the methods adopted earlier for carrying out these studies in the Kiel Fjord may not have sufficiently been satisfactory e.g. ^{14}C-bicarbonate technique, oxygen exchange method (KARG 1979). Revised techniques implying to these important studies were required. Hence, the present study was carried for estimating the benthic primary production in the Kiel Fjord, with the help of microprofile technique "light-dark shift method" (REVSBECH et al. 1981). Review of literature indicates that till date glass microsensors have been popularly used for the measurement of benthic primary production. However, the present study is related to the pioneer use of the needle electrode for the measurement of the microphytobenthos production.

Following objectives of the present study were conducted at two different types of wave-washed sandy beach sediments of the Kiel Fjord:

1) Seasonal variations in the benthic primary production and O_2 uptake with consideration of physical, chemical and biological parameters.

2) Spatial and temporal variations of the microphytobenthos biomass with the factors responsible for species abundance and distribution.

3) Ecological significance of benthic microalgae as primary producers, and their role in the energy budgets, in comparison to phytoplankton.

2 MATERIALS AND METHODS

2.1 TOPOGRAPHY

THE KIEL FJORD

The Kiel Fjord (54° 21' N, 10° 10' E) is an extended, narrow, southwestern part of the Kiel Bight (western Baltic Sea), running around 17 km from north to south and finally terminating at its southern end in the town of Kiel (Fig. 1). From its mouth, between Bülk and Laboe, roughly 8 km wide the Kiel Fjord tapers in a funnel shape up to its narrowest part at Friedrichsort, the width here being only little more than 1 km. This constriction divides the Fjord into two more or less equal sections forming a demarcation between the outer and the inner Fjord. The latter part broadens out again inwards to a width of about 2.5 km and finally ends in a narrow tongue, projecting into the centre of the town called Hörn (LENZ 1977). The depth here being 7 to 9 m. This innermost section of the Kiel Fjord is more heavily polluted by the river Schwentine and smaller effluents from land, everyday ship traffic and ship industry (HDW) than its outer section. The quality of water on its outer part is better than on its inner part. The average depth of the Kiel Fjord is 15 m. The area and volume of the Kiel Fjord (STIENEN 1986) is given in Tab.1.

Tab. 1: Kiel Fjord: Area and volume

Depth (m)	**Area (km^2)**	**Volume (10^6 m^3)**	**Volume %**
0 - 10	15.0	129.78	84
10 - 15	11.1	23.16	15
> 15	.945	2.01	1
		154.95	

The hydrography of the Kiel Fjord has been well discussed by KÄNDLER (1959) and OHL (1959). As regards bottom topography, the Kiel Fjord is open towards the Kiel Bight, without any sill to act as a barrier. As a prolongation of the Fjord, there extends a 17-20 m deep basin into the Kiel Bight, enclosed by low banks between 10-13 m deep. Only in the northeast,there is a 15 m deep relatively narrow outlet, which leads it into the deeper parts of the Kiel Bight.

Due to this small outlet, exchange of water between the Fjord and deeper parts of the Bight is not unimpeded as is at its surface (LENZ 1977).

Freshwater input into the Kiel Fjord comes from one minor source, the river Schwentine, which is eutrophic and flows on its eastern side. The rainwater drainage of Kiel municipality contributes a negligible quantity of the freshwater. Similarly, on its western side, overflow of water from the Kiel Canal (Nord-Ostsee-Kanal) is irrelevant, since the water in question is brackish, albeit with a low salt content.

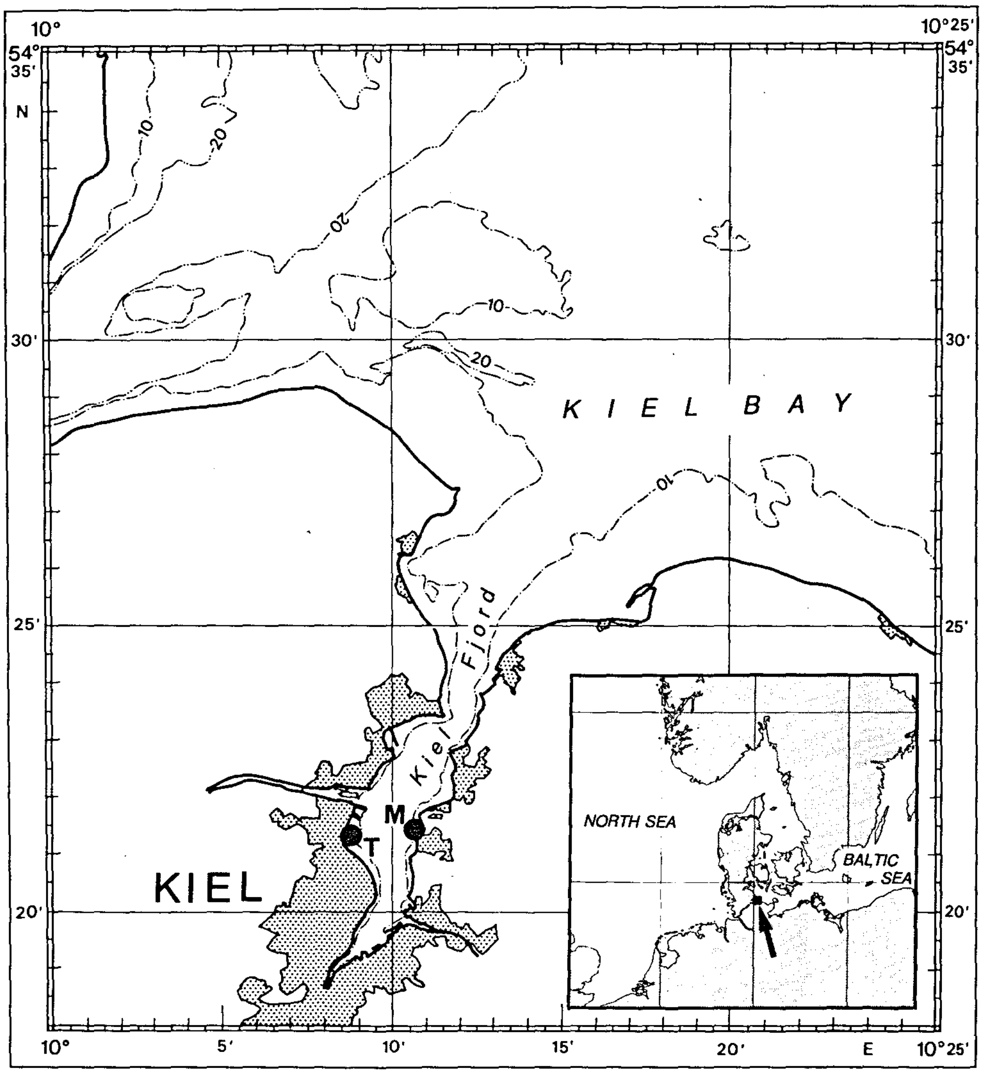


Fig. 1: Map of Kiel Fjord, showing the 2 sampling sites.

The Bathymetry and the sediments of the Kiel Fjord have been studied by KÖGLER & ULRICH (1985). The Kiel Fjord beaches are similar to other sandy beaches and are dominated by sand having grain size ranging from 0.208 to 0.489 mm (mean grain size 0.293 mm) and grain shape (62% of grains with rounded edges) (MEYER-REIL et al. 1980). On its eastern side, at water depths of < 10 m, sediments constitute mainly of sand and coarse material (SEIBOLD et al. 1971).

2.2 STUDY SITES AND SAMPLING LOCALITIES

During the present studies samples were collected once or twice a month from the two different sandy, wave-washed shallow water localities on both sides of the Kiel Fjord (Fig.1), Mönkeberg (54° 21.18' N, 10° 10.75' E) and Tirpitzmole (54° 21.25' N, 10° 8.55' E). The sampling was conducted at a water depth varying from 20 to 50 cm from April 1994 to July 1995, respectively. However, for the comparison of the microprofile technique "Light-Dark Shift method" (*precision of the glass and needle microsensor*) extra samples were collected from the Tirpitzmole in August and November 1995. For each sample acquisition approximately 1 m^2 area was selected, depending upon the rich development of the microphytobenthos populations.

The study stations differ not only in their sites but also in their sediment and wave exposure. Mönkeberg (M) is an exposed beach, situated on the eastern side, clean with coarse sandy sediments, predominated by small *"epipsammic"* diatoms and being to a larger extent influenced by the strong hydrodynamic forces which keep its sediments oxygenated. It is therefore referred to as *high energy window*, in contrast to the fine sandy grain sediments of the Tirpitzmole (T), which is a sheltered site, placed on the western side of the Fjord, with ample of anthropogenic waste matter and dominated by larger sized "*epipelic*" diatoms and designated here as *low energy window.*

2.3 PHYSICAL AND CHEMICAL PARAMETERS

2.3.1 IRRADIANCE

A daily average value (Wm^{-2}) i.e. from sunrise to sunset for the respective sampling day was calculated from the data obtained from the Meteorological Department of the Institut für Meereskunde, Kiel with the aid of pyranometer (CM 11, KIPP & ZONEN, GERMANY).

2.3.2 TEMPERATURE

Sediment temperature (uppermost sediment layer *ca.* 1 cm) was determined each time ***in situ*** with a (1103 TESTO TERM) thermometer.

2.3.3 WIND DIRECTION AND SPEED

The data for the wind direction and speed was achieved by courtesy of the Meteorological Department of the Institut für Meereskunde, Kiel. On account of the rapid changes in both these respective parameters, from the gathered data for the respective sampling day, a mean value was further calculated for the time period between 00:00 AM to 12:00 PM. Whereas, due to the frequent changes in the wind direction on 28 July 1994 and 10 August 1994 mean was calculated from 06:00 AM to 12:00 PM and 08:00 AM to 12:00 PM, respectively.

2.3.4 SEA-LEVEL

Data for the sea-level for the respective sampling day was collected from the Meteorological Department of the Institut für Meereskunde Kiel. From the achieved data, a mean was further calculated from 00:00 AM to 12:00 PM.

2.3.5 SALINITY

Salinity was measured with the help of a salinometer (BECKMAN INSTRUMENTS MODEL- RS - 7B) in the laboratory for which water samples were collected from both the sampling sites. The salinometer was calibrated by using Standard Seawater (obtained from IAPSO STANDARD SEAWATER OF THE OCEANIC SCIENTIFIC INTERNATIONAL, UK).

2.3.6 SEDIMENT PARAMETERS

2.3.6.1 GRAIN SIZE ANALYSIS

The grain size distribution of sediment was carried out by an initial splitting of the sediment sample (upper surface layer 0 to 1 cm, 100-200 g sediment) into sand fraction (particles > 63 µm) and silt-clay fraction (particles < 63 µm) which was achieved with the 63 µm sieve, employing a wet sieving method (with simultaneous washing). The fraction > 63 µm was then dried, while the remaining fraction < 63 µm was allowed to settle out for several days. The overlying water was then decanted, the remaining fraction < 63 µm was dried and weighed. The washed and dried > 63 µm was then sieved through a stacked set of 6 grade sieves (mesh sizes 2000, 1000, 500, 250, 125, 63 µm; HAVER & BOECKER, GERMANY), with the aid of an electromagnetic sieving apparatus (RETSCH, GERMANY). The material on each individual sieve was then weighed and noted together with any material < 63 µm which may have passed into the closing pan at the bottom of the sieve stack. The mean size was calculated from the curve obtained by plotting grain size against frequency of grain size classes. Mean, median, sorting, skewness and kurtosis were calculated according to FOLK & WARD (1957) and FOLK (1974).

2.3.6.2 POROSITY

Water or the moisture content is the difference between the wet weight (WetWt) - dry weight (DryWt) of the sediment and is expressed as the percentage of the wet weight, while *porosity* is the percentage volume of pore space or void space in the total volume of the sediment. Thus, the porosity of a sediment is the volume of water needed to saturate a given weight of dry sand (HULINGS & GRAY 1971). It depends on the arrangement of individual grains, in other words sediment packing. The packing of a sediment in turn is related to both sorting and shape of sand grains, and also to the manner of sediment deposition. Porosity varies markedly with the depth of the sediment.

During the studies, undisturbed sediment samples were collected by making streaks carefully with the help of three 5 ml plastic syringes (1.2 cm diameter; top cut off) on the surface of sandy sediments 0-1 cm depth in an approximately marked 1 m^2 area at three different locations as referred earlier. The overlying seawater of each sample was carefully removed, then from the collected sediment samples the upper 1 cm^3 layer was carefully cut and separated. These separated sediment layers were then put into preweighed aluminium containers and weighed for their (WetWt), while (DryWt) was determined after drying at 60°C for 24 hrs. On dividing, the difference between (WetWt-DryWt) with the specific density of seawater (DIETRICH et al. 1975) and the average density of sediment (HOLME & MCINTYRE 1984) gave the volume percent of the liquid phase. Assuming, that the salinity of the interstitial water is similar to the overlying water, the weight could be converted to volume using seawater density tables (HOLME & MCINTYRE 1984). The dry weight of the sediment could be converted to approximate volume by assuming a mean grain specific gravity of 2.97 (sand).

In the present study, the density of water was calculated assuming salinity 35 PSU. Moreover, if salinity between 10-20 PSU is taken into consideration as commonly found in the western Baltic Sea, a small error of *ca.* 1.0-1.7% exists.

$$\frac{(WetWt - DryWt/1.025)}{(WetWt - DryWt/1.025) + DryWt/2.97} = Vol\,\% \qquad \text{equation 1}$$

where

$WetWt$ = wet weight

$DryWt$ = dry weight

Density of the seawater (at salinity 10 PSU) = 1.008 g cm^{-3}

Density of the seawater (at salinity 15 PSU) = 1.012 g cm^{-3}

Density of the seawater (at salinity 20 PSU) = 1.015 g cm^{-3}

Density of the seawater (at salinity 35 PSU) = 1.025 g cm^{-3}

Density of the solids (sand) = 2.97 g cm^{-3}

The porosity phi (Φ) which is further required for calculating the diffusive fluxes in the sediment, is obtained on dividing the volume percent by 100.

$$\Phi = \frac{Vol.\%}{100} \qquad \text{equation 2}$$

2.3.7 ORGANIC CARBON AND NITROGEN

After measuring the porosity of the collected 3 samples, the dried samples were then pulverized with the help of mortar and pestle. Owing to the very low organic content in the sandy sediments of the Kiel Fjord, for the estimation of the organic carbon (Corg) 15-20 mg of the each sample was weighed in silver cylinders. The organic carbon content was then determined by a "CHN-ANALYZER" (CARLO ERBA NA-1500) according to VERARDO et al. (1990), after removing the carbonates by acidification with HCL (1N) within silver cylinders and dried prior to analysis. The CHN analyser was calibrated with acetanilide (10.36% nitrogen, 71.09% carbon).

2.3.8 CARBON : NITROGEN RELATIONSHIP

The atomic ratio of carbon and nitrogen ratio was obtained by dividing the measured weight values of carbon and nitrogen by their respective atomic weights.

2.3.9 TOTAL CARBON AND NITROGEN

The pulverized samples used for the determination of the organic carbon were also used for the determination of the total carbon (TC) and total nitrogen (TN). For the estimation 15-20 mg of the each sample was weighed in tin cylinders as described above. The total carbon (TC) and nitrogen (TN) was determined with the aid of CHN analyser (CARLO-ERBA-NA-1500) without acidification. The calibration was performed as described above. Inorganic (carbonate) carbon was derived from the difference between total carbon and organic carbon. Percent calcium carbonate is then calculated according to VERARDO et al. (1990).

$$CaCO_3\% = 8.33 \times (TC - C_{org}) \qquad \text{equation 3}$$

Where:

8.33 = factor
TC = total carbon
$Corg$ = organic carbon

2.4. BIOLOGICAL PARAMETERS

2.4.1 THE OXYGEN MICROPROFILE METHOD

The oxygen microprofile method (REVSBECH et. al 1981, REVSBECH & JØRGENSEN 1983) was used to measure the photosynthesis (microphytobenthos production) in the sediments. This new technique has been successfully used by REVSBECH et. al (1981), REVSBECH & WARD (1984), LINDEBOOM et al (1985), BAILLIE (1986), PEEKEN (1989), JENSEN & REVSBECH (1989), HOFMAN et al. (1991), PINCKNEY & ZINGMARK (1991,1993), LASSEN et al.1992), GLUD et al (1992), GÄTJE (1992), BRUNS (1994), LORENZEN et al. (1995) and EPPING & JØRGENSEN (1996) for the analysis of microbenthic photosynthesis.

The photosynthetic activity of the microphytobenthos is measured with the help of the "light -dark shift method" (REVSBECH et al. 1981) employing oxygen microsensors (*glass or needle*), which have proved to be very powerful tools for the analysis of oxygen dynamics in the sediments. Polarographic Clark-type oxygen microsensors have been used since the last decade (REVSBECH &JØRGENSEN 1986). On account of the introduction of a guard cathode and more use of insulating glasses (REVSBECH 1989), the performance of the Clark-type oxygen microsensors has ameliorated. The oxygen microsensors have now stable signals, which often exhibit less than 2% drift per day (REVSBECH 1994). Two parameters could be achieved, while using the microsensors for determination of the photosynthetic rates in the benthic communities of microorganisms:

a) ***Net photosynthesis*** (the net flux of oxygen out of the photosynthetic community)

b) ***Gross photosynthesis*** (as determined by light and dark shift technique (REVSBECH & JØRGENSEN 1986)

The oxygen production or photosynthesis within the sediment can be measured with excellent spatial and temporal resolution with the help of a glass oxygen microsensor, having a guard cathode on account of its stable signal, < 2% drift per day, response time of < 0.1 sec and with a tip diameter of <10 µm. In the present study, it was not possible to measure the oxygen production in the coarse sandy sediments (mean grain size 0.516 mm) of the station Mönkeberg with the glass microsensor, having a tip diameter of <10 µm because of its extremely fragile nature. Therefore, all the photosynthesis measurements were performed with the needle microsensors of DIAMOND GENERAL, USA, having a tip diameters of 0.89 mm each, also differing in their response times (Tab. 2). From May to July 1994, *needle microsensor-type A* with a response time of ≤ 6 sec and from August 1994 to July 1995 *needle microsensor-type B* with ≤ 3 sec were used for the measurements (Tab. 2). On account of their different response times (i.e. ≤ 3 and ≤ 6 sec) and for the accuracy of our results especially during the dark phase, which was given for 10 seconds instead of 1 or 2 sec (REVSBECH & JØRGENSEN 1983), for determining the rate of photosynthesis at various depths. An extra experiment (described later) was executed for evaluating the over - or under estimation of the rate of photosynthesis, when a longer dark period is given and a needle sensor is used instead of a glass microsensor.

Tab. 2: Characteristics of the sensors used in the present study

TOPIC	CLARK-STYLE GLASS OXYGEN MICROELECTRODE	OXYGEN NEEDLE ELECTRODE TYPE -A	OXYGEN NEEDLE ELECTRODE TYPE-B
Material	Glass, length 9.4 cm	Stainless steel, needle length 3.81 cm	Stainless steel, needle length 3.81 cm
Measurement period	August 1995 and November 1995	May 1994 to 10 August 1994	30 August 1994 to November 1995
Company *	Diamond General, USA	Diamond General, USA	Diamond General USA
Product No *	737 GC with a guard cathode Clark style	768-20R with internal reference non Clark-style	768-20R with internal reference non Clark-style
Reference electrode* (Anode)	Ag/AgCl	Ag/AgCl	Ag/AgCl
Cathode diameter *	Approximately 5 μm, platinum with gold plated	25 μm gold-plated on platinum recessed and protected by oxygen - permeable membrane	25 μm, gold-plated on platinum recessed and protected by oxygen - permeable membrane
Response time	95% in ≤ 1 sec	90% in ≤ 6 sec	90% in ≤3 sec
Tip diameter *	5-20 μm	0.89 mm	0.89 mm
Sensitivity to stirring *	< 3%	< 5%	< 5%
Motion artifact sensitivity *	< 2%	10%	10%

* according to Diamond General, USA

2.4.1.1 EXPERIMENTAL SET-UP

A simple set-up for measuring oxygen in a sediment core is shown in (Fig. 2). Oxygen needle or (*steel type*) electrode, PRODUCT NO. 768-20R (e.g. DIAMOND GENERAL, ANN ARBOR, USA) as described above was operated at a polarization voltage -0.75 V, and was introduced vertically into the sediment from above with the aid of a motordrive micromanipulator (MÄRZHAUSER WETZLAR, GERMANY), which could be used to introduce the microelectrode tip into the substratum, with a depth resolution of better than 10 µm. The microsensor could thus be continuously moved up and down to measure the oxygen concentration. The sensor current (readings) was measured with a picoammeter similar to MODEL- 480 (KEITHLEY INSTRUMENTS, GERMANY) having a range of 10^{-6} to 10^{-12} A, connected to a strip chart recorder (LINSEIS, GERMANY), to record the amplified signals.

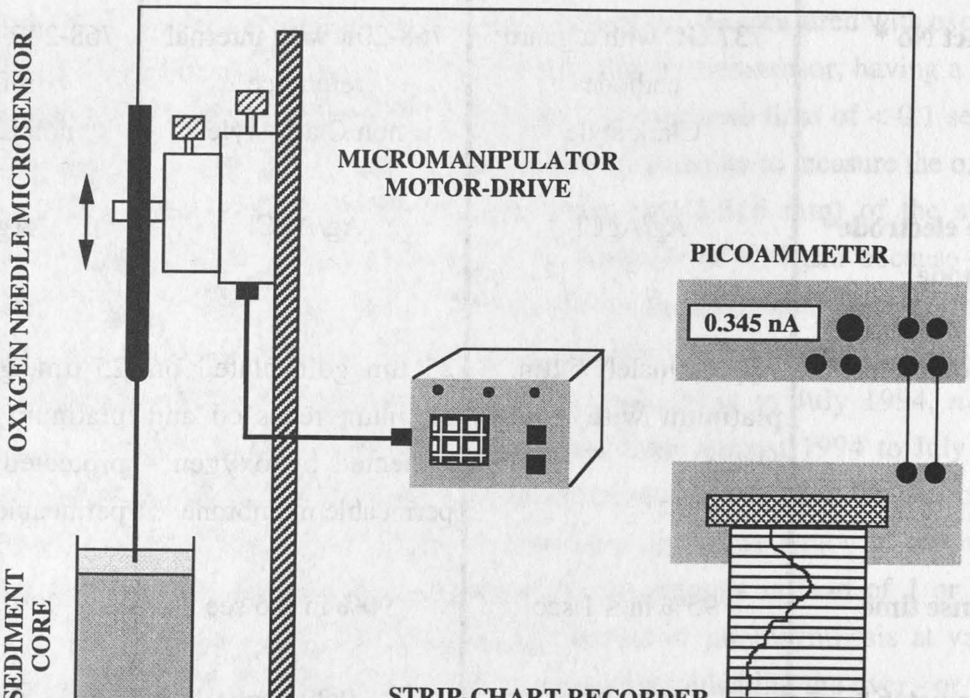


Fig. 2: A simple set-up for measuring oxygen in a sediment core with the aid of oxygen microelectrodes.

2.4.1.2 POSITIONING OF MICROSENSOR ON THE SEDIMENT SURFACE

In order to position the microsensor exactly in correspondence to the sediment-water interface, the sediment and the electrode tip was simultaneously observed under a dissecting microscope. For further confirmation, the differences in oxygen gradients (Fig. 3.), due to the altered conditions for diffusion were also used for indicating the position of the sediment surface. As close to the sediment-water interface, the linear concentration gradients of dissolved oxygen are steeper in the sediment as compared to those in the overlying water column.

2.4.1.3 MEASURING PRINCIPLE, RESPONSE TIME AND CALIBRATION

MEASURING PRINCIPLE

Clark electrodes may be classified either as *polarographic* electrodes or *galvanic electrodes*.

Polarographic electrodes consist of a platinum cathode and a silver anode, both immersed in a solution of saturated potassium chloride. When two electrodes (i.e. cathode and anode) are polarized with a potential of slightly less than -1.0 Volt in a electrolytic solution containing dissolved oxygen, the current will flow as a result of the reduction of oxygen at the cathode (negatively polarized surface). A suitable polarization voltage of -0.75 V (versus Ag/AgCl) between the anode and the cathode is necessary which selectively reduces oxygen at the cathode:

$$O_2 + 2H_2O + 4e^- \rightarrow 4OH^- \text{ cathode}$$

$$4Ag + 4Cl^- \rightarrow 4AgCl + 4e^- \text{ anode}$$

equation 4

These redox reactions (equation 4) result in the production of a current that is quantitatively proportional to the concentration of dissolved oxygen in the reaction vessel.

RESPONSE TIME

The *response time* was measured by quickly moving the electrode tip from the water saturated with oxygen in a nitrogen sparged "Zero" solution. This was practised 3 times. The thinner the electrode and the shorter the distance from the cathode to the tip of the electrode, the faster is the response (Tab. 2).

CALIBRATION

The electrodes were calibrated by assuming a linear relationship between the oxygen concentration and output signal (REVSBECH & JØRGENSEN 1986). A two point linear calibration was done for each O_2 profile between the overlying water of known concentration and the anoxic layer within the sediment. Currents (readings) obtained at each depth were recorded and recalculated to the corresponding oxygen concentration, assuming a linear current relationship. The actual oxygen concentration in the overlying water was determined by Winkler titration.

2.4.2 BENTHIC PRIMARY PRODUCTION

Undisturbed sediment samples were collected by pushing gently the Plexiglas cylinders (inner diameter 4 cm, length 6.5 cm) with hand into the fine ripples, exhibiting prominent yellowish brown patches of microphytobenthos from the different locations of the selected 1 m^2 area as described earlier. After removal, the cores were stopped with the silicon corks at the bottom and on top to maintain the *in situ* environmental conditions, leaving approximately 3 to 4 cm sediment layer and 1 to 2 cm of overlying water enclosed in each core. The cores were then immediately brought to the laboratory, where they were submerged in the waterbath exhibiting *in situ* temperature and were kept sealed outside the laboratory under natural varying light conditions. All the measurements for the gross oxygen production were made within the same day in the laboratory.

Photosynthetic activity of the microphytobenthos was measured with the help of the microprofile method (REVSBECH et al. 1981, REVSBECH & JØRGENSEN 1983), which permitted determination of short term variations in the oxygen concentration at various sedimental layers during light & dark shifts. Each step consisted of 500 µm depth size, alternating light and dark cycles The sensor was introduced into the sediment and the oxygen concentration was recorded assuming a steady state before darkening. The rate of decrease in oxygen concentration recorded after the sediment was darkened for 10 sec, corresponded to the photosynthetic rate. Hence, the photosynthetic activity in each sedimental layer, was calculated from the rate of decrease in oxygen concentration after 10 sec of dark incubation. The exact time for extinguishing the light was monitored by a stopwatch. Three oxygen profiles were measured at random positions in each of the core, due to the patchiness of the microphytobenthos. For the oxygen concentration, all the profiles were measured starting from the water column to the sediment which was showing zero oxygen reading. The benthic primary production was calculated according to following equations:

$$GPR\,(mmolO_2\,m^{-2}\,h^{-1}) = \Sigma\,(P(x)\,(mmol\,O_2\,l^{-1}\,h^{-1}) * \Phi * \delta Z) \qquad \text{equation 5}$$

$$GPR\,(mgCm^{-2}h^{-1}) = \frac{mmol\,O_2\,m^{-2}h^{-1}}{PQ} * 12 \qquad \text{equation 6}$$

Where:

GPR = gross photosynthetic rate

$P(x)\,(mmol\,O_2\,l^{-1}\,h^{-1})$ = oxygen production in the whole sedimental layer

Φ = porosity

δZ = 500 µm (movement of the electrode between the two measuring points)

PQ = $\frac{moles\ of\ O_2\ liberated\ during\ photosynthesis}{moles\ of\ CO_2\ assimilated} = 1.2$

12 = conversion factor (1mol CO_2 corresponds to 12 gC)

The PQ value of 1.2 STRICKLAND & PARSONS (1972), HARRIS (1978), MORRIS (1981) for phytoplankton has also been used frequently for microbenthic algal studies by REVSBECH et al.(1981), ASMUS (1982), DAVIS & MCINTIRE (1983), PEEKEN (1989), ASMUS (1992), GÄTJE (1992), CAHOON & COOKE (1992).

2.4.3 METHOD COMPARISON AND TECHNIQUES EMPLOYED

Sediment oxygen production rates and actual oxygen concentrations can be measured directly in the sediments with the oxygen microsensors. Comparisons have been performed mainly to

A) *Estimate the error in the rate of photosynthesis (i.e. the measured gross photosynthetic rate) while employing a needle sensor instead of a glass microsensor*

B) *Determine the over or under- estimation in the rate of photosynthesis, when a longer dark period of 10 seconds is given instead of 1 or 2 seconds*

Undisturbed sediment samples were collected from the station Tirpitzmole in the month of August and November 1995, oxygen microprofiles in the sediment were measured as described above in the laboratory. The calibration and the response time of the microsensors were determined as described earlier. The oxygen production measurements were performed with the glass microsensor (Clark-style), non Clark-style (Needle electrode type B) (Tab. 2.). The glass microsensor was used prior to needle sensor on account of its fine tip diameter of ≤ 25 µm. While introducing the needle microsensor, it was also made sure that the needle sensor was fixed in close proximity to the area where the measurements with glass microsensor were performed to estimate the difference in the photosynthetic rates with both the microsensors.

In the *first* experiment the whole oxygen profiles with light and dark shifts were measured by introducing the microsensors (glass and needle) stepwise into the sediment under the natural light conditions. Photosynthetic activity within the sediment was measured in 500 µm depth increments until measured rates approached zero. The photosynthetic rate at each depth was obtained by the continuous measurement of O_2 concentration during 10 sec of dark incubation and were then calculated with the change in the oxygen concentration at various dark incubations i.e. 1 to 10 seconds for the glass and 3 to 10 sec for the needle microsensor, respectively. The rate of oxygen disappearance during 10 sec of dark period was equal to the rate of oxygen production. The differences between the light and dark readings in each respective profile were used to estimate the actual primary production. In each core two or three oxygen profiles per electrode were measured at random positions on account of the microphytobenthos patchiness, which could result in the over or under-estimation of photosynthetic rate.

The ***second*** experiment was conducted according to the *fixed point technique* (REVSBECH et al. 1981, GLUD et al. 1992). The main goal of this experiment was to determine the change in the rate of O_2 disappearance (i.e. the measured gross photosynthetic rate) with the needle and glass microsensors, for different duration's of dark incubations. The microsensors were fixed one after the other approximately at the same angle, at a certain depth in the sediment (within the photic zone), beginning from the sediment surface The glass microsensor was introduced prior to the needle as described above. The rates were calculated for time interval ranging from 2 to 10 sec for glass and 3 to 10 sec for needle microsensor. The rate of O_2 disappearance after each second was calculated according to REVSBECH et al. (1981) & GLUD (1992). From this method it can be deduced, how long the assumptions of equation 7 about constant rates of diffusive loss and oxygen consumption are valid, pertaining to this experimental study when longer periods of dark incubations were given. If they are valid then the rate of decrease in oxygen concentration must be linear with time (REVSBECH et. al. 1981). This method requires one light-dark cycle at each depth with the dark period of 10 sec. After each dark period of 10 sec, the sediment was illuminated with the natural daylight for at least 10 minutes to re-establish the steady state of oxygen profile. At each depth two or three replicates per sensor were obtained and the mean value was calculated. By measuring the rate of oxygen disappearance at different depths in the photic zone, i.e. by integrating the equation with respect to x (REVSBECH et al. 1981, REVSBECH & JØRGENSEN 1986), the rate of photosynthesis in the sediment was calculated according to equation 7.

$$P(x) = -\frac{\partial C(x,t)}{\partial t} \qquad \text{equation 7}$$

Where:

$P(x)$ = the measured rate of photosynthesis at depth x after t sec

$\frac{\partial C}{\partial t}$ = change in the concentration after t sec

2.4.4 OXYGEN CONSUMPTION

The microelectrodes have proved to be a very powerful tool for the analysis of oxygen dynamics in sediments (REVSBECH & JØRGENSEN 1986). The flux of oxygen into the sediment is a fundamental measure of benthic community respiration, which can be calculated from the O_2 microgradients. For measuring these, sediment cores were collected as mentioned under primary production heading. Two oxygen microprofiles per core at two different positions were measured by darkening the sediment with the aid of a black box for 5 min. Before darkening, it was made sure with the help of a binocular that the microsensor was accurately positioned approximately 2 mm just above the sediment-water interface. Immediately after 5 min of darkening, microprofiles were measured at depth intervals of 500 µm with the aid of a needle microsensor, which was moved into the sediment with the help of a motor driven micromanipulator.

The difference in oxygen gradients, due to the altered conditions for the diffusion, indicated the position of the sediment surface as discussed earlier. All the profiles of oxygen concentration were measured, starting from approximately 2 mm above the sediment-water interface into the sediment layer showing zero oxygen reading. The oxygen consumption rates were calculated from the oxygen gradient at the surface below the point where the net flux of oxygen across the sediment surface equals zero (REVSBECH et al. 1980). Decrease in oxygen in the upper part of the profile is almost linear (Fig.3). The slope of the gradient was calculated by taking at least 3-4 measuring points into consideration. In the sediments the oxygen consumption can thus be calculated, from the sediment molecular diffusion coefficient, and the porosity using the Fick's first law of diffusion (REVSBECH & JØRGENSEN 1986).

$$J(x) = -\Phi D_s(x) \frac{\delta C(x)}{\delta(x)} \qquad \text{equation 8}$$

where:

$J(x)$ = oxygen flux (mmol O_2 m^{-2} h^{-1})

Φ = porosity

D_s = the molecular sediment diffusion coefficient of oxygen at depth x. The molecular diffusion coefficient is constant over the oxic sediment-layer

$\frac{\delta C(x)}{\delta(x)}$ = O_2 concentration gradient over depth interval x or linear portion of oxygen gradient in the top layer of the sediment

In the present study, the whole sediment molecular diffusion coefficient D_s of the respective sample was empirically determined on multiplying the molecular diffusion coefficient for oxygen Do dependant on temperature and salinity of seawater (RAMSING & GUNDERSEN 1994) by its porosity.

$$D_s = D_o * \Phi \qquad \text{porosity} < 0.75 \qquad \text{(LERMAN 1975)} \qquad \text{equation 9}$$

$$D_s = D_o * \Phi^2 \qquad \text{porosity} > 0.75 \qquad \text{(LERMAN 1975)} \qquad \text{equation 10}$$

Where :

D_s = molecular sediment diffusion coefficient

D_o = molecular diffusion coefficient for oxygen at a particular temperature and salinity of seawater (RAMSING &GUNDERSEN 1994)

Φ = porosity of the sediment

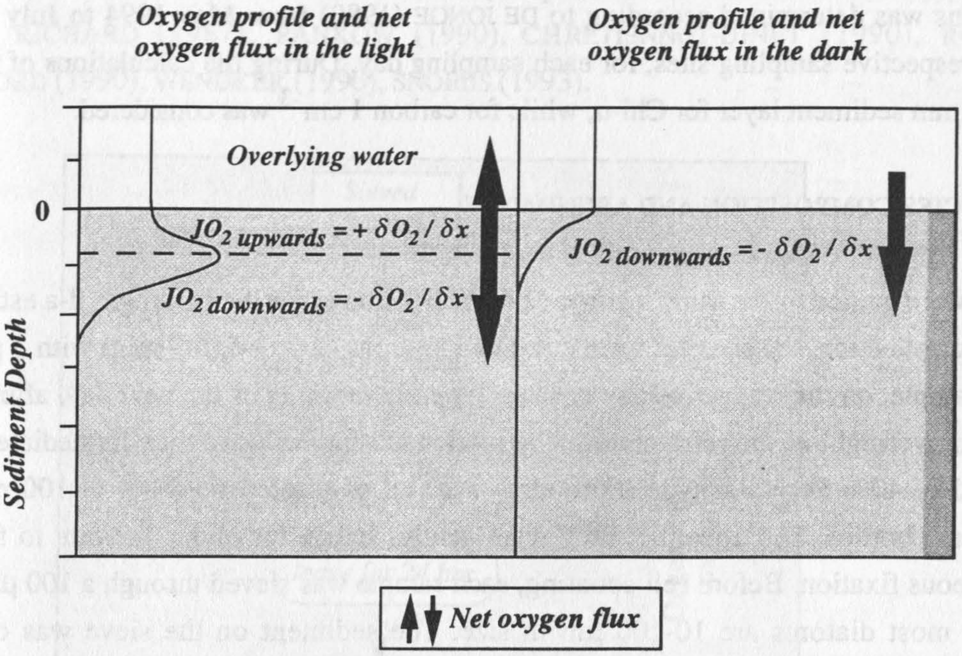


Fig.3: Schematic representation of oxygen concentrations and oxygen fluxes $J(x)$ during the light and dark measured with the oxygen microsensor.

2.4.5 CHLOROPHYLL-A

Chlorophyll-a as an important parameter for the microphytobenthos biomass was measured by the method of JEFFREY & HUMPREY (1975). Undisturbed sediment samples were collected by pressing 5 ml plastic syringes (1.2 cm diameter; top cut off) into the ripples at the different sites within an area of $1 m^2$ at three different locations of the sediment. The overlying water of each sample was removed and the uppermost layer was carefully cut and separated into 4 sections (0-3, 3-6, 6-9, 9-12 mm) with 3 parallels each. These cut sediment samples were then immediately deep-frozen in 10 ml plastic centrifuge tubes at -22 °C. For the measurements, the sediment sections were placed in 10 ml of 90 % acetone and a few glass pearls were added to the aliquot. To ensure complete extraction each sample was then homogenized in a VIBROGEN ZELLMÜHLE for 3-4 min. The extracted pigments of the aliquot were then centrifuged at 4000 rpm for 10 min at 0 °C. The absorbance of the supernatant was measured as quickly as possible in a 1 cm or 4 cm cuvette (depending upon the concentration) at selected wavelengths of 750, 663, 647, and 630 nm with the (SHIMADZU DOUBLE BEAM UV-150-01) spectrophotometer (LORENZEN 1967, STRICKLAND & PARSONS 1968).

2.4.6 CARBON TO CHLOROPHYLL - A RATIO

Organic carbon (mg C cm^{-3}) to Chl-*a* (µg Chl cm^{-3}) ratio for the microphytobenthos populations was determined according to DE JONGE (1980) from May 1994 to July 1995 at both the respective sampling sites, for each sampling day. During the calculations of C:Chl-*a* ratio, 0-9 mm sediment layer for Chl-*a*, while for carbon 1 cm^{-3} was considered.

2.4.7 SPECIES COMPOSITION AND ABUNDANCE

Samples were gained in the same manner as described above for the chlorophyll-a estimation. Following collection, the samples were cut into 3 sections (0-3, 3-6, 6-9 mm) with 3 parallels of each sample, on the respective day or latest by early morning of the next day, after having kept them overnight in the refrigerator. The sectioned samples were then immediately fixed with 2 ml of 40% Formaldehyde (Formalin) + 20 ml of filtered seawater in 100 ml dark-brown glass bottles. Subsequently, they were gently shaken for about 1-2 min to facilitate instantaneous fixation. Before cell counting, each sample was sieved through a 100 µm nylon mesh, as most diatoms are 10-100 µm in size. The sediment on the sieve was carefully washed 3-4 times with filtered seawater, to separate the microphytobenthos from the sediment. The bottles containing the filtrate were shaken in jerks to evenly distribute the particles and then poured into the sedimentation chamber. This consisted of combined plate chamber (HYDRO-BIOS, KIEL) with a top cylinder (sedimentation cylinder) of 10 and 20 ml (10 ml for the station Tirpitzmole and 20 ml for Mönkeberg) capacity and a bottom-plate chamber, respectively. The cell counting was done under the inverted microscope (UTERMÖHL METHOD 1958) modified by SANDGREN & ROBINSON (1984) after sedimentation for 24 hrs, as the settling time is dependant on the size of the chamber and preservative used (LUND et al. 1958).

Only living cells, which could be distinguished from the dead ones by intact chloroplasts, were counted. Cells were counted forming two crossed transects (vertical crossed by horizontal) on the area of the chamber. Cells falling in these transects were easily countable under the inverted microscope by moving the mechanical stage horizontally to give one transect and then vertically to give the second one, at least 400 cells and valves were counted, giving an approximate error of ± 10% (VENRICK 1978). However, at the time of scanty growth of microphytobenthos, at least 100-200 cells were counted, which result in an approximate error of ± 20 % (VENRICK 1978). During the dense population of the microphytobenthos, counting was done by taking either random fields or by counting one transect (vertical or horizontal) of the chamber area. This examination was done under a 400-fold magnification. The quantitative estimation of the cell counts was obtained according to EDLER (1979). Permanent slides were also made for the further identification and confirmation of the microphytobenthos algae (Fig. 4.). Microphytobenthos were identified according to HUSTEDT (1959, 1961-66), HENDEY (1964), VAN DER WERFF & HULS (1957-74), KRAMMER (1985, 1986), THRONDSEN (1985) unpublished, THRONDSEN (1993), SOURNIA (1986), RICHARD (1987), PANKOW (1990), CHRÉTIENNOT-DINET (1990), ROUND & CRAWFORD (1990), WENDKER (1990), SNOEIJS (1993).

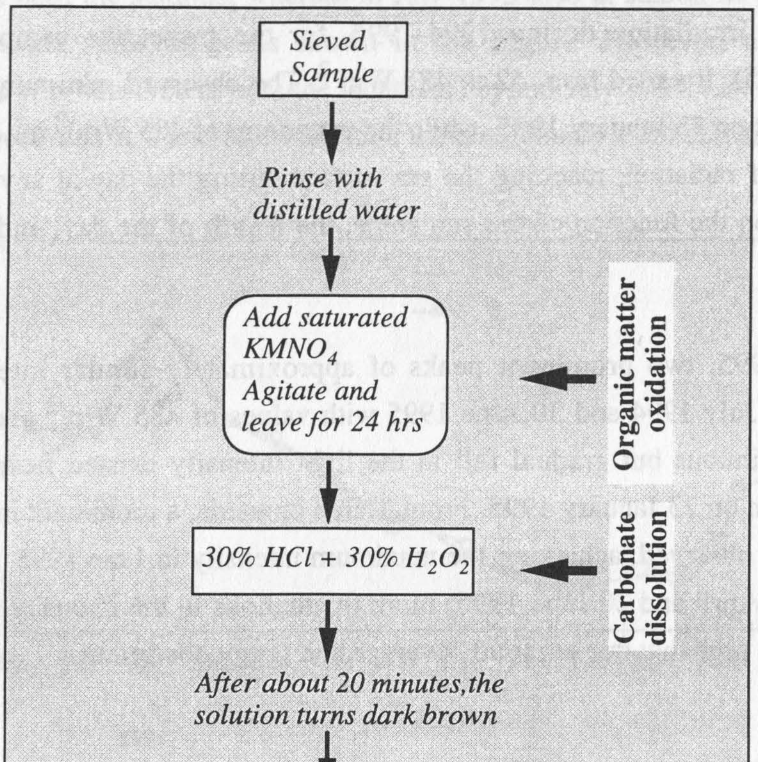


Fig. 4: Diagramatic presentation for cleaning diatom cells and preparing slides after SIMONSEN (1974).

3 RESULTS

3.1 PHYSICAL AND CHEMICAL PARAMETERS

3.1.1 IRRADIANCE

The daily averaged irradiation during 1994-1995, for the respective sampling days is summarized in (Fig. 5). It varied from 42 to 485 Wm^{-2}. The observed minimum intensity of 42 Wm^{-2} was evident on 23 January 1995, while the maximum of 485 Wm^{-2} on 12 July 1994. The actual amount of radiation, reaching the sea surface during the day at any point of the surface, depends upon the function of the sun angle, the length of the day, and the weather conditions.

During 1994 and 1995, two prominent peaks of approximately similar intensities were accomplished on 12 July 1994 and 30 June 1995 with values of 485 Wm^{-2} and 483 Wm^{-2}, respectively. A continuous but gradual fall in the light intensity existed from June 1994, touching its minimum on 23 January 1995. From March onwards, a prominent increase in the intensity was clearly observed, achieving the maximum intensity in June 1995. Besides this, during 1995 (i.e. 18 April and 20 June 1995) more fluctuations in the intensity of light were observed which were probably due to cloud coverage and foggy conditions.

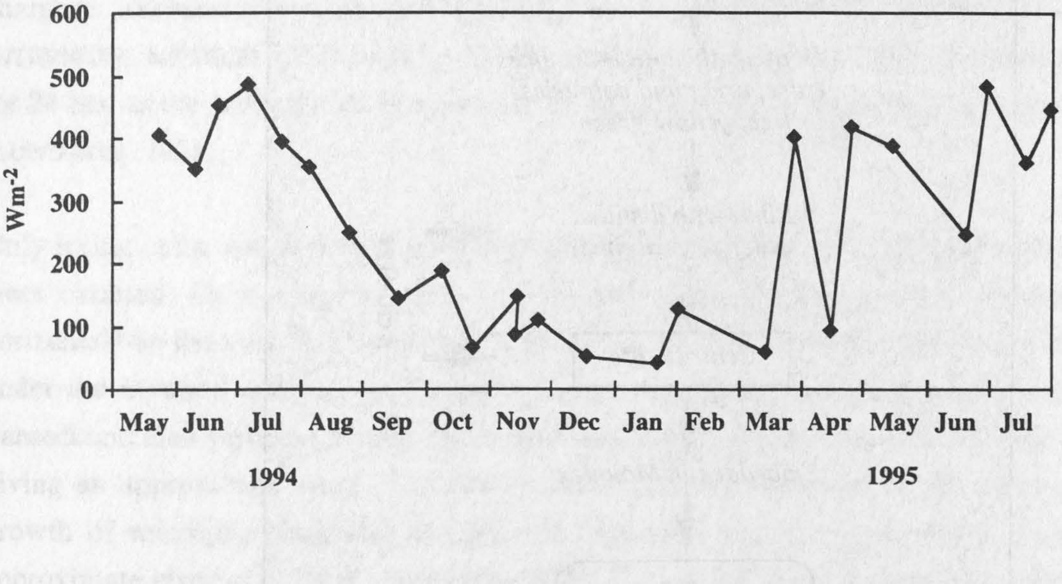


Fig. 5: Irradiance (daily averaged) for the investigation location (inner Kiel Fjord). Values gathered from (Meteorological Department of the Institut für Meereskunde, Kiel).

3.1.2 TEMPERATURE

During experimental investigation period of 1994-1995, sediment temperature generally varied from 2.8 °C to 23.5 °C at the sampling station M, while at T it varied in the similar manner i.e. 3.0 °C to 23.5 °C (Fig. 6). In July 1994 and 1995, two peaks showing maximum temperature at each study site were obtained. On 28 July 1994, 23.5 °C temperature was recorded at both the stations, whereas in July 1995 also at station M and T the temperature was within the same range as shown in the Figure. However, a gradual decrease in temperature was observed at both the locations beyond July 1994. Lower temperatures below 3 °C were recorded at T and M during high winter (January and February) of 1995.

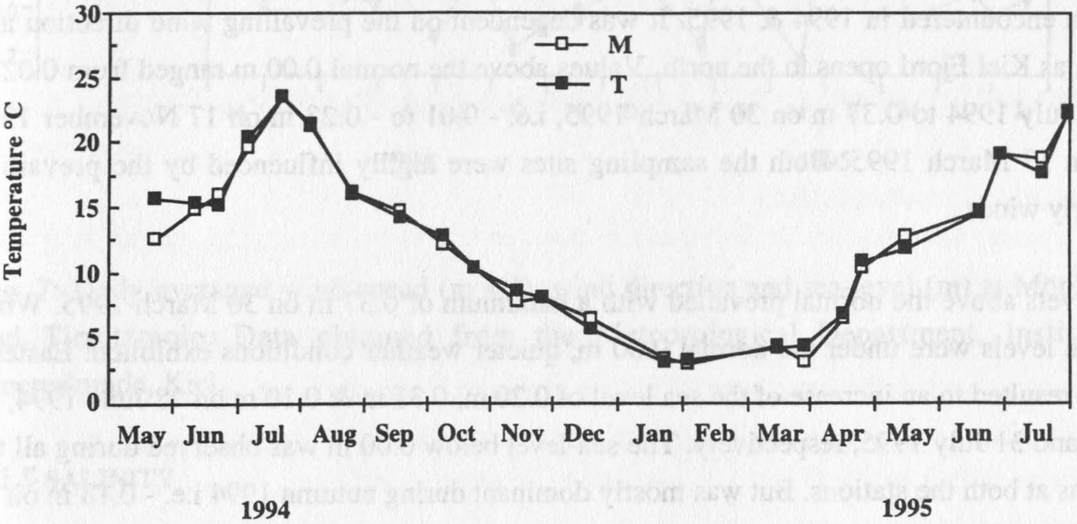


Fig. 6: Seasonal distribution of sediment temperature (°C) at Mönkeberg and Tirpitzmole.

3.1.3 WIND DIRECTION AND SPEED

Data for the wind direction shown in (Fig. 7) indicate a domination of southerly and south westerly winds on both the study locations. Westerly winds are generally connected with low pressure, low irradiance and higher velocity winds. On the contrary, the easterly are with high pressure, stronger irradiance and weaker velocities. These were not commonly observed during the present investigation. Influence of the easterly winds was accomplished only on 3 instances i.e. 28 June 1994, 27 April and 31 July 1995, respectively. On these specific days comparatively placid conditions prevailed and a remarkable increase in the water level was noticed.

The average wind speed at the sampling days in 1994-1995 was mostly below 6.0 ms^{-1}, while more than 7.0 ms^{-1} was registered only twice (Fig. 7). The data was collected from the

Meteorological department of the Institut für Meereskunde, Kiel. It ranged from 1.0-8.0 ms^{-1}, with the minimum value of 1.0 ms^{-1} on 28 June 1994, while the maximum of 8.0 ms^{-1} on 17 March 1995. The maximum wind speed is very well correlated with southern westerly winds coming from 180°- 250°. Between 30 May to 12 October 1994, it was 1.0 to 4.0 ms^{-1}, with an increase observed on 27 October and on 17 November 1994, being 6.0 and 5.0 ms^{-1}, respectively. Wind speeds with greater magnitude (7.0 - 8.0 ms^{-1}) were recorded between late winter and early spring (January and March 1995).

3.1.4 SEA-LEVEL

The averaged sea-level data presented in (Fig. 7) show values below and above the normal 0.00 m encountered in 1994 & 1995. It was dependent on the prevailing wind direction and speed, as Kiel Fjord opens to the north. Values above the normal 0.00 m ranged from 0.02 m on 28 July 1994 to 0.37 m on 30 March 1995, i.e. - 0.01 to - 0.23 m on 17 November 1994 and on 17 March 1995. Both the sampling sites were highly influenced by the prevailing westerly winds.

Sea levels above the normal prevailed with a maximum of 0.37 m on 30 March 1995. When the sea levels were under the normal 0.00 m, quieter weather conditions exhibited. Easterly winds resulted in an increase of the sea level of 0.20 m, 0.31 m & 0.10 m on 28 June 1994, 27 April and 31 July 1995, respectively. The sea-level below 0.00 m was observed during all the seasons at both the stations. But was mostly dominant during autumn 1994 i.e. - 0.18 m on 12 October and in spring 1995 (- 0.23 m on 17 March 1995). Influence of south westerly winds coming from 180° to 270° brought the sea-level below the normal 0.00 m.

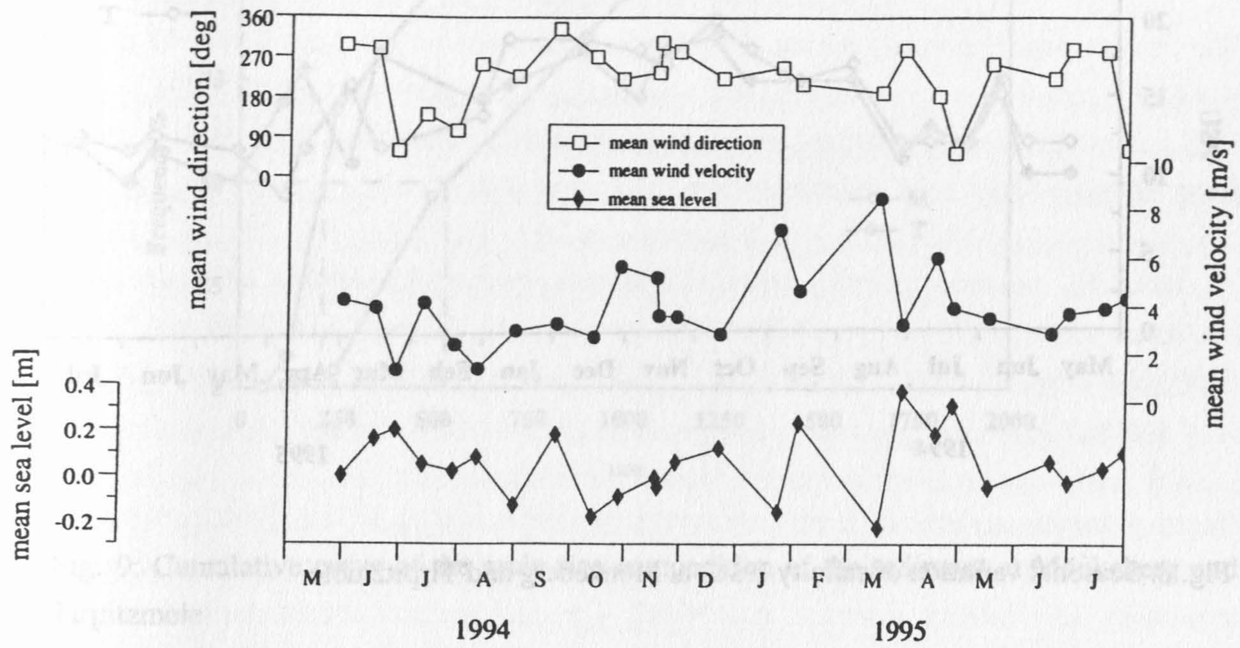


Fig. 7: Daily averaged wind speed (m s^{-1}), wind direction and sea-level (m) at Mönkeberg and Tirpitzmole. Data obtained from the Meteorological Department, Institut für Meereskunde, Kiel.

3.1.5 SALINITY

Salinity data at the stations M and T are depicted in (Fig. 8). Salinity during the different seasons of 1994-1995 varied from 10-19 PSU at station M, while at station T it was 9-20 PSU.

At the station M, the minimum salinity values of 10 PSU was obtained in May and June, during both the years 1994 and 1995, respectively. The maximum value touching 19 PSU was encountered on 27 October 1994. Comparatively, higher salinity values occurred between October 1994 and March 1995. On an average gradual decrease in salinity occurred from March to July 1995.

At station T, the minimum salinity value of 9 PSU was accounted on 27 April 1995, while the maximum value of 20 PSU on 27 October 1994. Higher salinity values existed between October 1994 and January 1995. However, continuous fall in the salinity was observed from February to July 1995.

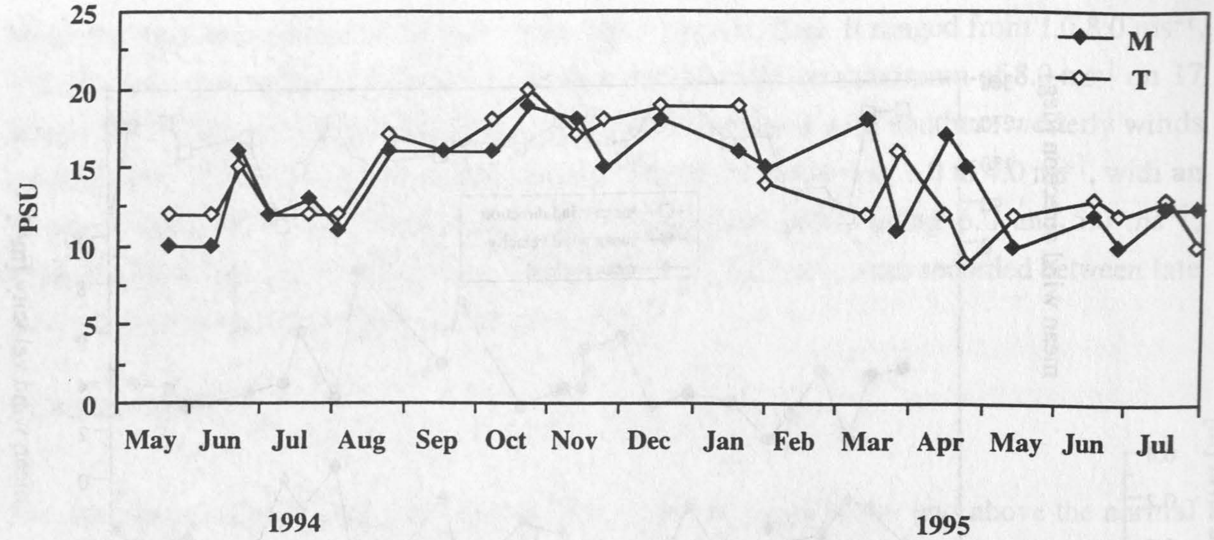


Fig. 8: Seasonal variation of salinity (PSU) at Mönkeberg and Tirpitzmole.

3.1.6 SEDIMENT PARAMETERS

3.1.6.1 GRAIN SIZE ANALYSIS

Surface sediments in the upper intertidal zone at the study site during the present study (1994-1995) consisted primarily of sand, with the mean grain size of 516 µm at M, while at T it was 214 µm as shown in the Fig. 9. At station M the surface sediments were coarser than at T during all the seasons.

The sediments of the respective stations were moderately well sorted and had the ranges of 0.50-0.71 (for sorting classes see HOLME & MCINTYRE 1984). Station T showed negative skewness while M positive skewness. A positive value of the skewness indicates that the mean quartile lies to the right of the Md and hence prefixed as '+', when lying to the left then prefixed '-'. At both the stations, the values of the kurtosis (K_G) were found to be in the range 0.67-0.90, during the investigation and therefore classified as platykurtic. Kurtosis- "which measures the ratio between the sorting in the tails as well as in the central portion of the distribution. When the central portion is better sorted than the tails - '*leptokurtic*', if the tails are better sorted than the central portion - '*platykurtic*'" (LINDHOLM 1987).

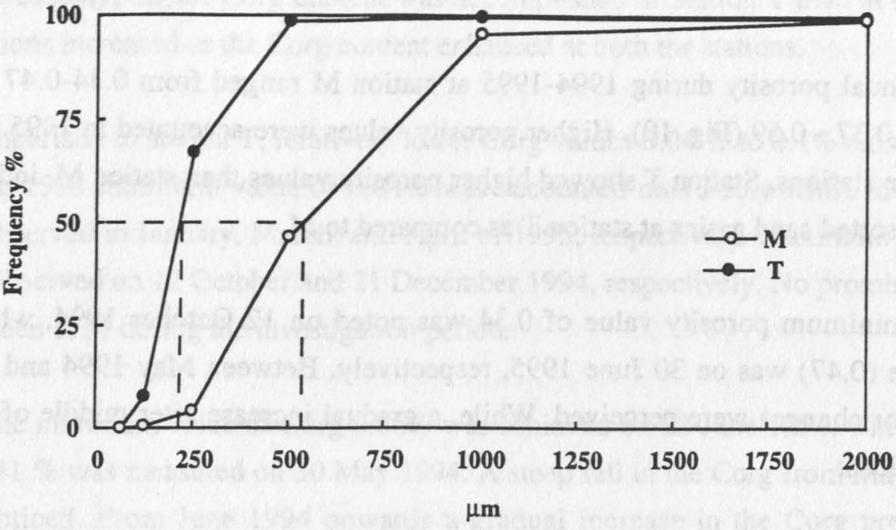


Fig. 9: Cumulative curve of the grain size composition of the sediment at Mönkeberg and Tirpitzmole

Tab. 3: Summary of sediment grain size analysis in the top cm of the sediment (*sieve analysis data*) at Mönkeberg and Tirpitzmole. Median and mean grain size are expressed in µm, while measures of sorting, skewness and kurtosis are dimensionless.

Parameters	**Station M**	**Station T**
Median (Md)	526	205
Mean size (Mn)	516	214
Sorting	0.637	0.603
Skewness (Skq)	0.059	0.158
Kurtosis (K_G)	0.828	0.936

3.1.6.2 POROSITY

The average annual porosity during 1994-1995 at station M ranged from 0.34-0.47 and at station T it was 0.37 - 0.59 (Fig. 10). Higher porosity values were accounted in 1995 than in 1994, at both the stations. Station T showed higher porosity values than station M, indicating finer and better sorted sand grains at station T as compared to M.

At station M, minimum porosity value of 0.34 was noted on 12 October 1994, while the maximum value (0.47) was on 30 June 1995, respectively. Between May 1994 and March 1995, only minor changes were perceived. While, a gradual increase after middle of March 1995 was significant.

Contrary to this at station T, minimum porosity value was 0.37 on 30 May 1994 and maximum 0.59 on 30 June 1995. From November 1994 to March 1995 insignificant changes in porosity were noticed. However, after March, a gradual decrease and an eventual increase (0.45-0.59) in the porosity was seen.

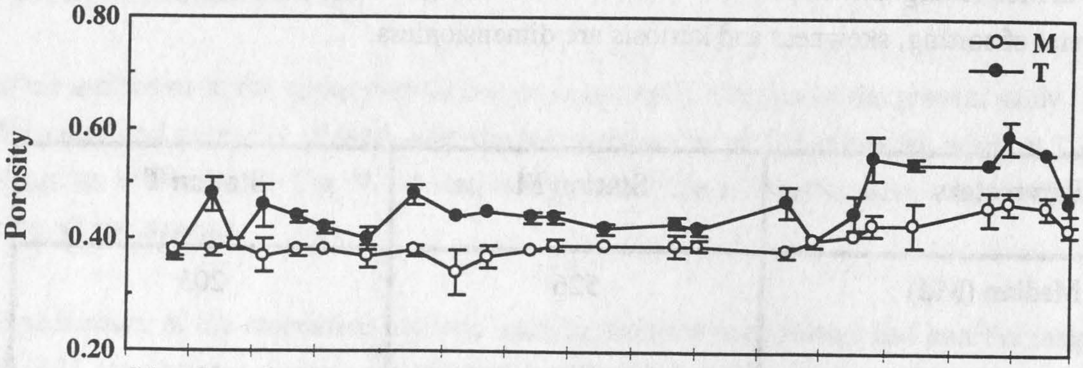


Fig. 10: Sediment porosity at Mönkeberg and Tirpitzmole.

3.1.7 ORGANIC CARBON

3.1.7.1 SEASONAL VARIATION IN THE ORGANIC CARBON (CORG) CONTENT

Fig. 11 shows the mean organic carbon content (Corg) during 1994-1995. Station M showed < than 0.1% (Corg), while T < 0.4 % except for 30 May 1994 when value > 0.9 was recorded. During winter comparatively lower Corg content was accounted at both the sites.

Conspicuously, higher Corg content was accomplished at Station T than at M. The standard deviations increased as the Corg content enhanced at both the stations.

In comparison to station T, relatively lower Corg values 0.04 % to 0.1% existed at station M. During 1994 minimum value of 0.04% was accounted on 12 July while lower values were also observed in January, March, and April of 1995, respectively. Maximum values of 0.09% were observed on 12 October and 21 December 1994, respectively. No prominent fluctuations were seen at M during the investigation period.

At T the minimum value of Corg 0.06% was achieved on 28 June 1994, while the maximum of 0.941 % was measured on 30 May 1994. A steep fall in the Corg from May and June 1994 was noticed. From June 1994 onwards a gradual increase in the Corg prevailed, with an obvious small peak in September 1994. Between October 1994 to March 1995 it mostly remained low. The values increased after March 1995 reaching maximum in June 1995.

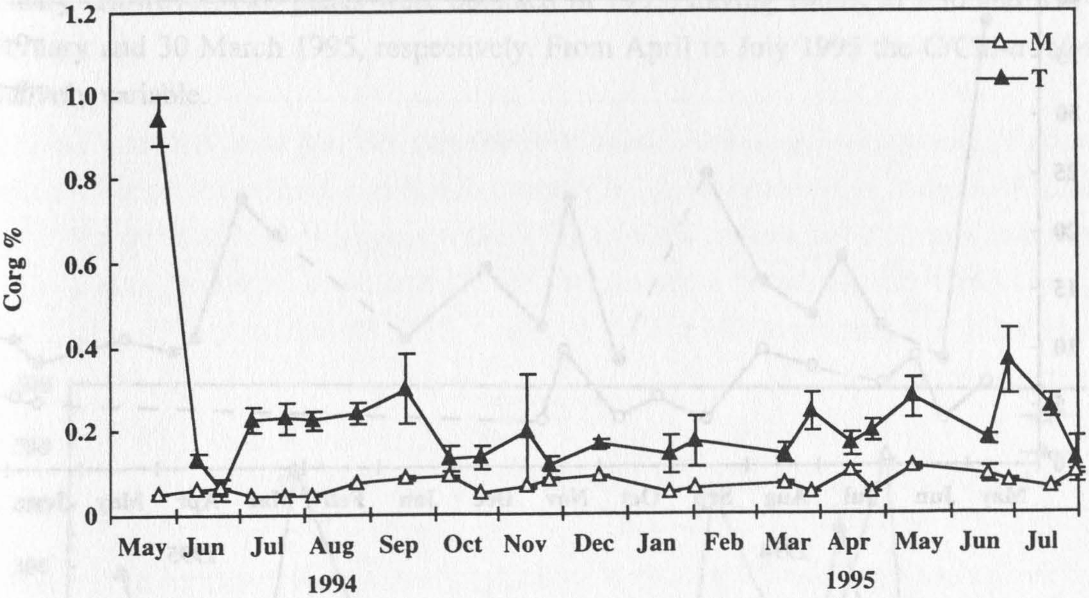


Fig. 11: Seasonal variation of organic carbon (Corg) in the upper 1 cm sediment layer at Mönkeberg and Tirpitzmole.

3.1.7.2 SEASONAL VARIATION IN THE CARBON TO NITROGEN RATIO

The average atomic ratio of organic carbon to nitrogen (C/N) during 1994-1995 at station M and T is presented in Fig. 12. Due to relatively low concentration of nitrogen in the sediment samples at both the study sites, it was not possible to evaluate the C/N ratio in all the respective samples. Therefore, for the C/N ratio only those sediments were taken into consideration, where nitrogen was measurable, while the rest were omitted.

Station T showed relatively higher C/N ratios than M, which may be due to the different sites (*i.e. exposed and open, discussed later)*. In general the C/N ratio at both the study sites was found to be < 25, with an exception on 30 May 1994.

At station M, minimum value of 4 existed on 17 June, 22 September, 27 October and 28 November 1994, respectively. The maximum C/N ratio 10 was accounted on 17 November and 30 August 1994. During 1995 it ranged from 6-15. The minimum value of 6 was accounted in June, while the maximum C/N ratio of 15 in July 1995.

At station T, relatively higher C/N ratios 9-38 were accomplished. The C/N ratio of 9 prevailed on 17 June and 27 October 1994, while the peak with maximum value of 38 was on 30 May 1994. In September and November 1994, C/N ratios > 20 were accounted. During 1995 C/N ratios ranged from 9-23, the C/N ratio 9 was accounted on 20 June &31 July 1995, while 23 was on 30 March 1995.

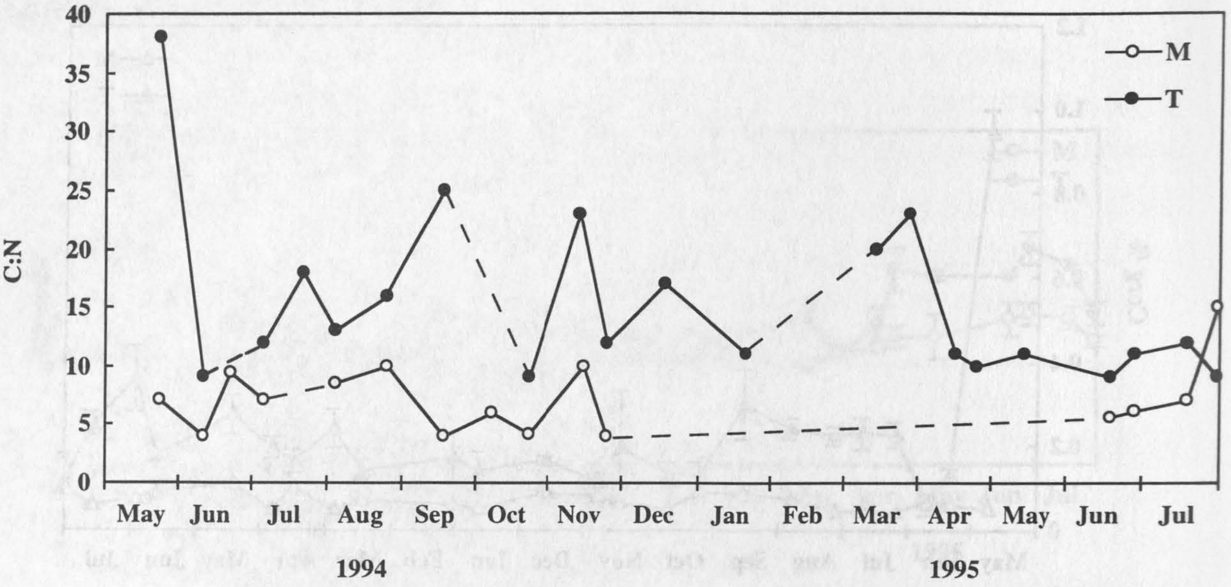


Fig. 12: Atomic C/N ratio in the upper 1 cm sediment layer at Mönkeberg and Tirpitzmole from May 1994 to July 1995. Dotted lines indicate missing values.

3.1.7.3 FLUCTUATION IN THE MEAN ORGANIC CARBON TO CHLOROPHYLL-A RATIO FOR SEDIMENTS

Fig. 13 shows the organic carbon (Corg) to chlorophyll-a ratios (C/Chl-*a*) averaged for 0-9 mm sediment depths during the investigated period (1994-1995) at both the sampling stations M and T. C/Chl-*a* at both the respective sites varied both spatially and seasonally. Generally higher values were obtained at station T (36-454) as compared to M (36-490), indicating a higher amount of microphytobenthos and detrital matter within the sediment. Interestingly, higher C/Chl-*a* ratios were found during spring and summer at T, whereas at M during spring.

At station M, the minimum C/Chl-*a* ratio of 36 existed on 12 July & 17 November 1994, whereas the maximum of 490 prevailed on 18 April 1995, respectively. Observations revealed that the values were <100 throughout 1994-95. However, from December 1994 to April 1995, a gradual increase in the C/Chl-*a* ratio prevailed with the ratios exceeded the values of 100 in March, April and May 1995. After the peak in April a sudden fall accounted in the later part of the same month and the value decreased by a factor of 5.56. Nevertheless, the C/Chl-*a* ratio remained on the lower side between June and July 1995.

At station T, the minimum C/Chl-*a* ratio of 36 was observed on 27 April 1995 while the maximum value recorded was 454 on 10 August 1994, respectively. The values were on the lower side during June & July, 1994. Subsequently, an increase in the C/Chl-*a* ratio reaching the maximum 454 on 10 August was observed. Lower values existed from September to January. However, two peaks were obtained in 1995, having values of 430 and 371 on 3 February and 30 March 1995, respectively. From April to July 1995 the C/Chl-*a* ratio was relatively variable.

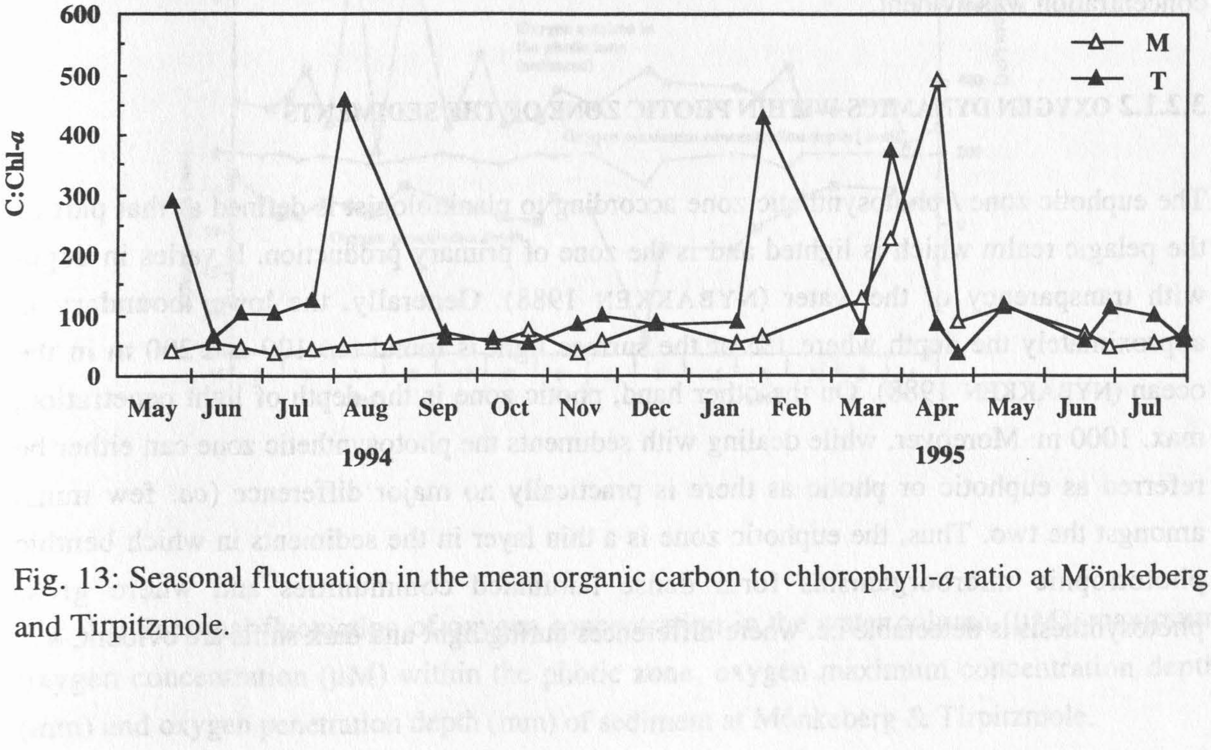


Fig. 13: Seasonal fluctuation in the mean organic carbon to chlorophyll-*a* ratio at Mönkeberg and Tirpitzmole.

3.2 BIOLOGICAL PARAMETERS

3.2.1 OXYGEN CONCENTRATION AT THE SEDIMENT WATER INTERFACE

3.2.1.1 SEASONAL VARIATION IN THE OXYGEN CONCENTRATION

Fig. 14 illustrates the seasonal variation in the oxygen concentration at both the respective stations, during 1994-1995. The oxygen concentration in the water column at station M varied from 216 to 413 µM, while at T from 167 to 406 µM. At both the study sites, relatively higher oxygen concentrations were measured in 1995 than during 1994. Station M showed relatively higher oxygen concentrations than T. At both the research areas the whole water column was well mixed and oxygenated during winter, spring and autumn than in the summer.

The minimum concentration of 216 µM was recorded on 30 August 1994 at station M, while the maximum concentration of 413 µM was attained on 31 July 1995. Nonetheless, the value increased from August 1994 upto 30 March 1995. After this a decrease was seen which resulted in the minimum of 284 µM.

At station T, minimum oxygen concentrations of 167 and 199 µM were encountered on 12 July and 30 August 1994, respectively. However, after this a gradual increase in oxygen concentration with low temperature during windy and stormy periods of autumn, winter and spring was observed. As during these seasons the water masses were well mixed, which probably led to a maximum of 406 µM on 30 March 1995. From March 1995, a fall in the concentration was evident.

3.2.1.2 OXYGEN DYNAMICS WITHIN PHOTIC ZONE OF THE SEDIMENTS

The euphotic zone / photosynthetic zone according to planktologist is defined as that part of the pelagic realm which is lighted and is the zone of primary production. It varies in depth with transparency of the water (NYBAKKEN 1988). Generally, the lower boundary is approximately the depth where 1% of the surface light is found *ca.* 100 and 200 m in the ocean (NYBAKKEN 1988). On the other hand, photic zone is the depth of light penetration, max. 1000 m. Moreover, while dealing with sediments the photosynthetic zone can either be referred as euphotic or photic as there is practically no major difference (*ca.* few mms) amongst the two. Thus, the euphotic zone is a thin layer in the sediments in which benthic phototrophic microorganisms form dense laminated communities and where gross photosynthesis is detectable i.e. where differences during light and dark shifts are evident.

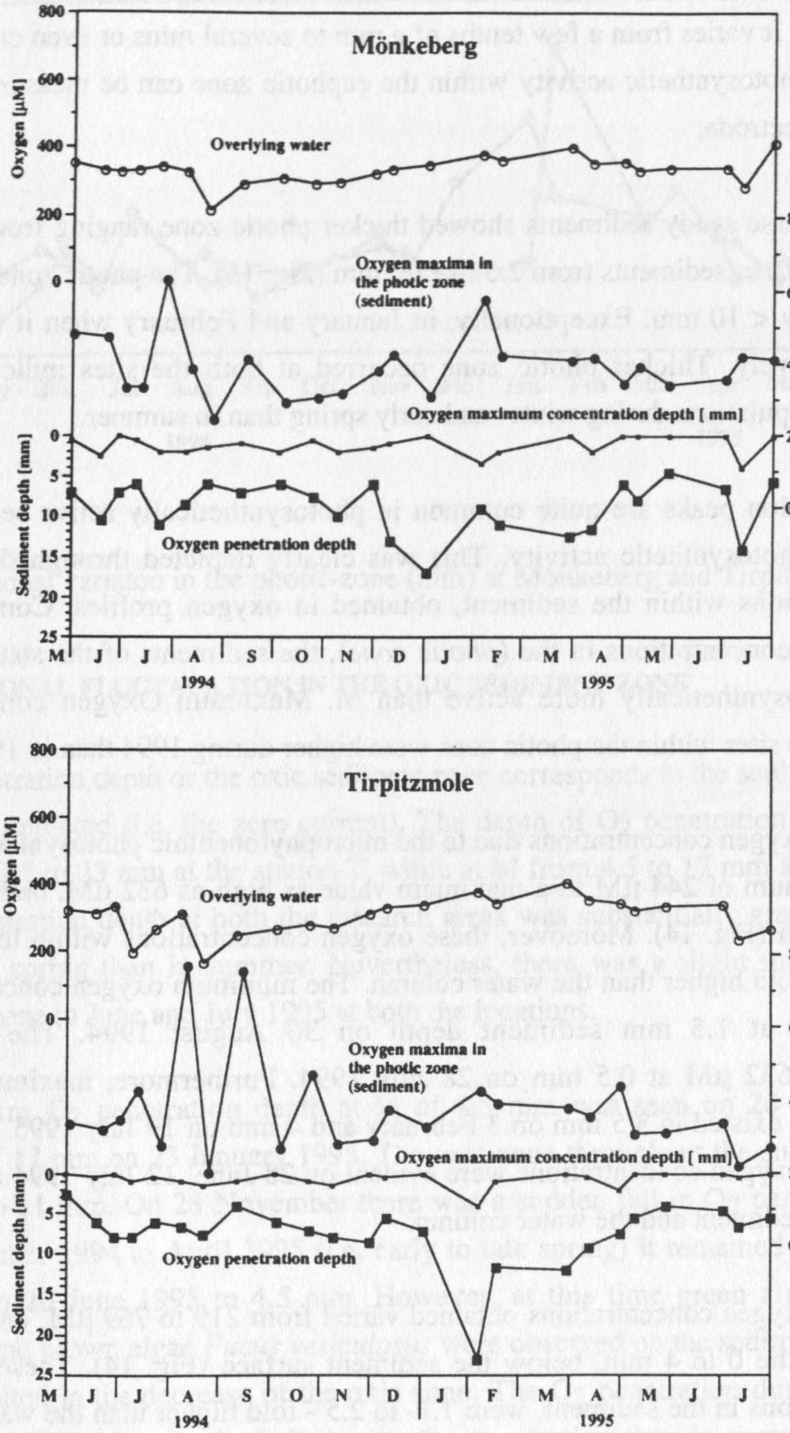


Fig. 14: Seasonal fluctuation of oxygen concentration in the water column (µM), maximum oxygen concentration (µM) within the photic zone, oxygen maximum concentration depth (mm) and oxygen penetration depth (mm) of sediment at Mönkeberg & Tirpitzmole.

The thickness of the euphotic zone varies with sediment type, photon flux, absorption/ scattering of the light and density of the photosynthetic communities (REVSBECH & JØRGENSEN 1986). It varies from a few tenths of a mm to several mms or even cms (LASSEN et al. 1992). The photosynthetic activity within the euphotic zone can be measured with the help of the microelectrode.

Station M with coarse sandy sediments showed thicker photic zone ranging from 4 to 16.5 mm than at T with finer sediments from 2.5 to 21.5 mm (Fig. 15). The photic zone at both the stations was mostly < 10 mm. Exceptionally, in January and February when it was 21.5 & 16.5 mm, respectively. Thicker photic zone occurred at both the sites indicating more scattered diatom populations during winter and early spring than in summer.

Oxygen concentration peaks are quite common in photosynthetically active sediments on account of high photosynthetic activity. This was clearly depicted through the elevated oxygen concentrations within the sediment, obtained in oxygen profiles. Comparing the maximum oxygen concentrations in the (*photic zone*), the sediments of the station T were found to be photosynthetically more active than M. Maximum Oxygen concentrations obtained at both the sites within the photic zone were higher during 1994 than in 1995.

At station M, the oxygen concentrations due to the microphytobenthic photosynthetic activity ranged from minimum of 244 µM to a maximum value as high as 632 µM, between 0 to 4 mm sediment depth (Fig. 14). Moreover, these oxygen concentrations within the sediment were 1.1- to 1.8 - fold higher than the water column. The minimum oxygen concentration of 244µM prevailed at 1.5 mm sediment depth on 30 August 1994. The maximum concentrations of 632 µM at 0.5 mm on 28 July 1994. Furthermore, maximum oxygen concentrations also existed in 3.5 mm on 3 February and 4 mm on 19 July 1995. No distinct differences in the oxygen concentrations were evident on 28 June, 12 July 1994 and 31 July 1995 between the sediment and the water column.

At station T, the oxygen concentrations obtained varied from 219 to 769 µM, on account of photosynthesis in the 0 to 4 mm, below the sediment surface (Fig. 14). These accounted oxygen concentrations in the sediment, were 1.1- to 2.5 - fold higher than the water column. The minimum value of 219 µM was recorded on 19 July 1995 and maximum value of 425 µM on 3 February 1995 at 4 mm sediment depth. Maximum oxygen concentrations of 769 µM on 10 August and 751 µM on 22 September 1994 existed at 1 mm, below the sediment surface. However, on 12 October 1994, 18 April & 30 June 1995 no significant differences in the oxygen concentrations in the sediment and the water column were observed.

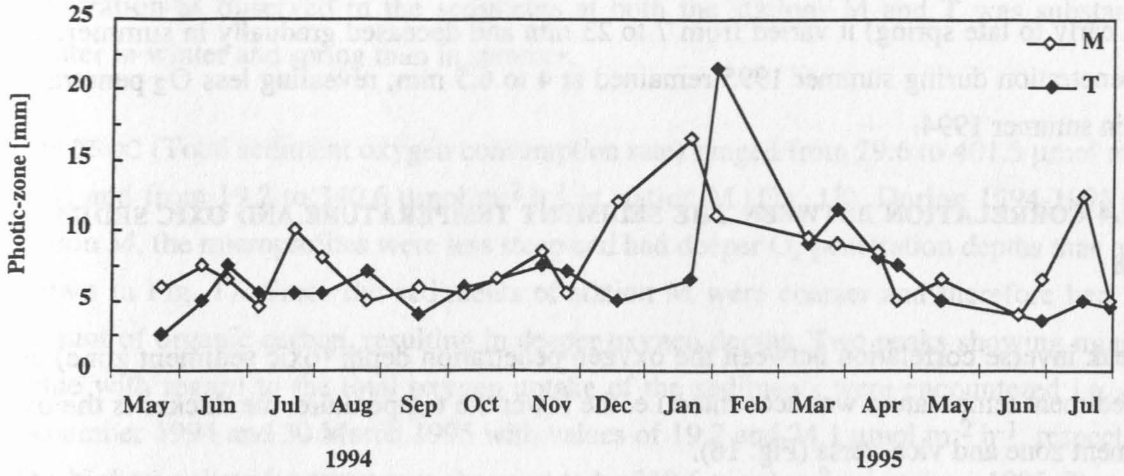


Fig. 15: Seasonal variaton in the photic-zone (mm) at Mönkeberg and Tirpitzmole.

3.2.1.3 SEASONAL FLUCTAUATION IN THE OXIC SEDIMENT ZONE

Oxygen penetration depth or the oxic sediment zone corresponds to the sediment depth, where oxygen gets depleted (i.e. the zero current). The depth of O_2 penetration into the sediment varied from 2.5 to 23 mm at the station T, while at M from 4.5 to 17 mm as shown in fig.14. The O_2 penetration depth at both the research areas was substantially greater during winter and in early spring than in summer. Nevertheless, there was a slight increase in the oxic penetration zone in June and July 1995 at both the locations.

The minimum O_2 penetration depth at M of 4.5 mm was seen on 20 June whereas the maximum of 17 mm on 23 January 1995. The oxic zone throughout the summer 1994 varied between 6 to 11 mm. On 28 November there was a sudden fall in O_2 penetration of 6 mm. From December 1994 to April 1995 (i.e. early to late spring) it remained at 9-12.5 mm and decreased on 20 June 1995 to 4.5 mm. However, at this time green algae *Enteromorpha intestinalis* and brown algae *Fucus vesiculosus* were observed on the sediment surface, which perhaps resulted in the decrease of the oxic zone. The O_2 penetration during summer 1995 varied from 4.5 to 14 mm, depicting more O_2 penetration than in summer 1994. The O_2 penetration augmented once again in later part of June 1995 (6.5 mm) and remained so till middle of July (14 mm).

At station T, the minimum O_2 penetration of 2.5 mm existed on 30 May 1994 and maximum of 23 mm on 3 February 1995. The thickness of the oxic zone throughout the summer 1994 remained at 6 to 8 mm, but reached a new minimum (4 mm) on 22 September (Fig 14).

During winter, oxygen penetrated slowly deeper into the sediment, with an exception on 21 December, when it suddenly reduced to 5.5 mm. But from January 1995 to April 1995 (i.e. from early to late spring) it varied from 7 to 23 mm and deceased gradually in summer. The O_2 penetration during summer 1995 remained at 4 to 6.5 mm, revealing less O_2 penetration than in summer 1994.

3.2.1.4 CORRELATION BETWEEN THE SEDIMENT TEMPERATURE AND OXIC SEDIMENT ZONE

A weak inverse correlation between the oxygen penetration depth (oxic sediment zone) and the sediment temperature was accounted i.e. the lower the temperature, the thicker is the oxic sediment zone and vice-versa (Fig. 16).

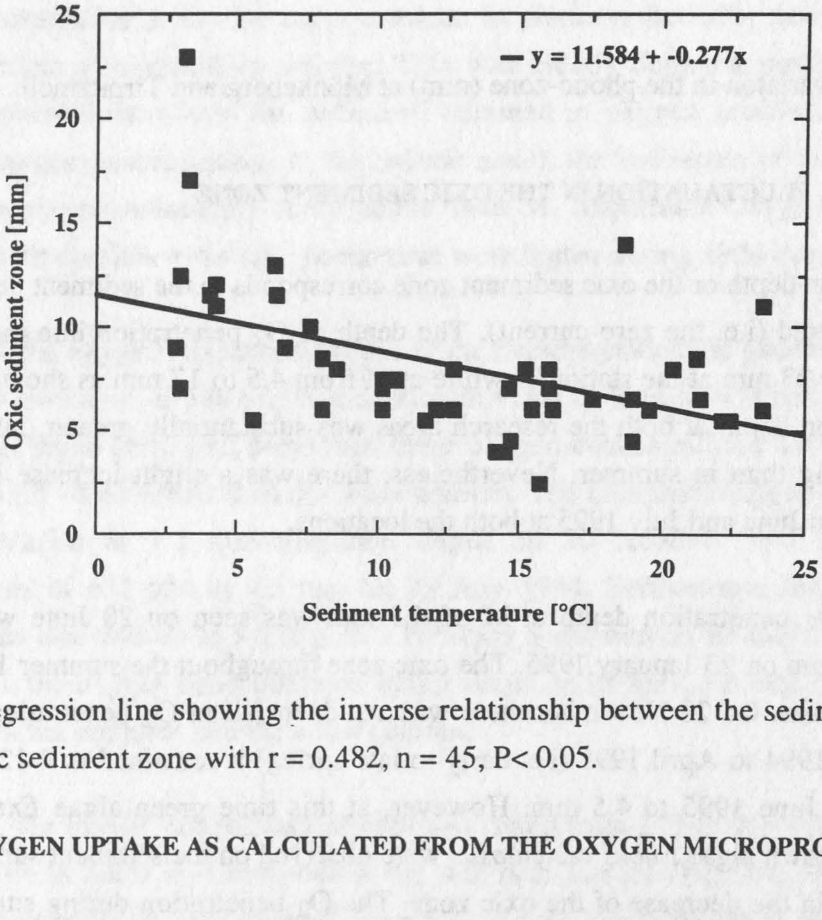


Fig. 16: Regression line showing the inverse relationship between the sediment temperature and the oxic sediment zone with $r = 0.482$, $n = 45$, $P < 0.05$.

3.2.1.5 OXYGEN UPTAKE AS CALCULATED FROM THE OXYGEN MICROPROFILES

The flux of oxygen into the sediment is a fundamental measure of benthic community respiration. It fluctuated significantly over time at both the stations. The rate of O_2 consumption in the sediment was calculated from the O_2 microprofiles assuming a diffusive uptake of O_2 into the sediments. The presented O_2 microgradients . at both the study areas showed decreasing O_2 concentrations into the sediment as shown in Fig. 17. Oxygen gradients were steeper in the sediment as compared to the overlying water at T than at M. Besides this, the seasonal changes in the oxygen uptake of the sediments at both the sites could not be caused by the fluctuations in the sediment temperature alone. The depth of O_2 penetration as observed in the sediments at both the stations M and T was substantially greater in winter and spring than in summer.

The TSOC (Total sediment oxygen consumption rate) ranged from 29.6 to 401.5 µmol m^{-2} h^{-1} at T, and from 19.2 to 340.6 µmol m^{-2} h^{-1} at station M (Fig. 18). During 1994-1995 at the station M, the microprofiles were less steep and had deeper O_2 penetration depths than at T as shown in Fig. 17. Since the sediments of station M were coarser and therefore had lower amount of organic carbon, resulting in deeper oxygen depths. Two peaks showing minimum value with regard to the total oxygen uptake of the sediments were encountered i.e. on 21 December 1994 and 30 March 1995 with values of 19.2 and 24.1 µmol m^{-2} h^{-1}, respectively. The highest values for TSOC was observed to be 340.6 µmol m^{-2} h^{-1} in June 1995. Two more peaks with lower values of 91.1 µmol m^{-2} h^{-1} and 91.8 µmol m^{-2} h^{-1} on 28 July occurred on 10 August 1994, respectively. From late August till February 1995 a fall in TSOC rates was observed. On 3 February 1995, the oxygen consumption rate at station M was higher than at T by about 1.36 times, as shown in the Fig. 18. However, during winter the trend at both the stations M and T with the exception of lower values varying between 19.2 to 40.3 µmol m^{-2} h^{-1} at M.

Station T showed 1.2-1.5 fold higher oxygen consumption rates than at M. From the O_2 profiles it can clearly be illustrated that the diffusive O_2 uptake rates at station T were significantly higher in the summer than in winter, when the sediments contained low organic content. Lowest benthic metabolic activity 29.6 µmol m^{-2} h^{-1} was recorded on 3 February 1995, while the highest value of 401.5 µmol m^{-2} h^{-1} on 30 June 1995. However, two prominent peaks with maximum TSOC occurred in July 1994 and June 1995 as shown in the Fig 18. Subsequently, after July 1994, TSOC deceased dramatically, which eventually resulted in 45.9 µmol m^{-2} h^{-1} on 30 August 1994. Following this an increase on 22 September 1994 (152.9 µmol m^{-2} h^{-1}) was accomplished. These rates being (2.64-fold) higher than at M. From September 1994 to February 1995 lower values in the diffusive oxygen uptake prevailed. Furthermore, during spring 17 March 1995 increase in the O_2 uptake was evident with an oxygen penetration depth of 13 mm, though the temperature was still low i.e. 4.0 °C. It was also observed that during winters when the temperatures were low the penetration depth was higher. On the whole, after the minimum value in February 1995 a steady increase in the TSOC resumed, resulting in the maximum on 30 June 1995 when the sediment temperature was 19 °C. However, within 2 weeks, in the month of July, TSOC decreased by 2.5 fold to 159 µmol m^{-2} h^{-1} with the sediment temperature being the same at 19°C .

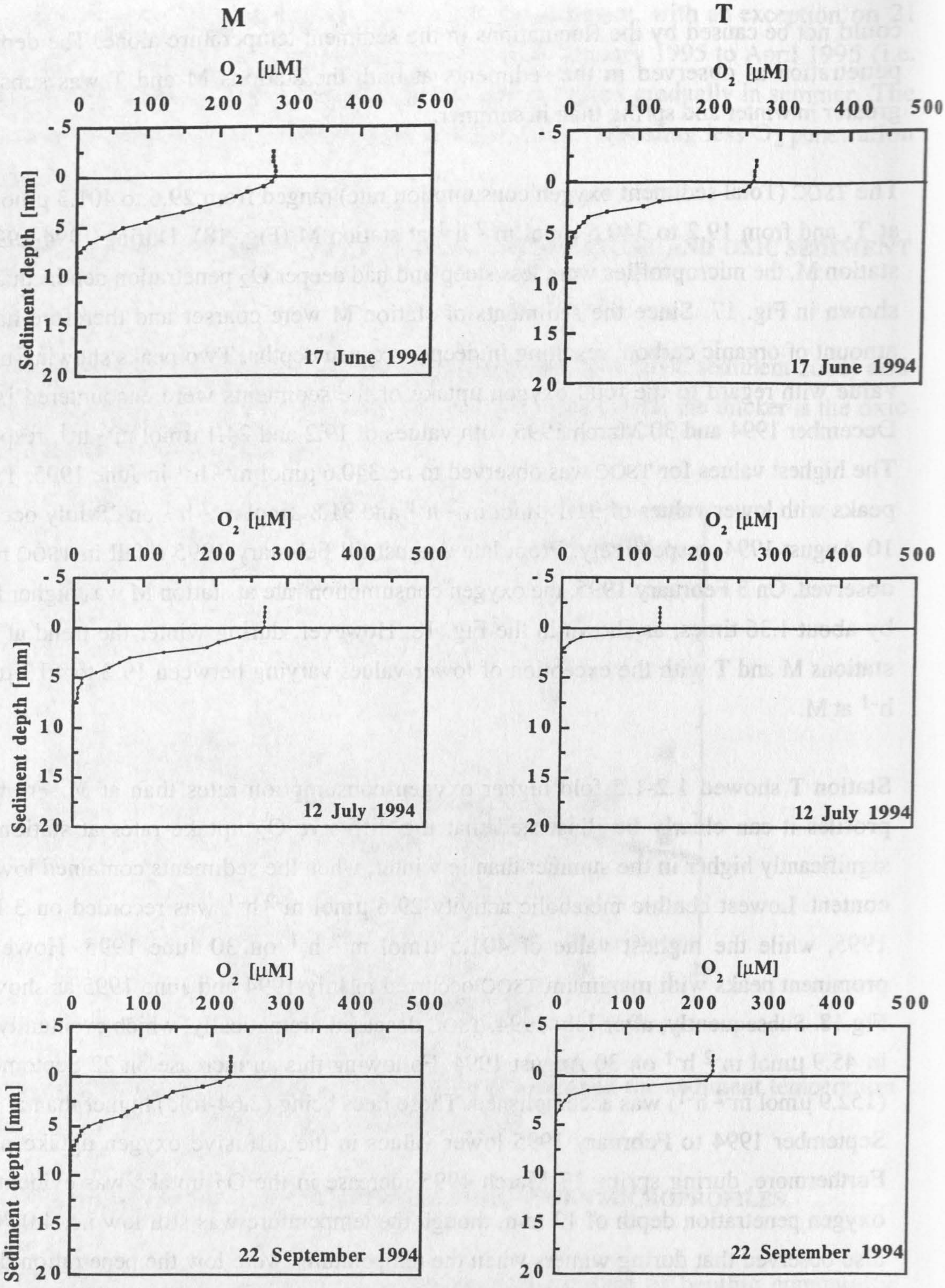
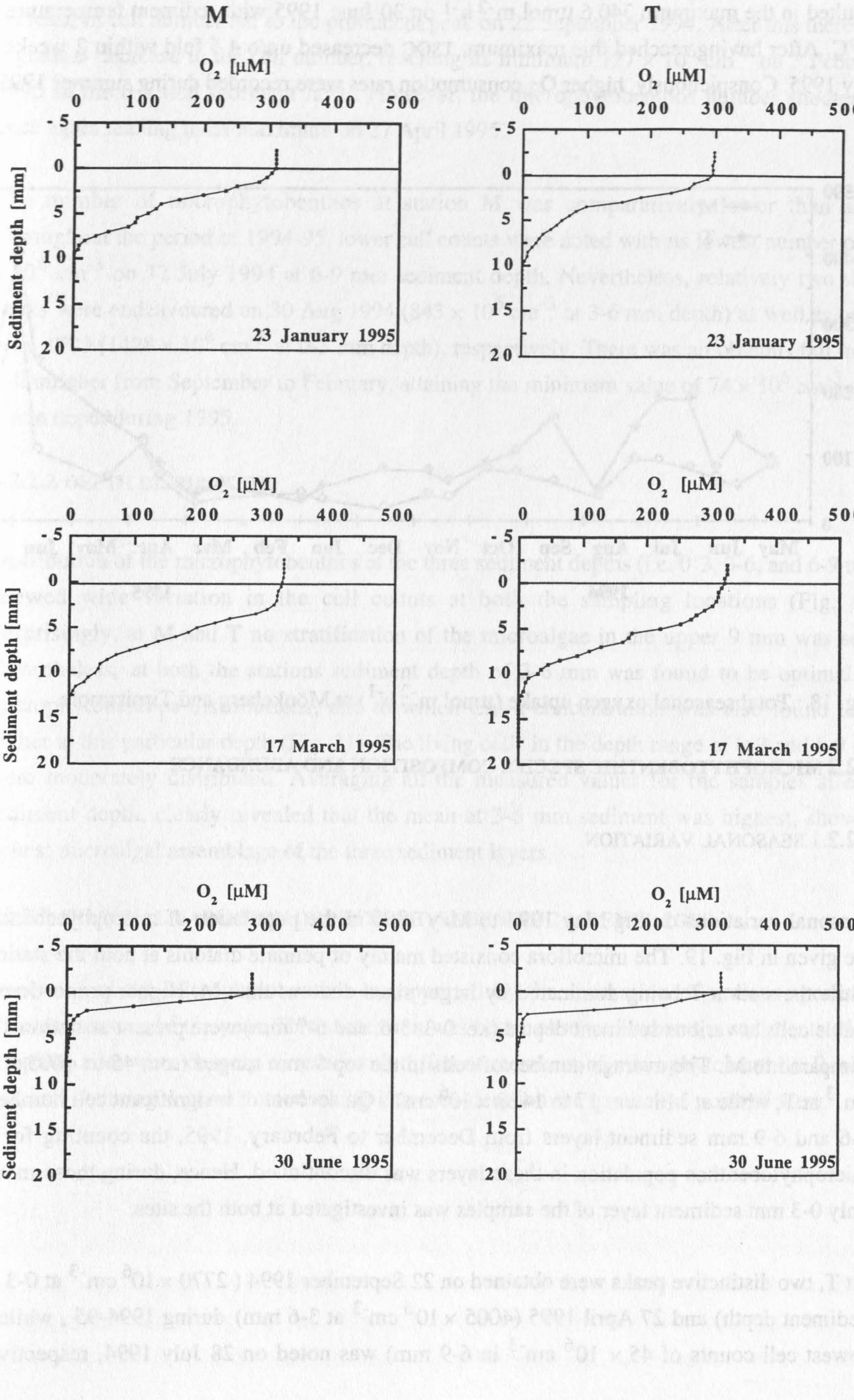


Fig. 17: Profiles of oxygen concentration measured in the dark on (*a*) 17 June 1994 (*b*) 12 July 1994 (*c*) 22 September 1994 (*d*) 23 January 1995 (*e*) 17 March 1995 (*f*) 30 June 1995 were used to calculate the diffusive oxygen uptake within the oxic sediment layer at Mönkeberg and Tirpitzmole. Negative depths represent measurements above the sediment-water interface.


M
T
O$_2$ [μM]
0
100
200
300
400
500
-5
0
5
10
15
20
Sediment depth [mm]
23 January 1995
17 March 1995
30 June 1995

A steady increase in the total oxygen uptake from December onwards was noticed which resulted in the maximum 340.6 µmol m^{-2} h^{-1} on 30 June 1995 with sediment temperature of 19°C. After having reached this maximum, TSOC decreased upto 4.5 fold within 2 weeks in July 1995. Conspicuously, higher O_2 consumption rates were recorded during summer 1995.

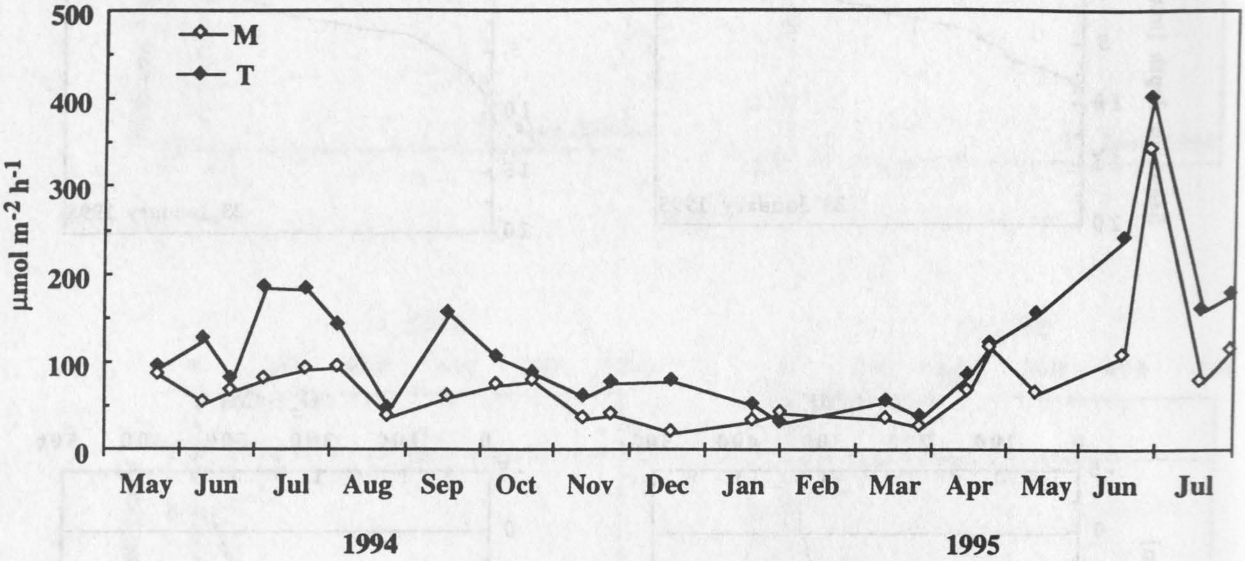


Fig. 18 : Total seasonal oxygen uptake (µmol m^{-2} h^{-1}) at Mönkeberg and Tirpitzmole.

3.2.2 MICROPHYTOBENTHIC SPECIES COMPOSITION AND ABUNDANCE

3.2.2.1.SEASONAL VARIATION

Seasonal variations during May 1994 to May 1995 in the population of microphytobenthos are given in Fig. 19. The microflora consisted mainly of pennate diatoms at both the stations, while the station T being dominated by larger sized diatoms than M. Higher proportions of viable cells at various sediment depths (i.e. 0-3, 3-6, and 6-9 mm) were present at station T, as compared to M. The average number of cells in the top 9 mm ranged from 45 to 4005 × 10^6 cm^{-3} at T, while at M it was 17 to 1428 × 10^6 cm^{-3}. On account of insignificant cell number in 3-6 and 6-9 mm sediment layers from December to February, 1995, the counting for the microphytobenthos population in these layers was discontinued. Hence, during these months only 0-3 mm sediment layer of the samples was investigated at both the sites.

At T, two distinctive peaks were obtained on 22 September 1994 (2770 × 10^6 cm^{-3} at 0-3 mm sediment depth) and 27 April 1995 (4005 × 10^6 cm^{-3} at 3-6 mm) during 1994-95 , while the lowest cell counts of 45 × 10^6 cm^{-3} in 6-9 mm) was noted on 28 July 1994, respectively.

Lower number of microphytobenthos prevailed from May to 30 August 1994. A sudden increase in cell number led to the prominent peak on 22 September 1994. After this there was a gradual decrease in the cell number, reaching its minimum 127 × 10^6 cm^{-3} on 3 February 1995 in the 0-3 mm sediment layer. However, the microphytobenthos number shooted up once again leading to its maximum on 27 April 1995.

The number of microphytobenthos at station M was comparatively lower than at T. Throughout the period of 1994-95, lower cell counts were noted with its lowest number of 17 × 10^6 cm^{-3} on 12 July 1994 at 6-9 mm sediment depth. Nevertheless, relatively two short peaks were endeavoured on 30 Aug 1994 (843 × 10^6 cm^{-3} at 3-6 mm depth) as well as on 16 May 1995 (1428 × 10^6 cm^{-3} at 0-3 mm depth), respectively. There was an obvious fall in the cell number from September to February, attaining the minimum value of 74 × 10^6 cm^{-3} at 0-3 mm depth during 1995.

3.2.2.2 DEPTH DISRIBUTION

Distribution of the microphytobenthos at the three sediment depths (i.e. 0-3, 3-6, and 6-9 mm) showed wide variation in the cell counts at both the sampling locations (Fig. 19). Surprisingly, at M and T no stratification of the microalgae in the upper 9 mm was seen. Nevertheless, at both the stations sediment depth of 3-6 mm was found to be optimal for microphytobenthos distributions, due to which Chl-a concentration was also found to be higher at this particular depth (Fig. 21). The living cells in the depth range of 0-3 and 6-9 mm were moderately distributed. Averaging all the measured values for the samples at each sediment depth, clearly revealed that the mean at 3-6 mm sediment was highest, showing richest microalgal assemblage of the three sediment layers.

3.2.2.3 SEASONAL VARIATION OF MICROPHYTOBENTHIC ASSEMBLAGES

Dynamics of the microphytobenthos is supported by the succession of various species at different seasons of the year. This succession was better observed, when the sediments of the sampling sites were densely covered with different members of microphytobenthos. Besides this, cell counting was conducted taking into consideration the qualitative point of view.

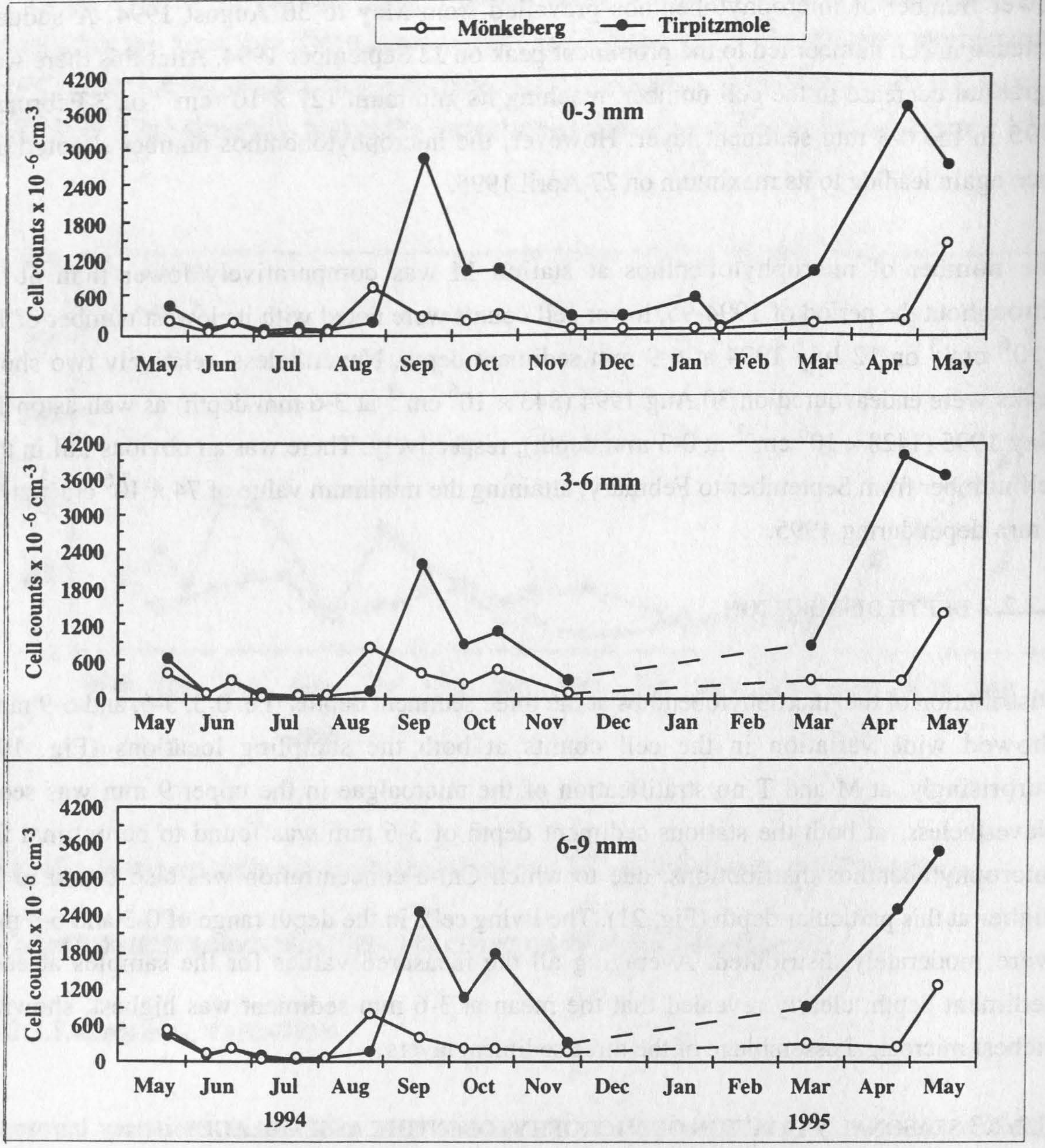


Fig: 19: Seasonal distribution of the microphytobenthos cell number (× 10^6 cm^{-3}) at three sediment depths (0-3, 3-6, 6-9 mm) at Mönkeberg and Tirpitzmole. Dashed lines indicating missing cell counting.

During the investigation, station T showed richer population dominated by motile epipelic species (Fig. 20b) with bimodal size spectrum i.e. small and large in size, but often dominated by large sized diatom cells e.g. *Amphiprora* sp., *Amphora* sp., *Cocconeis* sp., *Mastogloia* sp., *Navicula* sp., *Nitzschia* sp., *Pleurosigma* sp. etc. In contrast to its counter part M, with smaller diatoms (Fig. 20a)*Achnanthes* sp., *Amphora* sp., *Rhabdonema* sp., *Navicula* sp., etc. However, besides the above mentioned diatoms minor portions of planktonic diatoms (i.e. *Actinoptychus senarius*, *Chaetoceros* sp., *Thalassiosira baltica*, *Coscinodiscus* sp.,

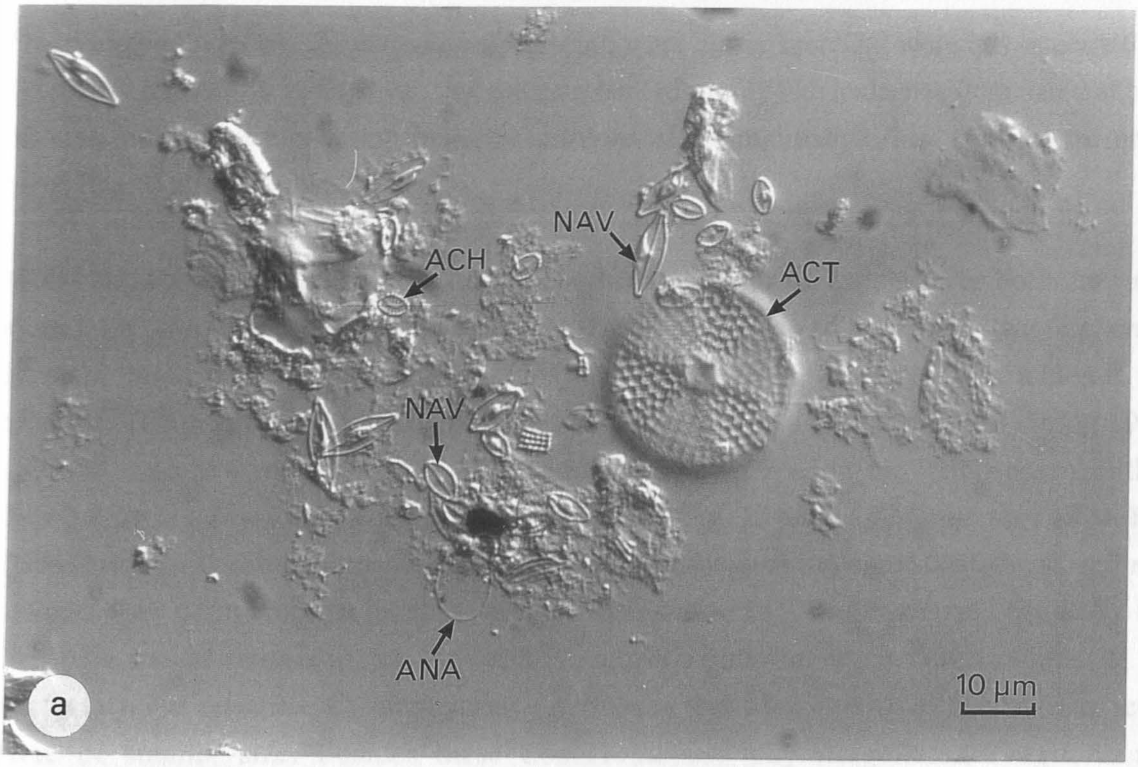


Fig. 20a: Microphytobenthos assemblage from [0-9 mm] sediment depth at Mönkeberg characterized by sparse and small sized taxa such as of *Achnanthes* sp., *Actinoptychus senarius*, Cyanophyceae - Anabaena, *Navicula* sp.

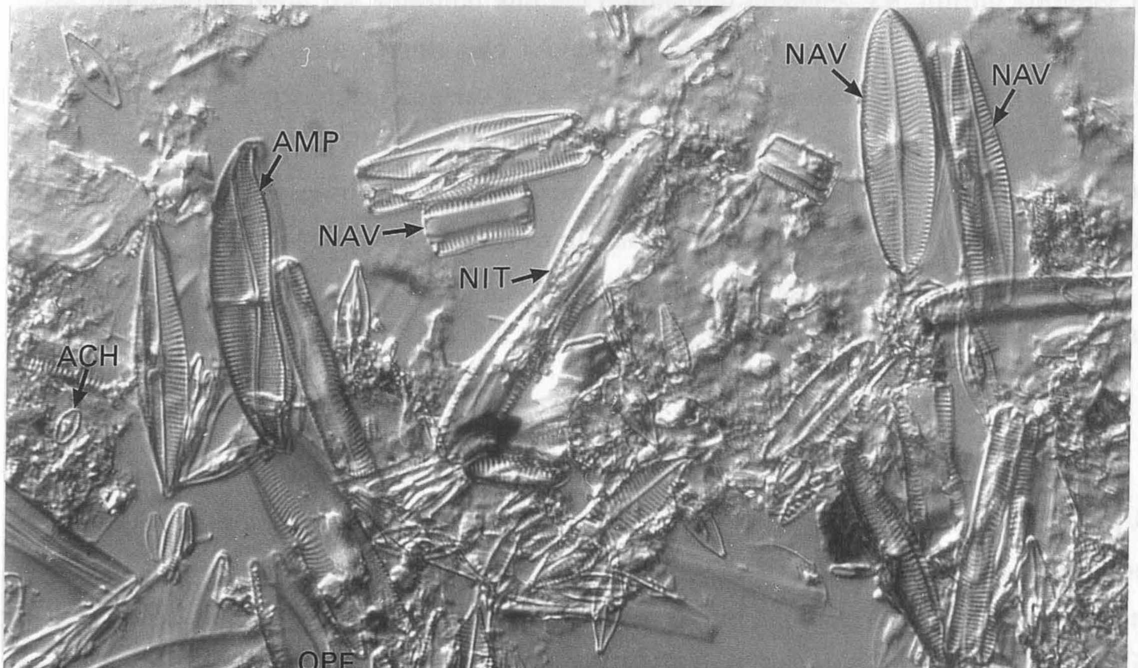


Fig. 20b: Microphytobenthos assemblage from [0-9 mm] sediment depth at station Tirpitzmole consisting of *Achnanthes* sp., *Amphora* sp., *Navicula* sp., *Nitzschia* sp., *Opephora* sp. Assemblage was heavily dominated by large sized and abundant pennate diatoms.

Prorocentrum minium , *Stephanodiscus* sp. etc.) were rarely seen and were also included for the investigation. It was observed that the members of family Naviculaceae dominated at both the stations and were covering major proportions of the microalgal flora than the members belonging to other families.

Most frequent and ubiquitous diatom genera throughout the investigation at both the study areas was *Navicula,* having approximately (10 to 30 µm) size and rarely > 30 µm (e.g. on 28 June, 10 August, 22 September 1994, 23 January 1995 etc.), which specially added to the biomass. The growth of Microphytobenthos varied extensively with the season during 1994-1995 at both the research sites. This mainly depended upon the microphytobenthos distribution in the sediments of the sites as shown in (Fig. 20 a,b) of 22 September 1994. Fig. 20b illustrates that the sediments of station T were dominated by large sized, dense and rich assemblages of microphytobenthos having (*Achnanthes* sp., *Amphora* sp., *Navicula* sp., *Nitzschia* sp., *Mastogloia* sp., *Opephora martyi, Pinnularia* sp. etc.) while at M (*Actinoptychus senarius*, Cyanophyceae - Anabeana and Merismopedia, *Navicula* sp. etc.) were of smaller size. Besides these *Coscinodiscus,* phytoflagellates, *Fragilaria* sp., *Rhabdonema* sp, *Melosira* sp. were also prevelant during autumn.

The microphytobenthos species at both the stations changed from larger to smaller and vice-versa, depending upon the seasonal and environmental changes .i.e. during summer large sized microphytobenthos dominated (*Amphiprora* sp., *Cocconeis* sp., Cyanophyceae-Anabeana, Merismopedia, *Epithemia sorex, Fragilaria* sp., *Gyrosigma* sp., Phytoflagellates-Porocentrum minimum, *Pleurosigma* sp., *Tabularia* sp., *Tetraselmis* sp., *Navicula* sp., *Navicula humerosa, Stauroneis sp.* etc.) were noticed. Comparatively, in winter the number of species reduced (i.e. *Achnanthes* sp., *Fragilaria* sp., *Navicula* sp. (small sized), *Opephora martyi, Rhabdonema* sp., *Tetraselmis* sp.) they were relatively smaller in size. It was also accounted that the species type present in the sediments during spring, summer, autumn and winter were dependent on the season.

The species prevailing during spring (*Atheya decora, Biddulphia* sp., *Cyclotella* sp., *Cylindrotheca* sp., *Cymbella* sp., *Diatoma* sp., *Diploneis* sp., *Eunotia* sp., *Licmophora abbreviata,* Phytoflagellates - *Heterosigma* sp., *Melosira* sp., *Nitzschia closterium, Synedra* sp. etc.) were absent or rarely present in other seasons. In addition to this, the changes in the species composition along the depth gradient (0-3, 3-6, 6-9, 9-12 mm) was a significant feature at both the stations.

3.2.3 CHLOROPHYLL-A

3.2.3.1 SEASONAL VARIATION

Chlorophyll-a data were collected to provide an estimate of the standing stock of microalgae living on and in the shallow water sediments of the study sites (M and T). Spatial and seasonal variations of the mean Chl-*a* concentrations in the upper 0 to 12 mm sediment layer at both stations are presented in Fig. 21. A subjective assessment of the graphs exhibited dissimilarity in Chl-*a* concentrations among both the stations. Significantly, higher Chl-*a* concentrations were accounted at T (2.06 to 29.07 µg Chl-a cm^{-3}) with finer sediments than at M (0.95 to 13.17 µg Chl-*a* cm^{-3}) with coarser and sandy sediment. The graphs illustrate that the standard deviations increased with increasing Chl-*a* concentrations.

At station M relatively low Chl-*a* concentrations between 5.43 and 9.22 µg Chl-*a* cm^{-3} were prevalent during summer 1994 (Fig. 21). However, a progressive increase in the Chl-*a* concentrations from 10 August was noted, which subsequently resulted into the maximum value of 13.17 µg Chl-*a* cm^{-3} on 12 October at 6-9 mm sediment depth. Succeeding this the concentrations rapidly decreased to (4-5 µg Chl-*a* cm^{-3}) on 27 October. However, in November the chlorophyll a concentrations reached a value of 12.42 µg Chl-*a* cm^{-3} at 9-12 mm, after which it gradually fell down, showing the minimum concentration of 0.95 on 18 April 1995 in the 0-3 mm sediment layer. A slow and continuous increase in the concentration was noted upto 20 June 1995, when the second peak with 9.53 µg Chl-*a* cm^{-3} was perceived at 3-6 mm sediment depth.

During 1994-1995 at station T, two distinctive peaks were observed on 22 September 1994 (29.07 µg Chl-*a* cm^{-3}) at 0-3 mm and 27 April 1995 (28.72 µg Chl-*a* cm^{-3}) at 3-6 mm sediment depth, respectively. Nevertheless, the minimum value prevailed on 28 June 1994 (3.33 µg Chl-*a* cm^{-3}) and on 3 February 1995 (2.06 µg Chl-*a* cm^{-3}) at 0-3 mm sediment depth each. During summer and winter comparatively lower Chl-*a* concentrations were noted than in other seasons.

An increase in the Chl-*a* concentration was observed on 12 July (10.38 µg Chl-*a* cm^{-3} at 0-3 mm), after which values declined between July and August 1994. Subsequently, after this in September there was an increase in the Chl-*a* concentration reaching the maximum. After this month onwards a precipitous reduction in the concentration prevailed, resulting in the minimum value on 3 February 1995. From February until 27 April 1995 there was a steady increase in the Chl-*a* concentrations (28.72 µg Chl-*a* cm^{-3}) at 3-6 mm sediment depth.

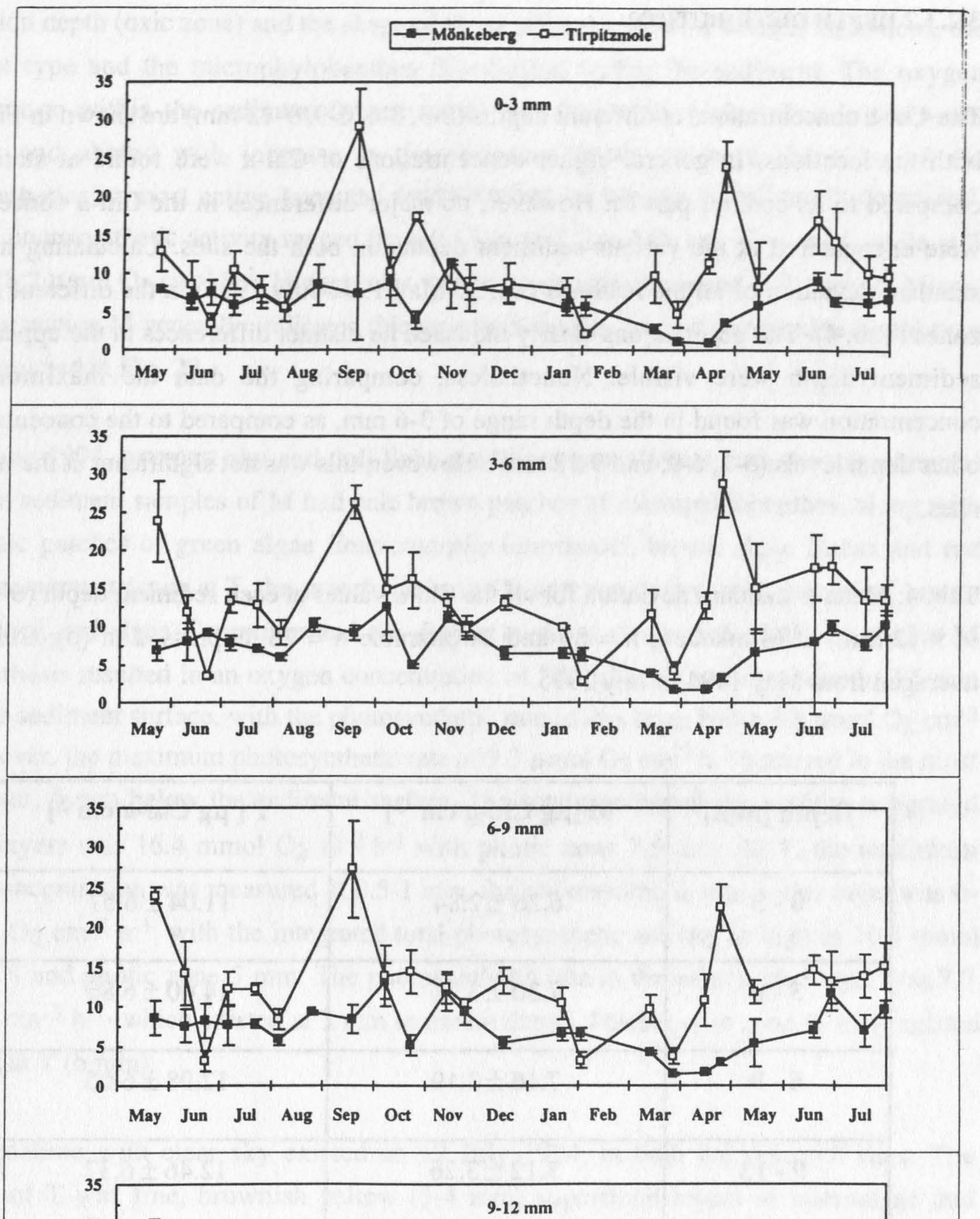


Fig. 21: Mean Chlorophyll-a concentrations (µg Chl-*a* cm^{-3}) with standard deviations in 4 sediment depths (0-3 mm; 3-6 mm; 6-9 mm; 9-12 mm) at Mönkeberg and Tirpitzmole.

3.2.3.2 DEPTH DISTRIBUTION

The Chl-*a* concentrations at different depths (0-3, 3-6, 6-9, 9-12 mm) are shown in Fig. 21 for both the locations. In general higher concentrations of Chl-*a* were found at station T as compared to its counter part M. However, no major differences in the Chl-*a* concentrations were encountered at the various sediment depths on both the sites. Calculating mean and standard deviation of all the readings (i.e. 30 May 1994-July 1995) in the different sediment zones (Tab. 4). The observations clearly indicated no distinct differences in the upper 0-9 mm sediment depth were visible. Nonetheless, comparing the data the maximum Chl-*a* concentration was found in the depth range of 3-6 mm, as compared to the concentrations at other depth levels (0-3, 6-9, and 9-12 mm). However, this was not significant at the respective sites.

Tab. 4: Mean ± standard deviation for all the Chl-*a* values at each sediment depth (0-3, 3-6, 6-9, 9-12 mm) at Mönkeberg n = 80 and Tirpitzmole n = 76, expressed in (µg Chl-*a* cm^{-3}) averaged from May 1994 to July 1995.

Depth [mm]	**M [µg Chl-*a* cm^{-3}]**	**T [µg Chl-*a* cm^{-3}]**
0 - 3	6.26 ± 2.84	11.04 ± 6.57
3 - 6	7.30 ± 3.01	14.00 ± 6.86
6 - 9	7.16 ± 3.19	12.98 ± 6.05
9 - 12	7.12 ± 3.26	12.46 ± 6.37

3.2.4 BENTHIC PRIMARY PRODUCTION

3.2.4.1 MICROPROFILES OF PHOTOSYNTHESIS

Oxygen microprofiles of photosynthesis, measured at M and T showed temporal and spatial variations during the different seasons of 1994-1995 are illustrated in Fig. 22. The oxygen microprofiles of the two respective sites under dark and light phase depicted no distinct differences, with an exception on 17 March, when the fluctuations were observed in dark Fig. 22. The oxygen concentration, photosynthetic rate, photosynthetically active layer, penetration depth (oxic zone) and the shape of the profiles varied with weather conditions, the sediment type and the microphytobenthos distribution within the sediment. The oxygen concentration within the sediment (photic zone) was frequently higher than in the water column, and abated with increase in the sediment depth. At both the sides of the photosynthetically most active layer the concentration of oxygen significantly decreased. Rates of photosynthetic activity ranged from 0.13 to 16.7 µmol O_2 cm^{-3} h^{-1} at M, while at T 0.06 to 18.2 µmol O_2 cm^{-3} h^{-1}. Higher rates were occasionally measured at T than M. Microprofiles at station M generally indicated thicker oxic zone (i.e. oxygen penetration depth) than at T as depicted in Fig. 22.

On 17 June 1994, overcast sky and dull light conditions prevailed at both the experimental sites. The sediment samples of M had pale brown patches of microphytobenthos, along with the mosaic patches of green algae *Enteromorpha intestinalis*, brown algae *Fucus* and red algae *Ceramium strictum* at T, the superficial layer (1 mm) was brown, with patches of brown algae *Fucus,* red algae *Ceramium* and the deeper layers were greyish black. At station M photosynthesis resulted in an oxygen concentration of 380 µM at a sediment depth, 2.5 mm below the sediment surface, with the photosynthetic rate in this layer being 4.8 µmol O_2 cm^{-3} h^{-1}. However, the maximum photosynthetic rate of 9.3 µmol O_2 cm^{-3} h^{-1} occurred in the most active layer, 5 mm below the sediment surface. The total photosynthetic activity integrated over all layers was 16.4 mmol O_2 m^{-2} h^{-1} with photic zone 7.5 mm. At T, the maximum oxygen concentration was measured at 0.5-1 mm, the photosynthetic rate in this layer was 0-1.3 µmol O_2 cm^{-3} h^{-1}, with the integrated total photosynthetic activity as high as 10.4 mmol O_2 m^{-2} h^{-1} and photic zone 5 mm. The photosynthetic rate in the most active layer was 7.7 µmol O_2 cm^{-3} h^{-1}, which existed at 3 mm sediment depth. Thicker oxic zone (8 mm) existed at M than at T (6 mm).

Bright sunshine with clear sky existed on 12 July 1994, at both the research sites. The sediment of T was fine, brownish yellow (3-4 mm) superficial layers of microalgae and greyish black deeper layers, with anthropogenic matter. However, this sediment also included large numbers of green algae *Enteromorpha intestinalis, Ulvaria* and brown algae *Fucus* patches. At M, sediment was coarse, clean with no anthropogenic matter and less prominent yellowish-brown microphytobenthos patches with meagre amount of green *Cladophora, Enteromorpha intestinalis, Ulvaria* and brown algae *Fucus.* At station M maximum O_2 concentration of 337 µM existed at 0.5 mm and the photosynthetic rate within this layer was as high as 0.26 µmol O_2 cm^{-3} h^{-1}, while the maximum photosynthetic activity of 10.6 µmol O_2 cm^{-3} h^{-1} in the most active layer, 1.5 mm below the sediment surface (Fig. 22).

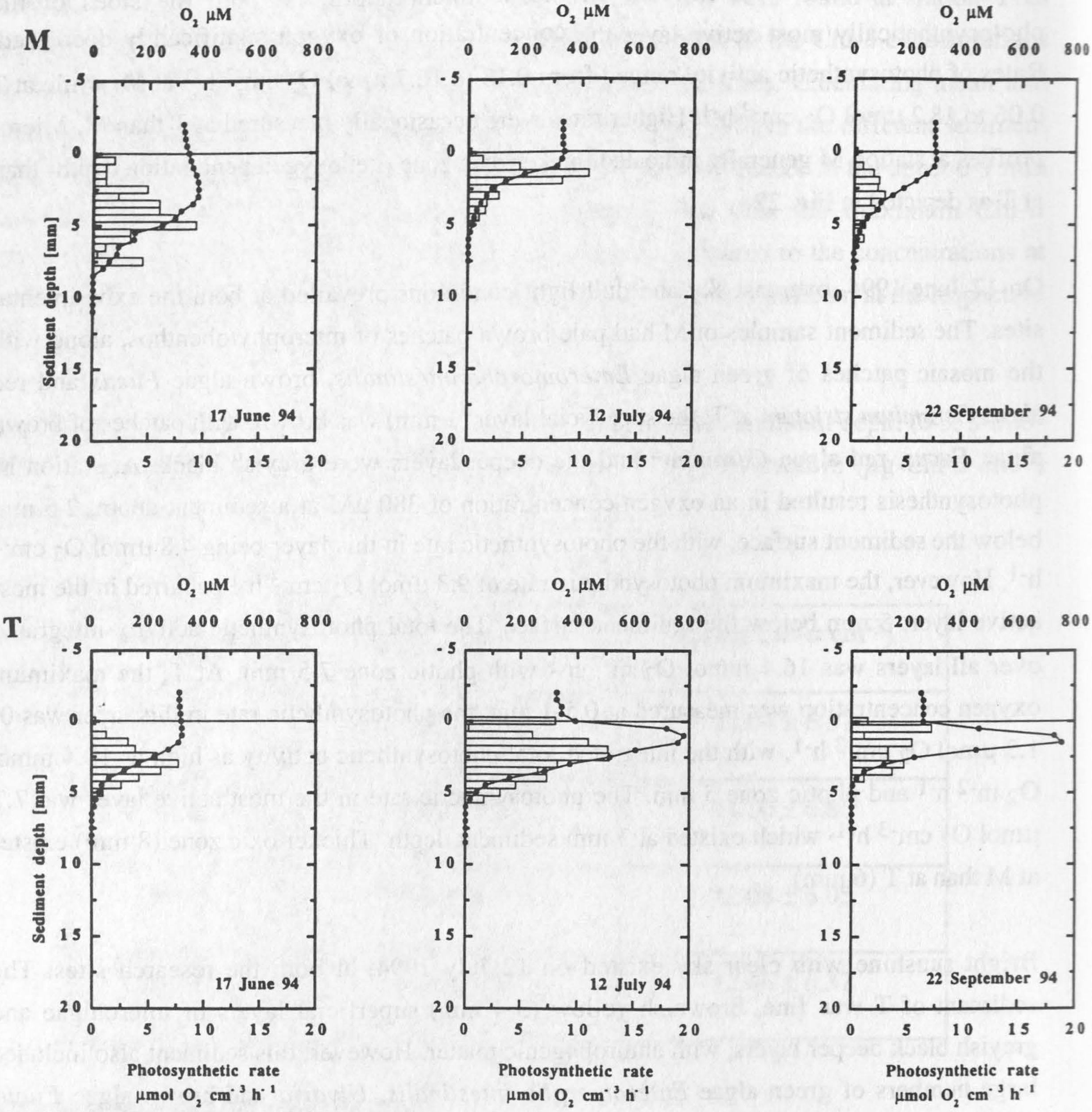
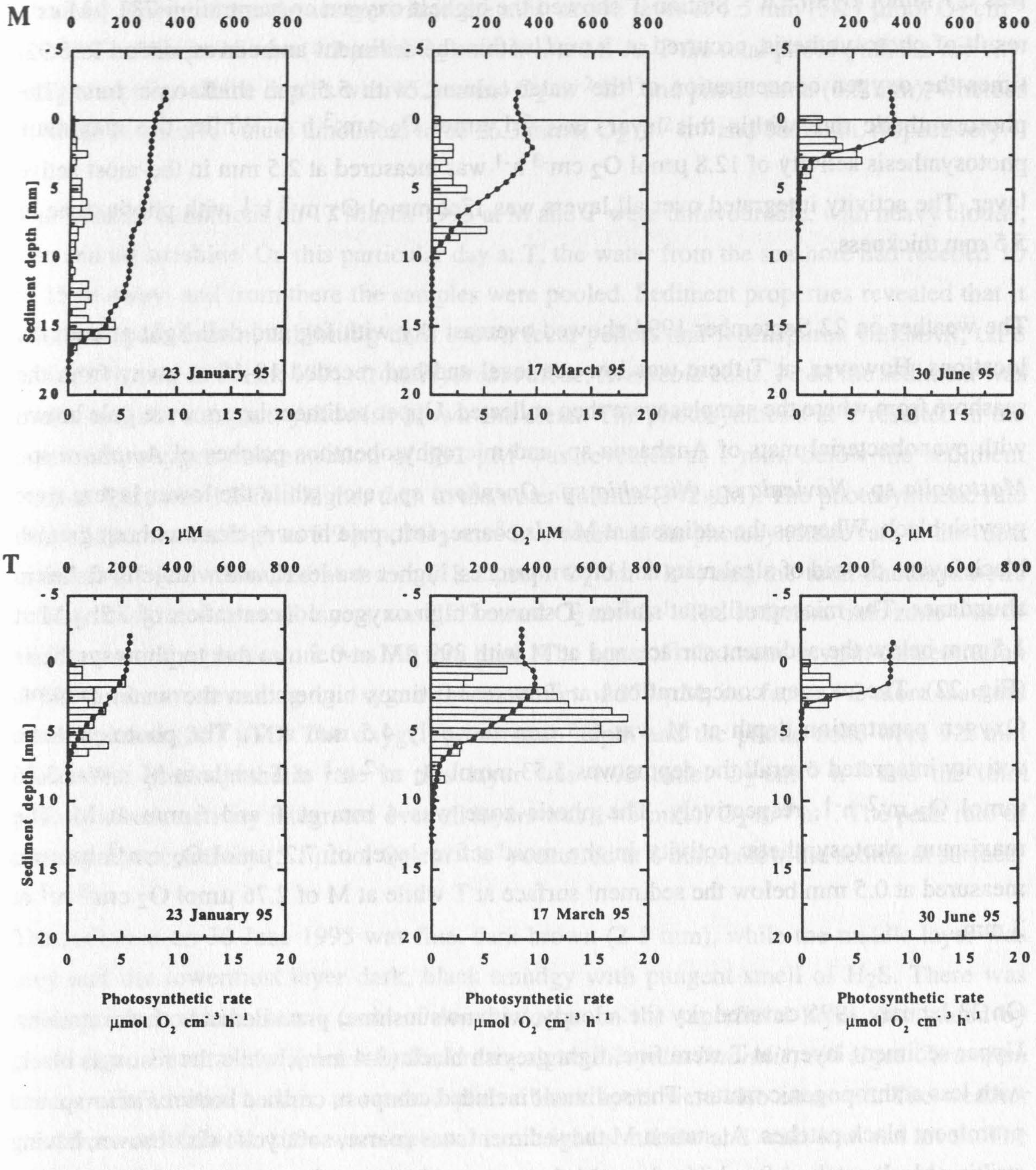


Fig. 22: Vertical oxygen profiles of oxygen concentration during light (filled circles) and photosynthetic activity (bars) in shallow, sandy sediments of the stations Mönkeberg and Tirpitzmole, indicating seasonal changes from May 1994 - July 1995.


M
T
O₂ µM
0
200
400
600
800
Sediment depth [mm]
-5
0
5
10
15
20
23 January 95
17 March 95
30 June 95
Photosynthetic rate
µmol O₂ cm⁻³ h⁻¹

Apparently no major differences in the oxygen concentration between the water column and the uppermost sediment layers were seen. However, a gradual decline in the oxygen concentration was obvious indicating no peak. The oxic zone was only 5.5 mm, while the photic zone was 4.5 mm. The total photosynthetic activity integrated over all sediment layers was 6.7 mmol O_2 m^{-2} h^{-1}. Station T showed the highest oxygen concentration 781 µM as a result of photosynthesis, occurred at 1 mm, within the sediment and corresponded to 3.92-times the oxygen concentration of the water column, with 5.5 mm thick oxic zone. The photosynthetic rate within this layer, was 6.1 µmol O_2 cm^{-3} h^{-1}. While, the maximum photosynthesis activity of 12.8 µmol O_2 cm^{-3} h^{-1} was measured at 2.5 mm in the most active layer. The activity integrated over all layers was 17.2 mmol O_2 m^{-2} h^{-1} with photic zone of 5.5 mm thickness.

The weather on 22 September 1994 showed overcast sky with fog and dull light at both the locations. However, at T there was low sea-level and had receded 10-15 m away from the seashore from where the samples were then collected. Upper sediment layers were pale brown with cyanobacterial mats of Anabaena sp. and microphytobenthos patches of *Amphora* sp., *Mastogolia* sp., *Navicula* sp., *Nitzschia* sp., *Opephora* sp., etc., while the lower layers were greyish black. Whereas the sediment at M was coarse, soft, pale brown, clean without greyish black layers, devoid of algal mats and brown patches, higher sea-level, and with jelly-fishes in abundance. The microprofiles at station T showed high oxygen concentration of 751 µM at 1.5 mm below the sediment surface and at M with 299 µM at 0.5 mm due to photosynthesis (Fig. 22). The oxygen concentrations at T were 3.0 times higher than the water column. Oxygen penetration depth at M was 6.5 mm and only 4.5 mm at T. The photosynthetic activity integrated overall the depths was 5.53 mmol O_2 m^{-2} h^{-1} at T while at M it was 3.56 mmol O_2 m^{-2} h^{-1}, respectively. The photic zone was 4 mm at T and 6 mm at M. The maximum photosynthetic activity in the most active layer of 7.2 µmol O_2 cm^{-3} h^{-1} was measured at 0.5 mm below the sediment surface at T while at M of 2.76 µmol O_2 cm^{-3} h^{-1} at 3 mm.

On 23 January 1995 covered sky (i.e. cloudy, with no sunshine) prevailed at both the stations. Upper sediment layers at T were fine, light greyish black (3-4 mm), while the rest was black, with less anthropogenic matter. The sediment included compost, crushed brown *Fucus* sp. and prominent black patches. At station M the sediment was coarse, soft, yellowish brown, having striking black patches. It exhibited scanty decomposed leaves and crushed brown algae *Fucus* sp. Furthermore, the water column at both the locations exhibited higher oxygen concentrations than the sediment, without eminent oxygen concentration peaks. Maximum oxygen concentration due to photosynthesis was found to be in the uppermost sediment layer, 0.0 mm. Oxygen concentration of 217 µM existed in the uppermost sediment layer, 0 mm at station T, i.e. a factor 1.1 less than in the water column, with photosynthetic rate within this layer was 0.26 µmol O_2 cm^{-3} h^{-1} and the oxygen penetration depth 7 mm. The maximum oxygen concentration at M within the sediment was 309 µM, 1.1 fold less than its water column, rate of photosynthesis within this layer accounted was 0.3 µmol O_2 cm^{-3} h^{-1} and with 17 mm oxic penetration depth. A zig-zag pattern of the profile, with no oxygen peak was obtained. The photosynthetic rate within the most active layer at 1.5 mm (5.27 µmol O_2 cm^{-3} h^{-1}) at T, while at 15 mm (4.3 µmol O_2 cm^{-3} h^{-1}) at M. At T the total photosynthetic activity integrated over all the depths was 15.2 mmol O_2 m^{-2} h^{-1} and photic zone (6.5 mm), whereas at M the respective values amounted to be 26.3 mmol O_2 m^{-2} h^{-1} and 16.5 mm, respectively.

The weather conditions on 17 March 1995 at M and T were unfavourable, with heavy clouds, rain and no sunshine. On this particular day at T, the water from the seashore had receded 10 to 15 m away, and from there the samples were pooled. Sediment properties revealed that it was fine, pale brown, exhibiting dark brown fecal pellets and lebenspuren GERMAN, LIFE TRACES (GAGE & TYLER 1991) from *Hydrobia ulvae, Arenicola* casts. At M the sediment was coarse and not compact, yellowish brown and clean. The photosynthesis at T resulted in the maximum oxygen concentration of 392 µM was revealed at 1 mm, below the sediment surface. This was 1.2-fold higher than in the water column (342 µM). The photosynthetic rate in this layer was as high as 3.9 µmol O_2 cm^{-3} h^{-1}, whereas the photosynthetic rate in the most active layer was measured at 4 mm (18.2 µmol O_2 cm^{-3} h^{-1}) and the total photosynthetic activity integrated over all layers was 75.9 mmol O_2 m^{-2} h^{-1}. The sediment oxic zone was of 11.5 mm and the photic zone was 7.5 mm thick. The zone of maximum oxygen concentration at M was 2 mm, revealing an oxygen concentration of 377 µM, i.e. factor 1.2 more than the water column (361 µM). The oxygen penetration depth and the photic zone were 9.5 mm thick. The photosynthetic rate in this layer was 1.93 µmol O_2 cm^{-3} h^{-1} and the total photosynthetic activity integrated over all layers was 14.3 mmol O_2 m^{-2} h^{-1}. The peak rate of photosynthetic activity (5.1 µmol O_2 cm^{-3} h^{-1}) occurred at 8 mm, below the sediment surface.

The sediment on 30 June 1995 was fine, dark brown (2-5 mm), while the middle layer was grey and the lowermost layer dark, black smudgy with pungent smell of H_2S. There was anthropogenic matter, heavy casts of *Arenicola* sp. on the superficial layer, dominated by green algae *Enteromorpha intestinalis*, brown algae *Pilayella littoralis*, red algae *Ceramium strictum.* In addition to this, at random places black spots were also observed. The weather conditions at both the sites were optimal i.e. bright sunshine and with low sea level. The sediment of M was clean, not compact, coarse with upper layers of approximately 4 cm yellowish brown, while the deeper layers were black, without H_2S smell. The overlying water was turbid. No prominent microphytobenthos patches were noticed on the sediment surface, while the algal patches of green algae *Ulvaria, Enteromorpha intestinalis,* brown algae *Zostera marina (sea grass), Fucus, Pilayella littoralis* sps. were common. No conspicuous differences in the oxygen concentrations between the water column and (uppermost 0.5 mm) sediment layer with 332 µM were observed at station T, where a relatively thin oxic zone of 3.0 mm was found. The photosynthetic rate within this layer was 0.7 µmol O_2 cm^{-3} h^{-1} (Fig. 22). The highest photosynthetic rate of 5.7 µmol O_2 cm^{-3} h^{-1} was measured at 2 mm, in the most active layer below the sediment surface. Besides this, at station M the highest oxygen concentration of 355 µM, 0 mm on the sediment surface. The photic zone and oxic zone in the sediment were 6.5 mm thick each. Peak rate of photosynthesis in the most active layer was 5.9 µmol O_2 cm^{-3} h^{-1}, 3 mm below the sediment surface. The total photosynthetic activity integrated over all layers was 4.5 µmol O_2 cm^{-3} h^{-1} at T and 8.61 µmol O_2 cm^{-3} h^{-1} at M, respectively.

3.2.4.2 SEASONAL PRIMARY PRODUCTION CYCLE OF MICROPHYTOBENTHIC ALGAE

Results given in Fig. 23 depict the seasonal variations in the benthic primary production of the experimental stations M and T. Both the stations were readily accessible under all weather conditions and enabled the measurements throughout the year. The benthic primary production ranged during the period of May 1994 to July 1995 from (38.6 to 284.8 mg C m^{-2} h^{-1}) and 15.3 to 454.3 mg C m^{-2} h^{-1} at M and T, respectively. Overall observations of the two respective locations, clearly indicated that the amount of production at T was generally higher than M. Throughout the investigation period, it was accounted that the microphytobenthos production was lesser during summer and autumn, while it was higher during the months of winter and spring, respectively.

At station M, the minimum gross productivity of 38.6 mg Cm^{-2} h^{-1} was observed on 12 October 1994 ,while the maximum of 284.8 mg C m^{-2} h^{-1} was attained on 23 January 1995, respectively. The productivity increased significantly 3.4 -fold in June 1994. However, this value remained on the higher side even in July. Lower productivity existed between October and November 1994. Following this, the productivity augmented during the months of December 1994 and January 1995, and attained a peak of 284.8 mg m^{-2} h^{-1}. During these months such results were not observed at T. After which the primary production once again abated, reaching a secondary peak of 58.4 mg C m^{-2} h^{-1} on 27 April.

At station T, the minimum value of 15.3 mg C m^{-2} h^{-1} existed on 30 May 1994, while the sharp peak with maximum production of 454.3 mg C m^{-2} h^{-1} was accounted on 17 March 1995, respectively. From May 1994 a gradual increase in the benthic production was noticeable until reaching its maximum on 12 July 1994. Besides this, a prominent decrease in the production was obvious from July till end of August. From January to March a dramatic increase in the benthic primary production took place, which led to the formation of the second peak on 17 March 1995. This peak was 2.1 - fold higher than the previous peak of 12 July 1994. Nonetheless, this value suddenly deceased by 2.5 - fold on 30 March 1995, which kept on further dwindling and ultimately reaching a value of 43.3 mg C m^{-2} h^{-1} on 19 July 1995.

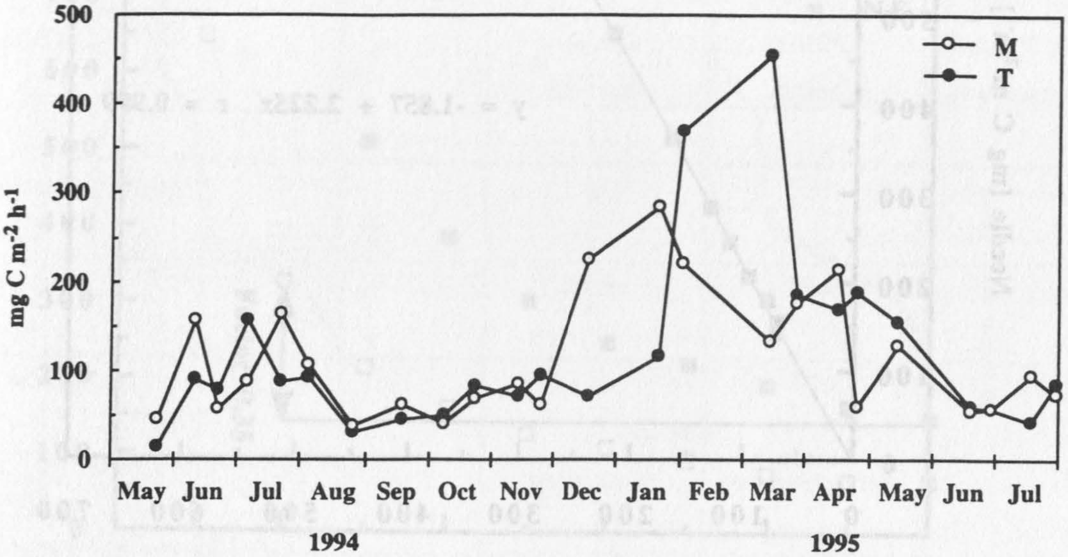


Fig. 23: Seasonal primary production cycle of microphytobenthos at Mönkeberg and Tirpitzmole.

3.2.4.3 COMPARISON AND ERROR IN THE PRIMARY PRODUCTION MEASURED WITH GLASS AND NEEDLE MICROSENSORS

The first experiment conducted to compare the rate of photosynthesis within the sediments of station T, with the aid of two different microsensors i.e. *glass* and *needle* (steel type) in light and dark shifts, indicated that the photosynthetic activity measured by the needle sensor was factor 2 higher than with the glass sensor, with 10 sec of dark phase at each sediment depth of 500 µm, when integrated over all the depth intervals yielded a gross primary production of 77± 8.54 with glass and steel 154.33 ± 12.66 mg C m^{-2} h^{-1}, n= 3. Furthermore, taking only one measurement into account a factor difference of 2.2 in gross production i.e. 76 mg C m^{-2} h^{-1} for glass, needle 152 mg C m^{-2} h^{-1} was estimated i.e. the longer the dark period the lesser is the benthic primary production taking only one oxygen microprofile into account as Fig 24. It was also observed that the overestimation by 2 or 2.2- fold in the photosynthetic activity came irrespective of the existing duration of the dark period i.e. 3 to 10 sec and remained constant irrespective of the increase or decrease in the primary production.

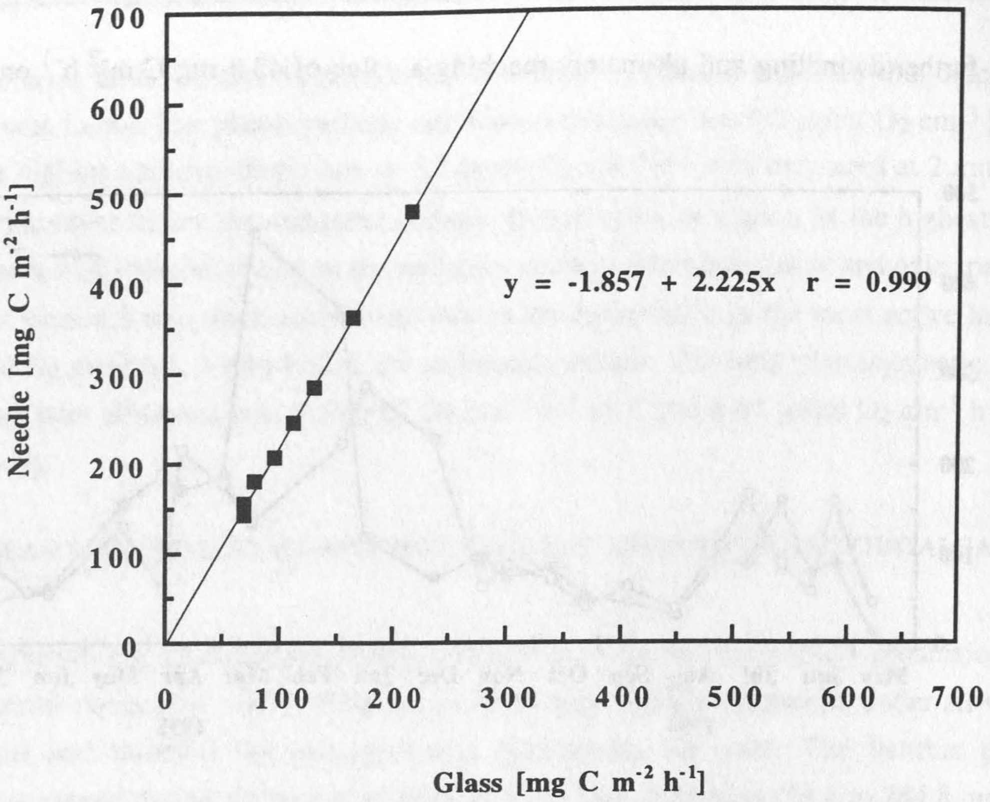


Fig. 24: Estimated gross production mg C m^{-2} h^{-1} measured with needle and glass microprobe and plotted against each other. Regression line indicates an overestimation by a factor 2.2 in the gross primary production measured with needle compared to glass microprobe, with 10 sec of dark phase at each sediment layer, taking one measurement into consideration. Each point represents the calculated production every sec i.e. from 3 to 10 sec of dark period. The coefficient of determination r = 0.999.

With the *fixed point microsensor technique*, the slope of the recorded current gave the oxygen accumulation rate at fixed depths of the sediment, and the initial slope to estimate the rate of oxygen production, when the light was turned off for 10 seconds , after the sediment had already been exposed to light for 10 minutes. The calculated rates showing the change in oxygen concentrations with time revealed that the highest oxygen concentration below the sediment surface existed at 0.5 mm and at 1 mm with glass and needle, respectively. However, the glass microsensor responded by showing the change in the oxygen concentrations at a particular depth of the sediment after 1-2 sec as compared to the needle where it was 3 to 4 sec, after the illumination was extinguished. It was observed that the oxygen concentration remained almost constant after the mentioned time till 10 seconds indicating steady state. The gross primary production calculated from the measurements conducted by the two respective sensors indicated that the estimated production measured with the needle sensor, after having given 10 seconds of dark phase at each sediment depth, showed lower primary production as compared to the glass sensor, when it was given 2 sec of dark phase Fig. 25 and Tab. 5. Thus the gross primary production when measured with needle was *underestimated* by factor of 0.35 ± 0.14 (n= 7) as compared to the glass.

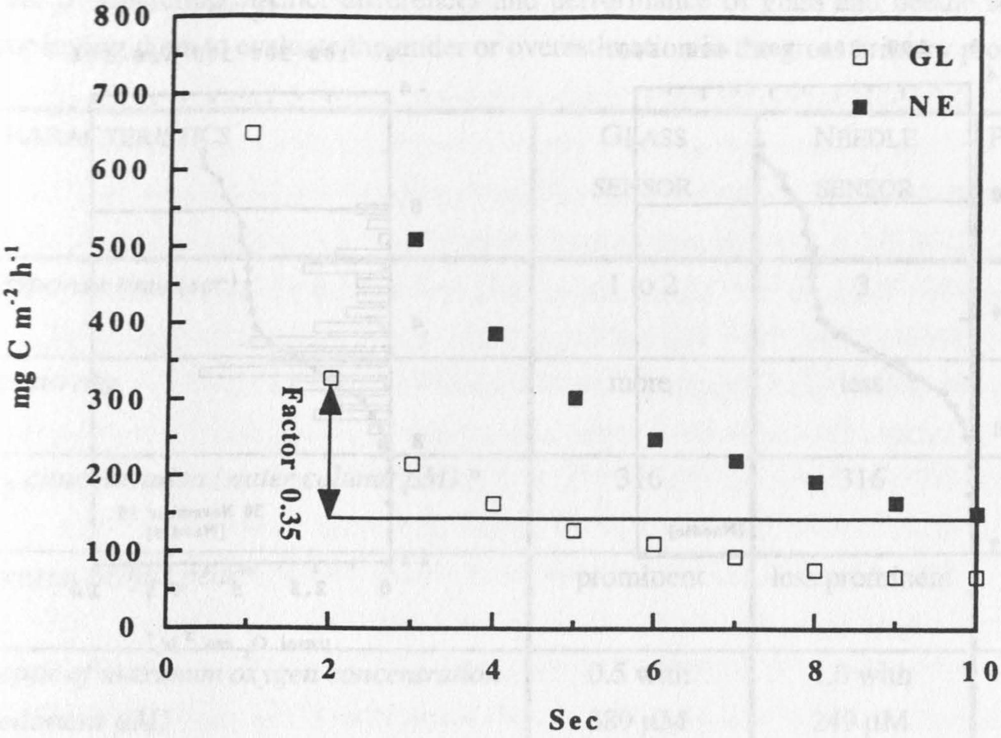


Fig. 25: Gross primary production (mg C m^{-2} h^{-1}) measured with needle and glass microprobes Vs time (sec). Plot shows the underestimation in the gross primary production by mean factor 0.35, when the sediment was incubated for 10 sec at each depth interval instead of 2 sec. Average incident light intensity = 53 Wm^{-2}; temperature 4.3 - 5.3 °C.

3.2.4.4 DISTINCTION BETWEEN THE OXYGEN PROFILES MEASURED BY GLASS AND NEEDLE MICROSENSORS

The major differences observed amongst the microprofiles measured by both the sensors are depicted in Fig.: 26 and Tab. 5. A prominent O_2 peak of 389 µM at 0.5 mm sediment depth was measured when the glass microsensor was employed, while maximum O_2 concentration of 249 µM at 1.0 mm depth was recorded with the needle sensor. However, no prominent peak was obtained by this microsensor. Peak rates of photosynthesis in the most active layer measured by both the sensors were of similar magnitude (glass 6.4 µmol O_2 cm^{-3} h^{-1} at 3 mm; needle 6.5 µmol O_2 cm^{-3} h^{-1} at 5.5 mm). The only distinction was evident in the depth where these respective peaks existed. Besides this the oxygen concentration within the sediment measured by the needle was factor 1.56 times less than the glass microsensor. Major differences accounted amongst both the sensors have been summarized in the following Tab. 5.

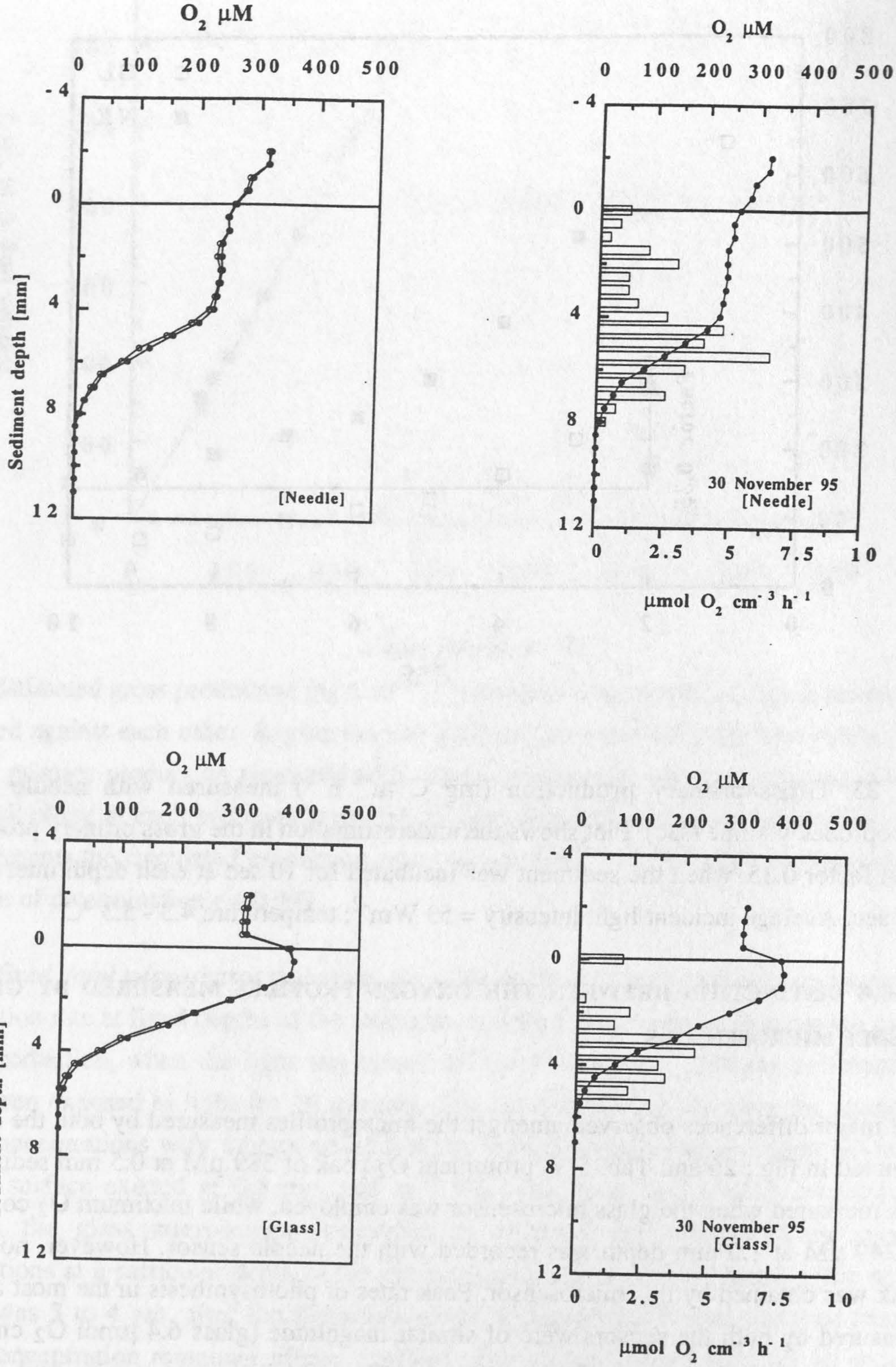


Fig. 26: Oxygen profiles during light and dark phase, and photosynthetic activity measured with needle and glass microsensor, with 10 sec of dark period within the sediment of Tirpitzmole. The porosity of the sediment was 0.48, the average incident light intensity was 53 Wm^{-2}. The temperature of water ranged from 4.3 to 5.3 °C. Oxygen concentrations during light (filled circles) and dark (open circles), photosynthetic activity (bars).

Tab. 5: Depicting distinct differences and performance of glass and needle sensors, while employing them to evaluate the under or overestimation in the gross primary production.

CHARACTERISTICS	GLASS SENSOR	NEEDLE SENSOR	PERFORMANCE OF NEEDLE SENSOR (FOLD)
Response time (sec)	1 to 2	3	
Sensitivity	more	less	
O_2 concentration (water column μM) *	316	316	-
*Oxygen profile peak**	prominent	less prominent	-
Depth of maximum oxygen concentration (sediment μM)	0.5 with 389 μM	1.0 with 249 μM	< 1.56
*Photosynthetic activity (μ mol cm^{-3} h^{-1}) and most active layer (mm)**	6.4 at 3 mm	6.5 at 5.5 mm	-
Oxygen production (μM) *	8	11	> 1.38
*Oxygen penetration depth (mm)**	5.5	8.0	> 1.45
*Photic zone (mm)**	5.5	7.5	> 1.36
Mean benthic primary production (mg C m^{-2} h^{-1}); 10 sec dark phase; n=3	77 ± 8.54	154.3 ± 12.66	> 2 overestimated
Mean benthic primary production (mg C m^{-2} h^{-1}); dark phase 2 or 10 sec; n=7	435.3 ± 95.22 2 sec	147.3 ± 23.68 10 sec	< 0.35 underestimated

* within same sample

4 DISCUSSION

4.1 EXPOSURE TO METEOROLOGICAL, HYDROGRAPHICAL & TOPOGRAPHICAL FACTORS

The western Baltic Sea is a channel like, strongly stratified, southernmost part of the transition zone between Baltic Sea and Kattegat. It is influenced by local winds, sea-level differences between Kattegat and Baltic proper, and also by baroclinic pressure gradient sustained by outflowing freshwater and inflowing saline water (FENNEL & STURM 1992). A prominent feature of the Baltic is the presence of seiches i.e. pronounced oscillations which are strongly stimulated by sea-level changes and wind stress conditions in the northern Kattegat. Due to these forced oscillations Kiel Bight gets "filled" and also "emptied" (WERNER et al. 1987, LASS & MAGAARD 1996) from time to time. However, both the study locations during the studies were dominated by southwesterly winds. These easterly and southerly winds along with the wind velocity play a key role in regulating different parameters i.e. salinity, oxygen concentration, nutrients etc. in the Kiel Fjord. North easterly winds are connected with high sea-level, while south westerly with low sea-level. However, this does not holds always true and should be applied cautiously, as the changes in sea level are delayed to the changes in the wind vector.

4.1.1 SEDIMENT CHARACTERISTICS

Shallow-water environments are extremely dynamic (JING et al. 1996), associations of micro- and macro-habitats, each performing its own role, but all interacting in a unity as material for energy transfer among themselves (ABOOD & METZGER 1996).

Populations of microphytobenthos living on tidal flats and shallow water localities are exposed to the water currents and waves which transport sand and generate ripples. Sediment stability, water currents (ADMIRAAL 1984, DE JONGE & VAN DEN BERGS 1987, SUNDBÄCK & JÖNSSON 1988, DELGADO et al. 1991b) and sediment type (AMSPOKER & MCINTIRE 1978, LÄNGE & LENZ 1980, PATERSON & UNDERWOOD 1990) etc. may be important parameters influencing the development and the growth of the microphytobenthos. Sediments with small grain-size allow only limited light penetration, and thus are not suitable for colonisation of cyanobacteria, but the rapidly moving diatoms adapt well in such environments (PATERSON 1989, PINCKNEY & ZINGMARK 1991). Subsequently, growth and metabolism of micro-organisms in coastal sediments have been conceived to influence sediment transport as well as coastal morphodynamics (PATERSON 1989, YALLOP et al. 1994). On the other hand, colonization of sediment particles and excretion of extracellular polymeric affect the sediment erodibilty (DADE et al. 1990).

During the present study, it was observed that the characteristics of sediments e.g., sediment movement, sediment type, water content, influence of wind and water turbulence due to shallow depths, caused frequent sediment resuspension, and also affected the distribution of benthic diatoms in the sediment thereby directly affecting the benthic primary production. The sediment analysis depicted that the mean grain size at both the sites ranged from 0.214 to 0.514 mm (see Section 3.1.6.1). Similar results have been reported in the sandy beach sediments of the Kiel Fjord and Kiel Bight earlier (KARG 1979, MEYER-REIL et al. 1980). Moreover, variations in the mean grain size are more dependent on location than on seasonal variations (MEYER-REIL et al. 1978). Fine sediments at station Tirpitzmole (T) were influenced by smooth swash actions of waves with little turbulence, hence providing more suitable habitat for the beach flora and fauna than at Mönkeberg (M). Increasing particle size with harsh swash climate not only affected the species composition but also reduced their number and size. Similar observations were also made by (MCLACHLAN 1996).

During the studies, higher porosity was accounted during 1995 than in 1994 at both the research sites (M & T). Nevertheless, station T showed relatively higher value than at its counter part M (see Section 3.1.6.2). This could be attributed to the fact that station T was a sheltered station with less influence of wave action, while M was an exposed one with greater influence of wave action. The amount of variability at a location that can be ascribed to any single factor varies with season (VAN ES 1982), as well as with the mean grain size of the sediment (DAVIS & MCINTIRE 1983, SHAFFER & ONUF 1983). Similarly, the relative importance of these variables can differ between adjacent habitats (SULLIVAN & MONCREIFF 1988, PINCKNEY & ZINGMARK 1993a). This might be due to varied grain sizes and their arrangement, investigated at both the stations. It was clear from the investigation that porosity depended upon the size, sorting and packing of the sediment, the finer the sediment the lesser are the chances of the still finer particles filling the voids, as also reported by CRISP & WILLIAMS (1971), MCLACHLAN & TURNER (1994). However, depending upon this, station T showed higher porosity. It was recorded from the present study that the porosity at both the locations was maximum during June 1995, which might have been on account of the calmer prevailing conditions, with well sorted grains. From earlier studies, it is well known that there tends to be an increase in porosity with the decrease in mean grain size (WEBB 1958).

4.1.2 RESUSPENSION

Resuspension can be a quantitatively an important mass flux (MACINTYRE et al. 1996) in the shallow water ecosystem. Benthic diatoms are the major component of the microphytobenthos, inhabiting in the boundary layer between the sediment and the water, hence are susceptible to resuspension (DE JONGE 1994). Resuspension may be caused by winds (PEJRUP 1986, DE JONGE 1992, ARFI et al. 1993, ARFI et al. 1994), tides (SANFORD et al. 1991, LITAKER et al. 1993) and anthropogenic activity e.g. dredging (DE JONGE 1994, MACINTYRE et al. 1996) and boat traffic (ANDERSON 1976). In aquatic environments, it plays a pivotal role by cycling the sediments, nutrients, carbon and contaminants (SANFORD 1992).

Sediment surface, particularly in shallow tidal waters may be disturbed by turbulent water currents, especially those generated by wind waves regulate resuspension (DELGADO et al. 1991a). The degree of disturbance depends upon sediment type and hydrodynamic conditions (e.g., water currents, sea level, wave height) and influenced by macrofaunal abundance and their activity. It is impossible to judge the impact of a single parameter responsible for resuspension due to different frequencies with which these factors interact with each other. Higher percentage of suspended matter at both the locations in the Kiel Fjord was predominantly influenced by wind induced wave and tidal resuspension. Tides play only a minor role in the western Baltic Sea ranging *ca.* 10-15 cm (LENZ 1977). Still, the impact of tidal resuspension could be at times significant. However, effect of boat traffic at M cannot be neglected as it being more important.

In the present study impact of all these mentioned factors probably triggered resuspension at both the stations, but it was more pronounced at M as compared to T. Thus, a significant loss of microphytobenthos populations at both the sites might have also been due to the resuspension. As a result of which probably the cells were mixed in the water column. Similar results were also obtained by CADEÉ & HAGEMAN (1974), DEMERS (1987). Besides this, DE JONGE (1985) estimated that the total amount of benthic (i.e. pennate) diatom cells present in the water column of Ems Estuary can equal the total amount present in the 0.5 cm top layer of the sediments. Under higher angular velocity at the sediment surface, DELGADO et al. (1991a) found that maximum microphytobenthos resuspension in terms of cell numbers was up to 45 % , while sediment chlorophyll-a upto to 11% and 6% in the 0.5 mm top layer of the sediment. Despite this, in shallow waters under natural conditions resuspension begins with current velocities as low as *ca.* 10 cm s^{-1} (DE JONGE & BERGS 1987).

The role of these resuspended populations for the pelagic systems has been earlier discussed BAILLIE & WALSH (1980), ADMIRAAL (1984), DE JONGE (1985), DE JONGE & VAN BEUSEKOM (1992). Resuspended microphytobenthos may contribute significantly to the primary productivity in shallow water column (SHAFFER & SULLIVAN 1988), with an exception of St. Lawrence Estuary, where no change in the water column primary productivity was seen succeeding microphytobenthos resuspension (DEMERS et al. 1987). Resuspended microphytobenthos contributes, on an average, 30% of the Chl-*a* and annual primary production of the water column, in the lower reaches of the Ems estuary, while *ca.* 85% in the Dollard estuary (DE JONGE 1994). Consequently, from this it can be concluded that perhaps in the present study, due to resuspension at times less Chl-*a* and primary production was accounted.

At times, resuspension makes the overlying water turbid by transporting the cells into the water column and subsequently reducing the irradiance that penetrates the benthos and thereby indirectly affecting the primary production (MACINTYRE et al. 1996). On the other hand, the resuspended viable microphytobenthos in the water column might play an important role by enhancing the food chain efficiency of shallow water ecosystems, where at times phytoplankton biomass is relatively low specially during winters. This is in accordance with the observations made by GABRIELSON & LUKATELICH (1985) and DEMERS et al. (1987).

Turbid conditions were mostly observed during late summer, more often at Tirpitzmole (T) than at Mönkeberg (M). When the number of the stabilizers (microphytobenthos) is reduced due to grazing and nutrient limitation. The diatom films (thicker microphytobenthos population) help to increase the sediment stability, thereby suppressing resuspension of the sediment and diatoms (DELGADO et al . 1991a, MILLER et al. 1996). Therefore, chances of the remaining low microphytobenthos populations to be displaced and resuspended in the water column are greater at T (fine sand) than at M (coarse sand). In addition to this, finer particles are resuspended faster than the coarser ones. On the other hand, Station M predominately consisted of small episammic diatoms, living attached to sand grains and having capability to resist resuspension forces (DELGADO et al. 1991b). However, the sediment movement can also keep the sand grains free from diatoms (MEADOWS & ANDERSON 1968). But, as they are only tenaciously attached to the sand grains the chances to be resuspended due to frequent resuspension and being carried away to the deeper parts (SUNDBÄCK & JÖNSSON 1988) are higher than at T. In addition to this, as a consequence of frequent sediment instability and lower diatom abundance in the high energy habitats, the possibility of biofilms to remain intact is very low.

4.1.3 SALINITY

The diatom flora of the Baltic Sea is representative of low salinity conditions. Therefore, the distribution of diatom species along the Baltic Sea salinity gradient is determined more by their absolute salt tolerances than by their ability to tolerate salinity fluctuations (SNOEIJS 1994). He further confirmed that nearly all diatoms species in the Baltic Sea are cosmopolitan. Salinity becomes an important physical factor to diatoms in estuaries, by influencing the species composition and their abundance (HOPKINS 1964, MCINTIRE & OVERTON 1971, WHITING & MCINTIRE 1985, OPPENHEIM 1991, ASMUS & BAUERFEIND 1994, MONTI et al. 1996).

During the studies it was observed that maximum salinity occurred at both the stations Mönkeberg (M) and Tirpitzmole (T) in October, while low values of salinity were encountered during summer (see Section 3.1.5). Salinity variations (M: 10-19 PSU, T: 9-20 PSU) in this study are in accordance with the pervious studies performed in the Kiel Fjord. High and low salinity values during different months, in the present studies could be on account of it being influenced by easterly and westerly winds, which bring about salt rich water from Kattegat into the Kiel Bight. Nonetheless, the salinity record taken from the study sites, clearly depicts that salinity fluctuated frequently on account of shifting water, specially more at station M being an exposed station. Such shifts of water masses and salinity fluctuations were also observed earlier in reference to Kiel Fjord by OHL (1959), KÄNDLER (1959), KARG (1979), MOIGIS (1983) and STIENEN (1986).

In the present study, a weak correlation between salinity and density of benthic diatoms was found. Relatively low population of microphytobenthos among other factors could be as a result of low salinity values coupled with high temperatures and calm weather conditions in summer, which probably deceased the cell division capacity of the microalgae and lowered its photosynthetic activity. This is in accordance with the reports of COLIJN & VAN BUURT (1975), ADMIRAAL & PELETIER (1980a) that some benthic diatoms are inhibited by high summer temperature.

There is a possibility that such prevailing conditions were ideal for the growth of grazers, which might have suppressed the number of microphytobenthos cells during summer. Although, in the present study it seemed that a correlation existed between salinity and the cell number during summer i.e. with the decrease in the salinity there was a decrease in the cell number. Moreover, low salinity conditions coupled with low nutrient concentration (specially silicate) and high temperature were ideal for the growth and multiplication of ciliates and phytoflagellates e.g. *Heterosigma* sp. etc. Therefore, salinity alone may not be the single factor responsible for decrease in cell density. This is in accordance with the citations of SIMONSEN (1962), WENDKER (1990) who found that the species richness of the benthic diatoms was not affected by salinity in the Schlei Estuary (western Baltic Sea 3-18 PSU). Similarly, SNOEIJS (1994) reported that epiphytic diatoms as a group are not stressed by salinity in the Baltic sea. In the present study, it was also observed that with the maximum salinity value at both the stations, high number of cell were accounted. This could be on account of high tolerance against the salinity fluctuations as also experienced by ADMIRAAL (1977a), LÄNGE (1983). According to them, the estuarine benthic diatoms were able to withstand the salinity fluctuations. Consistent with other studies (MCINTIRE 1978, ADMIRAAL & PELETIER 1980b, OPPENHEIM 1991, UNDERWOOD 1994) who also accounted that different salinity promoted the domination of certain species at the expense of others in the mixed assemblages of epipelic diatoms in estuarine mudflat.

Furthermore, in an experimental study, Admiraal (1977a) accounted an insignificant impact of a wide range of salinity (4-60 PSU) on the photosynthetic rate of the benthic diatoms, measured as oxygen production. Besides this, ADMIRAAL (1977a), ADMIRAAL & PELETIER (1980b) noticed that the growth rate and photosynthetic activity of *Navicula arenaria, Navicula phyllepta*, *Gyrosigma fasciola* was retarded, in the salinity range below 2-8 PSU. This is in agreement with the presence of *Navicula* sp. and *Gyrosigma* sp. during the present study in the higher salinity variability period. Similar observations have been also made by GÄTJE (1992). Williams (1964) also accounted higher division rate (6-68 PSU) than at (1-2 PSU).

In the present study maximum Chl-*a* value and primary production was accounted between the salinity range of 15-17 PSU. In contrast, VAN ES (1982), COLIJN & DE JONGE (1984) accounted these from < 1 to 17 PSU in the Ems Dollard. On the other hand, RASMUSSEN et al. (1983) found maximum photosynthesis at salinities between 15 and 30 PSU and decreased to 37% at a salinity of 50 PSU. Distinction in the species composition and the diversity of microalgal assemblages at both the sites was probably related to the specific salt concentration of the overlying water. It has been also cited by MCINTIRE & OVERTON (1971), and WILDERMAN (1987).

4.1.4 ORGANIC CARBON

The supply of organic material is a major factor determining the structure and activity of benthic microbial communities (MEYER-REIL 1991). Coastal sediments may be a significant reservoir for the cycling of organic matter (BLACKBURN 1988, SEITZINGER 1988, LOHSE et al. 1996), the mineralization rate of which depends primarily on the quantity and quality present (BOUDREAU 1992, MIDDELBURG 1989, 1996). Organic sources of nitrogen are more significant for the microphytes inhabiting estuarine and marine sediments, rather than for the phytoplankton (ADMIRAAL et al. 1987). Benthic microflora constitutes a major source of organic input via primary production in the interstices (MCLACHLAN & TURNER 1994), while being insignificant at exposed beaches but are extremely important in sheltered areas (STEELE & BAIRD 1968)

Our results of the low Corg content are in accordance with the earlier studies conducted in the western Baltic Sea. ZEITZSCHEL (1964) reported low amount of Corg (0.58-1.45%) in the sandy sediments of the Baltic Sea. The presence of higher Corg content at station Tirpitzmole (T) could be attributed as it being calm, protected locality, consisting of finer sandy sediment which generally contain higher organic content (RIZZO & WETZEL 1985, RIZZO et al. 1992, RIZZO et al. 1996), higher microbial activity (due to the greater surface area for bacterial attachment of the fine sediments) and less influence of harsh windy waves causing sediment disturbances than its counter part Mönkeberg (M). This is in accordance to the reports of MEYER-REIL et al. (1980) who also found not only low values ranging from 0.43-2.40 mg g^{-1} but also higher microbial activity in the finer sediments of the Kiel Bight and Fjord. They further stated that Corg and microbial activity deceased with the increase in distance from the inner part to the outer part of the Kiel Fjord. BALZER (1978) also observed low Corg values ranging from 0.60-0.90 % in the Kiel Bight at 20 m sediment depth. High organic content in the sediment was mostly connected with an increase in the porosity.

Station T consisted not only anthropogenic waste matter (due to human activities and land waste) but might also be associated with enhanced nutrient concentrations i.e. NH_4+ or phosphorus releases. This is in accordance with RIZZO et al . (1996). The minimum value in the Corg content accounted during summer 28 June 1994 might have been due to enhanced bacterial activity and decomposition of the organic matter (see Section 3.1.7.1). However, it could also be speculated as a grazing affect of deposit feeding organisms (e.g., *Arenicola* sp., *Hydrobia ulvae*, *Pygospio* sp.) as also reported by VARELA & PENAS (1985). Interestingly, this decrease in the Corg was correlated with the fall in Chl-a content. A close relation between chlorophyll and POC (particulate organic carbon) existed as also observed by STEELE & BAIRD (1968). During both summers 1994-1995, Corg content remained around 0.2 % except for the minimum value discussed above. This relatively higher content could also be associated with the influx of dense populations of macroalgae such as *Enteromorpha* sp. and Sea grass *Zostera* sp. during these months, which might have got buried into the sediment as a result of slight intermixing. Similarly, DAVIS & MCINTIRE (1983) also accounted maximum organic matter during summer as a result of macroalgae.

Station M depicted relatively uniform concentration of Corg of (< 0.1%) in the period of investigation (see Section 3.1.7.1). This may be due to the coarser sandy sediments with lot of intermixing as a result of which most of the fresh organic matter is transported into the deeper parts of the basin, leaving behind coarse and clean sand. Moreover, in such sandy systems where there is low percentage of Corg, the living substance is of more importance as compared to the muddy sediments.

Interestingly, both the sites depicted low nitrogen content. Nitrogen is probably assimilated by the micro and macro algae at a faster rate or lost from the sediment either through denitrification, particle resuspension or mineralization processes as also mentioned by NIELSEN et al. (1995). Besides this, benthic nutrient remineralization is more dependent on nitrogen than on carbon supply (HARGRAVE 1980, GRAF et al. 1983). It has been demonstrated by KRISTENSEN & BLACKBURN (1987) that particulate organic nitrogen (PON) decay constants are 2-3 times higher than those for particulate organic carbon (POC). Furthermore, it has been also proved in anexic cultures (ADMIRAAL et al. 1984, 1986) that the benthic diatoms utilize amino acids as nitrogen source. Similarly, SEITZINGER (1988, 1990) speculated from her data taken from the Baltic Sea and 6 estuaries in the different parts of the world that 40 to 50% of the estuarine nitrogen load is retained by nitrification.

Station T depicted relatively higher C/N ratio than M, which may be due to the different location sites *(i.e. exposed and open, discussed earlier)*. In general the C/N ratio at both the study sites was found to be < 12 (see Section 3.1.7.2). The samples with values > 12 are probably be due to the significant contribution of the refractory organic matter i.e. detritus derived from terrestrial vascular plant material (BURRELL 1988) namely leaves, wood residues etc. (containing low nitrogen content cellulose and rich phenolic compounds and lignin). Similarly, POCKLINGTON & LEONARD (1979) accounted a C/N value of 20 in the innermost sediments of Saguenay Fjord (Quebec) on account of discharges of numerous wood and pulp directly into the Saguenay river. Moreover, higher C/N ratios ranging from 1.21-95.9 have also been accomplished in the sandy beach sediments of the Kiel Fjord and Kiel Bight by MEYER-REIL et al. (1980). In the Westerschelde Estuary, Middelburg et al. (1996) also found higher molar C/N ratios ranging from 13.2 to 22.3, while on their sandy station Bath mean C/N value of 15.4 ± 1.1, POC (Wt %) 1.5±0.5 and TN (Wt %) 0.11 ± 0.04 existed. On the other hand, in the present study the mean total nitrogen TN (wt %) ranged from 0.00 to < 0.01 at both the stations. The mean total carbon TC (wt %) varied from 0.15 ± 0.02 to 0.57 ± 0.32 at M, while from 0.08 ± 0.00 to 1.63 ± 0.01 at T, respectively.

Contrarily, in the mud flats relatively low C/N ratios (6-10) were accounted by CAMMEN & WALKER (1986) indicating a rapid recycling of the organic matter. The C/N value of 38 obtained on May 1994 after spring bloom sedimentation at station T indicated an effective remineralization of organic nitrogen or might have been due to some refractory material as mentioned earlier. Nonetheless, the contribution of macroalgae should not be neglected. It is possible that the macroalgae i.e. *Fucus vesiculosus*, *Ulvaria* sp. contributed to higher C/N ratios, specially during winter. GRAF et al. (1983), ABELE (1988) also accounted an increase in the OM content in the sediments of the Kiel Bight a result of macroalgae.

4.2 SPECIES COMPOSITION AND ABUNDANCE OF THE MICROPHYTOBENTHOS

4.2.1 ABUNDANCE, COMPOSITION AND PHYSIOLOGICAL ADAPTATIONS OF MICROALGAL COMMUNITIES

The microflora mainly consisted of pennate diatoms (both motile and epipsammic species) at both the stations, Mönkeberg (M) and Tirpitzmole (T) of the Kiel Fjord. Station M (sandy coarse sediments, exposed and high energy window) was predominated by small epipsammic grain-adhering diatoms, while T (fine sediments, sheltered and low energy window) often consisted of epipelic (often larger sized) motile diatoms. Protected habitats of these two locations with finer sand depicted higher cell density (STEVENSON 1984, WASMUND 1984, MACINTYRE et al. 1996) than open with coarse sand. However, MACLULICH (1987) found higher density and greater variety of microphytobenthos at exposed sites with more waves.

Temporal and spatial variations in the species composition and abundance are correlated with physical and biological factors i.e. light (ADMIRAAL 1977a, COLIJN & VAN BUURT 1975, KAWAMURA & HIRANO 1992), temperature (HOPKINS 1964, ADMIRAAL & PELETEIR 1980a, SNOEIJS 1989), salinity (MCINTIRE & OVERTON 1971, AMSPOKER & MCINTIRE 1986, UNDERWOOD 1994), sediment characteristics (AMSPOKER & MCINTIRE 1978, WHITING & MCINTIRE 1985, GÄTJE 1992, ASMUS & BAUERFEIND 1994), desiccation (MCINTIRE 1978 UNDERWOOD 1993), hydrodynamics i.e. water currents, waves (BAILLIE & WELSH, 1980, AMSPOKER 1977, COLIJN & DIJKEMA 1981, DE JONGE 1994), immigration rates (STEVENSON, 1984), organic pollution (SULLIVAN 1982, RIAUX 1983), nutrients (ADMIRAAL 1977d, SUNDBÄCK & SNOEIJS 1991, BRUNS 1994, HOLLINDE 1995), allopathic factors (DE JONG & ADMIRAAL 1984, SABUROVA 1995) which have a strong impact on the microphytobenthos assemblages.

Station Mönkeberg (M) showed as expected lower number of cells according to its exposed position, with sandy coarse sediment composition (see Section 3.2.2.1). It is subjected to more hydrodynamic processes i.e. abrasion, frequent resuspension of the cells in the water column due to the turbulent water currents and intermixing of the sediments. As a result of this, the viable cells are transported from the wave washed localities to the deeper sites leaving behind only coarser sand. Another reason for the lower cell number at M could be due to sand motion (SUNDBÄCK & JÖNSSON 1988, DELGADO et al. 1991b) and physical processes i.e. sediment intermixing due to harsh swash climate (i.e. water movement) and boat wash (ANDERSON 1976), which might damage microalgal cells and transport them into the deeper sediment layers. COLIJN & DIJKEMA (1981) reported 50% decrease in microphytobenthos biomass in the sediment top layer due to a storm event in April 1973. In high energy environments with well mixed sandy sediments, a uniform distribution of viable microalgae was accounted to tens of centimeters (STEELE & BAIRD 1968, FENCHEL & STRAARUP 1971, FIELDING et al. 1988, MACINTYRE et al. 1996). Contrarily, at Tirpitzmole (T) low energy station the microalgae was mostly found concentrated in the upper few oxygenated sediment layer.

The abundance of microphytobenthos found at T (sheltered, low energy window) could be due to finer sediment composition, low sea level, less turbulence and shear stress produced by strong winds and water currents or boat wash. As a result of these favourable environmental conditions, the mucilaginous films of muco-polysaccharides secreted by the microalgae on the sediment surface, stabilize and smoothen the sediment surface, thereby protecting them against the dynamic estuarine conditions i.e. erosion, stress, resuspension and scouring. These stabilizing properties of the microphytobenthos have been well observed in the laboratory (HOLLAND et al. 1974, DELGADO et al. 1991a) and in the field studies (FROSTICK & MCCAVE 1979, GRANT et al. 1986, PATERSON 1989). It may be possible that during unfavourable weather conditions the microphytobenthos (epipelic diatoms) might migrate downwards and hence protect themselves against the mentioned parameters. HECKMAN (1985) proposed that vertical migratory evolved as an adaptation to escape resuspension. Motile benthic diatoms are capable of rapid movement (1-25 $\mu m\ s^{-1}$), which varies from sediment type, location and time of the year (PINCKNEY et al. 1994). They further postulated that the migration was basically limited to the upper 3 mm of the sediment with *ca.* 33 % of the total biomass in the upper 1 mm undergoing migration. In contrast to this, JOINT et al. (1982), WASMUND (1984) found the vertical migration as deep as 15 mm. DELGADO et al. (1991a) suggested that vertical migration may provide "inoculations" of diatoms from deeper sediment and thus promote the development of new populations in surface sediments. STEVENSON (1984) found higher immigration (autogenic and allogenic enhancement) rates of diatoms at the protected areas which increased rapidly during the taxocene development compared to an exposed station.

The density of the microalgae varied spatially and temporally in the upper 0-9 mm sediment layers, being greatest in spring and autumn while least in summer. Similar peaks have been encountered by several authors (*mentioned later*). Microphytobenthos were homogeneously distributed in the upper sediment layers, depicting no signs of stratification at both the stations. In addition to this, viable cells were accounted uptil 9 mm. This could be an indirect effect of the physiological stress conditions i.e. fluctuating light intensities, water currents, desiccation, sediment intermixing resulting into deposition and renewal of attached diatoms to sand grains which probably prompted vertical and downward migrations of the microalgae more pronounced at Tirpitzmole (T) than at Mönkeberg (M). Thus, depicting a homogenous distribution in these sediment layers. Wasmund (1984) also found microphytobenthos to be homogeneously distributed in the upper 10 mm of sediment at an exposed station.

Dense population of microphytobenthos was found at 3-6 mm (see Section 3.2.2.2), which might be due to more sediment stability within this layer, or an impact of wind induced sediment erosion bringing about short term fluctuations. Furthermore, it can also be attributed that this sediment layer might be optimal for the microalgal populations as adequate light conditions, temperature and nutrient supply from the deeper sediment layers as a result of bioturbation prevail. Distinct differences in the species composition at both the stations existed which were presumably due to the degree of exposure affecting the granulometric composition of sediments or indirectly altering the chemical conditions of the habitat. Subsequently, inspite of an indirect impact of eutrophication the species composition has not been affected in the Kiel Fjord i.e. similar species were identified as reported earlier by KARG (1979) and BOOTH (1985), but a dramatic increase in the cell number has been observed.

Microalgae species stratification along the depth gradient was a common feature (i.e. genus dominating in the 0-3 mm was either absent or rarely present in the rest of the sediment layers or vice-versa), varied immensely at both the respective sites. The selectivity of taxa for specific depths has been observed (ALEEM 1950, ROUND 1961, SIMONSEN 1962, STEVENSON & STOERMER 1981). Such distributions might have resulted due to different physiochemical conditions along the depth gradients. Similar results were also accounted by STEVENSON & STOERMER (1981). In addition to this, it seemed that microalgae probably exhibits a phenomenon to orient themselves in the different sediment layers as per their light requirement (quality and quantity), even if the sediment is disturbed as a result of intermixing. Hence, light requirement could also be responsible for the differences in species composition with depth.

In the present study nutrients were not estimated, but there may exhibit specific patterns of variations that could influence microalgae distribution varying from species to species. Shallow water sediments are self-sustaining, where a major role in the nutrient regeneration for the marine ecosystem is mediated by the activity of benthic bacteria (MEYER-REIL 1987). As a result of microbial activity there is a regular release of the nutrients required by microalgae for their metabolism. Despite this, benthic microalgae are also reported to compete with the pelagic phytoplankton for the regenerated nutrient pool (SUNDBÄCK & GRANÉLI 1988). Sheltered beaches exhibit the highest nutrient concentration (MCLACHLAN & TURNER 1994). This could perhaps be attributed due to increased abundance of macrofauna which probably enhance the regenerated nutrients by bioturbation . This is in accordance with ALLER & YINGST (1985). The greater the interstitial water circulation and more rapid the flushing rate, the lower is the nutrient concentration. Furthermore, SUNDBÄCK & SNOEIJS (1991) observed in an experimental study that the addition of nutrient inorganic nitrogen (IN) and inorganic phosphate (IP) to the water column stimulated the microalgal growth and addition of N + P favoured larger cells. Major sources of the nutrient in the Kiel Fjord is the heavily polluted river Schwentine and smaller effluents from land, everyday ship traffic and rainfall (an important source of nitrogen). On the other hand, KAWAMURA & HIRANO (1992) found in Aburatsubo Bay that the seasonal changes in the density of benthic diatoms were not influenced by the inorganic nutrients.

Moreover, thick populations of diatoms were accounted, inspite of very low phosphate concentration. Moreover, SOMMER (1996) from his nutrient competition experiments conducted with periphytic microalgae from the Kiel Fjord concluded that diatoms were found to be dominant competitors at high Si:N ratios (N-limited conditions) and high Si:P ratios (under P-limited conditions). While blue greens (cyanobacteria) were dominant at low N:P ratios under low silicate supply. Furthermore, during his studies he also observed that the nitrogen source (ammonium or nitrate) did not affect the competition.

During summer relatively low number of viable cells were accounted, which could be due to grazing (VAN DEN HOEK et al. 1979, MCCLATCHIE et al. 1982, LÄNGE 1983, UNDERWOOD 1984, BAILLIE 1987). Probably, calm and sunny conditions, with low salinity were optimal for the multiplication of the grazers. The possibility for the summer decline could also be ascribed to nutrient limitation after the spring blooms. But, since the inner Kiel Fjord is greatly influenced by eutrophic river Schwentine, the chances of the nutrient limitation are precluded during summer (STIENEN 1986), who reported that during summer ammonium made up some 50% of the whole nitrogen load. In contrast, CHENG et al. (1993) recorded microphytobenthos peaks during summer. Moreover, ANTOINE & BENSON-EVANS (1985) also recorded higher cell counts during summer and lower ones during winter. However, they also observed the grazing impact of zoobenthos during the warmer months which reduced the total number of viable cells, although other environmental and nutritional conditions further favoured the growth and multiplication of the algal communities. On the other hand, the sediments inhabited by microphytobenthos depict lower rates of nutrients i.e. ammonium, phosphate, nitrate and nitrite release to the water column, thereby become rather sinks for nutrients than sources on many occasions (SUNDBÄCK & GRANÉLI 1988, NILSSON et al. 1991, RIZZO et al. 1992, 1996). Similarly, BRUNS (1994) speculated that nitrogen might have been be a limiting factor for the growth of microphytobenthos in late summer.

Dull light conditions, bad weather with rain, storms, higher sea-level and the resulting physical disturbances of the sediment (VARELA & PENAS 1985, DE JONGE & COLIJN 1994) or nutrient limitation i.e. silicate, might probably led to low cell counts at both the sites. However, this effect was more pronounced at M. May be as a result of abrasion, the tenaciously attached episammic diatoms to the sand grains were washed away by storm and waves as also reported in the other high energy habitats (MEADOWS & ANDERSON 1968, WEISE & RHEINHEIMER 1978, DE JONGE & VAN DER BERGS 1987). Contradictory to this, (MACLULICH 1987) accounted greatest density of cells during winter in an intertidal rock platform near Sydney (Australia).

Peaks obtained during spring and autumn (see Section 3.2.2.1) at both the sites were probably correlated to the calm weather conditions i.e. low sea level, less waves and currents, wind direction i.e. north easterly winds, sediment disturbances and rich in nutrients (ammonia, phosphate, silicate) which were probably optimal for the microphytobenthos growth. Under calm conditions, the phytoplankton in the water column could sink to the bottom and become incorporated into the microphytobenthos (MACINTYRE et al. 1996). At both the stations, the bloom began in March, reaching maximum in May. Similar seasonal pattern was also seen by COLIJN & DIJKEMA (1981), ADMIRAAL et al. (1982). Spring peaks were also accounted by SNOEIJS & KAUTSKY (1989), GÄTJE (1992). GrØntved (1960), TAASEN & HØISÆTER (1981), Riaux (1983), LÄNGE (1983), SUNDBÄCK & JÖNSSON (1988), ASMUS & BAUERFEIND (1994) found microphytobenthos peaks during spring and autumn.

The abundance of microalgae depends upon location, season and sediment characteristics, ranging usually from 10^5 to 10^7 cells cm^{-3} (MACINTYRE et al. 1996) within the upper 5 to 10 mm of the sediment surface layers. Benthic microalgae have much higher population densities upto (10^5 to 10^6 cells cm^{-2}) as compared to phytoplankton (TAASEN & HØISÆTER 1981, ADMIRAAL 1982, SABUROVA et al. 1995). In our studies, higher proportions of viable cells i.e. 45 to 4005 × 10^6 cm^{-3} were present at station T (sheltered, fine sand, less sediment flushing), as compared to M (exposed, coarse sand, more sediment flushing) varying from 17 to 1428 × 10^6 cm^{-3}. Higher cell densities were accounted as compared to other studies (i.e. KARG 1979, LÄNGE 1983, GÄTJE 1992). Moreover, studies of these authors reported higher cell counts in the finer sediments as compared to coarse sediments. Similarly, (HOPKINS 1963, 1964a) accounted mean cell counting values of 93 × 10^6 cm^{-3} and 694 × 10^6 cm^{-3}, respectively. This might apparently be related to the shallowness of the area, hydrography and may be an indirect influence of eutrophication (STIENEN 1986, GERLACH 1990) in the Kiel Fjord and Bight (STIENEN 1986, GERLACH 1990, HANSEN 1996). In an experimental study conducted on eutrophication, SUNDBÄCK & SNOEIJS (1991) found that nutrient addition to the water column stimulated the diatom growth. Despite of higher nutrient concentration in the pore water than the water column, the diatoms are not nutrient saturated.

The methods for sampling and processing of diatoms (quantitatively and qualitatively) have not yet been standardized (ASMUS & BAUERFEIND 1994) till date. On account of different methods adopted by various authors for counting i.e. fluorescent microscopy (FENCHEL & STRAARUP 1971), Utermöhl technique (UTERMÖHL 1958) and separating the microphytobenthos i.e. ludox-method (DE JONGE 1979), ultrasonification (COLOCOLOFF & COLOCOLOFF 1973), sieving method (present study), it becomes rather difficult to compare the cell counts of the different studies performed. The results either show an under- or overestimation. In spite of the methodological discrepancies, the general seasonal cycle (peak and fall) can be compared with the other studies.

Microphytobenthos vegetation changed continuously along the environmental gradients and time axis (see Section 3.2.2.3). The changes in the species composition along the depth gradient (0-3, 3-6, 6-9 mm) was a significant feature at both the study sites. On comparing the entire microphytobenthos species spectrum obtained in this study depicted interesting features, the diversity of genera was higher in spring i.e. the species prevailing in spring

(*Atheya decora*, *Cyclotella* sp., *Diploneis* sp., *Licmophora* sp., etc.) were either absent or rarely present in other seasons. Besides this, the same species of microalgae were seen in both the seasons. This might have been probably due to the physical and chemical gradients which are indispensable for their growth and survival. This type of population dynamics is indispensable for succession of the species as well as for speciation and hence plays a significant role for the food chain in the shallow water ecosystem. On the contrary, MACLULICH (1987) found the highest variation in summer.

Members of the family Naviculaceae were most dominant and highly adaptable, during all the seasons, at both the study sites as also reported by KARG (1979) in the Kiel Fjord. *Navicula* sp. was reported to be a most tolerant and ubiquitous genus under all the weather conditions, as also cited earlier by KARG (1979) and RIAUX (1983). In an experimental channel, WENDKER (1992) found *Navicula* sp. to be unaffected by different current velocities. KRAMMER & LANGE-BERTALOT (1986) also reported the same observation and explained it on account of gelatinous layers, which protected the algae. On the other hand, SUNDBÄCK (1984) noted *Nitzschia* sp., SUNDBÄCK & JÖNSSON (1988) *Navicula* sp. and *Nitzschia* sp. to be most dominant. While, GRØNTVED (1960) found *Melosira sulcata* and *Cyclotella caspia* to be the most dominant. Moreover, COLIJN & DIJKEMA (1981), WHITING & MCINTIRE (1986) and ASMUS (1992) observed *Achnanthes hauckiana* Grunow to be most dominant and tolerant species, whereas *Gyrosigma* and *Pleurosigma* sp. was reported by CAMMEN & WALKER (1986) for the sediment surface of a mudflat.

4.2.2 CHLOROPHYLL-A DISTRIBUTION

Microalgal biomass was expressed as concentration of Chl-*a* in the sediment. Chlorophyll-a is a bulk parameter, with a drawback that the cells containing higher or lower chlorophyll-a per cell cannot be distinguished. The seasonal variations of Chl-*a* concentration (10-291 mg $m^{-2)}$ during the study are within the same range as observed by COLIJN & DIKJKEMA (1981), RIAUX (1982), DAVIS & MCINTIRE (1983), VARELA & PENAS (1985), HOLLINDE (1995), and BROTAS et al. (1995), in the different intertidal ecosystems (Tab. 6). Moreover, is also comparable with the Chl-*a* content data accounted in the Kiel Fjord, by KARG (1979), MEYER-REIL et al. (1980) Kiel Fjord and Kiel Bight and SUNDBÄCK (1984) for sandy substrates in shallow water (< 1 m) of the western Baltic Sea.

The spatial variation in microbenthic biomass (Chl-*a* content) is related to sediment type (MEYER-REIL et al. 1980, LÄNGE 1983, SHAFFER AND ONUF 1983, SUNDBÄCK 1984, GÄTJE 1992, BROTAS et al. 1995) tidal height or sea-level (COLIJN & DIJKEMA 1981, DAVIS & MCINTIRE 1983, SHAFFER & ONUF 1983, BROTAS et al. 1995) and wave action (LÄNGE 1983, WASMUND 1984, MCLACHLAN 1996), resulting into variable values of Chl-*a* as obtained from the respective research areas in the present study. Moreover, there are other factors such as temperature, irradiation and resuspension, grazing which might have an indirect impact on the microalgal distribution and thereby affect the Chl-*a* concentration. The spatial distribution of Chl-*a* depicted low concentration on the exposed stations than the sheltered stations (CADÉE & HAGEMAN 1977, COLIJN & DIJKEMA 1981, MACINTYRE & CULLEN 1995, SUNDBÄCK et al. 1991, MACINTYRE et al. 1996). The main factors that are responsible for the such distributions are sediment type and sea-level.

Significantly, higher chlorophyll-a concentrations were accounted at station (Tirpitzmole) T, which consisted of finer sediments as shown by RIZNYK & PHINNEY (1972), COLIJN & DIJKEMA (1981), DAVIS & MCINTIRE (1983), SHAFFER & ONUF 1983, FIEDLING et al. 1988 and in calmer conditions with slack tidal currents. This correlates to the reports of GRANT et al. (1986) where also calmer weather of spring and summer might have enhanced the biological processes in controlling the dynamics of the chlorophyll sediment. Furthermore, at station T (sheltered station) the decrease in Chl-*a* content probably was not due to the disturbance by wave action, but rather due to the sediment turnover by animal activity this is in accordance with the assumptions of JOINT (1978). However, at Mönkeberg (M) which showed relatively lower concentrations of Chl-a, may be on account of coarser sediments and more degree of physical disturbance (HICKMAN & ROUND 1970, COLIJN & DIJKEMA 1981) or reworking of the sediments by wave action due to which the finer sediment particles are washed away and transported into the deeper sediments (GRAF et al. 1982) resulting into cleaner sand with coarse sediment.

The pattern of temporal variations of Chl-*a* was very much alike and depicted characteristic features. This is in accordance with COLIJN & DIJKEMA (1981), DAVIS & MCINTYRE (1983). Higher values of Chl-*a* were accounted during spring. Similar peaks were also obtained by JOINT (1978), COLIJN & DIJKEMA (1981), RIAUX (1982), DAVIS & MCINTYRE (1983), SHAFFER & ONUF (1983), VARELA & PENAS (1985), and in autumn (COLIJN & DIJKEMA 1981, DAVIS & MCINTYRE 1983, BROTAS et al. 1995). Peaks obtained during spring and autumn at both the sites are probably correlated with the calmer weather conditions i.e. low sea-level, less waves and currents, wind direction (north easterly winds), sediment disturbances and enough nutrients (phosphate, silicate, ammonia) which were probably ideal for the microphytobenthos growth. In accordance to this, UNDERWOOD (1984) found that the Chl-*a* concentration deceased with an increase in the intertidal height. Higher concentration of Chl-*a* was also accounted in spring (CAMMER & WALKER 1986). They further noticed a positive correlation between the Chl-*a* and bacteria cell number i.e. with the increase in the Chl-*a* the bacteria number also augmented vice-versa. Similarly, MEYER-REIL (1988) also observed that the benthic bacterial populations were immensely influenced by certain ecological situations and events i.e. phytoplankton blooms in autumn and spring. Most of the microphytobenthos populations show a biomass peak either in spring or summer. However, this does not always hold good i.e. LUKATELICH & MCCOMB 1986 accounted a peak in winter/spring. They further reported that the seasonal fluctuations were largely controlled by nutrient availability coupled with the light. In contrast to this, STEELE & BAIRD (1968) accounted no seasonal fluctuations on a sandy beach.

During the present studies, lower concentration of Chl-*a* was recorded during summer 1994-1995 at both the stations (see Section 3.2.3.1). However, during 1995 relatively higher concentrations existed than 1994. A weak correlation between the sediment concentration of Chl-*a* and temperature was noticed. In contrast to this, UNDERWOOD & PETERSON (1993) found a positive correlation in the Severn Estuary. Increase in Chl-*a* concentrations during summer months also have been reported by COLIJN & DIJKEMA (1981), ADMIRAAL et al. (1982) MONTAGNA et al. (1983), BROTAS et al. (1995), HOLLINDE (1995) in the estuarine sites. Summer declines in the microphytobenthos populations, thereby resulting into Chl-*a* fall, could probably be due to the consumption by grazers i.e. *Arenicola* sp., *Hydrobia* sp., Mussels (JOINT 1978). This was in correspondence to the earlier reports of DAVIS & LEE (1963), DAVIS & MCINTIRE (1983), where apparent depression of Chl-*a* with intact cores have demonstrated a remarkable effect of infauna on the microalgal abundance and production, which could account for this decrease in summer. The summer decline in the Chl-*a*. concentration could also be due to nutrient limitation or overcast sky and periods of high wind speed resulting into sediment intermixing. This is in accordance with DE JONGE & COLIJN (1994). Furthermore, according to FROSTICK & MCCAVE (1979) the microalgal biomass in the sediment was also affected by the interaction with the macrophytes i.e. *Enteromorpha prolifera* and *Zostera marina*, which at times (June and July) shaded the sediment by competition for space, thereby trapping large amounts of sediment locality. Analogously, at times both the stations were densely covered with dense patches of macrophytes (*Enteromorpha intestinelis, Fucus vesiculosus* and *Fucus serratus, Ulvaria* sp., *Zostera marina etc.)* which might have also been the cause for the decrease concentration of Chl-*a* . Besides this, at times these macrophyte patches made the rest sediment beneath them anoxic, revealing black spots at random places, with pungent smell of H_2S specially at station T. In addition to this, black spots were mostly found during the warmer months (June, July and August) and also at times during late winter (January) being significant feature of station T han at M. Similarly, black spots have also been noticed in the Wadden Sea (HÖPNER 1996).

The estimation of Chl-*a* in winter at both the sites revealed low concentration, while BROTAS et al. (1995) obtained maximum values in Tagus Estuary. Low values obtained might be due o low cell numbers on account of the unfavourable environmental conditions, namely low emperature and diminishing irradiance (RIAUX 1983), frequent harsh physical disturbances i.e. strong winds with rain which rupture coherent sediment layers stabilized by a film of diatoms (HOLLAND et al. 1974), thereby hampering the growth of microphytobenthos and

Tab.:6 Variabilities in sediment chlorophyll-a concentration (mg m^{-2}) in the different estuarine ecosystem. ‡ Estimated from a figure, * Chl-*a* in μg g^{-1}

Location	**Sediment type**	**Sediment slice thickness (cm)**	**Chlorophyll - a (mg m^{-2})**	**Source**
Loch Ewe, Scotland	Sand	2	< 0.1-19 μg g^{-1}‡*	Steele and Baird (1968)
S. W. England	Estuarine mudflat	0.5	25-80 μg g^{-1}*	Joint (1978)
Kiel Fjord, Germany	Fine-coarse sand	0.3	3-223	Karg (1979)
Kiel Fjord & Kiel Bight, Germany	Sand	0.7	0.10-2.94 μg g^{-1}	Meyer-Reil et al. (1980)
Dutch Wadden Sea, Netherlands	Sand & mudflats	2	10-240	Colijn & Dijkema (1981)
North Brittany, France	Estuarine-mudflats	0.5	25-250	Riaux (1982)
Netarts Bay, Oregon, USA	Sand Silt	1	10-130 30-320	Davis & McIntire (1983)
Elbe Estuary, Wadden Sea	Mud Muddy sand Sand	1	300 270 90	Länge (1983)
Mugu Lagoon, California	Sand & mudflats	0.5	5-50 μg g^{-1}*	Shaffer & Onuf (1983)
Falsterbo Peninsula, SW Sweden	Sand	0.5	23-258	Sundbäck (1984)
Mikolajskie Lake	Shallow litoral zone	1	1-114	Wasmund (1984)
Ria Arosa, Spain	Sand flat	1	25-100	Varela & Penas (1985)
Elbe Estuary, Wadden Sea	Sand Mud	0.5	27-185 3-818	Gätje (1992)
Ems-Dollard Estuary, Netherlands	Sand & mudflats	0.5	< 10-420 ‡	de Jonge & Colijn (1994)
Sylt-Rømø Wadden Sea, Germany/ Denmark	Sand Mixed sand Mud	*ca.* 10	5-278 28-208 14-486	Hollinde (1995)
San Antonio Bay, TX USA	Sand	0.2	1-15	MacIntyre & Cullen (1995)
Tagus Estuary, Portugal	Estuarine flats	1	20-300	Brotas et al. (1995)
Kiel Fjord, Germany	Sand	1.2	10-291	Present study

resuspend or transport of the diatoms into deeper water depths. A pattern of low Chl-*a* concentration has also been reported by LÄNGE (1983), GÄTJE (1992). Similarly, these factors might have led to the decrease in Chl-*a* concentration during autumn after the peak.

It is, however, interesting to note that under the overcast weather with low sea-level higher Chl-*a* concentrations perceived at both the study sites. This could be attributed on account of the reduced growth of microphytobenthos as on an overcast sky, due to which the cells tend to build up more pigments. Hence, the diatoms show vertical migration (PINCKNEY & ZINGMARK 1991) from the bottom to the top, to compensate for the reduced supply of incident quanta. These features are in good accordance with the peak of autumn.

At both the stations, there existed no stratification in the Chl-*a* of the upper 1.2 mm of the sediment. Chl-*a* was found down to 1.2 cm into the sediment with the Chl-*a* concentration being highest at 3-6 mm depth at both the locations. This is in good agreement to the results obtained by LÄNGE (1983), who also found maximum Chl-*a* concentration at 5-7 mm sediment depth in the sandy sediments while in the finer sediments at 3-5 mm. In addition to this, GÄTJE (1992) also accounted a homogenous chlorophyll-a distribution in the uppermost 0-5 mm of the sandy sediments. Moreover, it also appeared the microalgae tends to compensate for their low levels of light reaching the deeper sediment layers by incorporating higher pigments. Probably, due this higher amount of Chl-*a* was also accounted in the deeper sediment layers. At the same time, in such systems the microalgal mixing in the upper sediment layers is faster as compared to its degradation. Subsequently, considerable amount of Chl-*a* was found at 3-6 mm sediment depth. This may be due to the intermixing of the sediment by water currents and waves that generate sediment transport by bed-load (moving sand ripples) and suspension transport. According to SUNDBÄCK & JÖNSSON (1988), DELANGO et al. (1991b) such transport processes and especially that of sand may influence the development of the microphytobenthos in various ways. As a result of these processes the upper 0-3 mm sediment layer gets disturbed and to avoid such sediment instabilities the microphytobenthos simply migrate to the layer where they can probably get adequate light conditions and sufficient nutritional supply (N and P) from the deeper sediment layers as a result of remineralization processes.

Besides this, a homogenous distribution of Chl-*a* was also observed at deeper depths. Similar observations were also accounted by PEEKEN (1989). Moreover, SKJOLDAL (1982) also found uniform contents of Chl-*a* and ATP in the uppermost 2 and 4 cm. As it is well known in the shallow water systems, the upper most layers are mostly well mixed due to the wave action. In the laboratory experiment, JENNESS & DUINEVEILD (1985) showed that a constant velocity of 20 cm s^{-1} at 15 cm above the sediment surface was sufficient for the ripple formation and incorporating the algae into the sediment to a depth of 5 cm, when the algae was introduced into the system at this particular velocity. This reworking of the sediment fraction and the associated microflora regulation by wave action, results in the microalgae migration into deeper depths as a result of which a homogenous distribution of Chlorophyll-*a* prevails. Similar homogenous distributions at sheltered and exposed stations have also been accounted (MACINTYRE AND CULLEN unpubl. data in MACINTYRE & CULLEN 1995). In an experimental study, MACINTYRE AND CULLEN (1995) found physical mixing over periods of less than 24 h was responsible for the homogenous distribution of chlorophyll.

The presence of Chl-*a* at deeper depth 1.2 cm is comparable to the studies of HOPKINS (1963), STEELE & BAIRD (1968), LEACH (1970) where they also found the functional Chl-*a* far below the euphotic zone, which was in sediment 2 to 5 mm depth (TAYLOR & GEBELEIN 1966, FENCHEL & STAARUP 1971), or 10 mm (DAEHNICK et al. 1992) upto 7 cm (MEADOWS & ANDERSON 1968, VARELA & PENAS 1985). The presence of Chl-*a* in the deeper sediment layers could be explained due to intermixing of the sediment stimulated by bioturbation, (resuspension i.e. wind-and tide driven currents) which could drag the microalgal cells into the deeper sediment layers. Moreover, such episodic events resulting into intense sediment shuffling might be a regulating factor responsible for the microflora deposition below the mixed layer, as a result of which the flora is either transported on the sediment surface or could be dragged into the deeper sediment layers. Living cells were found in deeper layers of the sediment to be viable for long periods of time (ADMIRAAL 1984) or the capability of heterotrophic assimilation microalgae (LEWIN & LEWIN 1960, DARLEY et al. 1979, VARELA & PENAS 1985). The occurrence of such viable buried cells represents a vital source of potential photosynthetically active populations (CADÉE & HAGEMANN 1974, FIELDING et al. 1988). Furthermore, BROTAS & SERÔDIO (1995) found Chl-*a* higher burial rates v (0.23-0.31 mm d^{-1}) and lower decay rates k at the sandy stations. Perhaps, this might hold true for our stations too. Nevertheless, the burial rate is greatly dependent upon the systems characteristics i.e. currents and the type of fauna present. MAHAUT & GRAF (1987) found the burial rates of tracers (0.14-0.16 mm d^{-1}) in the Baltic Sea due to bioturbation.

Qualitatively similar seasonal fluctuation trend amongst Chl-*a* and cell counts representing some relationship was accounted at both the stations and a correspondance between both the parameters was seen (FENCHEL & STRAARUP 1971, HICKMAN & ROUND 1970, RIZNYK & PHINNEY 1972a). Both the stations revealed varying values of Chl-*a* concentration, nevertheless the same trend in their spatial and temporal patterns was observed. M with coarse sediment showed relatively lower chlorophyll concentration than T. Which could be attributed as at T, the benthic microflora might compensate for lower light levels reaching the sediment surface by incorporating higher concentrations of pigments into the light harvesting complexes, i.e. higher Chl-*a* per cell content (BRODY & EMERSON 1959). In aggreement with this interpretation, SHAFFER & ONUF (1983) found the concentrations of chlorophyll-a in the fine sediments to be double and triple than in the coarse sediments.

On comparing the seasonal changes accounted in the Chl-*a* by various authors, it can be deduced that in the colder regimes such variations are of shorter duration, while with the increase in the latitude such variations are either absent or exist irregularly. As also cited by BROTAS et al. (1995), MACINTYRE et al. (1996). More reliable estimates of biomass, or preferably biovolume, can be gained by cell counts paired with Chl-*a* data. However, due to the difficulty in calculating the biomass from microphytobenthos, the use of cell-counting in most of the investigations is impractical. Despite variability in the relations amongst Chlorophyll-*a*, biomass, and cell abundance. Chlorophyll-*a* provides a useful index of the photosynthetic potential of a population and gives a sufficiently accurate estimate of biomass for these studies (UNDERWOOD & PETERSON 1993, BROTAS & SERÔDIO 1995, MACINTYRE et al. 1996) or marker for the diatom biomass (KOWALEWSKA et al. 1996).

4.2.3 CARBON TO CHLOROPHYLL-A RATIO

Carbon/Chlorophyll-*a* or C:Chl-*a* ratios could be applied to determine the microphytobenthos biomass fluctuations expressed as carbon (DE JONGE 1980, DE JONGE & COLIJN 1994). Ratios of C:Chl-*a* (50-80) are commonly used to convert one biomass estimate to another (HARRIS 1986). According to DE JONGE (1980) the use of yearly C:Chl-*a* averages to estimate biomass could lead to errors of 34-50%. In addition to this, C:Chl-*a* ratios vary with the nutrient concentration, microphytobenthos populations and abiotic factors (DE JONGE 1980). This is a good reason for the variable C:Chl-*a* ratios found in the literature.

Furthermore, the major source of error in C:Chl-*a* ratios in this study was that it was impossible to determine how much of the organic carbon is living or detrital, due to lack of appropriate technique to differentiate amongst the two. Which is probably an obstacle in the benthos as well as that in the water column. Hence, the C:Chl-*a* ratios were calculated as mentioned earlier (see Section 2.7.7). C:Chl-*a* ratios estimated for the microphytobenthos ranged from 56-454 at Tirpitzmole (T), whereas at Mönkeberg (M) from 36-490, revealing seasonal variations, which were more prominent at M than at T (see Section 4.2.3). Higher C:Chl-*a* ratios estimated in this study as compared by DE JONGE (1980) were due to the methodological discrepancies. Station T showed higher C:Chl-*a* ratios indicating a higher amount of detrital matter derived from either dead algae or pigment derivatives than at M. Mostly the values found were below 120. Results accomplished in the present study are comparable to C:Chl-*a* ratios obtained by other authors i.e. 10-154 (DE JONGE 1980), 18.7-60.4 (GOULD & GALLAGHER 1990) etc. Values more than 150 were probably on account of the decrease in the Chl-*a* content (reduced growth rate) and increase in the cell-carbon. For some of the phytoplankton species GOLDMAN (1980) concluded that C:Chl-*a* ratios 150 or more were associated with relative low growth, while ratios of 40 were associated with relative high growth rate. Similarly, higher values were also accounted such as 55-500 (THOMAS & DODSON 1972).

Higher values found during summer at T could be an indirect impact of either nutrient limitation or increase in the Cyanophyceae members i.e. *Merismopedia* sp. (DE JONGE 1980). Furthermore, he stated C:Chl-*a* of Cyanophyceae (*Merismopedia* sp.) is relatively higher than that of the benthic diatoms. However, as mentioned earlier the possibility of nutrient limitation is unpredictable in the Kiel Fjord or in an Estuary.

Peaks obtained during spring might have been due to the increase in the biomass and deceased growth rate. Similarly, during spring bloom incubations GOULD & GALLAGHER (1990) found the lowest growth rates (0.06 d^{-1} and 0.09 d^{-1}) to be consistent with high biomass of 1.16×10^{-3} and 1.54×10^{-3} biomass and high C:Chl-*a* ratios (54.4 and 60.4), respectively.

In the present study, low C:Chl-*a* ratios < 50 depicted that the samples constituted mainly of the living microphytobenthos and were probably devoid of detritus, which is quite common feature of the sandy sediments as compared to the muddy sediments which contain high concentrations of the organic matter.

4.2.4 GRAZING

Marine meiobenthos are supposed to having a close trophic coupling with microbial communities GERLACH (1978), MONTAGNA (1984). Sediment bacteria and benthic diatoms are the most common producers in marine sediments and thus play a pivotal role in trophic linkages and secondary production ZOBELL & FELTHAM (1942), MONTAGNA et al. (1983), MILLER et al. (1996). Sediment diatoms are most suitable food for the meiofauna because of their apt size (SCHWINGHAMER 1981). In addition to this in Kiel Bight GRAF et al. (1983), MEYER-REIL (1983) found that the supply of organic material to be a dominating factor for determining the structure and the activity of benthic communities. The balance between consumption of microphytobenthos by macrofaunal grazing and resupply is a scale dependent phenomenon (GRANT 1983, 1985). Diatoms are the preferred food for most grazers and form the basis of food chains which are 'beneficial' to man (DOERING et al. 1989).

Grazing is an important factor in reducing diatom biomass VAN DEN HOEK et al. (1979), TAASEN & HØISÆTER (1981), MCCLATCHIE et al. (1982), UNDERWOOD (1984), ASMUS &

ASMUS (1985), BAILLIE (1987), KUWAMURA & HIRANO (1992), GÄTJE (1992), ASMUS & BAUERFEIND (1994), BROTAS et al. (1995). The impact of grazing on microphytobenthos depends not only on the abundance and distribution of the biotic components (grazers and burrowers) but also on the growth and transport of the microphytobenthos. Changes in the relative availability of benthic microalgae in the upper few mm of the sediments may be of importance to the foraging strategies of the surface deposit feeders (PINCKNEY et al. 1994).

The present study indicated that the cell number and chlorophyll-*a* (biomass), during summer was lower at both the locations (see Section 3.2.2.1 and 3.2.3.1). However, the concentration of mentioned parameters was relatively higher, at Tirpitzmole (T) than at Mönkeberg (M). Grazing and bioturbation could be the factor during the studies for these accounted low values. This has also been cited by COLIJN & DIJKEMA (1981), UNDERWOOD & PATERSON (1993b), ASMUS & BAUERFEIND (1994).

The density of deposit feeders (*Arenicola* sp., *Hydrobia ulvae*), suspension feeders (*Macoma baltica, Mya arenaria*), crustaceans, nematodes, polychaetes i.e. *Pygospio* sp. (Spionidae) at T, and at M (*Hydrobia ulvae, Macoma baltica, Mytilus edulis,* crustaceans) increased in summer. Hence, grazing could probably be a regulating factor responsible for the abrupt fall in the biomass peaks at both the stations, subsequently followed by an increase in the biomass. Such abrupt fall and increase in the pheopigment content was also observed by BROTAS et al. (1995). Station M was predominated by *Hydrobia ulvae,* while T by *Arenicola* sp. and *Hydrobia ulvae.* Specially during June and July, polychaetes *Pygospio* sp. (Spionidae) reached their maximum abundance at station T. Increase in the polychaete density during June was also experienced by STEPHAN (1980) in the Nordstander Watt. LÄNGE & LENZ (1980), and BROTAS et al. (1995) observed that microphytobenthos population was affected by *Hydrobia ulvae* .

The increase in grazing during summer can also be coupled with the low salinity concentration and high temperature as such conditions were optimal for their survival and reproduction. Besides this, GRAF (1983) reported that oxygen concentration to be also a vital factor, as macrobenthos and meiobenthos mortality during summer and autumn is controlled by its concentration. Despite of these assumptions, it is doubtful that grazing alone is responsible for these fluctuations in the biomass concentrations and cell numbers during summer. It is more likely that at times strong reductions in the microphytobenthos population (i.e. directly affecting the biomass) in the upper sediment layers might be connected with the hydrodynamic processes i.e. wind-induced waves. From the variations in the wind speed accounted during this study i.e. 17 June, 12 July 1994 (see Section 3.1.3), it can be concluded that the decrease in the microphytobenthos population might have been as a result of intermixing caused by wind induced waves. This accords with the findings of LÄNGE & LENZ

(1980), DE JONGE & COLIJN (1994). According to ADMIRAAL et al. (1988) when the microphytobenthos suspended into the water column, is subjected to planktonic grazing and filter-feeding macrobenthos prefer suspended microphytobenthos over phytoplankton. Research sites T and M revealed low biomass during winters. This could be accounted because of bad weather with rains and storms, resulting into physical disturbances of the sediments and also dull light conditions. Besides this, DELAGADO et al. (1991b) illustrated that the sand motion on its own can damage the microphytobenthos cells, thereby leading into a decrease in the biomass.

The high trophic relevance of microphytobenthos for meiofauna have been stressed by BLANCHARD (1991). According to MILLER et al. (1996), the decrease in the microphytobenthos population may be due to the meiofauna. Meiofauna are mostly considered to have metabolic demands at least at par with those of macrofauna in the sandflat community or shallow water system (MCINTYRE 1969, FENCHEL 1978). However, in contrast to this ADMIRAAL et al. (1983) reported no impact of meiofauna on the microphytobenthos in Ems-Dollard Estuary. In addition to this, GALLAGHER et al. (1983, 1990) concluded that the limiting resource for the competition between juvenile (meiofauna-size) polychaetes (the ampharetid *Hobsonia florida*) and oligochaetes were sediment diatoms.

According to MONTAGNA (1984) grazers are food selective, he also found that the traditional meiofauna taxa (nematodes, copepodes, ostrapods) prefered diatoms 8 times more than the bacteria. Similarly, some nematode taxa are known to prefer diatoms as food (TIETJEN & LEE 1973). The specialized herbivorous nematodes increased with the abundance of the diatoms in the sediment of the Ems estuary (BOUWMAN et al. 1984), revealing successional adaptation to the food spectrum. In laboratory microcosms, it has been shown that the growth rate of the microphytobenthos was stimulated by *Macoma baltica* grazing (JASCHINSKI 1989). Identical results were also obtained by ASMUS (1992) in the Wadden Sea, where the dominating role of *Achnanthes haukiana* was accounted to the grazing effect of *Hydrobia ulvae.*

Microphytobenthos is also a good source of food for the infauna feeding above the sediment surface. It was demonstrated by MUSCHENHEIM (1987a, b) and LEVINTON (1991) that facultative feeders often switch from deposit feeding to suspension feeding in response to flow and movement of the sediment particles.

The role of ciliates in benthic trophic-dynamics is well documented by FENCHEL (1969), FENCHEL & JØRGENSEN (1977) and SICH (1985). It is plausible that "selective grazing" between April and May might have resulted into succession of species. Due to which the relative frequency of *Navicula* sp. deceased and was subsequently replaced by *Cylindrotheca* sp. and *Nitzschia closterium* being long and spiny cells to defend themselves against the predators. Similar observations have also been made by ADMIRAAL (1977d) and GÄTJE (1992).

4.3 BENTHIC PRIMARY PRODUCTION AND ITS ECOLOGICAL SIGNIFICANCE

4.3.1 OXYGEN MICROPROFILE METHOD-ADVANTAGES AND DISADVANTAGES, NEW DEVELOPMENTS IN THE FIELD OF MICROSENSORS

In the present study, gross primary productivity was measured with the aid of the oxygen profile technique (REVSBECH et al. 1981, REVSBECH & JØRGENSEN 1983). A completely new approach "light-dark shift method" developed by REVSBECH et al. (1981) was adopted, to estimate benthic photosynthesis from oxygen measurements of the sediment. Due to several disadvantages to the oxygen exchange method (POMEROY 1959, PAMATMAT 1968, HARGRAVE 1969, HUNDING & HARGRAVE 1973) and bicarbonate tracer method (STEEMANN NIELSEN 1952), the oxygen microprofile method was adopted. The main source of error in the oxygen exchange method is that the rate of respiration and the chemical oxidation may not be identical in the light as in the dark (REVSBECH & JØRGENSEN 1981, EPPING & JØRGENSEN 1996). Moreover, the oxygen consumption rate may be higher in light than in dark (HUNDING 1973, COHEN et al. 1977). All these factors may then lead to underestimation of the benthic primary production. On the other hand, the bicarbonate tracer method (STEEMANN NIELSEN 1952) successfully used till date for the estimation of the phytoplankton primary productivity by incubating water samples in the light and dark with the aid of bicarbonate traced by ^{14}C. This method has been also used for microphytobenthos (GRØNTVED 1960, 1962, CADÉE & HEGEMAN 1974, 1977, LÄNGE 1983, COLIJN & DE JONGE 1984, MACINTYRE & CULLEN 1995). The major source of error in this method is the inaccuracy in determining the labelled and unlabelled HCO_3^- in the most active photosynthetically layer (REVSBECH et al. 1981).

Ever since the last decade, polarographic Clark-type oxygen microsensors have been extensively used in the study of microbenthic photosynthesis and respiration (REVSBECH & JØRGENSEN 1986a). Specially, in the marine sediments, REVSBECH et al. (1980) employed these cathode-type O_2 microelectrodes and further developed Clark-type oxygen microelectrodes with improved characteristics (REVSBECH & WARD 1983, REVSBECH 1989a). The utilisation of more insulated glasses and guard cathode has ameliorated the performance of the microsensors (REVSBECH 1989a, 1994). The O_2 microelectrodes have excellent measuring properties namely, a small tip diameter of < 10 μm, a 90% response time of < 1 s, and small stirring sensitivity of < 1 % (REVSBECH 1989a). Thus, all these features make O_2 microelectrodes ideal tools for their application in the aquatic environments (KLIMANT et al. 1995) as well as in benthic microbiology (GLUD et al. 1996).

Advantages of the microprofile method : (1) It is a fast technique, with simple equipment, leaves the sediment virtually undisturbed, and is most suitable for analyzing the diurnal variations in the photosynthetic activity (REVSBECH et al. 1981). (2) Unlike ^{14}C methods, this method is non-destructive and permits multiple measurements on the same sample over time (PINCKNEY & ZINGMARK 1993c). (3) Oxygen production rates and oxygen concentrations can be determined with high vertical resolution in 100 µm steps or less. In addition to this, repetetive measurements can be conducted in a few minutes due to its rapid response (HOFMAN & DE JONG 1993). (4) The most prominent feature of this method over the other methods is that all the measurements are performed within the photosynthetically active layer (REVSBECH & JØRGENSEN 1981). Furthermore, this method depicts rapid response of photosynthesis to the changes in irradiance (REVSBECH & JØRGENSEN 1983), thereby providing a useful means of elucidating the environmental influence on primary production (GRANT 1986). (5) It reflects simultaneous information about the thickness of the photic zone, O_2 dynamics within in the aerobic layer and other processes involved in the sediment, biofilms or boundary layer. A high spatial resolution of 2-10 µm-wide oxygen microelectrodes has enabled direct measurements of distribution and dynamics of the O_2 in the diffusive boundary layer (DBL), within the viscous sublayer above the sediment surface (JØRGENSEN & REVSBECH 1985, GUNDERSEN & JØRGENSEN 1990, GLUD et al. 1994). This may obstruct the O_2 availability to the benthic microbial communities. (6) A new method for measuring the community respiration (REVSBECH et al. 1989b, HOFMAN 1990, 1991) with the help of microelectrodes has been recently developed. Apparent sediment diffusion coefficient of oxygen in the porewater can be determined from the oxygen gradient measurements. The sediment oxygen consumption can be quantified through the mineralization and respiratory processes in the light and in the dark. (7) Furthermore, oxygen microsensors are not only an optimal tool for estimating the benthic primary production, but were also recently used in accounting the vertical distribution of benthic ciliates (BERNINGER & EPSTEIN 1995) in response to the oxygen concentration in the sediments of North Sea.

New developments in the field of microsensors: (1) Fiber-optic microprobes are also a new tool for studying the optical properties and distribution in the cyanobacterial mats (JØRGENSEN& DES MARAIS 1988) and sediments (LASSEN et al. 1992). (2) A new fiber-optic oxygen microsensor (microoptrode) based on dynamic fluorescence quenching has been developed to measure oxygen gradients in marine sediments and microbial mats (KLIMANT et al. 1995). Oxygen profiles obtained from the measurements with microoptrodes depicted a good correlation to profiles measured with oxygen microelectrodes. The presence of silicone overcoat makes the sensing tips flexible and hence are not readily breakable. Besides this, they can become an ideal tool for the coarse sediments superior to O_2 glass microsensor, if the response times are improved. Due to the relatively slow response time of 5-30 sec (KLIMANT et al. 1995) microoptrodes are not that ideal for the use in photosynthesis measurements, where response times < 0.5 sec. are required (REVSBECH & JØRGENSEN 1983). (3) Planer optrodes are a new tool for measuring O_2 dynamics in two dimensions at a high spatial and temporal resolution in the benthic microbial communities (GLUD et al. 1996). (4) To investigate the temperature distribution with high spatial resolution a new temperature microoptrode has recently been developed (HOLST et al. 1996). Subsequently, the first direct temperature compensated oxygen measurements in the aquatic films and sediments has been conducted with the aid of a special combination of a Clark-type oxygen microelectrode with a built- in- temperature microoptrode by HOLST et al. (1996).

Disadvantages of the microprofile method (1) A continuous supply of microsensors is required due to their fragile nature and they are also very expensive (REVSBECH & JØRGENSEN 1981). (2) Densely populated meio- and macrofauna at times could be an obstacle in the measurements due to their bioturbation and irrigation activity and thereby cause sediment instabilities of the oxygen microprofiles in the surrounding substratum (REVSBECH & JØRGENSEN 1986). (3) In comparison to the bicarbonate method this is an insensitive method. But to be sufficiently sensitive the microprofile method requires high photosynthetic rates per unit volume, preferably > 2 mmol O_2/ l· h (REVSBECH & JØRGENSEN 1986). In other words < 2 mmol O_2/ l· h approximately *ca.* 0.05 mmol O_2/ m^2· h cannot be measured accurately with this method. (4) The ^{14}C method gives an adequate information about the gross primary production, but microalgal respiration taking place is neglected. Furthermore, till today no such method *in situ* is available which could deliver both the data simultaneously. (5) Oxygen consumption rates cannot be obtained directly, the oxygen gradients measured have to be converted to fluxes using the appropriate sediment diffusion coefficient (HOFMAN et al. 1991). (6) Due to unstable environmental conditions namely wavering light intensities, drifting clouds in the outdoor experiments, which makes it difficult to get stable readings (REVSBECH & JØRGENSEN 1986), and could result into underestimation of the benthic primary production. Therefore, the experiments should be preferably conducted under simulated *in situ* laboratory conditions.

Looking into the discrepancies in the benthic primary production methodology, uncertainties and disadvantages with the oxygen exchange method and ^{14}C method, we opted to use oxygen microprofile method in this study. Nevertheless, it was not possible to measure the gross photosynthesis and oxygen consumption because of the sandy beach stations Mönkeberg (M) and Tirpitzmole (T) having mean grain size (0.214 to 0.516 mm), with the aid of O_2 glass microsensor, due to its fragile nature. Thus, we decided to employ oxygen needle electrodes, which are suitable for coarse-grained sediments exhibiting a good spatial resolution of 0.25 mm (HELDER & BAKKER 1985). Nonetheless, we were successful in achieving good and comparable results and oxygen consumption values for the shallow water systems of the Kiel Fjord (western Baltic Sea). Similarly, the needle electrodes have also been successfully employed for measuring oxygen profiles in the intertidal sediments (BROTAS et al. 1990).

4.3.2 MICROPHYTOBENTHOS: THEIR ROLE AS PRIMARY PRODUCERS AND ECOLOGICAL SIGINIFICANCE

There is a wide recognition that the primary production of benthic microflora is important in the shallow water (SHAFFER & ONUF 1983, CAHOON & COOKE 1992) and periodically flooded habitats (SHAFFER & ONUF 1983). The production in shallow waters is mainly contributed by microphytobenthos (GAŘGAS 1972, PLANTE-CUNY & BODOY 1987, MACINTYRE & CULLEN 1995, SUNDBÄCK et al. 1996). The microphytobenthos contributes a major portion to the primary productivity in a variety of shallow water habitats and add a vibrant pool of energy producers. Hence, they play a significant role in ecological food web and have been largely investigated for over the past 35 yrs (MACINTYRE et al. 1996) in different localities, as reported by KARG (1979), PEEKEN (1989), GÄTJE (1992), ASMUS & BAUERFEIND (1994), BROTAS & CATARINO (1995).

The microphytobenthos is indispensable as far as food source for benthic invertebrates is concerned e.g. ranging from protozoans, ciliates to the members of the meio-and macrofauna (MONTAGNA 1984, SUNDBÄCK & JÖNSSON 1988, SULLIVAN & MONCRIEFF 1990, MILLER et al. 1996). Regional distribution and the production of microalgae is basically dependent upon the seasonal variations and the environmental factors. Seasonal productivity in shallow waters elicits a seasonal pattern of activity in benthic community (GRAF 1989a). Moreover, the relationship amongst photosynthetic rate and photon flux in this study clearly depicted that the benthic microalgae were probably able to maintain maximum production over a wide range of fluctuating light intensities. This is in accordance with the results of RASMUSSEN et al. (1983).

Present research observations dealt with the benthic primary production in shallow waters revealed that a lower gross primary production of 571 ± 22 g C m^{-2} y^{-1} was accounted at M (exposed, with coarse sediment, more influenced by the hydrodynamic forces) than at T (sheltered, with fine sediments, with relatively less physical disturbances) with 640 ± 37 g C m^{-2} y^{-1}, respectively. Similarly, Karg (1979) found higher primary production values measured with the ^{14}C and O_2 exchange method at a sheltered station than at an exposed one in the Kiel Fjord. This is in accordance with the reports of CADÉE & HAGEMANN (1977), REVSBECH et al. (1988), PINCKNEY & ZINGMARK (1993a), IANNUZZI et al. (1996), MACINTYRE et al. (1996), SUNDBÄCK et al. (1996), who also reported higher primary production values at their sheltered station than at the open ones. In contrast to this STEELE &

BAIRD (1968), SHAFFER (1984) measured higher values at exposed stations. Our results are comparable to the results of other authors in Tab. 7.

Tab. 7: Values of microphytobenthos production measured at the various geographical areas with different techniques, ^{14}C: Bicarbonate method; O_2: Oxygen exchange method; ME: Oxygen microprofile method.

LOCATION	DEPTH [m]	HOURLY PRODUCTION [mg C $m^{-2} h^{-1}$]	METHOD	AUTHOR
Niva Bight, Denmark	> 0.5	135-290	^{14}C	Gargas (1970)
Wadden Sea, Netherlands	intertidal flats, <0.5	50-100 (winter) 100-1100 (summer)	^{14}C	Cadée & Hageman (1974)
Kiel Fjord, Germany	0.2-0.7	3-545 12-533	O_2 ^{14}C	Karg (1979)
Natarts Bay, Oregon	1.0-1.5	< 5-88†	O_2	Davis & McIntire (1983)
Kiel Bight, Germany	18	0.2-107	^{14}C	Schulz (1983)
Bay of Fundy, Canada	intertidal flats	10-800	O_2	Hargrave et al. (1983)
Elbe Estuary, Germany	<1	1-25	^{14}C	Länge (1983)
Ems Dollard Estuary, Netherlands	intertidal flats	1-120	^{14}C	Colijn & de Jonge (1984)
Chesapeake Bay, Virginia	0.9	< 2-170†	O_2	Rizzo & Wetzel (1985)
Ria de Arosa, Spain	intertidal flats 0.5	3-44	^{14}C	Varela & Penas (1985)
Barther Bodden, Germany	0.15-0.2	34	O_2	Wasmund (1986)
Laholm Bay, Sweden	2-5	max. 24	^{14}C	Sundbäck & Jönsson (1988)
Mittelgrund & Schleimünde,	6 to14	2.86 - 8.37	O_2	Peeken (1989)
Schleimünde, (Kiel Bight) Germany	6	18	ME	
Elbe Estuary, Germany	< 1	0-395	ME	Gätje (1992)
Nordsylter-WaddenSea	0.1	88-132	ME	Bruns (1994)
Tagus Estuary, Portugal	1-4	11-13	O_2	Brotas (1995)
Kiel Fjord, Germany	< 0.5	38-285 15-454	ME	This study

†Estimated from a figure

The mean integrated photosynthetic rates at Mönkeberg (M) were relatively uniform and ranged from 3.8 to 28.5 mmol O_2 m^{-2} h^{-1}, while at Tirpitzmole (T) 1.5 to 45.4 mmol O_2 m^{-2} h^{-1}. The photosynthetic activity ranged from 0.13 - 16.7 µmol O_2 cm^{-3} h^{-1} at M, while 0.06-18.2 µmol O_2 cm^{-3} h^{-1} at T. Our results are comparable with tidal flat sediments inhabited by pennate diatoms (REVSBECH et al. 1988) measured considerably lower photosynthetic activity, with the rates being only 6 µmol O_2 cm^{-3} h^{-1} while the integrated activity was 7 mmol O_2 m^{-2} h^{-1} than the finer sediments with 98 µmol O_2 cm^{-3} h^{-1} and 27 mmol O_2 m^{-2} h^{-1}. respectively. In the four cyanobacterial mats of Solar Lake, Sinai JØRGENSEN et al. (1983) found the total photosynthetic rate varying from 1.2-17.6 mmol O_2 m^{-2} h^{-1}, the photosynthetic rate within the mat was 0.53- 49 µmol cm^{-3} h^{-1}. In the Oosterschelde Estuary (Netherlands), HOFMAN et al. 1991, measured a production rate ranging from 10.6-18.0 mmol O_2 m^{-2} h^{-1} in April. BRUNS (1994) found integrated photosynthetic rates ranging from *ca.* < 1 mmol O_2 m^{-2} h^{-1} to 15.50 mmol O_2 m^{-2} h^{-1} in the different sediments and the photosynthetic activity varied from *ca.* < 2.3 - 55 µmol O_2 cm^{-3} h^{-1} in the different sediments of the Wadden Sea. In the Kiel Bight, PEEKEN (1989) accounted the integrated photosynthetic activity ranging from 1.659-1.925 mmol O_2 m^{-2} h^{-1} on April 1989, in the fine sediments of the Schleimünde at 6 m water depth. The photosynthetic rate within the sediment ranged from 0.00-88 µmol O_2 l min^{-1} on 30 April 1989. On the other hand, YALLOP et al. (1994) obtained 14-125 µmol cm^{-3} h^{-1} from all the profiles measured in Texel.

The maximum production during spring on 17 March 1995 at station Tirpitzmole (T) was 454.3 mg C m^{-2} h^{-1} with the total photosynthetic activity integrated for all the layers being 75.9 mmol O_2 m^{-2} h^{-1}, in comparison to M with 132 mg C m^{-2} h^{-1} and 14.3 mmol O_2 m^{-2} h^{-1} (see Section 3.2.4.1 & 3.2.4.2), respectively. The maximum oxygen concentration was found at 1 mm depth, within the sediment surface with the photosynthetic rate being only 3.9 µmol O_2 cm^{-3} h^{-1} at station T. The sediment temperature at both sites was 4.0 °C (see Section 3.1.2) and the mean light intensity was 58 Wm^{-2} *in situ* (see Section 3.1.1). High primary productivity found at T might have been due to the observed pale brown patches of thickly growing microphytobenthos tufts of *Navicula* sp., *Amphora* sp., *Fragilaria* sp. etc., with relatively higher viable cell counts. Similarly, REVSBECH et al. (1988) also cited that the benthic microalgae often depicted highest standing stock in early spring, before the grazers impact becomes significant. On the other hand, a slight grazing may also enhance the primary production by mobilization of nutrients (FENCHEL & KOFOED 1976).

Furthermore, on this specific day the oxic sediment zone at both the locations was relatively thick *ca.* 11 mm each (see Section 3.2.1.3). From this it can be concluded that the viable microphytobenthos were present in the deeper layers at M as well as at T, which holds good with the cell counts and Chl-a concentration at both the sites. Active upward migration of the benthic diatoms is a key mechanism for restoring the oxygenation of the sediment surface by photosynthesis (SUNDBÄCK et al. 1996). At Mönkeberg (M), the estimated benthic primary production was factor 3 lower than at Tirpitzmole (T), inspite of oxic zone being comparatively thick. Low primary production at M could be attributed to the scanty number of viable and photosynthetically active microphytobenthos cells in the sediment. The sediment intermixing caused by wave activity probably transported most of the diatoms into the deeper sediment depths. This was clearly observable from the peak rate of photosynthetic activity at 8 mm. Another reason could be the instability of the sediment, which is reported to be a major limiting factor for the benthic primary production (ADMIRAAL 1980, in REVSBECH et al. 1988).

In the sandy beach sediments of station T higher rates of integrated gross photosynthesis existed, consequently as a result of thicker photic zone and oxygen penetration depth, which may be due to the vertical migrations of microphytobenthos at various sediment depths in order to avoid the unfavourable weather conditions. In Texel, YALLOP et al. (1994) also accounted higher integrated gross photosynthesis as a result of greater photic zone and with bimodal peak rates of distribution, the maximum peak rates at both the stations were identical. Contrarily, the peak rates encountered at M and T were never identical.

During the present study, both the sites revealed higher gross primary productivity in summer 1994 as compared to summer 1995 (see Section 3.2.4.2). The higher productivity accounted on certain sampling occasions (M: 17 June, 28 July; T: 12 July 1994) at both the stations during summer 1994 was on account of thicker photic and oxic sediment zone (see Section 3.2.1.2. & 3.2.1.3). Whereas, low productivity during summer may be due to thin photic zone and oxic sediment zone, or grazing effects (*Hydrobia ulvae*, *Arenicola* sp., *Pygospio* sp. etc.) which probably resulted in sudden vanishing of algal blooms. On the other hand, one of the most common feature for the primary production limitation during summer is the water column turbidity, owing to resuspension (wave induced) of finer particles, microphytobenthos or sedimented phytoplankton, which at times can hinder the minimum required light for the microphytobenthos production, as only < 3 % of incident light is transmitted through the sediment (MACINTYRE & CULLEN 1995). However, the presence of the photosynthetically active microalgae well below the photic zone within the sediment has been mentioned earlier (PAMATMAT 1968, STEELE & BAIRD 1968, CADÉE & HAGEMAN 1974, RIAUX-GOBIN et al. 1993).

Observations taken in autumn on 22 September 1994 revealed that at T the sediment surface consisted of dense, dark green filamentous mats of cynaobacteria, with thick compaction of photosynthetic organisms e.g., *Navicula*, *Nitzschia*, *Amphora* sp. etc. with high oxygen concentration of 751 µM at 1.0 mm, which was factor 3 times higher than in the water column. In the shallow cyanobacterial mats (dominated also by *Navicula*, *Nitzschia*, *Amphora* sp. etc.) of Solar Lake in Sinai similar magnitude oxygen concentration peaks at 0.4 mm were found JØRGENSEN et al. (1983). On this particular day, low sea-level existed and the seawater had receded about 10 to 15 m away from the seashore. Despite of cell number, Chl-*a* concentration and oxygen production being high (see Section 3.2.4.1), the gross productivity was relatively low (45 mg C m^{-2} h^{-1}), under the mean *in situ* light intensity of 142 Wm^{-2} with cloud coverage. The low productivity was probably not due to the nutrient limitation as can be depicted from the thick population of microphytobenthos. As a result of low-level and dim light conditions the microphytobenthos migrated upwards (PINCKNEY et al. 1994) and formed thick patches, and reduced the oxic sediment zone to 4 mm. Subsequently, making the rest of the sediment anoxic.

Similarly, LASSEN et al. (1992a) observed that under dim light *Oscillatoria* sp. migrated upwards and a dense surface film of cyanobacteria developed. Phototactic migration, with different species-specific responses, may result in a surface maximum and microzonation of species and size (HOPKINS 1963, ROUND 1979a, b, ADMIRAAL et al. 1984). Low benthic production on the cloudy days is in accordance with the results of CAHOON & COOKE (1992). Consistent with this, MACINTYRE et al. 1996 stated that the total primary production enhanced with the irradiance. In addition to this, under the low light conditions the benthic microalgae have the ability to compensate for the lower levels of light reaching the sediment surface by incorporating higher pigment concentrations, i.e. higher chlorophyll a per cell content (BRODY & EMERSON 1959, SHAFFER & ONUF 1983). Station M depicted slightly higher gross production (62 mg C m^{-2} h^{-1}) which can be due to thicker oxic zone (7 mm) as a result of coarser sediment, uneven distributions of diatoms in the sediment layers due to the wave activity as compared to station T. In addition to this, microphytobenthos, response to incident radiation may be different with the locations (SHAFFER & ONUF 1983) as light is less likely to be limiting in coarse grained than at the locations with fine grained sediments.

On the other hand, station M indicated highest production during late winter (see section 3.2.4.2). The maximum gross productivity of 285 mg C m^{-2} h^{-1} in late winter (23 January 1995) seems to be unusual, but the careful examinations of the oxygen microprofiles as shown in Section 3.2.4.1 suggested that the production in January at M was not exceptionally high, as only 1.1 fold less oxygen concentration in the sediment existed as compared to the water column, indicating no production peak. In addition to this, a zig-zag pattern of profile was measured revealing that the photosynthetic rate within the most active layer being as high as 4.3 µmol O_2 cm^{-3} h^{-1} at 15 mm sediment depth. Moreover, thicker photic zone of 16.5 mm and oxygen penetration depth of 17 mm also existed. Higher rates of integrated gross photosynthesis of 26.3 mmol O_2 m^{-2} h^{-1} prevailed which may be due to greater photic zone (YALLOP et al. 1994) and thicker sediment oxic zone. Besides, a weak correlation between the O_2 penetration depth and the sediment temperature was accounted i.e. with the decrease in the oxygen penetration depth an increase in the sediment temperature was evident (see Section 3.2.1.4). Similar correlation revealed by GÄTJE (1992) in the Elbe Estuary.

From all the mentioned parameters, it can be attributed that hydrodynamic forces (MCLACHLAN & TURNER 1994, IANNUZZI et al. 1996) namely strong south westerly gales with mean wind velocity of *ca.* 7 m/sec (see Section 3.1.3) kept the exposed sandy beach sediments oxygenated and hence causing sediment instability (VARELA & PENAS 1985). Such harsh weather conditions were probably responsible at both the stations (M & T) in transporting the viable microalgal cells from the photic zone into the deeper (aphotic) sediment layers hence reducing the cell number. Similar observations were also made by CADÉE & HAGEMANN (1974), BAILLIE & WELSH (1980). Moreover, they can survive the long dark periods without damaging their photosynthetic capacity (ADMIRAAL 1984d, SUNDBÄCK & GRANÉLI 1988). Such continuous sediment intermixing might have resulted in the distribution of the microalgae (in and out, up and down) as well as of oxygen in the deeper sediment layers (PINCKNEY & ZINGMARK 1991, PINCKNEY et al. 1994). Furthermore, sediment transport plays a vital role in the microdistribution of the diatoms and may limit to the primary production (GRANT et al. 1986). Thus all these factors were responsible for the higher gross production at both the sites during winter. The high winter production rates especially demonstrated that light and temperature were not the limiting factors at both the sites. This is in accordance with BRUNS (1994).

4.3.3 IMPLICATIONS OF THE BENTHIC PRIMARY PRODUCTION

Furthermore, the microlagal productivity in winter may especially be of importance to other trophic levels as the decomposition processes are highly temperature dependent. Thus, the possibility of organic matter availability from detritus may be limited (RIZZO et al. 1996) in winter. The high gross primary productivity in January is not correlated with the low *in situ* irradiance (42 W m^{-2}). The importance of light relative to temperature in benthic primary production is less clear (GRANT 1986). Light conditions, such as intensity of light and photoperiod are important influencing environmental factors for the photosynthetic rate and growth rate of marine benthic diatoms (COLIJN & VAN BUURT 1975, ADMIRAAL 1977g, ADMIRAAL & PELETIER 1980a). Inconsistent with this, MACINTYRE et al. (1996) stated that the net primary production will only be significant, where there is adequate light reaching the sediment surface and above the compensation irradiance, primary production is expected to increase with the increasing irradiance. Interestingly, in this study no significant relationship between the primary production and total solar radiation was found. Similar results were obtained by VARELA & PENAS (1985). The photosynthetic rate of benthic microalgae living on the sediment surface is not affected by the light energy as also indicated by RASMUSSEN et al. (1983). The minimum sky irradiance in the field mostly exceeds the minimum light required by the microphytobenthos for their saturation (RASMUSSEN et al. 1983). Moreover, in laboratory experiments it has been demonstrated (COLIJN & VAN BUURT 1975) that there existed no correlation amongst irradiance and photosynthetic rate, especially, when the minimum saturation requirements exceeded a saturation level of 11-25 Wm^{-2} (COLIJN & DE JONGE 1984). In agreement with this (ADMIRAAL 1984d, RIVKIN & PUTT 1987b) found that benthic diatoms are able to compensate for low irradiance values by utilising organic substances. Besides this, the P-I parameters indicated that benthic microalgae are well adapted to their variable and stressful environmental conditions (BLANCHARD & CARIOU-LE GALL 1994).

4.3.4 RELATION OF MICROPHYTOBENTHIC PRIMARY PRODUCTIVITY TO THE ENVIRONMENTAL PARAMETERS

The physical removal of the sediment has also been recognized as an important limiting factor for microalgal production (RIZNYK et al. 1978). At Mönkeberg (M) the sediment disturbances caused during the summer due to the human activity, while at Tirpitzmole (T) clams and cockles should also not be ignored. Similar type of sediment disturbances have also been cited by VARELA & PENAS (1985). In addition to all these parameters at both the study the newly deposited fine material on the surface of the sediment as a consequence of sediment intermixing and wave action, could shadow the microflora beneath it. Thus, shadowing impact (VARELA & PENAS 1985) could relatively reduce production values, as the non-motile episammic diatom flora are not able to move upwards through the newly deposited material. Besides this, low gross productivity at M & T during the summer months may also be due to enhanced respiration rates. HICKMAN & ROUND (1970), RIZNYK et al. (1978) and SHAFFER (1984) also found lower net photosynthetic as a result of higher rates of respiration.

Observations in the literature suggest the roles of light, temperature, and nutrient limitations for benthic algal primary production (CAHOON & COOKE 1992). In addition to this, changes in the environmental variables within a season are as important as seasonal shift in determining the shape and magnitude of peaks in biological rates (GRANT 1986). A seasonal shift in the photosynthesis response to temperature by benthic microalgae has also been noted previously (PAMATMAT 1968). Higher values of productivity at both the regimes were encountered during winter and spring, when the temperature was low (see Section 3.1.2). In contrast to the studies of CAHOON & COOKE (1992) who reported that with lower temperatures (< 20 °C) production values were also lower as compared to the maximum production values.

During our study, in some of the incidences the productivity increased with an increase in the light intensity and the temperature. As observed in summer from June to August 1994, with an increase in temperature and light intensity (see Section 3.1.1) the productivity accelerated revealing at certain sampling days a correlation amongst temperature, light and the productivity. As temperature increased, an increase in the productivity was also noted. These reports are in correspondence with the reports of COLIJN & VAN BUURT (1975), RASMUSSEN et al. (1983), who also observed in their study that rise in temperature caused increase in the photosynthetic rate. In the present study, temperature coefficients (Q_{10} value) between the photosynthetic rate and temperature ranged from 1.45 at M to 1.74 at T. Whereas, DAVIS & MCINTIRE (1983) reported a Q_{10} of 2.05 for an intertidal assemblage in Oregon. GRANT (1986) found a Q_{10} of 2.0 and 3.3, respectively.

4.3.5 PHOTIC ZONE

Coastal sandy and intertidal sediments, both freshwater and marine, are often inhabited by phototrophic microorganisms (STAL et al. 1985, GARCIA-PICHEL & BEBOUT 1996). Photosynthesis in these environments takes place only within few millimeters from the surface, as beyond that the light is greatly attenuated (LASSEN et al. 1992a, KÜHL & JØRGENSEN 1994). Only about 1 % of the incident light reaches a depth of 3 mm in the sandy sediments (FENCHEL & STRAARUP 1971).

Measurements conducted with the aid of light microsensor have depicted that the light may penetrate down to *ca.* 4 mm, or more on account of scattering (KÜHL et al. 1994). Furthermore, KÜHL et al. (1994) examined that the light attenuation coefficients decreased with an increase in the particle size, and infrared light penetrated deeper in all sediments in comparison to the visible light. Intense scattering results in a maximum integral light intensity varying from 180% of incident irradiance in the coarsest sediments (250-500 µm) up to 280 % in the finest sediment (< 63 µm grain size) as measured with fiber-optic microprobes. This observation may hold meaning for sandy beach sediments Mönkeberg (M) & Tirpitzmole (T) of the Kiel Fjord.

The penetration of visible light (photic zone) in the Kiel Fjord is highly variable depending upon the season and time of the year. Thus the microphytobenthos production would be significant only where there is adequate light reaching the sediment surface. According to JUNGHANS (unpublished data) Secchi depth ranged in spring *ca.* 3-5 m, 2-4 m in summer, 2-7 in autumn, and 4-7 m in winter. Similarly, MOIGES (1983) found Secchi depth varying from 2.1 to 7 m, while STIENEN (1986) *ca.* 5 m in the Kiel Fjord. On the other hand, during summer in Laholm Bay SUNDBÄCK (1986) accounted the penetration of light up to 15 m. She further stated that 20 $\mu E\ m^{-2}\ s^{-1}$ (*ca.*1.4 $W\ m^{-2}$) was the lower limit for measurable microphytobenthos growth when the inorganic nutrients were not initially limited.

The thickness of the photic zone varies from sediment type (PINCKNEY & ZINGMARK 1993c), photon flux and intense absorption/scattering of the light (Tab. 8). In addition to this, the photic zone can also be reduced as a consequence of fine sediment deposition (SUNDBÄCK et al. 1996). A thicker photic zone ranging from 4 to 16.5 mm was accounted at station Mönkeberg (M) with coarse sandy sediments than at Tirpitzmole (T) with finer sediments from 2.5 to 21.5 mm (see Section 3.2.1.2). The photic zone at both the stations remained mostly < 10 mm. This is in accordance with the reports of JØRGENSEN et al. (1983) that the photic zone > 10 mm in the benthic ecosystem is quite unusual . In January and February when it was with 21.5 & 16.5 mm, respectively exceptionally deep. At both the stations (M & T) relatively thicker photic zone existed during winter and early spring than in summer. This was probably due to strong hydrodynamic forces as a result of which microphytobenthos populations were unevenly distributed within the sediment as compared to summer with relatively calmer conditions. Besides this, the photic zone in the silty (REVSBECH et al. 1988) and muddy sediments (FENCHEL & STRAAUP 1971, JØRGENSEN & DES MARAIS 1986) is < 1 mm. In addition to this, COLIJN (1982) measured the light penetration in the different sediments i.e. mud 0.14-0.5 mm, sand 0.8-1.1mm, coarse sand 1.2-3.0 mm in the Ems Dollard Estuary. Nonetheless, on comparing the photic zone data with the other authors it can be deduced that our results are overestimated. This probably resulted on account of employment of a needle microelectrode instead of the glass microsensor in this study. The reasons for the use of a needle microelectrode have been discussed earlier.

4.3.6 OXIC SEDIMENT ZONE

Diffusion may be a principal contributor of oxygen into the sediments from the overlying water or atmosphere in the case of intertidal areas while biological mechanisms are known to activate the molecular diffusion processes (BAILLIE 1986). Furthermore, the studies performed in the intertidal (RIEDL & MACHAN 1972, BAILLIE 1986) to deep coastal sediments (SILVERBERG et al. 1987) reached at the inference that other mechanisms than molecular diffusion are responsible for the transport of oxygen across the sediment-water interface. Contrary to this, BOOIJ et al. (1994) found that molecular diffusion is the predominant mechanism of transport of oxygen in a muddy sediment. Moreover, according to ZIEBES et al. (1996) advective oxygen transport may play a key role in the ecology of coastal sediments by expanding the oxic sediment volume far beyond the zone supplied by diffusion.

The availability of oxygen in the interstitial system is important in estimating the redox status of nutrients, the redox conditions and the microbial activity (MCLACHLAN & TURNER 1994) generally decreases with the depth of sediment.

Tab. 8: Comparison of photic zone (mm) of the various shallow coastal sediments determined by GE: Glass electrode, NE: Needle electrode.

Location	Sediment type	Technique	Photic zone (mm)	Source
Aalborg Bay, Denmark	Sand	GE	*ca.* 2.8	Revsbech &Jørgensen (1983)
Solar Lake, Sinai	Cyanobacterial mats	GE	0.8 - 10	Jørgensen et al. (1983)
Limfjorden, Denmark	Microbial mats on sandy sediments	GE	0.7 - 2.7	Lassen et al. (1992a)*
ElbeEstuary, Germany	Mixed & muddy coarse sand	GE	0.15 - 1.4 *ca.* 2.4	Gätje (1992)
Wadden Sea	Sand & Muddy sand	GE	1	Bruns (1994)
Portishead, Severn - Estuary, U.K.	Cohesive	GE	0.15-0.35	Yallop et al. (1994)
Texel, Netherlands	Non-cohesive		0.6-1.8	
Kiel Fjord, Germany	Coarse sand Fine sand	NE	4-16.5 2.5-21.5	This study

* Estimated from a figure

The studies conducted in coastal environments have depicted that oxygen usually do not penetrate deeper than 2 to 5 mm from the overlying water into the sediment by diffusion (REVSBECH et al. 1980, ANDERSON & HELDER 1987). It can be absent a few cm below the surface in low energy, fine sand beaches (FENCHEL & RIEDL 1970) or near saturation level more than 1 m below the surface in well drained, coarse-grained beaches (MCLACHLAN et al. 1979 in MCLACHLAN & TURNER 1994).

In the present study, the sediment oxic zone measured with the aid of needle microsensor in the sandy beach sediments of the Kiel Fjord varied from 4.5 to 17 mm at Mönkeberg (M), while at Tirpitzmole (T) from 2.5 to 23 mm (see Section 3.2.1.3). On the average thicker sediment oxic zone prevailed at M than at T. Similar ranges were found by BROTAS et al. (1990), who also measured oxygen profiles with the help of the needle microsensor and found in organically poor sand oxygen penetration depth varying from 3 mm in inundated cores to > 7 mm in exposed cores. On the other hand, in the muddy sediments the oxygen penetrated only uptil 1.5 mm. In addition to this, REVSBECH et al. (1981) in their measurements observed that the oxygen penetration depth varied with sediment type, season and oxygen consumption /production rate.

Since the O_2 profiles during the study were measured with the aid of needle microsensor, the oxygen penetration depth and photic zone were overestimated. Interestingly, the general trend (minimum and maximum peaks) in the oxygen penetration depth at station T coincided well with oxic sediment zone, measured with the glass microsensor by RASMUSSEN & JØRGENSEN (1992) in the coastal sediments of the Aarhus Bay at 15 m water depth. However, both the systems are not directly comparable, but in order to discern the impact of seasonal variations on the sediment oxic zone this was undertaken. The seasonal variations in the O_2 penetration depth depicted maximum oxygen penetration in winter and minimum during early fall. Nonetheless, during summer the oxygen penetration was relatively low and depicted a new minimum of 4 mm in September 1994. Similar observations were made by RASMUSSEN & JØRGENSEN (1992), where they accounted a minimum peak of 1.3 mm during September 1988. This sediment oxic zone value of 1.3 mm is comparable with the 4 mm at 0.5 m depth. As the measurements were conducted with the needle sensor, on recalculating this by the overestimation factor of 1.5 between needle and glass sensor (see Section 3.2.4.4, Tab. 5). The value fell at 2.7 mm approximately within the similar range. Similarly, MACKIN & SWIDER (1989) also found in Long Island Sound sediments substantially greater O_2 penetration depth during winter than in the summer.

A weak inverse relationship between the sediment temperature and sediment oxic zone was found (see Section 3.2.1.4). Similarly, GÄTJE (1992) in the Elbe Estuary sediments also found an inverse relationship amongst both the parameters with the sediment oxic zone ranging from 1.1-5.5 mm in thickness. The O_2 penetration in the sediment varied seasonally in close accordance with the O_2 concentration in the overlying seawater i.e. decrease in the O_2 concentration in the overlying seawater reflected a narrower oxic zone. Consistent observations made by REVSBECH & JØRGENSEN (1986) and RASMUSSEN & JØRGENSEN (1992) also found reduction in the oxygen penetration depth from 1.7 to 1.2 mm as a consequence of the decrease in the oxygen concentration at the sediment surface.

Oxic sediment zone varies considerably also with the microalgal distribution in the sediments. The denser the microphytobenthos populations, the narrower is the oxic sediment zone as observed on 22 September 1994 (see Section 3.2.1.3 & 3.2.2.1). Low oxygen penetration depth, i.e. 2.5 mm and 4 mm at station Tirpitzmole (T) on 30 May and 22 September 1994 was indicative of intense mineralization on account of dense microphytobenthos populations. Following sedimentation of fresh organic material (GRAF 1987a, MEYER REIL 1987) accounted a strong stimulation of the bacterial activity resulting into higher oxygen consumption and a shift of the redox layer to the sediment surface (GRAF 1989, KÖSTER 1993). This results in an immense decrease in the oxygen penetration depth (ENOKSSON 1987 in HOLLINDE 1995). Consistent reduction in the oxygen penetration depth to 7 mm was found (BRUNS 1994) in the sandy sediments, as a consequence of phytoplankton sedimentation.

LOHSE et al. (1996) reported an oxic sediment zone of 2.8 ± 0.5 mm on account of intensive respiration in the continental shelf sediments. While, in Aarhus Bay due to low oxygen uptake, the oxic zone up to 9.1 mm was observed (RASMUSSEN & JØRGENSEN 1992). The coarser the sediments, the greater is the oxygen penetration depth. Station M, being an exposed sandy beach, with coarser and organically poorer sediments, less microphytobenthos populations, is subjected to stronger hydrodynamic forces that keep its sediments relatively well oxygenated or flush the interstices with oxygen rich water (RIEDL et al. 1972, MALAN & MCLACHLAN 1991). On the other hand, BROTAS et al. (1990) found the major cause for the high oxygen penetration was the exposure of sand to the atmosphere, while comparing exposed and inundated conditions in the sediments of Ria Formosa. Besides, relatively less wave activity at station T (sheltered one) than at M (exposed one), pumping rhythm of the worms (JØRGENSEN & REVSBECH 1985) and bioturbation were probably responsible in transporting oxygen into the deeper sediment layers as oxygen is able to diffuse through the burrows walls of the burrowing macrofauna (FORSTER & GRAF 1992) into the ambient sediment.

4.4 OXYGEN CONSUMPTION

Oxygen is energetically the most favourable and vitally important, electron acceptor available in nature and is the first to be exhausted below the sediment surface (GLUD et al. 1994a). Hence, plays a major role in biological (REVSBECH & JØRGENSON 1986, ZIEBIS et al. 1996) and geochemical processes (ZIEBIS et al. 1996). Modification and decomposition processes of material in sediments are dominated by microorganisms (MEYER-REIL 1994). The O_2 uptake of sediments has been widely used as a measure of the total rate of mineralization and community metabolism (BOOIJ et al. 1994, GLUD et al. 1994a, RAMUSSEN & JØRGENSEN 1992, FORSTER & GRAF 1995). Several studies have recently been applied the O_2 microelectrode for estimation of the diffusive O_2 flux (REVSBECH et al. 1980b). In sediments, the oxygen flux is influenced by the apparent sediment diffusion coefficient, which might be several times higher than the molecular diffusion coefficient (HOFMAN & DE JONG, 1993). The O_2 fluxes are dependent upon the Corg content, bacterial activity and the temperature (WILTSHIRE, 1993). The O_2 transport through the thin oxic zone of impermeable sediments is regulated by diffusion, while due to the concurrent O_2 consumption (CRANK 1983) the O_2 concentration deceases with the depth.

Oxygen gradients were steeper in the sediment as compared to the overlying water at T than at (M). The steep O_2 gradients found may be associated to the intense O_2 consumption by the meiofauna in the surrounding environment. The stronger the curvature of the oxygen gradient, the higher is the respiration rate (JØRGENSEN 1994). The total sediment oxygen consumption rates (TSOC) ranged from 29.6 to 401.5 µmol m^{-2} h^{-1} at Tirpitzmole (T), while at Mönkeberg (M) from 19.2 to 340.6 µmol m^{-2} h^{-1} (see Section 3.2.1.5). Station T showed 1.60 fold higher oxygen consumption rates than at M. This may be due to high organic content and fine sand at the sheltered station T than at M. The finer the sand, the larger is the surface area and greater is the microbial population (DALE 1974). Thus fine sands tend to develop higher oxygen demands than the coarser ones (DAVIS & MCINTIRE, 1983, SHAFFER & ONUF 1983, MCLACHLAN & TURNER 1994, MACINTYRE et al. 1996). Similarly, HOFMAN et al. (1991) also found higher consumption rates at sheltered stations in their studies.

The enhanced O_2 consumption rates in summer existed probably due to high flux of reduced products (i.e. NH_4^+, Fe^{2+} or H_2S) diffusing up from the deeper layers to the oxygen respiring bacteria present at oxic-anoxic interface (RASMUSSEN & JØRGENSEN 1992, JØRGENSEN 1994). Besides this, at times high O_2 consumption rates were also observed, being more obvious at station T, on account of freshly settled detritus in early autumn, late spring, and early summer (see Section 3.2.1.5). This is also reported by REVSBECH et al. (1986). However, comparing the data with those of other authors (Tab. 9) from relatively low value of TSOC ranging from 0.46-8.18 mmol O_2 m^{-2} d^{-1} at M, while at T 0.71-9.64 mmol O_2

m^{-2} d^{-1} were obtained during the studies. It may be speculated that the gradient flux measured was purely a diffusive one. In addition to this, both the stations are influenced by waves. It is possible that probably on account of wave activity most of the organic material was transported to the deeper sediment layers or water depths of the Kiel Fjord. Specially at T, as a result of such wave activities the microphytobenthos might have migrated (predominated by motile diatoms) into the deeper sediment layers and consequently no drastic changes in the oxygen consumption rates of the upper 1 cm sediment layer were found. Besides this, bioturbation and bioirrigation should also not be neglected. The higher bioirrigation flux due to meiofauna (K_{bio} = 1.3 ALLER & ALLER 1992), which might have been the key factor responsible for increasing the oxygen consumption rate, being densely populated in the upper mm of the sediment layers.

Furthermore, bioirrigation, if important may enhance oxygen exchange rates between the sediment and the water compared to molecular diffusion (HULTH et al. 1994). Meiofauna and microorganisms also tend to increase the solute exchange rates through their movement in the interstices, though without visible effects on the colour of the sediment (ÖSTLUND et al. 1990, ALLER & ALLER 1992). Similarly, FORSTER & GRAF (1995) observed an increased flux due to surface microtopography and mixing by meiofauna by the order of 30%. Nonetheless, bioturbation could also result in lower consumption rates, but as the bioturbators i.e. polychaete worms and bivalves etc. are mostly found deeper in the sediments, hence the changes of them to increase the rate are sparse. It can be concluded that in the present study all the above mentioned factors lead to underestimation of the oxygen consumption rates of the microphytobenthos community. The fluxes of O_2 in the sediments were found to be highest during summer and lowest in winter at both the sites. This clearly depicted that the decomposition of organic matter as reflected in the oxygen consumption rate has minimum during winter and maximum after the spring blooms and during late summer. Interestingly, similar trends were accounted by POLLEHNE (1981) at 18 m water depth and BALZER (1984) at 20 m water depth of the Kiel Bight.

The seasonal oxygen consumption fluctuations in the boreal seas were found to be associated with the annual temperature cycle and revealed excellent correlation (WASSMANN 1984). Metabolic processes are temperature dependent, which is especially true for the respiratory enzymes at low temperatures (SOMERO et al. 1983). Lowest values of oxygen consumption (M: 19.2 µmol m^{-2} h^{-1} on 21 December 1994, T: 29.6 µmol m^{-2} h^{-1} on 3 Febuary 1995) may probably be related to the meagre amount of viable microphytobenthos and low benthic activity during these periods as a consequence of low temperature. Similarly, GRAF (1986) also accounted low benthic activity in February in the Kiel Bight. On the other hand, GRAF (1992) reported an increase in the benthic activity by a mean factor of 7 (GRAF et al. 1982, 1983) due to subsequent food input during sedimentation of the spring bloom to temperature increase of 1 to 2 °C at temperatures of 0-3 °C. This is comparable to the effect of temperature increase of 20 °C. Hence in this situation, food supply clearly dominated temperature effects on metabolism. On the other hand, KANNEWORFF & CHRISTENSEN (1986) accounted no immediate effect of sedimentation of spring bloom on respiration rates in Øresund sediment.

Tab. 9: Oxygen consumption rates (m mol m^{-2} d^{-1}) in the different shallow-water sediments

Location	Sediment type & Carbon content	m mol m^{-2} d^{-1}	Author
Chesapeake Bay, USA	Sand flat, C = < 0.5%	4.8 - 204*	Rizzo & Wetzel (1985)
Long Island Sound, USA	Mud, C = 14%	84 - 449	Baillie (1986)
Oosterschelde, Netherlands	Intertidal, n.d.	14 - 89	Hofman et al. (1991)
Böshrücken / Elbe, Germany	Mixed, C = 1.5 %	22 - 93	Wiltshire (1992)
Aarhus Bay, Denmark	Fine grained, OM = 7.7-10.1%	6 - 30*	Rasmussen & Jørgensen (1992)
Kiel Fjord, Germany	Sandy, $C \leq 1$	0.5 - 10	Present study

OM = organic matter, n.d = not determined, * = estimated from a figure

The calculated temperature coefficients (Q_{10}) values 1.91 at M to 2.14 at Tirpitzmole (T) for oxygen consumption agree with the literature values of 3-4 for the Kiel Bight sediments (BENGTSSON 1982, GRAF 1986). Similarly, Q_{10} values (HOFMAN et al. 1991) calculated for Oosterschelde intertidal sediments ranged from 1.4 to 3.2. On the other hand, Q_{10} value between 2-3 have also been accounted by (JØRGENSEN 1977, KANNEWORFF & CHRISTENSEN et al. (1986), HALL et al. (1989). However, GRANT (1986) found an Q_{10} of value of 6.5 indicating no acclimation within the season.

It is, however, interesting to note that the total sediment oxygen consumption rates (TSOC) of 0.46 to 9.64 mmol m^{-2} d^{-1} found in the present study are comparable with that of the Arctic sediments (Svalbard) at water depths of 170-2580 m ranging from 1.85 to 11.2 mmol m^{-2} d^{-1}

as measured by HULTH et al (1994) and continental shelf sediment oxygen fluxes of 4-19 mmol m^{-2} d^{-1} (ARCHER & DEVOL 1992). However, this 1.04-2.68 folds higher than that found in deep-sea sediments 0.48-3.6 mmol m^{-2} d^{-1} (REIMERS & SMITH 1986, SILVERBERG et al. 1987).

The total annual O_2 consumption of the sediment at M was 0.49 ± 8 mol O_2 m^{-2} y^{-1}, while at T 0.83 ± 18 mol O_2 m^{-2} y^{1} when integrated over the whole year. In contrast to this, RASMUSSEN & JØRGENSEN (1992) accounted relatively higher values of 10 mol O_2 m^{-2} y^{-1}. While on the other hand, MIDDELBERG et al. (1996) found the annual rates of organic matter mineralization varied from 8-339 mol C m^{-2} in the Westerschelde Estuary. Thus, it can be concluded from the present study that only a very small proportion 0.86% of total benthic microalgal production 571 g C m^{-2} y^{-1} (corresponds to 57 mol O_2 m^{-2} yr^{-1} assuming a photosynthetic quotient of 1.2) at M, while 1.30% of the 640 g C m^{-2} y^{-1} at T (corresponds to 64 mol O_2 m^{-2} yr^{-1},with photosynthetic quotient of 1.2) was remineralized. This suggests that probably a significant fraction of the organic C production got carried away by currents into deeper basin of the Kiel Fjord.

4.5 CARBON BUDGET OF THE SHALLOW WATER ECOSYSTEM (KIEL FJORD)

The microphytobenthos biomass (standing stock) expressed as organic carbon was estimated by multiplying the Chl-*a* values by the C:Chl-*a* ratio of 50 (DE JONGE 1980). However, DE JONGE & COLIJN (1994) demonstrated that the use of an incorrect C:Chl-*a* ratio (varied between 40 and 61) during the study can increase this deviation by a further 50%. Hence, the values obtained by taking into C:Chl-*a* 50 are also underestimated. The standing stock ranged from 2.93 to 23.64 at Mönkeberg (M), while at Tirpitzmole (T) they varied from 5.32 to 52.72 g C m^{-2}, calculated for the upper 1.2 cm of the sediment layer (Tab. 10). Average values over the total period of investigation (May 1994-July 1995) varied from 13.5 at M to 24.80 g C m^{-2} at T, respectively. The standing stock values estimated during the present study are comparable with the those of other authors, i.e. LÄNGE (1983) reported 0.1 to 25 g C m^{-2} using the C:Chl-*a* 50 in the Elbe Estuary. In BARETTA & RUARDIJ (1988) the total biomass in the 30 cm sediment column ranged from 2 to 25 g C m^{-2}, while in the upper 0.5 cm layer from 1 to 10 g C m^{-2}. On the other hand, DE JONGE & COLIJN (1994) found the microphytobenthos biomass ranging from 3.1 g C m^{-2} to 16.7 g C m^{-2} with the C:Chl-*a* 50 in the Ems Estuary.

In addition to this, from the results shown in Tab.10, it can be concluded that at both the stations (M & T), the microphytobenthos was most active during spring and the order of their activity deceased in the following pattern spring > winter > summer > autumn. Thus, during spring, the microphytobenthos would require less number of days for doubling the same amount of available biomass (g C m^{-2}), under the identical abiotic and biotic environmental variables. Furthermore from the Tab. 10, it can also be deduced that small-sized diatom cells at M were found to be more active than the larger ones at station T. Exceptionally, on account of minimum primary productivity of 0.18 g C m^{-2} d^{-1} and a high amount of the biomass (41.27 g C m^{-2}) measured during late spring 30 May 1994, a value as high as 224.5 days was estimated at T. On the other hand, rapid growth of the benthic microflora ranging from 0.14-3.2 doubling per day has been noticed by WILLIAMS (1964), ADMIRAAL (1977d), ADMIRAAL AND PELEITER (1980a).

Tab. 10: Seasonal impact on the microphytobenthos doublings (biomass/production ratio) in the sediments of the Kiel Fjord. A conversion factor C:Chl-*a* ratio of 50 (DE JONGE 1980) was used to convert the measured chlorophyll-a mg m^{-2} into (g C m^{-2}) as shown below:

$$\text{Doubling days (d)} = \frac{Chlorophyll-a\left(mg\,m^{-2}\right)*50}{Primary\ prod.\left(mg\ C\ m^{-2}\ d^{-1}\right)}$$

Station	Spring	Summer	Autumn	Winter
M (Doubling days)	1.4 - 7.30	2.7 - 37.1	10.2 -51.8	4.1 - 24.4
T (Doubling days)	3.8 21.87	6.8 -49.0	27.0- 98.3	1.2 - 27.0

Annual benthic microalgal productivity measured in the sediments of station M was 571 ± 22 g C m^{-2}, while at T it was 640 ± 37 g C m^{-2}. Moreover, productivity values as high as 892 g C m^{-2} y^{-1} have been registered by GRØNTVED (1962) with ^{14}C method and 800 mg C m^{-2} h^{-1} HARGRAVE et al. (1983) with O_2 exchange method. Furthermore, DAVIS & MCINTIRE (1983), SHAFFER & ONUF (1985), FIELDING et al. (1988), SUNDBÄCK & JÖNSSON (1988), RIZZO et al. (1992) obtained the benthic microalgal primary productivity values from *ca.* 100 to 300 g C m^{-2} y^{-1}. However, mean discrepancy of *ca.* 33% in the data between our results and authors cited may be on account of the microprofile method adopted in the present study. Besides this, the benthic primary production measured in the present study is also underestimated by a factor of 0.35 on comparing with GLUD et al. (1992) as mentioned earlier (see Section 3.2.4.3 Tab. 5).

Benthic trophic state index (BTSI) has been proposed to make general assessment of the degree to which sediments support ecological processes related to photoautotrophy (RIZZO et al. 1996). In the present study the production/respiration ratio was > 1.0 indicating photoautotrophical communities dominated at both the respective sites (M & T). Interestingly, the community respiration at M amounted to be only 0.86 % of the total benthic productivity, while at T it was as high as 1.3 % as mentioned earlier (see Section 4.4).

Moreover, macrophytobenthos and meiofauna standing stock are also a contributor to the carbon budget in the Kiel Fjord. However, the absence of any real information leads to fruitless speculations. On the other hand, depending on the water depth, macrophyte production varies from 37 to 387 g dry weight m^{-2} yr^{-1} (M. MEYER per. comm. in GRAF 1987b) in the shallow parts (≤ 13 m) in the Kiel Bight. Similarly, the meiofauna standing stock varied from 50-625 µg C cm^{-3} at a 10 m station (sand) in the Kiel Bight, being calculated assuming a C:ATP ratio of 250 (GRAF 1989b), from ATP-biomass values of GRAF et al. (1984). The heat loss of the shallow station at 10 m station was as high as 105 g C m^{-2} yr^{-1}.

On the other hand, phytoplankton production amounts about 200 g C m^{-2} y^{-1} (STIENEN 1986) Thus, it can be attributed that the microphytobenthos productivity is 2-2.3 folds higher than that of the phytoplankton. Hence, it can be concluded that microphytobenthos may be quantitatively a major source of fixed carbon for shallow water ecosystem of the western Baltic Sea. This is in accordance with the citations of GRAF et al. (1984). Similarly, PINCKNEY & ZINGMARK (1993b) have also stated the importance of the benthic microalgae in the carbon cycle and that it contributes disproportionately more organic matter to higher trophic levels (MONCREIFF et al. 1992). Besides this, the intertidal diatoms may contribute up to one-third of an estuary´s annual carbon budget (REISE 1985). Thus, the benthic microalgae are not only a food source in the shallow aquatic environment but can help to improve the water quality by stabilizing sediments and altering sediment-water nutrient fluxes (RIZZO et al. 1996). Furthermore, oxygen released as a by-product of photosynthetic activity serves an important function in estuarine areas influencing most of the processes at the sediment surface (GLUD et al. 1992). Moreover, as eutrophication is infact a severe problem in the western Baltic Sea (WEIGELT 1990, GERLACH 1990, BABENERD 1991, SCHULZ et al. 1992, HANSEN 1996). It can thus be speculated that high microalgal productivity in the shallow water system may help to override hypoxic and anoxia conditions and may exhibit a suitable oxic environment for the estuarine fauna in the western Baltic Sea.

However, the carbon pool produced by the microphytobenthos is not sufficient to nourish the whole ecosystem of the Kiel Fjord and Bight. As the distribution of benthic microalgae is only limited up to a certain depth in the western Baltic Sea, depending upon the transparency of water. Beyond which its role becomes unimportant due to light deficiency. Moreover, the high primary production measured in this study will hold meaningful for a small shallow belt along the beach. Furthermore, with the enhanced production of organic matter in the pelagic system followed by its sedimentation and decomposition, and subsequent transportation from the shallow water areas into the deeper basins. Which may deteriorate the oxygen conditions in the deep basins and would result into mortality of the benthic fauna. In addition to this, it may perhaps imbalance the food chain of this ecosystem. Looking into these problems further studies should not only be conducted in the shallow waters but also in the deeper basins of this system to see the impact on meio-and macrofauna under such adverse conditions i.e. oxygen deficiency. On the other hand, the role of nutrient distribution on the vertical migrations of the benthic microalgae remains unclear. Hence, it is advisable to perform future research work on this field, as microphytobenthos have been considered as the best indicator for recording the changes in the shallow water system.

5 SUMMARY

The main objective of this study was to investigate the physical, chemical and biological factors with regard to benthic primary production from two different sites, namely M: Mönkeberg (coarse, *high energy window*) and T: Tirpitzmole (fine, *low energy window*) of the Kiel Fjord (western Baltic Sea). Sediment samples were collected either once or twice a month on the same day from both the stations from 30 May 1994 to 31 July 1995. The benthic primary production was measured with the help of the microprofile method, by employing needle oxygen electrode instead of a glass microelectrode. This has been done for the first time as far as known from the literature.

1) The interstitial environment of the exposed locality is more influenced by hydrodynamic forces as compared to the sheltered one. Higher water content was noticed in the fine sandy sediments than the coarse sediments. Higher percentage of suspended matter in the sandy beach sediments is predominantly influenced by wind induced wave resuspension.

2) Both sediment types indicated a low Corg content ($< 1\%$), with fine sediments showing higher Corg content of $< 0.4\%$ than the coarser sandy sediments ($< 0.1\%$). Besides this, high organic content in the sediments was mostly connected with an increase in the porosity.

3) In general the C:N ratio at both the sandy beach sediments was found to be < 12. Moreover, values > 12 occurred on account of significant contribution of the refractory organic matter i.e. detritus derived from macroalgae, wood residues, vascular plant material etc.

4) The microflora mainly consisted of pennate diatoms (both motile and epipsammic species). The microphytobenthos community changed from larger to smaller species and vice-versa, depending upon the seasonal and environmental fluctuations at both the stations. Peaks were obtained during spring and autumn while a decline in the cell number was accounted in summer due to grazing. A common feature as a result of different physicochemical conditions was the species stratification along the depth gradient. The microphytobenthos activity decreased in the following order spring > winter > summer > autumn. Smaller microalgal cells are metabolically more active than the larger ones.

5) Coarse sandy sediments (exposed and *high energy window*) were predominated by small *epipsammic* grain-adhering diatoms ranging from 17 to 1428 $\times 10^6$ cm^{-3}, while fine sediments (sheltered and *low energy window*) often consisted of *epipelic* (often larger sized) motile diatoms varying from 45 to 4005 $\times 10^6$ cm^{-3}. The density of the microalgae varied spatially and temporally in the upper 0-9 mm sediment layers, depicting no stratification. Out

of the three sediment layers investigated, sediment layer 3-6 mm showed the richest microalgal assemblage. Members of the family Naviculaceae were most dominant, adaptable and played an integral role in the coastal sediments of the Kiel Fjord. The most tolerant, frequent and ubiquitous genus under all the weather conditions was *Navicula* sp.

6) Chlorophyll-a concentrations were higher in finer sediments ranging from 2.05 to 29.07 µg Chl-*a* cm^{-3} in comparison to coarser sandy sediments (0.95 to 13.17 µg Chl-*a* cm^{-3}). Nonetheless, the maximum Chl-*a* concentration was found in the depth range of 3-6 mm at both stations. The Chl-*a* concentration was directly proportional to the total cell number. Benthic microalgae tend to build up more photosynthetic pigments under dull light conditions as compared to in bright sunlight, to compensate for the reduction in available light energy.

7) On an average, thicker oxygen penetration depth (oxic sediment zone) into the sediment ranging from 4.5 to 17 mm at station M, while at T from 2.5 to 23 mm was estimated. It was found to be dependent upon the weather conditions, sediment type and microphytobenthos distribution within the sediment. A weak correlation existed between the oxygen penetration depth and the sediment temperature.

8) The photic zone at both the stations was mostly < 10 mm, varing with sediment type, photon influx and intense absorption/scattering of light. On an average, a deeper photic zone ranging from 4 to 16.5 mm was determined in the coarse sediments as compared to fine sediments where it varied from 2.5 to 21.5 mm.

9) Fine sands tend to develop higher total sediment oxygen consumption rate (TSOC) within the sediments ranging from 29.6 to 401.5 µmol O_2 m^{-2} h^{-1} as opposed to the coarse ones (19.2 to 340.6 µmol O_2 m^{-2} h^{-1}). The O_2 fluxes being highest during summer and lowest in winter. The higher bioirrigation flux due to meiofauna (K_{bio}) than the O_2 diffusive flux, being probably the key factor responsible for increasing O_2 consumption rates.

10) The photosynthetic activity measured with the needle electrode was a factor of 2 higher than with a glass electrode, irrespective of the existing duration of the dark period i.e. 3 to 10 seconds. The longer the dark period, the lesser is the benthic primary production. Thus, the gross primary production when measured with steel is underestimated by factor 0.35 ± 0.14 (n=7) when given 10 s of dark phase as compared to the glass electrode with 2 s. The sheltered locality (fine sediments, *low energy window*) showed a higher photosynthetic activity varying from 0.06 to 18.2 µmol O_2 cm $^{-3}$ h^{-1} and benthic primary production from 15.3 to 454.3 mg C m^{-2} h^{-1} than the exposed station (coarse sediments, *high energy window*) with 0.13 to 16.7 µmol O_2 cm $^{-3}$ h^{-1} and from 38.6 to 284.8 mg C m^{-2} h^{-1}, respectively. The

benthic microalgal productivity was found to be 3.2-fold higher than the phytoplankton productivity.

Thus, from this study it can be concluded that the microphytobenthos are an important contributor to primary production, living at the sediment water interface. They play not only a central role in the shallow water ecosystem of the Kiel Fjord but may also help to override the existing severe problem of eutrophication in this area.

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Appendix. Table 1: Characteristics of the (daily) averaged meteorological parameters *wind speed* (m s^{-1}), *wind direction*, *sea-level* (m) from 00:00 AM to 12:00 PM & *irradiance* (Wm^{-2}) from dawn to dusk for the respective sampling days. (Meteorological Department, Institut für Meereskunde, Kiel). Note data with symbols * and ** i.e. values averaged from 06:00 AM to 12:00 PM*; 08:00 AM to 12:00 PM**

Date	Wind speed [m/sec]	Wind direction	Sea-level [m]	Irradiance [W m^{-2}]
30.05.94	4.20	288	0.00	403
17.06.94	3.88	282	0.16	349
28.06.94*	1.28	58	0.20	450
12.07.94	4.10	138	0.05	485
28.07.94	2.35	103	0.02	393
10.08.94**	1.34	249	0.08	354
30.08.94	2.92	222	-0.13	247
22.09.94	3.22	326	0.18	142
12.10.94	2.68	265	-0.18	188
27.10.94	5.62	217	-0.09	65
17.11.94	5.18	231	-0.01	85
18.11.94	3.58	295	-0.05	147
28.11.94	3.54	277	0.06	108
21.12.94	2.83	219	0.12	53
23.01.95	7.16	241	-0.16	42
03.02.95	4.64	205	0.23	127
17.03.95	8.44	187	-0.23	58
30.03.95	3.22	280	0.37	400
18.04.95	6.01	180	0.18	91
27.04.95	3.92	56	0.31	418
16.05.95	3.51	250	-0.05	385
20.06.95	2.86	218	0.06	244
30.06.95	3.69	280	-0.03	483
19.07.95	3.91	275	0.03	359
31.07.95	4.32	62	0.10	446

Appendix. Table 2: Temperature (°C), salinity (PSU), porosity values recorded during the study at M & T from May 1994 to July 1995

Date	M °C	T °C	M: PSU	T:PSU	M [Porosity]	M:S.D	T [Porosity]	T:S.D
30.05.94	12.60	15.70	10	12	0.38	0.01	0.37	0.01
17.06.94	14.90	15.40	10	12	0.38	0.01	0.48	0.03
28.06.94	16.00	15.20	16	15	0.39	0.01	0.39	0.01
12.07.94	19.60	20.40	12	12	0.37	0.03	0.46	0.04
28.07.94	23.50	23.50	13	12	0.38	0.01	0.44	0.01
10.08.94	21.20	21.40	11	12	0.38	0.00	0.42	0.01
30.08.94	16.20	16.00	16	17	0.37	0.02	0.40	0.02
22.09.94	14.60	14.20	16	16	0.38	0.01	0.48	0.02
12.10.94	12.10	12.70	16	18	0.34	0.04	0.44	0.00
27.10.94	10.20	10.20	19	20	0.37	0.02	0.45	0.00
17.11.94	7.60	8.50	18	17	0.38	0.00	0.44	0.01
28.11.94	8.00	8.00	15	18	0.39	0.01	0.44	0.01
21.12.94	6.30	5.60	18	19	0.39	0.00	0.42	0.01
23.01.95	3.30	3.00	16	19	0.39	0.02	0.43	0.01
03.02.95	2.80	3.10	15	14	0.39	0.01	0.42	0.01
17.03.95	4.20	4.00	18	12	0.38	0.01	0.47	0.03
30.03.95	3.00	4.20	11	16	0.40	0.01	0.40	0.01
18.04.95	6.40	6.70	17	12	0.41	0.00	0.45	0.03
27.04.95	10.20	10.70	15	9	0.43	0.02	0.55	0.04
16.05.95	12.70	11.70	10	12	0.43	0.04	0.54	0.01
20.06.95	14.70	14.50	12	13	0.46	0.03	0.54	0.00
30.06.95	19.00	19.00	10	12	0.47	0.02	0.59	0.03
19.07.95	18.70	17.60	12	13	0.46	0.02	0.56	0.00
31.07.95	22.10	22.40	12	10	0.42	0.01	0.47	0.02

Appendix. Table 3: Mean values of Corg % and C:N measured at M and T from May 1994 to July 1995. Note S.D = Standard deviation

Date	M: Corg [%]	M: S.D	T: Corg [%]	T: S.D	M: C:N	T: C:N
30.05.94	0.050	0.001	0.941	0.059	7	38
17.06.94	0.058	0.002	0.131	0.014	4	9
28.06.94	0.067	0.001	0.060	0.026	9	-
12.07.94	0.043	0.000	0.227	0.029	7	12
28.07.94	0.047	0.002	0.230	0.036	-	18
10.08.94	0.046	0.001	0.225	0.022	9	13
30.08.94	0.075	0.000	0.243	0.025	10	16
22.09.94	0.087	0.006	0.300	0.085	4	25
12.10.94	0.090	0.003	0.132	0.030	6	-
27.10.94	0.050	0.001	0.135	0.027	4	9
17.11.94	0.066	0.001	0.197	0.134	10	23
28.11.94	0.083	0.001	0.118	0.017	4	12
21.12.94	0.093	0.000	0.164	0.010	-	17
23.01.95	0.050	0.000	0.143	0.046	-	11
03.02.95	0.060	0.000	0.173	0.061	-	-
17.03.95	0.073	0.001	0.143	0.023	-	20
30.03.95	0.050	0.000	0.241	0.046	-	23
18.04.95	0.103	0.008	0.166	0.028	-	11
27.04.95	0.050	0.000	0.197	0.027	-	10
16.05.95	0.110	0.008	0.275	0.047	-	11
20.06.95	0.093	0.020	0.175	0.014	6	9
30.06.95	0.076	0.003	0.362	0.078	6	11
19.07.95	0.062	0.000	0.254	0.028	7	12
31.07.95	0.094	0.005	0.126	0.054	15	9

Appendix. Table 4: Mean values of oxygen concentration (µM) water column, maximum oxygen concentration (µM) and its depth within the sediment (mm), oxic sediment zone (mm), Photic-zone (mm) from May 1994 to July 1995 at station M & T

	Oxygen concentration [µM] water column		Maximum oxygen concentration [µM] and its depth within the sediment [mm]				Sediment oxic zone [mm]		Photic -zone [mm]	
Date	M	T	M [µM]	T [µM]	M [mm]	T [mm]	M	T	M	T
30.05.94	355	323	480	336	0.5	0	7	2.5	6	2.5
17.06.94	330	312	471	319	2.5	0.5	10.5	6	7.5	5
28.06.94	329	335	330	345	0	0	7	8	6.5	7.5
12.07.94	333	199	332	428	0.5	1	6	8	4.5	5.5
28.07.94	345	268	632	275	2	0.5	11	6	10	5.5
10.08.94	328	312	384	769	2	1	8.5	6.5	8	5.5
30.08.94	216	167	244	199	1.5	1.5	6	8	5	7
22.09.94	295	247	413	751	1	1	7	4	6	4
12.10.94	312	268	293	269	2	0	6	6	5.5	6
27.10.94	291	281	303	472	0.5	1	7.5	7	6.5	6.5
18.11.94	298	269	314	278	2	1.5	10	8	8.5	7.5
28.11.94	322	315	379	290	1.5	0	6	8.5	5.5	7
21.12.94	336	330	424	375	1	0.5	13	5.5	12	5
23.01.95	347	339	309	325	0	0	17	7	16.5	6.5
03.02.95	378	379	576	425	3.5	4	9	23	11	21.5
17.03.95	361	342	419	392	2	1	11	11.5	9.5	9
30.03.95	401	406	407	379	0	0	12.5	12	9	11.5
18.04.95	352	352	416	353	2	0.5	11.5	9	8.5	8
27.04.95	358	344	344	440	0	2	6	7.5	5	7.5
16.05.95	331	324	391	307	0	0	8	5.5	6.5	5
20.06.95	341	334	341	311	0	0	4.5	4	4	4
30.06.95	340	341	355	340	0	0	6.5	4.5	6.5	3.5
19.07.95	284	234	419	219	4	0.5	14	6.5	12.5	5
31.07.95	413	265	413	270	0	0	5.5	5.5	5	4.5

Appendix. Table 5: Chlorophyll-a concentration (mean ± s.d) in the different sediment depths (0-3, 3-6, 6-9, 9-12 mm) at M and T from May 1994 to July 1995

Chl-a µg cm^{-3}	**0-3 mm**		**3-6 mm**		**6-9 mm**		**9-12 mm**	
Date	**M**	**M: s.d**	**M**	**M: s.d**	**M**	**M: s.d**	**M**	**M: s.d**
30.05.94	7.92	0.33	6.77	1.32	8.54	2.20	7.59	1.77
17.06.94	6.38	1.08	8.05	2.49	7.51	2.11	8.46	1.29
28.06.94	7.55	1.61	9.22	0.30	8.24	2.20	9.08	0.11
12.07.94	5.92	1.33	7.85	0.95	7.70	2.52	6.05	0.33
28.07.94	7.40	1.07	7.02	0.28	7.81	0.60	7.84	1.05
10.08.94	5.43	0.07	5.88	0.44	5.75	0.64	5.81	1.44
30.08.94	8.58	2.63	10.18	0.77	9.28	0.28	8.49	1.27
22.09.94	7.38	5.97	9.19	0.99	8.43	1.81	7.96	0.57
12.10.94	8.95	3.17	12.50	4.25	13.17	2.28	12.66	4.88
27.10.94	4.03	1.11	4.86	0.36	5.10	1.30	4.79	0.78
17.11.94	11.44	0.35	11.08	0.38	11.83	2.27	12.42	1.81
28.11.94	8.11	3.08	9.86	1.51	9.22	1.60	10.21	1.42
21.12.94	7.57	1.33	6.53	0.82	5.46	0.72	6.28	0.25
23.01.95	5.43	0.82	6.55	0.71	6.48	0.78	6.55	1.74
03.02.95	5.71	1.24	6.30	0.87	6.49	0.90	5.93	1.07
17.03.95	2.76	0.55	3.89	0.34	4.16	0.14	3.75	0.63
30.03.95	1.16	0.36	1.78	0.17	1.38	0.19	1.53	0.19
18.04.95	0.95	0.22	1.64	0.17	1.62	0.16	1.87	0.29
27.04.95	3.61	0.42	3.28	0.50	2.99	0.38	2.72	0.70
16.05.95	5.93	4.80	6.66	3.09	5.37	2.95	4.25	1.33
20.06.95	9.03	1.17	7.93	9.53	7.00	1.02	6.94	1.09
30.06.95	6.43	0.48	9.91	0.88	11.62	1.20	11.12	1.32
19.07.95	6.19	1.51	7.72	0.63	6.98	2.03	7.99	0.34
31.07.95	6.89	1.51	10.26	1.85	9.71	1.07	10.42	2.14

Chl-a µg cm^{-3}	**0-3 mm**		**3-6 mm**		**6-9 mm**		**9-12 mm**	
Date	**T**	**T: s.d**	**T**	**T: s.d**	**T**	**T: s.d**	**T**	**T: s.d**
30.05.94	12.83	2.58	23.74	5.34	23.94	0.97	22.04	8.66
17.06.94	8.53	3.08	11.86	2.25	14.17	4.01	20.28	7.16
28.06.94	3.33	1.34	3.33	0.19	3.08	1.21	2.80	0.75
12.07.94	10.38	2.43	13.27	1.53	12.17	2.21	9.17	3.36
28.07.94	7.54	2.05	12.72	2.80	12.19	0.70	9.91	3.25
10.08.94	5.74	1.95	9.18	1.62	8.46	1.28	11.64	4.68
30.08.94	-	-	-	-	-	-	-	-
22.09.94	29.07	4.90	26.34	2.16	27.26	6.18	22.77	5.17
12.10.94	10.30	3.13	14.91	5.52	13.90	3.80	10.82	1.77
27.10.94	17.40	0.51	16.15	3.70	14.40	2.65	14.04	5.16
17.11.94	8.32	2.78	13.15	1.17	12.42	2.06	12.31	1.52
28.11.94	8.01	1.40	9.71	0.96	10.34	0.52	9.57	1.38
21.12.94	8.71	2.67	13.13	0.88	13.28	1.70	10.77	2.65
23.01.95	8.03	1.43	9.92	0.17	10.40	2.02	11.03	1.14
03.02.95	2.06	0.20	2.79	0.45	3.13	1.02	2.67	1.11
17.03.95	9.68	3.44	11.53	3.32	9.70	1.70	10.34	1.71
30.03.95	4.76	1.72	4.17	1.17	3.67	0.99	3.18	1.43
18.04.95	11.27	1.26	12.77	1.73	10.75	3.33	9.66	3.26
27.04.95	23.88	3.32	28.72	4.46	22.39	2.92	23.54	2.26
16.05.95	8.29	5.97	15.04	5.90	11.83	1.41	12.19	5.91
20.06.95	16.77	4.03	17.76	4.22	14.56	1.82	13.94	1.77
30.06.95	14.22	4.26	17.95	2.38	13.21	3.79	11.39	3.63
19.07.95	10.08	2.44	13.52	4.32	13.82	2.76	13.50	3.77
31.07.95	9.58	1.69	13.58	2.02	15.16	2.94	14.95	3.14

Appendix. Table 6: Average values of microphytobenthos abundance (× 10^6 cm^{-3}) in the different sediment depths (0-3, 3-6, 6-9 mm) at M and T from May 1994-95

M	[cell counts 10 ^ 6/ cm ^3]			T	[cell counts 10 ^ 6/ cm ^3]		
Sampling date	**[0-3 mm]**	**[3-6mm]**	**[6-9mm]**	**Sampling date**	**[0-3 mm]**	**[3-6mm]**	**[6-9mm]**
30.05.94	226	426	509	30.05.94	454	645	421
17.06.94	68	89	106	17.06.94	100	78	82
28.06.94	210	292	217	28.06.94	210	292	217
12.07.94	42	30	17	12.07.94	96	83	78
28.07.94	66	72	50	28.07.94	124	69	45
10.08.94	53	73	56	10.08.94	84	53	56
30.08.94	747	843	783	30.08.94	207	123	147
22.09.94	285	417	376	22.09.94	2770	2198	2428
12.10.94	240	232	207	12.10.94	994	892	1054
27.10.94	324	474	206	27.10.94	1023	1091	1757
28.11.94	85	103	157	28.11.94	297	286	302
21.12.94	97	-	-	21.12.94	276	-	-
23.01.95	78	-	-	23.01.95	562	-	-
03.02.95	74	-	-	03.02.95	127	-	-
17.03.95	181	305	301	17.03.95	968	854	883
27.04.95	226	312	251	27.04.95	3577	4005	2503
16.05.95	1428	1415	1249	16.05.95	2670	3669	3469

Appendix. Table 7: List of the microphytobenthos species assemblages in the sediments of station M & T from May 1994 to May 1995

List of the microphytobenthos observed at station M and T
Achnanthes sp.
Actinoptychus sp.
Amphiprora alata
Amphora sp. (small)
Amphora sp. (big)
Atheya decora
Bacillaria sp.
Blue greens (Anabeana)
Biddulphia sp.
Chaetoceros sp.
Ciliates
Cocconeis sp.
Cylindrotheca sp.
Cyclottela sp.
Cymbella sp.
Diatoma sp.
Diploneis sp.
Epithemia sorex
Eunotia sp.
Flagellates (i.e. Heterosigma sp. etc)
Fragilaria sp.
Gyrosigma sp.
Licmophora sp.
Mastogloia sp.
Melosira sp.
Merismopedia
Navicula sp.
Navicula humerosa
Nitzschia closterium
Opephora martyi
Pinnularia sp.
Pleurosigma angulatum
Pleurosigma carinata
Rhabdonema sp.
Synedra tabulata
Tabularia tabulata
Tetraselmis

Appendix. Table 8: Microphytobenthos species composition in the (0-3, 3-6, 6-9 mm) sediment layers at M from May 1994 to May 1995. (vc: very common, c: common, r: rare)

Date	St. M: Dominant sp.	0-3 mm	3-6 mm	6-9 mm
30.05.94	Chaetoceros	r	-	-
	Cocconeis	c	c	-
	Cyclotella	r	r	r
	Melosira	r	r	-
	Navicula	c	r	r
	Opephora	r	r	-
	Rhabdonema	c	c	r
	Synedra	c	c	c
17.06.94	Achnanthes	-	-	r
	Biddulphia	vc	r	r
	Cocconeis	vc	vc	c
	Navicula	c	r	r
	Pleurosigma angulatum	c	vc	c
	Pleurosigma carinata	c	vc	c
	Tabularia tabulata	r	r	-
28.06.94	Amphiprora alata	r	c	r
	Amphora	r	r	-
	Navicula	vc	vc	vc
	Rhabdonema	vc	c	c
	Pleurosigma angulatum	c	vc	vc
12.07.94	Amphora	c	vc	vc
	Cyanophyceae (Anabaena)	c	r	r
	Licmophora	r	r	r
	Navicula	vc	vc	vc
	Rhabdonema	vc	c	-
	Phytoflagellates (Heterosigma)	vc	r	r
28.07.94	Amphora	vc	c	r
	Navicula	vc	c	vc
	Opephora	r	-	-
	Phytoflagellates (Heterosigma)	r	r	r
	Rhabdonema	r	c	r
10.08.94	Amphora	c	c	r
	Bacillaria	r	c	c
	Merismopedia	r	-	-
	Navicula	c	c	c
	Prorocentrum minium	vc	vc	c
	Stauroneis	c	c	c
30.08.94	Amphora	-	-	r
	Navicula	vc	vc	vc
	Prorocentrum minium	c	r	r
	Rhabdonema	vc	c	r
22.09.94	Amphora (small)	r	r	-
	Actinoptychus senarius	c	r	-
	Navicula	vc	vc	c
	Rhabdonema	vc	c	c
	Tabularia tabulata	r	r	-
12.10.94	Chaetoceros	c	r	-
	Coscinodiscus	r	r	-
	Navicula	vc	vc	vc
	Opephora	r	r	r
	Unidentified sp (< 10 µm)	vc	c	r
27.10.94	Amphora	r	r	r
	Fragilaria	c	c	c
	Navicula	vc	vc	vc
	Opephora	c	c	c
	Phytoflagellates	r	c	r
	Rhabdonema	c	c	c
28.11.94	Amphora (big)	vc	vc	c
	Chaetoceros	-	r	-
	Navicula	vc	vc	vc
	Nitzschia	-	-	c
	Tetraselmis	c	r	r
21.12.94	Achnanthes	c		
	Amphora	r		
	Navicula	vc		
	Phytoflagellates (Heterosigma)	r		
23.01.95	Fragilaria	r		
	Navicula	vc		
	Opephora	r		
	Phytoflagellates (Heterosigma)	c		
03.02.95	Fragilaria	c		
	Navicula	vc		
	Opephora	c		
	Phytoflagellates (Heterosigma)	c		
17.03.95	Chaetoceros	vc	vc	vc
	Eunotia	c	r	r
	Navicula	c	c	c
	Phytoflagellates (Heterosigma)	r	r	c
	Unidentified sp (< 10 µm)	-	r	r
27.04.95	Chaetoceros	c	c	c
	Licmophora	r	r	r
	Navicula	vc	vc	vc
	Opephora	r	r	r
	Phytoflagelltes (Heterosigma)	r	r	r
	Synedra	r	r	r
	Tabularia tabulata	r	r	r
16.05.95	Amphiprora alata	r	c	r
	Amphora (small)	c	c	c
	Chaetoceros	r	c	c
	Navicula	vc	c	vc
	Pinnularia	r	-	-

Appendix. Table 9: Microphytobenthos species composition in the (0-3, 3-6, 6-9 mm) sediment layers at T from May 1994 to May 1995. (vc: very common, c: common, r: rare)

Date	St. T : Dominant sp.	0-3 mm	3-6 mm	6-9 mm
30.05.94	Achnanthes	c	c	c
	Amphora	vc	c	c
	Amphiprora alata	c	-	c
	Biddulphia	vc	vc	r
	Chaetoceros	c	r	-
	Cocconeis	r	r	r
	Cylindrotheca sp.	vc	vc	vc
	Melosira	-	-	r
	Navicula	r	c	r
	Nitzschia closterium	vc	c	c
	Tabularia tabulata	-	c	r
17.06.94	Achnanthes	r	c	r
	Amphora	r	vc	r
	Chaetoceros	c	-	-
	Ciliates	vc	c	r
	Cocconeis	r	r	c
	Cymbella	r	r	r
	Navicula	c	r	r
	Pleurosigma angulatum	vc	c	vc
	Pleurosigma carinata	vc	c	vc
	Phytoflagellates	vc	c	r
	Rhabdonema	r	r	c
	Synedra	c	r	r
28.06.94	Amphora	vc	vc	vc
	Biddulphia	r	r	r
	Opephora	c	c	r
	Navicula	vc	vc	vc
	Rhabdonema	-	r	-
	Tabularia tabulata	c	c	-
12.07.94	Amphora	vc	vc	vc
	Navicula	vc	c	vc
	Cocconeis	-	r	r
	Cylindrotheca sp.	c	c	c
	Gyrosigma	r	-	-
	Navicula	vc	c	vc
	Opephora	c	c	vc
	Phytoflagellates	vc	vc	vc
	Tabularia	r	r	r
28.07.94	Amphiphrora	-	c	-
	Amphora	vc	vc	r
	Cyanophyceae	vc	vc	r
	Melosira	r	r	r
	Navicula	vc	vc	vc
	Opephora	c	c	_
	Phytoflagellates	vc	vc	r
	Pinnularia sp.	vc	c	vc
	Stauroneis	c	c	r
	Tabularia	c	r	c
10.08.94	Amphiprora sp	c	vc	vc
	Amphora (big & small)	vc	r	r
	Cocconeis	r	-	r
	Melosira	r	r	r
	Navicula humerosa	r	r	r
	Navicula	vc	vc	vc
	Opephora	r	r	r
	Pleurosigma	r	r	r
	Stauroneis	c	r	-
30.08.94	Amphiprora	vc	vc	r
	Amphora	vc	vc	vc
	Cocconeis	r	-	-
	Cyanophyceae (Anabaena)	vc	c	-
	Cylindrotheca sp.	c	r	r
	Fragilaria	-	-	vc
	Melosira	r	-	-
	Merismopedia	r	r	r
	Navicula	c	c	c
	Navicula humerosa	r	r	-
	Nitzschia	vc	r	c
	Opephora	vc	c	r
	Phytoflagellates	c	r	-
	Tetraselmis	vc	c	-
	Tabularia tubulata	r	r	-
22.09.94	Achnanthes	r	-	-
	Amphora	c	vc	c
	Cyanophyceae (Anabaena)	vc	c	c
	Mastogloia	c	r	-
	Merismopedia	c	r	r
	Navicula	vc	vc	vc
	Nitzschia	r	r	-
	Opephora	r	r	-
12.10.94	Amphora	c	vc	vc
	Melosira	r	_	r
	Navicula	vc	vc	vc
	Opephora	c	r	-
	Phytoflagellates (i.e.Heterosigma sp.)	r	-	-
	Stauroneis	-	r	r
	Tabularia	c	-	-
	Tetraselmis	c	-	-
27.10.94	Amphora (small)	c	c	c
	Anabaena	-	r	r
	Flagellates (Peranema sp.)	c	r	r
	Fragilaria	c	c	c
	Mastogolia	r	r	r
	Navicula	vc	vc	vc
	Opephora	c	c	c
	Pinnularia	-	-	r
	Unidentified sp.(5-10 µm)	c	r	r
28.11.94	Amphora	c	c	c
	Gyrosigma	-	r	r
	Navicula	vc	vc	vc
	Nitzschia	r	r	r
	Opephora	vc	c	-
	Rhabdonema	c	c	c
	Stauroneis	c	-	-
	Unidentified sp.(5-10 µm)	c	c	c
21.12.94	Amphora (small)	c		
	Ciliates	r		
	Fragilaria	c		
	Mastogloia	r		
	Navicula	vc		
	Phytoflagellates	c		
23.01.95	Amphora	r		
	Phytoflagellates i.e. Heterosigma sp.	c		
	Navicula	vc		
	Opephora	c		
03.02.95	Phytoflagellates i.e. Heterosigma sp.	r		
	Fragilaria	vc		
	Navicula	vc		
	Opephora	c		
	Phytoflagellates	c		
17.03.95	Amphora (small)	c	c	c
	Amphora (Big)	r	r	r
	Phytoflagellates i.e. Heterosigma sp.	vc	vc	vc
	Fragilaria	c	c	c
	Navicula	vc	vc	vc
	Tabularia	r	r	r
27.04.95	Amphiprora alata	c	c	c
	Atheya decora	c	r	r
	Amphora sp (big)	r	r	r
	Diatoma	c	r	c
	Diplonies	c	c	c
	Eunotia	r	c	r
	Epithemia sorex	c	c	-
	Gyrosigma	-	r	r
	Licmophora	r	r	-
	Pinnularia	-	-	-
	Phytoflagellates i.e. Heterosigma sp.	vc	vc	vc
	Navicula	c	c	r
	Nitzschia closterium	vc	vc	c
	Tabularia	r	r	c
16.05.95	Amphora (small)	vc	vc	vc
	Amphora sp (big)	r	r	r
	Biddulphia	r	c	r
	Epithemia sorex	c	c	-
	Cylindrotheca sp.	vc	c	c
	Gyrosigma	r	r	r
	Pinnularia	r	r	r
	Phytoflagelltes	r	r	r
	Navicula	r	c	c
	Nitzschia closterium	vc	c	vc
	Cyanophyceae	r	r	r
	Cyclottela	r	r	r
	Cymbella	r	r	c

Appendix. Table 10: Mean values of primary production (mg C m^{-2} h^{-1}), Oxygen uptake (µmol m^{-2} h^{-1}) and C:Chl-a ratio measured at M & T from May 1994 to July 1995

	mg C m^{-2} h^{-1}		**µmol m^{-2} h^{-1}**		**C/Chl-a**	
Date	**M**	**T**	**M**	**T**	**M**	**T**
30.05.94	45	15	83.8	91.7	40	287
17.06.94	157	91	52.4	123.4	54	64
28.06.94	58	77	66.0	78.5	45	101
12.07.94	66	215	78.5	182.9	36	103
28.07.94	205	88	91.1	181.2	43	122
10.08.94	80	93	91.8	140.3	48	454
30.08.94	41	32	36.3	45.9	51	-
22.09.94	62	45	57.8	152.9	69	60
12.10.94	38	42	73.3	104.8	52	60
27.10.94	77	51	77.1	86.3	74	54
17.11.94	89	71	34.3	58.9	36	83
28.11.94	64	96	39.3	75.1	57	98
21.12.94	224	72	19.2	76.6	87	85
23.01.95	285	117	32.0	49.3	51	86
03.02.95	248	369	40.3	29.6	63	430
17.03.95	132	454	34.6	53.5	127	79
30.03.95	176	165	24.1	35.3	226	371
18.04.95	58	169	65.9	83.8	490	83
27.04.95	214	188	114.7	120.0	88	36
16.05.95	127	151	62.6	153.8	113	117
20.06.95	55	55	106.0	239.4	69	57
30.06.95	57	57	340.6	401.5	47	111
19.07.95	119	43	75.9	159.0	51	98
31.07.95	75	69	112.7	176.4	67	56

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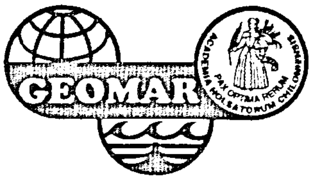

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