Role of benthic microalgae in a coastal zone : biomass, productivity and biodiversity

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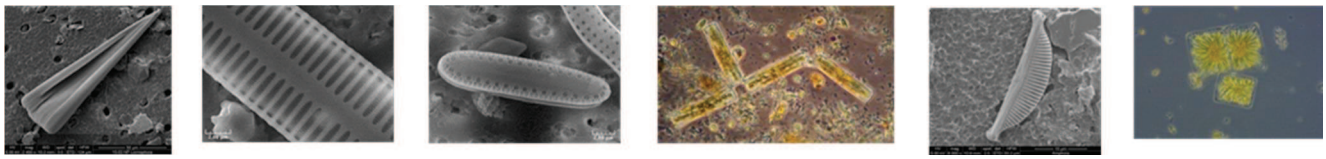
Rôle des micro-algues benthiques dans la zone côtière : biomasse, biodiversité, productivité



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Role of benthic microalgae in a coastal zone: biomass, productivity and biodiversity

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Extended abstract:

Le phytoplancton et le microphytobenthos (MPB) constituent les plus importants producteurs primaires des zones côtières (Pannard et al, 2008 ; Woelfel et al., 2010). Ils sont à la base de la chaine trophique et composent l'essentiel de la nourriture de la faune, en particulier des espèces économiquement importantes (Gillespie et al., 2000). Cependant, bien que le phytoplancton ait été largement étudié, le MPB est beaucoup moins connu. Il colonise tous les milieux (roche, vase, sable…) dès lors qu'il y a suffisamment de lumière pour la photosynthèse (Charpy et Charpy - Roubaud 1990, MacIntyre et al. 1996, MacIntyre et Cullen, 1996) et sa production peut égaler, voire même dépasser, la production du phytoplancton de la colonne d'eau qui le surplombe (Underwood and kromkamp, 1999).

Avec cette capacité de production élevée, les communautés de microalgues benthiques influencent profondément les flux, la consommation et la reminéralisation du carbone et des nutriments dans les zones côtières. Les producteurs primaires benthiques contribuent à la disponibilité de l'énergie et de la matière pour les réseaux trophiques benthiques et pélagiques.

Dans les eaux peu profondes, l'interaction entre les processus pélagiques et benthiques est plus intense, et en général favorise le benthos parce qu'il est beaucoup moins exposé aux perturbations physiques et biochimiques tels que l'évaporation, le vent,… que le phytoplankton (Molen, 2011). Parce que les microalgues benthiques peuvent éviter les processus d'advection et s'adapter aux changements de disponibilité de la lumière à des échelles de temps très courtes, leur importance est particulièrement renforcée (Phinney, 2004). Du fait de son importance dans les écosystèmes côtiers, et de son rôle fonctionnel, les études sur la diversité du MPB ont acquis une certaine importance dans les deux dernières décennies (Sundbaeck & Jönsson, 1988; Blanchard & Montagna 1992). Comme le phytoplancton, Le MPB est aussi un bon indicateur biologique de la qualité de l'eau, sa composition taxonomique variant en fonction de la teneur en nutriments (Kann, 1986).

Cependant, alors que l'importance du microphytobenthos a été particulièrement remarqué et étudié dans les zones intertidales (Herman et al., 2000), son rôle dans les zones subtidales est pratiquement toujours ignoré. En conséquence, peu de choses sont connues au sujet de sa biomasse et sa dynamique dans les zones subtidales.

La zone subtidale de la baie de Brest (Fig. 1) a été choisie pour cette étude parce qu'elle a été l'objet d'importants apports en azote lors du siècle dernier (Tréguer & Le Corre, 1975). Cependant, cette zone a étonnamment bien résisté à l'eutrophisation, bien que le rapport silicate/nitrate ait diminué au cours des 20 dernières années (Le Pape et al., 1996).

De récentes recherches ont étudié la répartition spatiale du MPB dans la Rade de Brest en termes de production primaire et de biomasse, à 2 saisons distinctes, mais dans le but de parvenir à une vision plus globale de ces photoautotrophes importants, une étude temporelle est nécessaire.

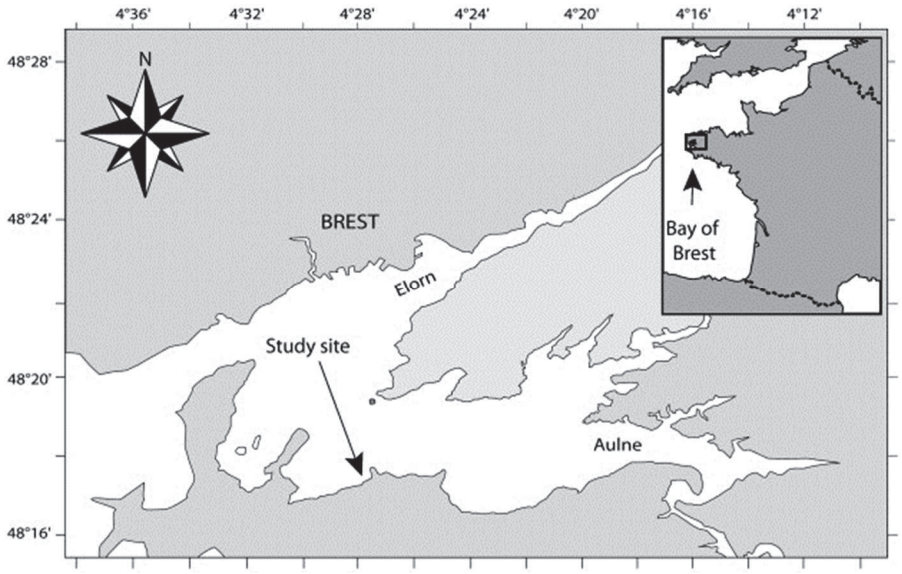


Fig.1 Site d'étude dans la Rade de Brest

Les objectifs de ma thèse étaient

- de caractériser la répartition temporelle du MPB en terme de biomasse, de production et de biodiversité dans la zone subtidale de la baie de Brest sur une échelle mensuelle,

- de comparer la dynamique du MPB et du phytoplancton de la colonne d'eau sus-jacente en fonction des différents paramètres de l'environnement, afin de mieux l'importance des fluctuations saisonnières de MPB et son rôle fonctionnel dans l'écosystème.

Notre étude a montré que la dynamique du MPB et du phytoplancton dans la zone subtidale étaient tout à fait différentes l'une de l'autre (Fig. 2). Le MPB est le premier à se développer dans la saison. Il constitue un apport important d'énergie dans l'écosystème dès le début du printemps (avec 60% de la biomasse totale jusqu'en Avril). Le système se déplace ensuite

d'un système dominé par la biomasse benthique au début du printemps vers un système où la biomasse pélagique prend le dessus.

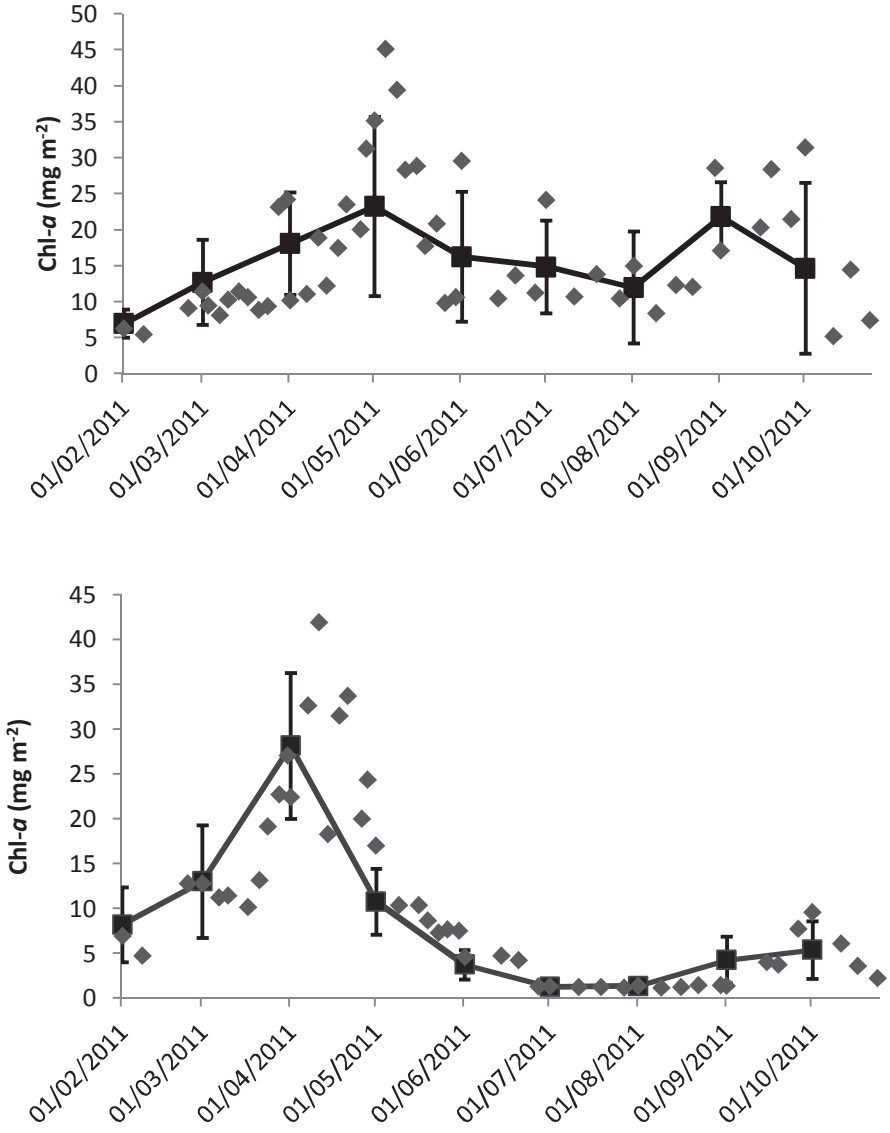


Fig. 2 Evolution saisonnière de la Chl-a (a) du phytoplancton de la colonne d'eau et (b) du MPB. Dots: données originales; ligne: moyennes mensuelles.

Parmi les ressources que le MPB et le phytoplancton ont à partager, la lumière semble être un des paramètres importants dans le déclenchement précoce de la floraison du MPB, par rapport au phytoplancton de la colonne d'eau.

En ce qui concerne les nutriments, le manque de phosphore peut être avancé pour expliquer le déclin de la biomasse MPB au début d'Avril, alors que le déclin du phytoplancton dans la première semaine du mois de Mai coïncide à une carence en acide silicique (Fig. 3). L'azote inorganique dissous devient ensuite potentiellement limitant dans la colonne d'eau jusqu'à la

fin d'Octobre. D'autres facteurs comme la compétition du MPB et des macroalgues, ou le grazing, peuvent sans doute aussi expliquer la différence de dynamique saisonnière entre le MPB et phytoplancton.

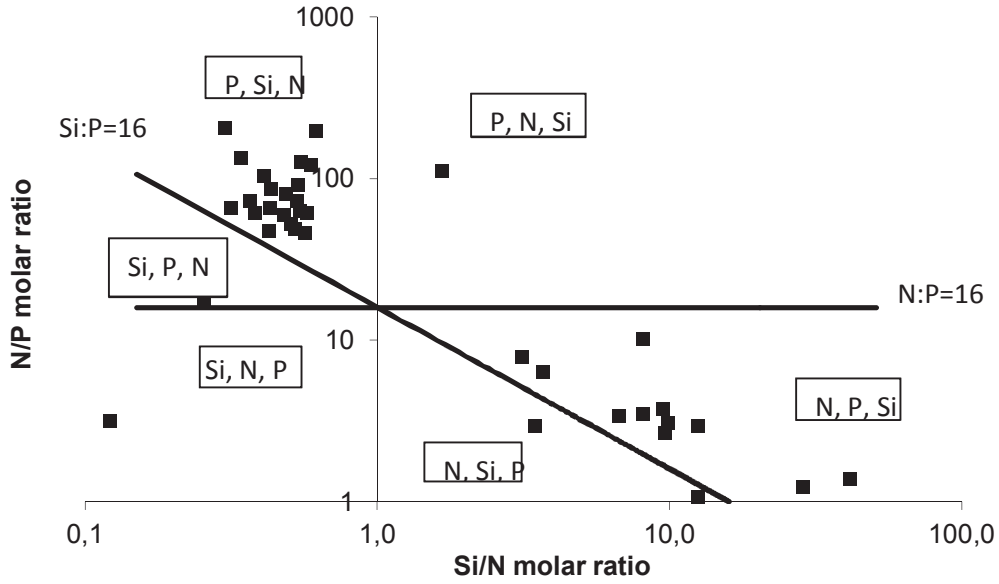


Fig. 3 Représentation des rapports molaires Si: N :P dans la colonne d'eau de Février à Octobre 2011. Chaque zone est délimitée par les rapports de Brezinski (1985) et Redfield et al. (1985) rapport Si: N: P = 16:16:01.

La production primaire maximale de MPB mesurée lors du suivi 2011 était de l'ordre de 100 mg C m^{-2} $jour^{-1}$ (Fig. 4). La production primaire du MPB atteint son apogée début Mai, juste après la pic de Chl-a. Après son pic de production, le MPB décline et suit à peu près les mêmes fluctuations que celles de la biomasse de Chl-a.

Des études antérieures ont montré que la température a un effet important sur la production de MPB. Dans notre étude, la production spécifique (production / biomasse) de MPB atteint son maximum en Août, lorsque la température a également atteint son apogée, ce qui suggère une dépendance partielle de la production du MPB avec la température.

Une limitation de la production spécifique du MPB par les nutriments est fort peu probable car la production est la plus forte en dépit de concentrations en DIN et DIP très faibles (Fig. 5).

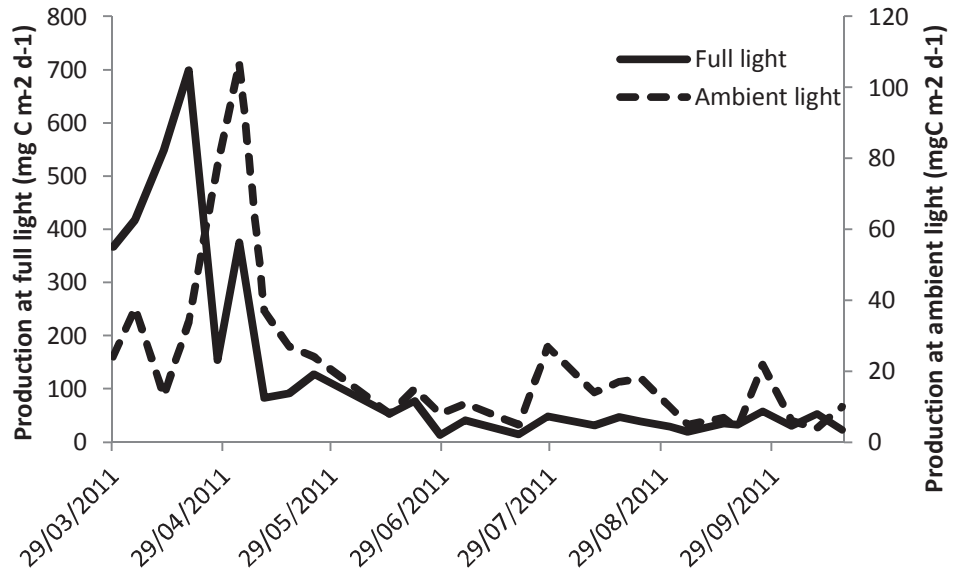


Fig. 4 Evolution saisonnière de la production primaire du MPB incubé en pleine lumière et à 11,4% du PAR

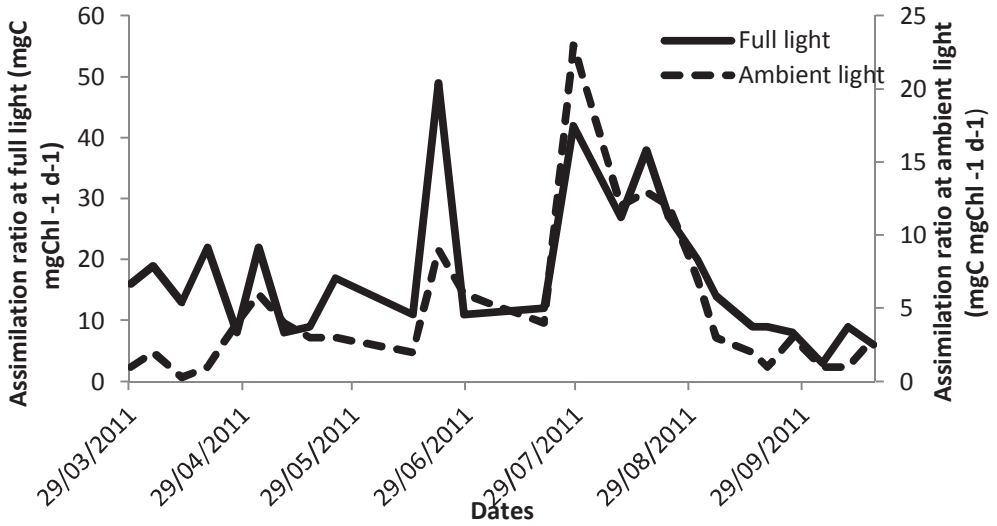
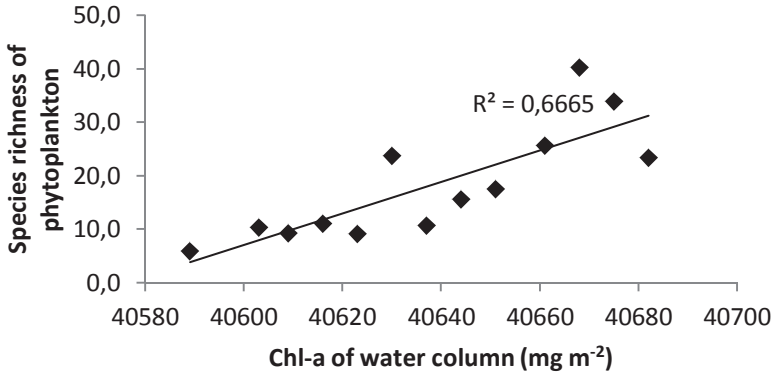


Fig 5. Production spécifique du MPB à pleine lumière et à 11.4% de la lumière incidente

Les paramètres photosynthétiques des communautés du MPB ont été étudiés. Les paramètres en tant que tels ne montrent aucune tendance saisonnière avec des valeurs fluctuantes tout au long de la période d'étude. Aucune relation n'a été trouvée entre le taux de transport photosynthétique (rETRmax) et le paramètre d'efficacité d'utilisation de la lumière α. Les variations de rETRmax ne coïncident pas non plus avec celles de la Chl-a , suggérant un contrôle « top down » du MPB. Une augmentation de rETRmax et α au cours du mois de Mars suggère que la lumière pourrait être le facteur déclenchant la floraison printanière.

Ek varie sur une échelle de valeur plus large, entre 59 et 355,3 pmol quanta m -2 s- 1, et dépasse même en quelques occasions, la valeur du PAR ambiant, avec un rapport maximum d'E/Ek atteignant 2.5, ce qui suggère une mauvaise photoacclimation du MPB. Les mesures de photosynthèse, avec les analyses de production spécifique, montrent que le grazing, plutôt que la limitation en ressources, serait une des principales raisons du déclin de la biomasse algale après la floraison printanière. Nos résultats appuient les travaux de Banse et English (2012), qui montrent que le grazing est certainement un facteur négligé pour expliquer la dynamique et la composition des communautés de microalgues marines. Le grazing n'affecterait pas seulement la disponibilité des ressources, mais aussi la structure et la composition des communautés.

On connait peu de choses sur la répartition temporelle et la diversité du MPB, par rapport au phytoplancton, en particulier dans les zones subtidales. Nous avons caractérisé, en parallèle, la diversité saisonnière de phytoplancton et des microalgues benthiques de la baie de Brest. Le phytoplancton comprend 74 espèces, dont 35 appartiennent à des dinoflagellés et 32 à diatomées, alors que la communauté de MPB est composée de 22 espèces, toutes des diatomées. La taille des cellules individuelles du phytoplancton varie de 42 μm^3 à 15.10^7 μm^3 et celle du MPB de 79 μm^3 à 3.10^4 μm^3 tout au long de la saison. Le phytoplancton est dominé par Chaetoceros sp. parmi les diatomées et Gymnodium sp. parmi les dinoflagellés, alors que pour le MPB, c'est Navicula sp. qui domine principalement pendant toute la période d'étude. Chaetoceros debilis et Chaetoceros didymus sont les deux seules espèces que l'on observe dans les 2 compartiments. On observe une corrélation entre la richesse taxonomique et la Chl-a du phytoplancton sur toute l'année, alors que la corrélation entre la richesse spécifique et la Chl-a du MPB n'est remarquable que jusqu'à la floraison au début du printemps. (Fig. 6).



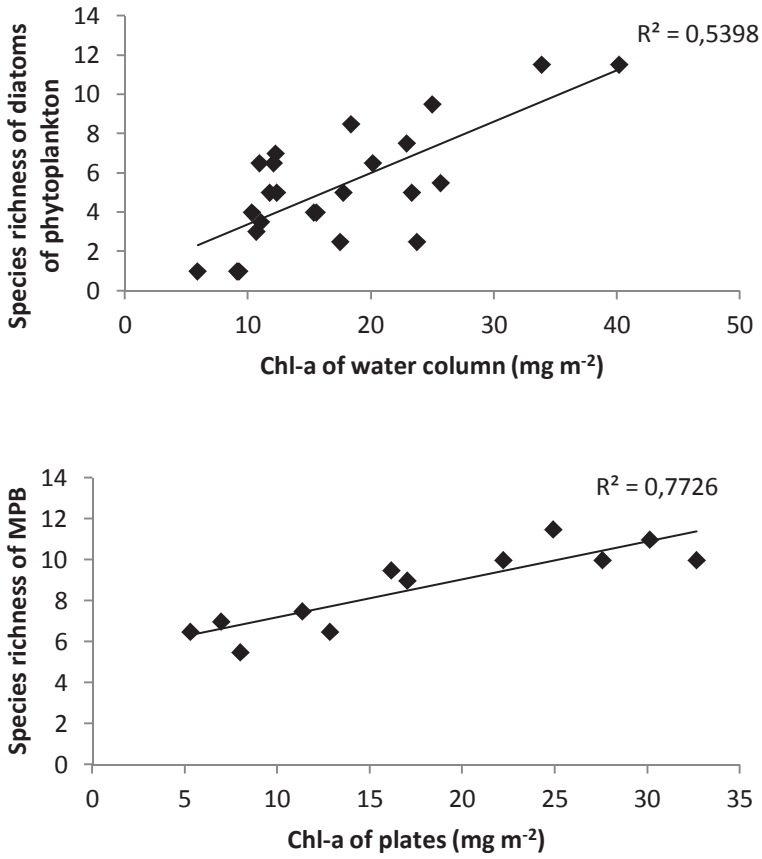


Fig. 6 Relation entre (a) la richesse taxonomique et la Chl-a du phytoplancton jusqu'en 2011 (b) entre la richesse taxonomique et la Chl-a des diatomées et de la communauté phytoplanctonique pendant toute la durée de l'étude et (c) entre la richesse taxonomique et la Chl du MPB jusqu'en mai 2011.

La composition des communautés phytoplanctoniques changent lors des différents pics saisonniers, passant de grandes cellules à de petites cellules avec une forte dominance d'une espèce. D'autre part, l'indice de diversité du MPB explique la dynamique de la Chl jusqu'à la floraison, et est aussi similaire à celle du phytoplancton jusqu'à ce moment. Après la floraison la biomasse décline et reste minime jusqu'en Septembre. Navicula sp. constitue une nourriture très appréciée du meiobenthos et l'absence d'espèces résistant au grazing pourrait expliquer l'incapacité de la communauté de MPB à soutenir sa biomasse après la floraison.

Bien que la composition taxonomique des communautés diffère complètement entre les communautés phytoplanctoniques et microphytobenthiques, les indices de diversité ont montré des tendances temporelles plus ou moins similaires, en particulier juste avant et pendant la floraison printanière. Cela suggère que la dynamique et le mécanisme de croissance pourrait être similaire pour les deux communautés. Cependant, la grande

différence de Chl du MPB et leurs indices de diversité après la floraison indique fortement l'influence du broutage empêchant la communauté MPB de se développer et maintenant une faible biomasse micro algale. Pour les études futures, il serait intéressant d'étudier la biodiversité par rapport à la productivité dans les différents sites d'échantillonnage. Tant que les raisons et les mécanismes de variations saisonnières de la diversité des algues - et comment ces mécanismes interagissent avec les facteurs affectant la productivité - ne sont pas connues en détail, il est très difficile d'argumenter sur les causes et les conséquences de la relation « diversité potentielle – productivité » provenant des tendances saisonnières.

En résumé, la communauté phytoplanctonique est sujète à un broutage sélectif après la floraison qui lui permet de subsider pendant l'été, ce qui n'est pas le cas pour le MPB. L'étude de la dynamique des micro-algues (croissance, production et biodiversité) de la communauté MPB indique que des études sur le grazing sont cruciales pour comprendre les modèles d'évolution des communautés microphytobenthiques. Ainsi, pour une meilleure compréhension de la dynamique de du MPB dans les zones subtidales des systèmes côtiers, les recherches devraient inclurent l'activité des brouteurs benthiques, ce qui permettrait de montrer davantage l'importance du réseau trophique benthique dans les écosystèmes côtiers.

Chapter 1

General Introduction:

Availability of ample food and easy accessibility fostered human habitation in the coastal areas for thousands of years. Although coastal regions account for only 20% of all land areas, nearly half of us live near the coasts (Pandolfi, 2003). Population density in the coastal regions is two times higher than the world's average (UN System-Wide Earthwatch, 2003). Moreover, between the years 2003 and 2025, the number of people living within 200 km of the coastline is predicted to double (Creel, 2003, PRB). Humans are dependent on the coastal water not just for food and livelihood; in fact huge economic activities are undertaken in the coastal regions. In the tropical developing countries of east Africa and Latin America, more than 50% of the GDP is generated in the coastal marine environments (CRTR, 2009, www.gefcoral.org). Income-generating activities in the coast include fisheries, tourism, community and recreational services, shipping etc. Nearly two thirds of all fish harvested depend on coastal wetlands (Hinrichsen, 1998). Specifically, temperate coastal zones are crucial for shellfish and fish farming. On the other hand, tourism is the fastest growing sector of global economy and coastal tourism involves *mass*, *i.e.,* 'touristic' visits as well as distinctive *adventure* or nature tourism. Summarily, coastal regions represent ***the*** global habitat where the prosperity of human communities is most closely and directly linked to the status of the natural habitat.

A. Ecological importance of coastal ecosystems:

The major ecological importance of the coastal ecosystems lies in their productivity. Coastal productivity by far exceeds that of the open oceans. The abundance of nutrients supports such huge productivity in the coastal water. Since secondary production is dependent on primary productivity, particularly in complex intertwined ecosystems the importance of coastal habitats cannot be ignored. Interestingly, coastal ecosystems often possess unique food-web structures showing biomass pyramid shapes. As depicted in figure 1, the increase in heterotrophic biomass is contributed primarily by zooplankton whereas protozoans have decreased abundance compared to that of open ocean ecosystems (Legendre, 2011).

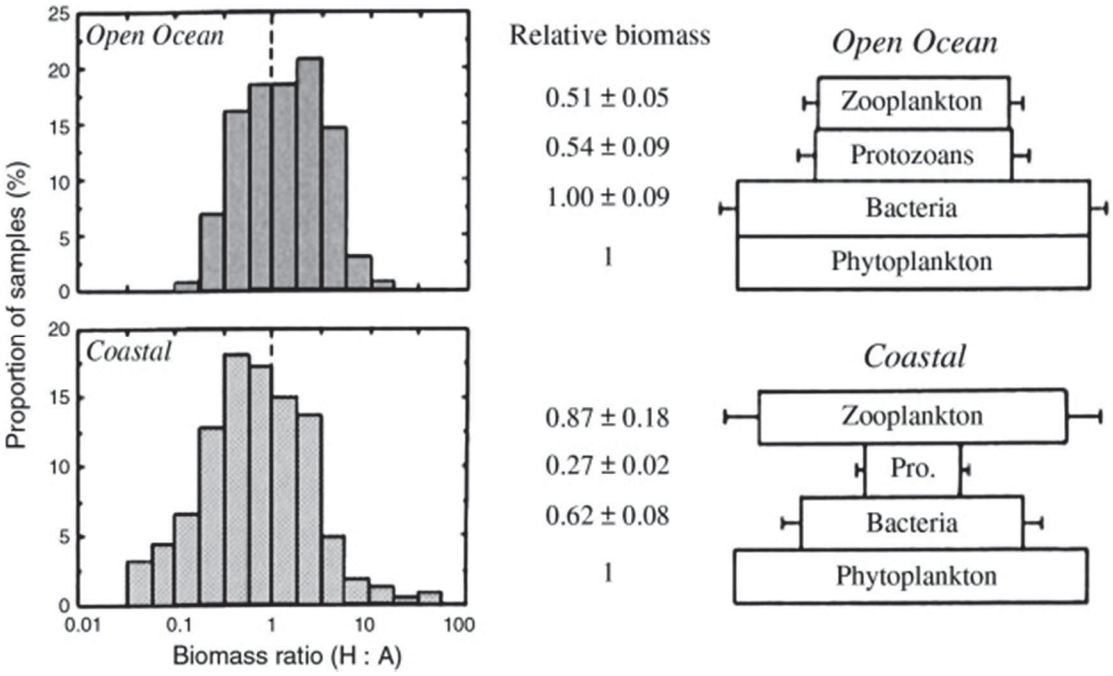


FIGURE 1. Left: Frequency distributions of samples with a given biomass ratio (heterotrophic:autotrophic) for open-ocean communities (upper panel) and coastal communities (lower panel). Middle: Mean biomasses (and standard deviation) of zooplankton, protozoans (heterotrophic protists), and heterotrophic bacteria, relative to autotrophic biomass, for open ocean communities (upper panel) and coastal communities (lower panel). (Gasol, 1997; Legendre, 2011).

Coastal zones are very rich in biodiversity; as a result they host tremendous biological activity. Physically the coastal habitat is traditionally divided into (a) the near-shore terrestrial zone which includes the dunes, cliffs, rocky shore, etc., (b) intertidal zone, this includes estuaries, deltas, lagoons, mudflats, salt marshes, mangrove forests, etc., (c) the benthic zone, includes coral reefs, seagrass beds, kelp forests etc., and lastly (d) the pelagic Zone (Burke, 2001, WRI). These zones however only represent physical habitats, meaning that a given ecosystem may encompass multiple physical zones. Generally, the exact limit of the coastal region is not universally demarcated but broadly it is said to encompass areas routinely inundated by saltwater - this includes "intertidal and subtidal areas on and above the continental shelf (to a depth of 200 meters) and immediately adjacent lands" (Burke, 2001). These areas provide extensive habitats of diverse characteristics and facilitate trophic linkages for a large variety of organisms ranging from microfauna to wading birds and demersal fish (Aberle, 2004). The coastal waters and resident biota are subjected to very

unique biological and physiochemical forces that render coastal ecosystems mechanistically distinctive. Shown in figure 2 is an example of how such diverse biological and physical forces shape the state and functioning of a typical estuarine ecosystem. Seasonality, acute climatic variations, nutrient loading, recycling and upwelling, benthic grazing and physical forces are some of the major determinants of the structure and function of coastal ecosystems.

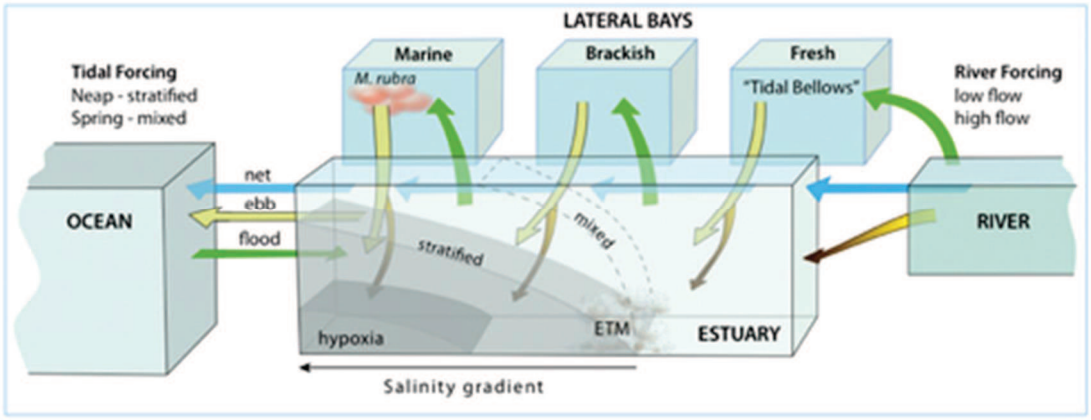


FIGURE 2: This figure shows how the function of the Columbia River estuarine bioreactor is controlled by three biological hotspots: lateral bays, estuarine turbidity maxima, and plankton blooms (CPOM, 2012)

However, although coastal ecosystems bear tremendous ecological significance, they have been constantly being subjected to severe anthropogenic stress in recent times. The two of the most important anthropogenic stress factors on coastal ecosystems are the direct stress factors and eutrophication

A.1 Direct anthropogenic stress factors:

Anthropogenic pressure is globally reshaping the marine coastal ecosystems. In particular, the shallow coastal areas of Western Europe are being subjected to remarkable levels of climate forcing and human-generated stress (Goberville, 2010). Global warming has led to increased melting of artic ice, which is already causing sea level rise, as shown in figure 3. A number of human communities and endemic biospheres are facing the chance of extinction owing to sea level rise. Over-accumulation of greenhouse gases in the atmosphere has

additionally resulted in ocean acidification. Both these two global changes in marine environment have direct consequences especially for the coastal ecosystems.

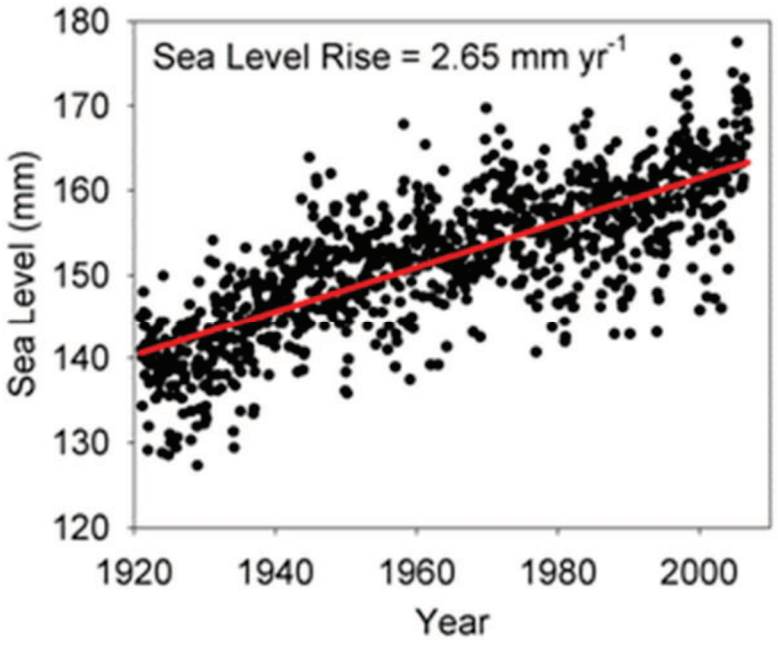


FIGURE 3: Sea level rise as measured in Boston, USA (Weston et al., http://www62.homepage.villanova.edu/nathaniel.weston/microbe.html, retrieved in July 15, 2013).

By 2050, 91% of the world's coastline is predicted to be negatively affected by construction and developmental projects (CRTR advisory paper, 2009, www.gefcoral.org). Coastal and inland construction often damages habitat irreversibly. Habitat degradation could also be invisible and indirect – e.g., removal of mangroves abolishes natural filtration thereby increasing pollution, damages the natural buffering capability against storm, tsunami and flood, and at the end establishes a beach system that requires periodic restoration and continuous management. WWF estimated in 2009 that land-based activities on its own contribute to 80% of marine pollution. Physical damage to the habitat could also originate from water-based human activity, e.g., fisheries. Specifically, 'bottom dragging' scrapes the ocean floor uprooting corals and sponges and effectively changing the species composition, biodiversity and ecosystem functioning within a very short span of time. Major sources of chemical pollution in the coastal environment are (a) sewage – more than 80% of sewage

enters the coastal ocean water directly without any treatment, outside of North America and Europe; (b) garbage and industrial debris whose rate of biodegradation is often very slow; (c) petroleum – mainly from the discharge of regular boat traffic, also from large oil spills and river-derived oil run-off; (d) fertilizers from lawns and farms that cause eutrophication and (e) other toxic chemicals such as pesticides. Invasive species in the coastal water are regarded as biological pollutants. They reduce local biodiversity, alter habitats, enhance biological completion and could potentially lead to extinction of endemic species. NCCOS in 2012 estimated that about half of the US species protected under the Endangered Species Act are effectively threatened by invasive species.

A.2 Eutrophication:

Eutrophic coastal water promotes very fast growth of algae that forms dense populations, called blooms. Occasionally the algal blooms pose serious harm for humans and local biota. Such harmful algal bloom (HAB) could release biotoxins that kill fish and shellfish and indirectly get incorporated in the food web ultimately affecting top predators and even humans. Identification of the relevant toxic species within a bloom and exact measurement of the toxin level are prerequisite for the forecast and management of toxic HABs. For example, *Pseudo-nitzschia* species in the Bay of Brest, where the field research pertaining to this thesis was carried out, produce a neurotoxin called Domoic acid or amnesic shellfish poison (Nezan, 2010). This poisonous amino acid bioaccumulates in mussels and human beings could die by ingesting such toxin-laden bivalves (Mos, 2001). In the US between 1991 and 1999, a cost of $300 billion was incurred on the economy for damaging impact of HABs on public health, tourism and loss for the seafood industry (McGinn, 1999). Even a bloom that is not producing toxins could be harmful because of the excessive growth of microalgae. These apparently non-toxic HABs could potentially suffocate fish, block light penetration, increased sedimentation of organic matter and lead to hypoxia. Typically dissolved O_2 level below 2mg/l is considered as hypoxic and generally this is correlated with a low pH.

Coastal and estuarine eutrophication adversely affects the overall biological productivity of numerous interconnected ecosystems because many organisms spend at least one trophic stage of their life-cycle in such habitat. Although eutrophication and HABs are natural

events, in the past decades their frequency and duration has increased significantly due to human activities (Figure 4).

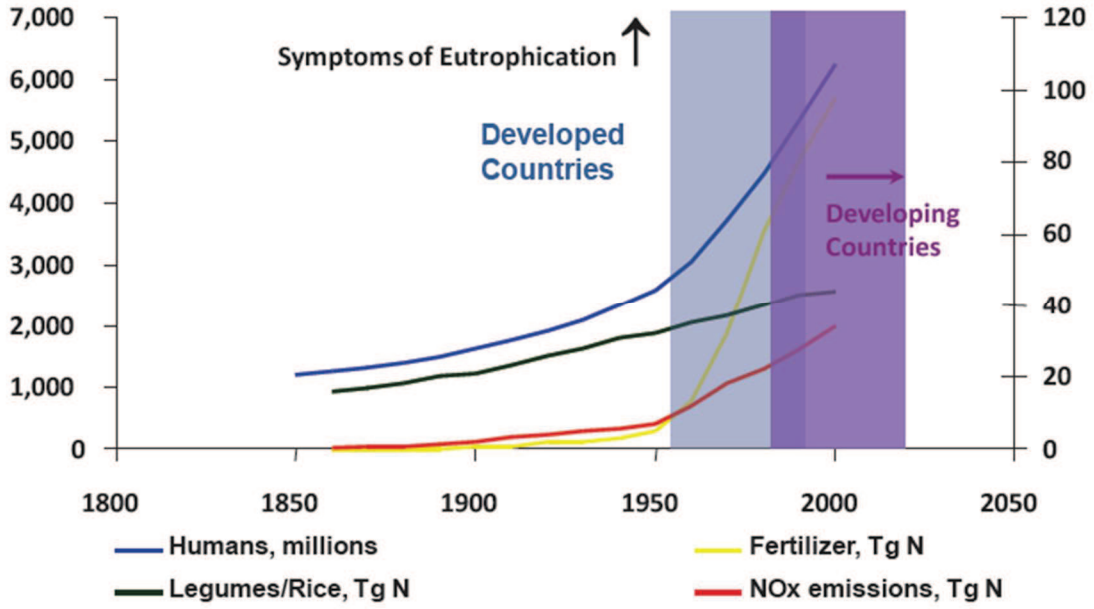


FIGURE 4: The occurrence of eutrophication and its symptom, i.e., hypoxia/anoxia are showing a trend of continued increase that began in developed countried and is currently shifting toward developing countires. (Adapted from Rabalais, 2010)

The major culprit for coastal eutrophication is nutrient loading. This often arises in the form of DIN (dissolved inorganic nitrogen: includes NO_3-*N* + NO_2-*N* + NH_4-*N*) and DIP (dissolved inorganic phosphate) from agricultural and livestock runoff. Altered N:P:Si ratio in ocean water owing to interaction between nutrient stressors and hydrology promotes the formation of HABs. The schematic in figure 5 illustrates the major sources and mechanism of coastal eutrophication.

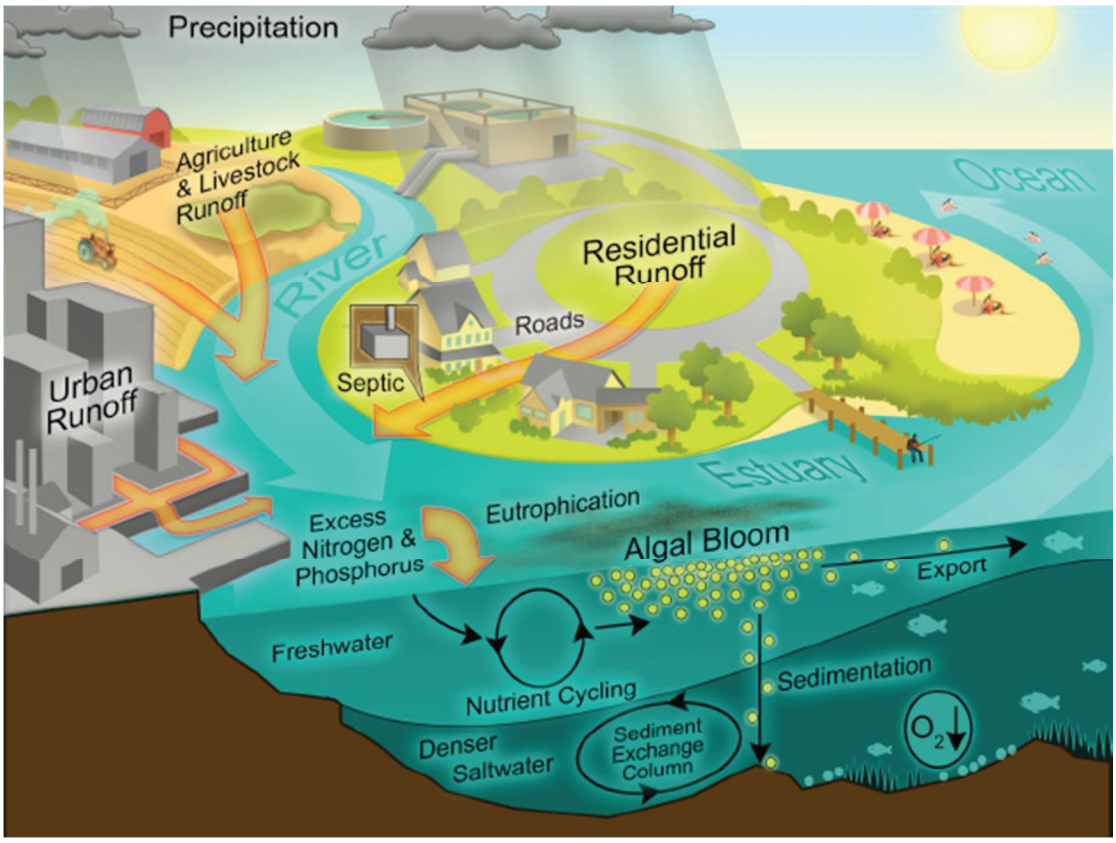


Figure 5: Schematic showing the various watershed and airshed anthropogenic nutrient sources, their input to estuarine and coastal waters via freshwater discharge, the establishment of hypoxia due to freshwater overlaying denser saltwater and the stimulation of primary production (eutrophication) and algal blooms due to coastal butrient enrichment (Kodu.ut.ee)

Notably, waste-water discharge and loading of untreated sewage, atmospheric deposition of dissolved NOx and overally change in global climatic patterns are presumed to contribute to eutrophication events. A pycnocline in the interface of the heavier, saltier, cooler bottom water and the lighter upper water prevents effective oxygen exchange. The dead algal cells settle down and decay in the denser bottom water depleting it of oxygen. Hypoxic water could form a dead zone and further release DIP from the sediment, facilitating a detrimental positive feedback. Benthic microalgae on which my research was primarily focused, suffers heavily from HAB events. HABs change their species composition, reduce depth distribution due to shading, promote the growth of epiphyte and nuisance macroalgae and may even cause mass death due to release of hydrogen sulphides (www.coastalwiki.org). The map in figure 6 below, underscores the state-of-the-art of eutrophication events in the Eurpean coast.

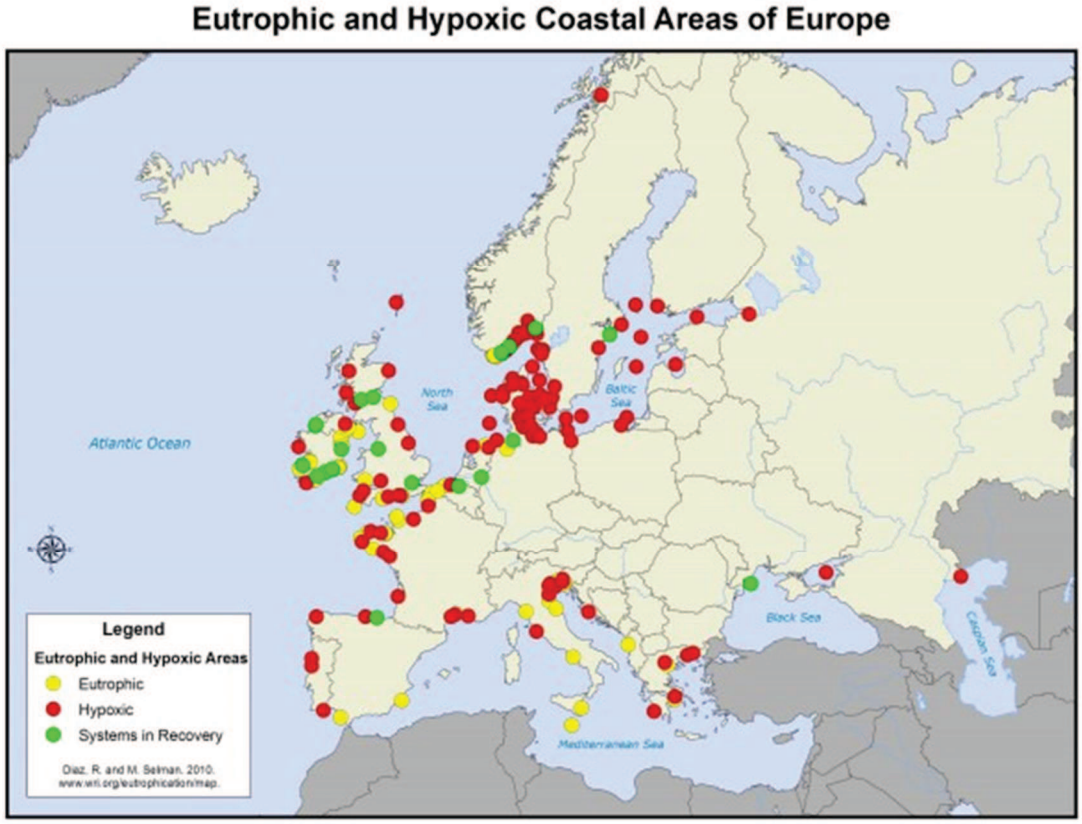


FIGURE 6: A map identifying 168 eutrophic and hypoxic coastal areas concentrated in the North and Northwest coastline of Europe (Adapted from Diaz, 2010).

Two of the most important primary producers in coastal ecosystems are phytoplankton and Microphytobenthos (MPB). Therefore, considering the contribution of coastal ecosystems and also the constant stress they are subjected to, the importance of studying these two living groups (phytoplankton and MPB) to get a detailed mechanistic view in different coastal ecosystems are increasing each passing day. The significance of both phytoplankton and MPB are discussed in the following section.

B. Phytoplankton:

Phytoplankton, the most abundant primary producers on earth are a free-floating aquatic microscopic diverse and polyphyletic group of mostly unicellular and colonial photosynthetic organisms (Falkwski, 1997) having a critical role in primary production, nutrient cycling, and food webs (Dawes 1998). In spite of constituting less than 1% of the Earth's photosynthetic

biomass, they make up a significant proportion of the global primary production (45% of annual net primary productivity; Field, 1998). Phytoplankton must be in the photic zone to entrap solar energy. A host of adaptations allow them to move into or to remain in the euphotic zone. Most phytoplankton species are motile and swim toward light; however, major movement is mostly through transport by water currents (Dawes 1998; Sandifer et al. 1980). Non-motile phytoplankton rely on physiological adaptations (production of mucilage and accumulation of lighter ions with a concomitant reduction of heavier ions or compounds), morphological characteristics (branching frustules, bladder-like cell shape, presence of gas-vaculoes), and physical factors (water viscosity, convection, wind-induced rotation) to reduce sinking rates (Dawes 1998).

B.1 Phytoplankton growth:

Phytoplankton growth outside the tropics is characterized by periodic oscillations. General patterns of phytoplankton dynamics in temperate water are well known (Reynolds, 1984; Sommer et al., 1986). Bloom events take place predominantly in spring and secondarily in autumn. A typical seasonal pattern phytoplankton in eutrophic and oligotrophic water is displayed in figure 7.

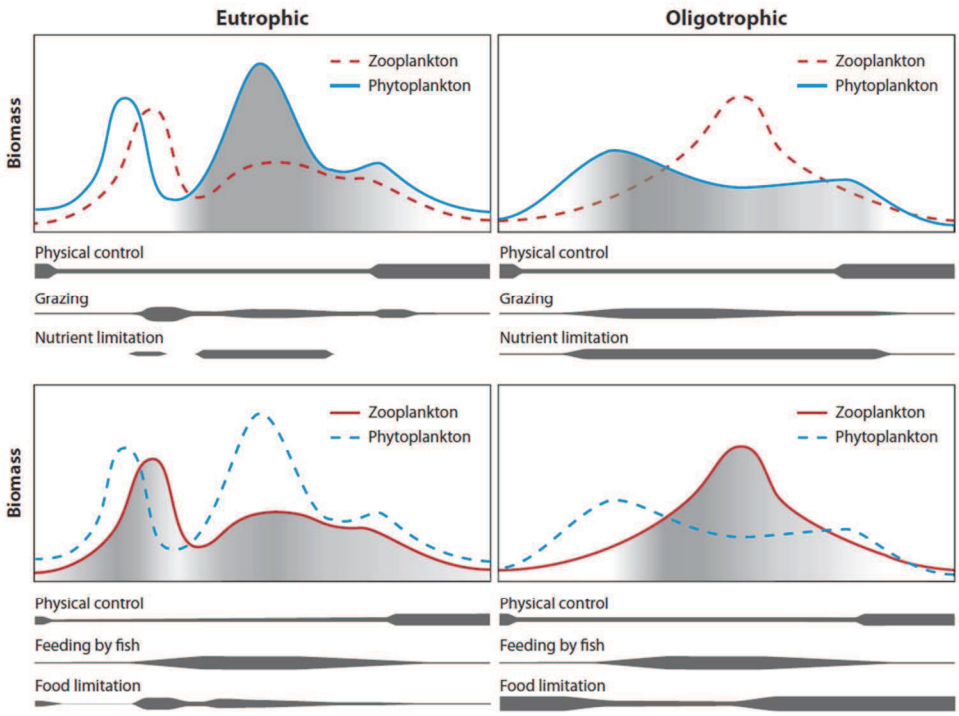


Figure 7 The PEG model: Biomass patterns of eutrophic (left) and oligotrophic (right) waters. The relative importance of physical factors, grazing, food limitation, fish predation and nutrient limitation are represented by the thickness of the horizontal bars. (Adapted from Sommer et al., 2012)

Sverdrup's critical depth hypothesis proposed in 1953 has been an effective albeit imperfect model to explain the phenomenon of seasonal blooms. The model is based on the idea of a critical depth, defined as the depth at which the integral of net growth rate over the water column becomes zero. The critical depth is a dynamic parameter - its value is maximal in spring, when increased solar radiation and decreased angle of incidence act together to enhance the depth of water column that can support phytoplankton growth. Before the onset of spring active turbulence homogenize the water column, giving rise to a mixed layer containing nutrients. In spring the depth of this mixed layer is smaller than the critical depth. The surface water is warmed by the sun, its density decreases and floats on top. Therefore, density dependent stratification of the water column because of a pycnocline caused by salinity and temperature differences prevents further mixing. It gives ample opportunity to the phytoplankton to actuate steep rise in cell division, *i.e.*, increase their number and abundance. This constitutes the primary bloom, which is often dominated by diatoms, cryptophytes, chrysophytes and chlorophytes. For every 10-degree rise in temperature the cell division rate of phytoplankton generally doubles. Particularly the upper limit of growth is

often determined by temperature (Harris, 1986). This peak is often followed by a "clear water phase" induced by the grazers in the late spring or early summer. During mid-summer there is no mixing of denser cooler nutrient rich water and the warm surface layer that becomes nutrient depleted due to phytoplankton overgrowth. Therefore the summer is often marked by a crash of the phytoplankton population. On rare accounts rain and remineralization processes may support continued sustenance of some phytoplankton communities in the summer. In autumn decreasing daylength leads to decrease in temperature so that the surface layer of water cools down and becomes denser. This often gives rise to a moderate level of mixing, bringing nutrient rich bottom water up. If enough light is still available, a secondary population bloom may ensue in this season. The winter is characterized by strong turbulence in the form of rain and storms that force a complete mixing between different layers of water. But scarcity of light prevents any growth in this otherwise nutrient enriched water (Grover and Chrzanowski, 2005). Coastal waters in winter occasionally register growth of phytoplankton such as *Skeletonema costatum*, which increase their assimilation rate of nutrients under cold environment, while keeping the cell-division rate largely unaffected (Goldman, 1977; Hitchcock, 1980). Interestingly, picoplankton keep a quasi-constant biomass throughout the year. It has been suggested that driven by a biological clock they divide daily and thus have a high turnover, but they could in fact be devoured by predators immediately (after being born) (Carpenter, 1998).

The simplified chain of events mentioned above clearly suggest that the growth and decay of phytoplankton population is controlled by multiple physiochemical parameters, including light, nutrient level, temperature, circulation, etc. and biological factors such grazing pressure, parasitic load etc. Phytoplankton requires both macro-and micronutrients for their growth. The availability of the nutrients is controlled by the balance upwelling and the biological pump. Biological pump refers to the marine snow, i.e., organic carbon in sinking particulate material and also include the downwelling of dissolved organic carbon. Upwelling brings the denser cooler nutrient rich bottom water toward surface owing to combined action of wind, Coriolis force and Ekman transport. It is noteworthy that while Critical depth theory has not yet been discarded, in recent times a number of alternative hypotheses have been put forward to account for the cyclical changes in phytoplankton growth over the course of a year. Prominent among these is the dilution recoupling hypothesis of Behrenfeld (2010). It posits that seasonally varying physical parameters spur the growth of predators and prey.

Increased light availability leads to a rise in the population of both in the spring. This in turn facilitates the interaction between them, i.e., recouples the predator-prey relationship. As a result the prey (phytoplankton) population suffers loss at the end of the spring bloom. In winter minimal stratification of water dilutes this coupling. This theory lays special emphasis on zooplankton biomass, grazing pressure and population loss of the phytoplankton in explaining the seasonal fluctuation of growth pattern.

N, P and Si constitute the growth regulating macronutrients. Generally these nutrients arise from weathering of rocks and atmospheric inputs, part of biogeochemical cycling. In addition to these, human activities can also import a huge amount of nutrients into the ocean. Most phytoplankton can not use aerial nitrogen gas directly, instead chemically reactive forms of nitrogen such as nitrates and ammonium ions are utilized by the microalgae. In most ocean water, growth is limited by N availability, but few specific regions, e.g., the eastern Mediterranean shows a P-limited pattern of microalgal growth. S On the other hand, Si determines the community composition as diatoms and silicoflagellates require considerable levels of Si for their growth. N level in the water is altered by vehicular exhaust, fertilizer and power generation facilities that primarily contribute nitrate, whereas animal manure provides ammonium ion. Detergents and sewage runoff generally boost the level of P in ocean water. Micronutrients include the trace metals Fe, Mn, Cu, Zn and Co and in addition to this vitamins, specifically Vitamin B. In the Southern hemisphere ocean Fe has been shown to be a limiting factor for phytoplankton growth (Dawes, 1998). Vitamins in spite of having a very low concentration in the ocean water are not known to be limiting because of their high turnover rate and low requirement. Apart from the usual recycling of nutrients, benthic flux of nutrients is another factor which influences both the community composition and biomass of phytoplankton (Claquin, 2010). In the Bay of Brest, *Crepidula fornicata* a molluscan grazer, influences Si flux (Claquin, 2010, Ragueneau, 2005). At the microscopic level, zooplankton and bacteria turn organic matter into CO2 and nutrients via respiration and bacterial decomposition respectively. These processes consume O2. If sunk, CO2 and nutrients are sometimes stored – 15% of CO2 taken up by photosynthesis is stored in this way. A small fraction of this settles and become sediment and an even smaller fraction ? turns into fossil fuels – gas, oil and coal.

The nutrient ratio has been shown to profoundly affect the community composition of phytoplankton. Ryther (1981) hypothesized that two distinctive categories of ecosystems could be formed based on nutrient availability and enrichment status. Phytoflagellate dominated system would prosper in nutrient rich water whereas Si-rich water would support specifically the diatoms. The former could lead to hypoxia whereas the latter is known to augment the output of fisheries. Mesocosm experiments later (Verity, 1998; Gray, 1982) verified this theory. Addition of anthropogenic pollutant (Cu and Hg) in controlled environment shifted nutrient ratio and changed the predominance from diatoms to flagellates. Such changes are bound mediate concurrent shift in food chain dynamics (Greve, 1977). In a longer timescale study in the Southern estuaries of USA, accelerated land-use over the course 25 years (in the seventies and eighties) was shown to generate increase in N load of the coastal water while Si did not show a concomitant increase (Windom, 1993). This suggests that the community structure and growth pattern of phytoplankton are changing. A comprehensive study investigated phytoplankton biomass at local, regional and global scales over the course of a century, since 1899 (Biyce, 2010). While decadal-scale fluctuations linked to climate forcing and strongly correlated with basin-scale climate indices was apparent, alarmingly a global rate of decline of ~1% per year was noted. This long-term declining trend was found to be related with increasing sea surface temperatures. This is of particular concern because as the environment changes the phytoplankton the biological changes also affect the working of the physiochemical environment. The famous CLAW hypothesis describes a feedback loop between particular phytoplankton growth under warm weather and variations in climate forcing. Blooms of certain phytoplankton, e.g., coccolithophoroids, under increased light availability and warmer temperature causes increased atmospheric release of a phytoplankton produced gas named DMS (Dimethyl sulfide) which is a byproduct of DMSP (Dimethylsulfoniopropionate), an osmolyte in certain phytoplankton cells. DMS is oxidized in the atmosphere to form SO2 leading to the generation of sulfate aerosols that nucleate cloud condensation. This acts to increase cloud albedo resulting in greater reflection of incident sunlight and at the end decrease in temperature (Charlson, 1987; Lovelock, 2006).

B.2 Phytoplankton diversity:

The apparent paradox of how unstructured marine environment offering little possibility for niche separation could support a high diversity has historically generated significant attention (Hutchinson, 1961). Scheffer (2003) proposed that ecological and environmental factors such as chaotic fluid motion, size-selective grazing, spatio-temporal heterogeneity, and environmental fluctuations continually interact such that the planktonic habitat fails to reach a static equilibrium favoring a single given species. The main global pattern of phytoplankton diversity is the latitudinal cline. With increasing latitude, diversity decreases. This pattern of diversity is shaped by the interplay of dispersal and competitive exclusion. Environmental variability modulates competitive exclusion – the largely uniform oligotrophic environment of the tropics allows more prolonged coexistence of competing species and the heterogeneous temperate zones favor the exclusion of slow growing species and homogeneous communities (Barton, 2010). On the other hand, lateral dispersal is prominent in regions of energetic ocean circulation that generate a collage of diversity hot spots on the global trend of latitudinal cline (Barton, 2010). Diversity and biomass of phytoplanktons have been shown to maintain a consistent unimodal relationship – intermediate biomass promotes the highest diversity while blooms harbor the lowest diversity (Irigoien, 2004). Surprisingly, no clear relation between phytoplankton and zooplankton diversity has been found (as shown in the figure below), while the biomass of zooplankton is an increasing saturating function of the phytoplankton biomass (Irigoien, 2004).

Phytoplankton comprise of microalgae and marine phototrophic eubacteria and archaebacteria. They include species from the following 8 major divisions: Cyanobacteria (blue-green algae), Chlorophyta (green algae), Prochlorophyta (prokaryotic picoplankton), Euglenophyta (euglenids and kinetoplastids), Pyrrhophyta (dinoflagellates), Cryptophyta (cryptomonads), Chrysophyta (golden algae), and Bacillariophyta (includes diatoms). Each group of phytoplankton shows characteristic colors, depending on the relative abundance of the resident photosynthetic pigments: green chlorophylls, yellow carotenes, or pink or blue phycobilins. Katz (2004) reported about 25000 morphologically distinct forms of phytoplankton, while at least 500 genera (Sournia, 1991) and 5000 marine species have so far been conclusively identified (Hallengraeff, 2003). Surprisingly, at least three times more planktonic species are known in the freshwater. This seems to be due to underestimation and lack of a focus on smaller species than true lack of diversity (Valout, 2001). In fact, only 40

picoplanktonic species are known - their classification is problematic and gradually being established (e.g., the new classes of Pelagophyceae and Bolidophyceae), and lastly they are not at all represented in standard cultures.

All phytoplankton do not share a common ancestor - successive events of endosymbiosis mark their evolutionary history and adaptive radiation (Simon, 2009). Based on cell-size phytoplankton are usually grouped into three categories. *Picophytoplankton* are the smallest, <2 micrometers (μm) in diameter and include the prochlorophytes and cyanobacteria; *nanophytoplankton* are intermediate sized, from 2-20 μm and include the flagellated cryptophytes, chrysophytes and prymnesiophytes; *microphytoplankton* are the largest and include those >20 μm in diameter and are made up mostly of diatoms and dinoflagellates. These two groups of diatoms and dinoflagellates generally comprises the bulk of a phytoplankton community (Figure 8)

B.2.1 Diatoms:

The diatoms are the most globally important planktonic primary producers in the ocean. Diatoms contain the chlorophyll-a and chl-c as well as a wide variety of carotenoids. Diatom cell shape follows one of two basic forms, radially symmetric *centric* or bilaterally symmetric *pennate* that bear a locomotory structure for gliding, called raphe. Pennate diatoms are often found on solid substrates, such as rocks, animals, or larger algae, while the centric forms are mostly pelagic. 29?Both types of diatoms have a SiO2 (silicon dioxide)-based bilayered external cell wall, called frustule, which is made up of a slightly larger epitheca fitting snugly over the hypotheca. The silicate frustule houses all the components of the cell. Surface of the frustule is generally decorated with fine lines, or striae, which are actually rows of tiny pores allowing exchanges across the frustule. The distribution of such morphological patterns is a key to the visual identification of diatom species.

B.2.2 Dinoflagellates:

The dinoflagellates are often brown in color and noticeably luminescent. Approximately half the dinoflagellates are strictly heterotrophic and lack chlorophyll, additionally the majority of the chl-containing species are mixotrophic, i.e. they carry out photosynthesis and consume

bacteria or other phytoplankton. Dinoflagellates are sometimes naked but usually have a porous cellulose cell wall, fitted with an equatorial groove that contains a ribbon flagellum. This groove compartmentalizes the dinophyte's ornate cell wall into the epicone and hypocone. A second groove perpendicular to the equatorial groove houses a longitudinal flagellum, used for movement.

B.2.3 Prymnesiophyceae

Another major group of eukaryotic marine nanophytoplankton is constituted by the Prymnesiophyceae, whose presence in marine waters is globally observed (e.g., the bloom-forming coccolithophorid *Emiliania huxleyi*). They all contain a pair of flagella and a thin filamentous peg-like appendage, called the haptonema. In contrast to dinoflagellates and diatoms, they are generally not present in the freshwater. Prymnesiophyceae cells are covered by organic scales that can be calcified (coccoliths). Phaeocystis, a genus of Prymnesiophyceae produces colonies whose polysaccharide matrix induces foam on the beaches of the North Sea (Lancelot et al., 1987). Toxic species, such as Chrysochromulina polylepis, may also bloom sporadically, as was the case in 1988 of Norway (Vaulot, 2001).

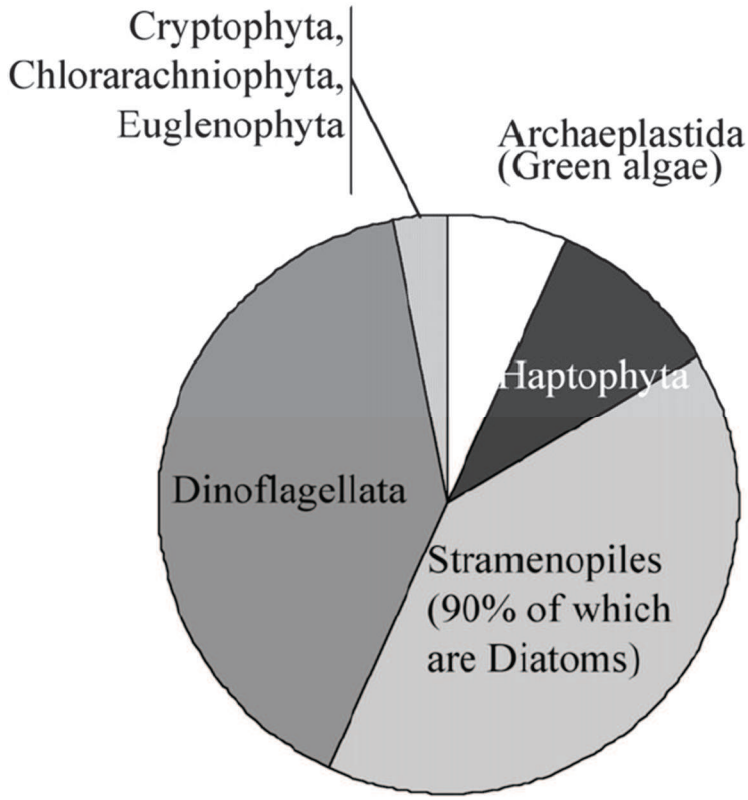


Figure 8 Distribution of different phytoplankton groups in the ocean. Adapted from Simon et al., 2009

C. Microphytobenthos:

Another important primary producer of the coastal regions are the benthic microalgae. These organisms inhabit the top few centimeters of the substrate layers (mud or sand) of marine sediment, given sufficient light for photosynthesis (MacIntyre et al. 1996, MacIntyre and Cullen 1996,Charpy and Charpy-Roubaud 1990). Benthic microalgaehave an important role as a food source for higher trophic levels in shallow water as well as estuarine food webs

(MacIntyre et al. 1996, Sorokin 1991, Charpy and Charpy-Roubaud 1990, Kang, 2003). Stable isotope tracer analysis has demonstrated that a host of benthic consumers including omnivores, suspension feeders and deposit feeders mostly rely on benthic microalgae for food (Sullivan, 1990). The cohesive nature of the benthic microalgae reduces resuspension and erosion of sediment layers, therefore promoting the stability of benthic habitats (Miller et al. 1996, Williams et al.1985). Mucilaginous films containing acidic "Extracellular Polymeric Substances" (EPS) (Paterson et al., 1990; Delgado et al., 1991; De Brouwer & Stal, 2001) glue these thin, dense microbial mats. The amount of EPS excretion by diatoms is often related to the rate of primary production (Cadée & Hegemann, 1974). By forming biofilms benthic diatoms modulate nutrient fluxes across the sediment–water interface – they function as an active biofilter and generally reduce the flow of inorganic nutrients into the pelagic zone (Facca et al. 2002; Nicholson, 1999; Sigmon and Cahoon 1997). Contrastingly, they also directly provide organic carbon to phytoplankton systems (Brandini, 2001). MPB can even determine the community structure of overlying pelagic phytoplankton assemblages by influencing the release of dissolved silica (Conley et al. 1993, Sigmon and Cahoon 1997). They can also exert an indirect impact on nitrate fluxes as oxygenation of surface sediments during photosynthesis can alter coupled nitrification–denitrification processes (sundback, 2000).

C.1 MPB GROWTH:

Sediment-dwelling MPB covers 70% of world's shelf regions (Emery, 1968). In a typical temperate bay (Onslow bay, North Carolina), 80% of the Chl-a related biomass was shown to reside in the sediment (Cahoon, 1990). In shallow coastal ecosystems, Chl-a related algal biomass in an integrated water column sample has systematically been shown to be much lower than Chl-a related algal biomass in sediments (Cahoon, 1990). The biomass of MPB could vary dramatically – reported values range from 85 mg Chl–a m^{-2} in a temperate bay in France to 1153 mg Chl-a m^{-2} in the Great Barrier Reef of Australia (Guarini, 1998; Woelfel, 2010).

A primary factor which is universally shaping the distribution and growth of MPB is light availability. As only the upper 0.2-2 mm of sediment generally has sufficient penetration by light, the distribution of benthic microalgae is restricted to this relatively thin surface layer

(Wolff, 1979; MacIntyre et al., 1996). The texture and relief of the sediment surface and its organic content also determine the vertical distribution of MPB communities. Within less than one centimeter of depth, the sediment properties change from fully oxygenated to anoxic conditions and pH, sulphide, irradiance, and nutrients also show strong vertical variability (Joergensen et al., 1983; Wiltshire, 1992; Wiltshire, 1993). As the top layers of the sediment represent a zone with such remarkably strong physicochemical gradients, most benthic microalgae show adaptive diurnal and tidal rhythms of vertical migration, moving in response to light, tide cycles, desiccation, predation and resuspension (Admiraal et al., 1984; Pinckney & Zingmark, 1991; Paterson et al., 1998). The speed at which MPBs migrate vertically is typically low - from 10 to 27 mm h^{-1} (Hopkins; 1963). Lastly, microscale horizontal gradients in nutrient, irradiance, water content and salinity are often overlaid upon the vertical gradients, in effect combinatorial shaping the growth of MPB communities (Wolff, 1979).

In general it is traditionally accepted that the growth of benthic microalgae is most probably not limited by nutrients, since nutrient concentrations in the interface water are usually high (Cadée & Hegemann, 1974; Admiraal, 1984). However, the unusually high concentration of diatoms in the upper layer of sediment may lead to temporary and heterogeneous nutrient depletion (Admiraal, 1977). Nutrient concentrations can differ as much as 10-times between the sediment-water interface and subsurface sediments (Sakamaki et al. 2006, Leynaert et al. 2009). Additionally, tidal oscillation in concentrations of key nitrogenous nutrients, particularly ammonium and nitrate in intertidal sediments are well known (Kuwae et al. 2003, Sakamaki et al. 2006). Therefore, in spite of having an overall nutrient-rich habitat, MPB could be effectively subjected to significant fluctuations in nutrient availability (Ni Longphuirt, 2009).

Seasonal variations in MPB biomass are well documented (Sullivan & Moncreiff, 1988; Cahoon & Cooke, 1992). Usually a single peak occurring in late winter or early spring characterizes their annual biomass dynamics. This peak is believed to be triggered by high nutrient concentration, increasing temperature and increasing day length coincident with the phytoplankton spring bloom in the water column. On the other hand, a decrease in biomass in late spring is generally attributed to increased grazing pressure as opposed to decreased production . In summer microphytobenthic biomass not only decreases, the MPB community also undergoes changes in composition such that the dominance of the diatoms is eroded and

Cyanobacteria and Euglenophytes coexist. The shift in the community composition is most probably linked to the decrease in silicon concentration in the overlying water (Barranguet, 1997).

C.2 Primary production of MPB:

MPB production is crucial and particularly relevant in shallow water systems including intertidal and subtidal marine ecosystems (MacIntyre, 1996; Underwood, 1999). The characteristic of benthic productivity is its direct coupling with the pelagic system – this renders benthic production susceptible to disturbances such as wind forcing and evaporation (Molen, 2011). Strong wind can resuspend MPB in the water column, generating a scenario in which MPB contributes to pelagic production (MacIntyre, 2007). The major factors affecting MPB production are parameters such as salinity, irradiance, temperature, DIN/DIP ratio, etc (Longphuirt, 2007). Globally MPB may contribute to (8.9 – 14.4 Gt C m^{-2} yr^{-1}) 20% of ocean's production and specifically subtidal MPB on continental shelves account for about 42% of total benthic primary production (Nelson, 1999; Cahoon, 1999). It is well known that in several shallow water strong-current systems, phytoplankton production is lower than that of benthic microalgae (Underwood, 1999). For example, on the pacific coast of the USA, Puget Sound's coarse sandy sediments have annual net benthic and pelagic primary production of 676 and 649 g C m^{-2} yr^{-1} respectively (Thom and Albright, 1990). Studies in the temperate zone demonstrated values for annual primary productivity as high as 892 g C m^{-2} yr^{-1} and hourly production rates matching 0.8 g C m^{-2} hr^{-1} (Hargrave, Prouse, Phillips, & Neame, 1983). Generally in temperate coastal regions as a rule of thumb, up to 20% of primary production can stem from the MPB. Examples are the Bay of Brest of Franceor where benthic primary production is estimated to be 57-111 mg C m^{-2} day^{-1}, which is 12-20% of total productivity (Longphuirt, 2007) or, in Weeks Bay, Alabama, USA, where benthic production was estimated at 90 g C m^{-2} yr^{-1} which is roughly 21% of total system production (Schreiber & Pennock; 1995). Production rate estimations for benthic microalgae in tropical waters are generally even higher - with annual values topping 3760 g C m^{-2} hr^{-1} (Hawkins & Lewis, 1982). As an example, MPB production in a Gulf of Mexico seagrass-dominated coastal ecosystem was estimated as 339 g C m^{-2} hr^{-1}, which is ten times higher than that of the in this study investigated temperate Bay of Brest (Daehnick, Sullivan, & Moncreiff, 1992; Moncreiff, Sullivan, & Daehnick, 1992).

C.3 MPB Diversity:

The microphytobenthos mainly includes Baccilariophyceae, but in algal mats a few other groups could be locally dominant, viz., Chlorophyceae, Haptophycaea, Cyanobacteria and Dinophyceae. Coccal and filamentous green algae and Cyanobacteria could outcompete other algal groups under specific seasonal conditions (Nozaki et al., 2003). Distinct taxonomic groups predominate depending on the nature of the physical habitat – however on sandy and muddy substrate it is generally the group of diatoms who are most abundant (Admiraal et al., 1984; Agatz et al., 1999). These diatoms are usually comprised of pennate and prostrate forms, which are either epipsammic or epipelic (Daehnick et al., 1992; Agatz et al., 1999). The actively motile epipelic forms use mucilaginous secretion of their paired raphes to move through the sediment (Round, 1971), they tend to dominate in relatively sheltered habitats. The smaller non-motile epipsammic diatoms grow on sediment particles being attached through mucilaginous pads or stalks and they tend to dominate in areas with strong water currents (Aberle-Malzhan, 2004). Such categories based on locomotor ability have no bearing on evolutionary relatedness among taxa because many diatoms such as Nitzschia sp., Navicula sp., and etc. have both epipsamnic and epipelic species (Wolff 1979). The MPB often forms a microbial mat or a biofilm characterized by a flat unstructured two-dimensional community with very few erect forms (Miller et al., 1987). Interestingly, MPB can occasionally appear in the water column, especially in shallow water systems with strong wave and current action (De Jong, 1995). Additionally, phytoplankton species too could settle down to benthic communities temporarily in calm waters. Actually, the same algal classes can be found in both the phytoplankton and the microphytobenthos and the basis of separating them are merely due to morpho-ecological characteristics (Aberle-Malzhan, 2004). Lastly, the diversity studies of MPB being focused on morphospecies, generally underestimate the diversity indices. DGGE-based molecular fingerprinting analyses have demonstrated the presence of prominent cryptic and pseudocryptic MPB species in a community, which could otherwise be not found by morphoecological studies (Sahan, 2007; Vyverman, 2011).

However, although the ecological importance of MPB has already been established as quite significant, there haven't been too many studies about their seasonal dynamics compared to their pelagic counterpart. On top of that, MPB studies in subtidal zones are extremely rare. Therefore, the focus of this thesis has been to understand the dynamics of MPB and to compare it with that of the overlying phytoplankton community in a typical temperate subtidal system of the North Atlantic, the Bay of Brest.

D. Bay of Brest:

The Bay of Brest is a temperate, semi-enclosed, shallow-water marine ecosystem off the coast of Brittany in northwestern France. It's 180 square-km in size, and its average (lowest) depth ranges around 8 m. The bay constitutes of a coastal macrotidal system, having the maximal tidal amplitude reaching over 8 m during spring, and the maximal tidal current nearing 2.6 m/s (Chauvaud, 2000). The rivers, Penfeld, Aulne and Elorn provide freshwater input, while the adjoining Iroise Sea remains connected via a narrow (1.8 km wide) strait, Goulet de Brest, that allows fast mixing exchanges with Atlantic water (Longphuirt, 2006; Longphuirt, 2007). The bay has notable interesting features: (a) presence of a number of pollutants including heavy metals and tributyltin which were used as biocides in anti-fouling bottom paints (Wikipedia, 2011). (b) Anthropogenic activity has dramatically increased the nitrogen and phosphorus load in the bay over the last 100 years (Treguer, 1989), resulting in a significant drop in the silica : (nitrate+nitrite+ammonium) molar ratio, particularly in the last 25 years. (c) In spite of this, the bay ecosystem has remained relatively resistant to eutrophication. (d) The shallow nature of the bay indicates the relatively higher contribution of benthic photoautotrophs in primary production. Nevertheless, the community structure of microphytobenthos in the Bay of Brest is only poorly known, and their influence on biogeochemical cycling is not fully understood; raising the necessity for holistic studies addressing their role in food-web dynamics and carbon cycle.

E. Objectives:

This thesis comprises the temporal dynamics of a MPB – ecosystem studied from January, 2011 to October, 2011 in terms of growth (biomass), physico-chemical parameters, primary production, photosynthetic performance and biodiversity. Along with that, to understand the comparative dynamics, the growth (biomass), physico-chemical parameters and the biodiversity of a phytoplankton system has also been investigated simultaneously. The respective following chapters include the:

1) The comparative dynamics of growth and physico-chemical parameters between the MPB and the phytoplankton communities of Bay of Brest

2) Primary production and photosynthetic performance of the MPB community in the Bay of Brest.

3) The seasonal distribution and diversity of the MPB and the phytoplankton communities in the Bay of Brest.

Chapter 2

Comparative dynamics of pelagic and benthic micro-algae in a coastal ecosystem

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Abstract:

Along with phytoplankton, microphytobenthos (MPB) play an important role in the overall food web structure of coastal ecosystems. MPB regulates nutrient fluxes, oxygen concentration and sediment stability in the ecosystem. Although there is a wealth of data on phytoplankton, MPB dynamics in the subtidal zone is largely unknown. In this study, we carried out a whole-year survey to investigate the seasonal dynamics of phytoplankton and MPB biomass simultaneously, in relation to the environmental physico-chemical parameters.

We show that phytoplankton and MPB do not follow the same dynamic at all. MPB is the first to rise in the season. It constitutes a large energy input to the ecosystem right from the beginning of spring (with 60% of the total biomass until April). The system then moves from a system dominated by benthic biomass in early spring to a system where the pelagic biomass takes over.

Among resources that MPB and phytoplankton have to share, light seems to trigger the MPB bloom as soon as maximum bottom PAR is reached, i.e. one month earlier than the phytoplankton bloom in the water column. As for nutrients, the lack of phosphorus can be put forward to explain the decline of MPB biomass at the beginning of April, whereas the phytoplankton decline in the first week of May coincides to silicic acid deficiency. Dissolved inorganic nitrogen then become potentially limiting in the water column till the end of October. Competition with macroalgae at the bottom and grazing were also considered as being possible factors for the disparate course of phytoplankton and MPB dynamics. Further investigations are needed in order to have a more detailed picture on the interactions and feedback loops between MPB and phytoplankton. However, although benthic-pelagic relationships are complex, this study points out the need to integrate such fundamental coupling to a thorough understanding of ecosystem dynamics and functions.

1. Introduction:

In coastal waters, both phytoplankton and microphytobenthos (MPB), are recognized as being principal components in the diet for higher trophic levels (Gillespie et al., 2000). Although phytoplankton has been vastly documented, MPB is often understudied. Because the presence of MPB is not always obvious, MacIntyre et al (1996) called it the "secret garden". However, in intertidal and some shallow subtidal systems, MPB can play an equally significant role: its biomass can be equal to or even surpass the biomass of the overlying phytoplankton (Cadee and Hegeman, 1977; Lukatelich and McComb, 1986; Underwood et al., 1998). By its photosynthetic activity, it also regulates the concentration of oxygen and nutrient fluxes at the sediment-water interface with a significant impact on their availability to phytoplankton in the water column (Ragueneau et al., 1994, Ní Longphuirt et al., 2009). MPB can affect the nutrient flux by assimilating nutrients from overlying water as well as from underlying porewater and also can influence the nutrient dynamics of the water column by the 'coupled nitrification-denitrification' pathway (Underwood, 2001). MPB differ from phytoplankton in terms of both ecology and taxonomy (MacIntyre et al., 1996; Cahoon, 1999; Underwood and Kromkamp, 1999). Some general patterns of phytoplankton dynamics in temperate natural reservoirs have already been established (Reynolds, 1984; Sommer et al., 1986). Spring bloom initiated by the abundance of nutrient and light, is generally comprised of diatoms, cryptophytes, chrysophytes or chlorophytes, which is followed by a "clear water phase" induced by the grazers in the late spring or early summer after which the summer brings in a period of stratification where nutrient limitation and grazing result in a controlled growth of phytoplankton which recovers a little in late summer and autumn due to deeper mixing before winter brings down the biomass of the community (Grover and Chrzanowski, 2005). Temperature and thermal stratification have been considered to be the two prime factors for the dynamics of phytoplankton in temperate areas along with nutrients, light and grazing to be the subsidiary ones (Reynolds, 1984; Sommer et al., 1986). Benthic flux is another factor which influences both the community composition and primary production of phytoplankton and MPB. Although, highly variable, the biological factors like bioturbation or bioirrigation have been observed to induce nutrient fluxes in specific time scales (Marinelli,1994; Ragueneau et al., 2005), as in the Bay of Brest *Crepidula fornicata* influences DSi flux and thus prohibit Dinophyta harmful algal blooms in summer months (Del Amo et al., 1997; Chauvaud et al., 2000; Ragueneau et al., 2005). However, although a wealth of data is available on global phytoplankton growth (Longhurst, 1995),

complementary benthic studies are rather scarce (Cahoon, 1999). Along with that, most of the work on MPB has been in interdidal zones, while subtidal zones have generally been neglected (Light and Beardall, 1998), except for a few studies (e.g. Sundback and Jonsson, 1988; Delgado, 1989; Cahoon et al., 1993; Schreiber and Pennock, 1995 etc.). The seasonal dynamics of subtidal MPB have been observed to be following the yearly pattern of irradiance and show higher degrees of seasonality compared to intertidal MPB which are subjected to extremes of irradiance exposures (Underwood, 2001). But, studies about the simultaneous dynamics and interactions between both pelagic and benthic compartments are missing. These investigations are important in coastal areas to better understand how phytoplankton and MPB share the resources necessary for their growth, that is to say, light and nutrients, for which competition is highly asymmetric. While pelagic algae intercept the flux of light from the surface to the bottom, benthic algae intercept the flux of nutrients from the sediment to the water column. These feedback loops can enhance the dominance of either algal group with major alterations to the entire trophic web (Reynolds, 2008).

The objective of this study has been to provide, from weekly to seasonal time scale, an overview of the phytoplankton and epipsammic (attached to hard surfaces) MPB dynamics (biomass, particulate matter and biogenic silica) in a subtidal area, in relation to the environmental physico-chemical parameters.

2. Material and methods:

2.1 Strategy of sampling

The Bay of Brest is a temperate, semi-enclosed, shallow-water marine ecosystem on the coast of Brittany in northwestern France. It's 180 km^2 in size, and its average depth ranges around 8 m. The bay constitutes a coastal macrotidal system, having the maximal tidal amplitude reaching over 8 m during spring, and the maximal tidal current nearing 2.6 m/s (Chauvaud, 2000). The rivers, Penfeld, Aulne and Elorn provide freshwater input, while the adjoining Iroise Sea is connected via a narrow (1.8 km wide) strait that allows fast mixing exchanges with Atlantic water (Le Pape et al., 1996).

The study site is located at Lanvéoc (48 ° 17'41 .23 "N - 4 ° 27'12 .63" W) in the southern part of the Bay of Brest (Fig. 1a). The fieldwork was carried out in 2011, from the beginning of February to the end of October. Samples were taken from the LEMAR or IUEM Research

vessels “Hesione” or “Albert Lucas”, once a week, intensified to twice a week for the period around the spring bloom (from March to May). Sampling was performed as much as possible at medium tidal coefficient and around mid-tide. These conditions were chosen to facilitate comparisons between the cruises. Water column samples were collected with a 12L Niskin bottle at 3 depths: surface, middle and bottom (9 m).

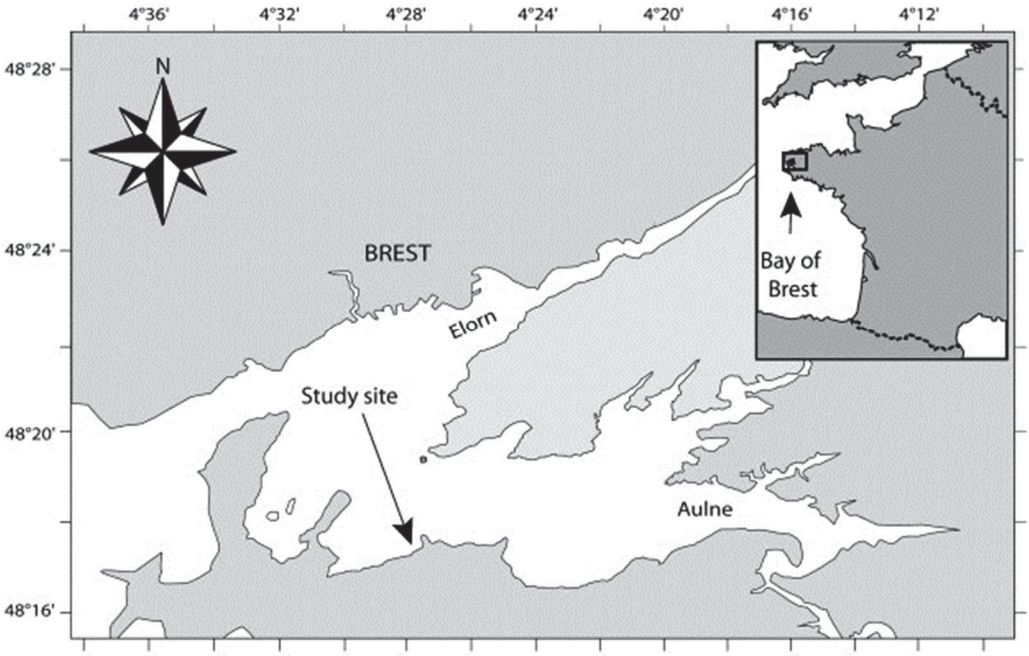


Fig. 1 (a) Map of the Bay of Brest (Adapted from Fouillaron et al., 2007). The arrow indicates the sampling station (Lanveoc).

MPB was studied on artificial support which simulated a hard surface substrat. A series of plexiglass plates (12X15 cm) were placed at the sediment surface at the site of sampling in June 2010, i.e. they were at least 6 months old when we started the survey (Fig. 1b). Such plates have been shown to be good mimics of the natural substrate (Cattaneo and Kalff, 1978) and allow overcoming the high variability of MPB population within sediment due to the heterogeneity of the substrate. One plate was taken out every week by scuba divers, starting from January 2011, and twice per week during the spring period. Immediately after collecting, the biomass was scrapped off by a standard toothbrush and suspended in 2 L of filtered (0.6 µm) bottom sea water. Subsamples were taken for subsequent analyses.

Fig 1 (b) Photograph of the series of plates at the sampling site used for the study of MPB

2.2 Physical parameters

A CTD profiler Sea-Bird SBE-911, equipped with a photosynthetically active radiation (PAR) sensor was used to measure salinity in a practical salinity scale, temperature and PAR (µmol photons m^{-2} s^{-1}). Light extinction coefficient "k" was calculated from these PAR profiles by the equation: k = (ln(surface PAR) – ln(bottom PAR))*$Depth^{-1}$. Surface PAR was also recorded continuously with a PAR sensor located at MAREL buoy in the Bay of Brest (http://www.ifremer.fr/mareliroise/index.html). Daily bottom PAR at 9 m depth was then calculated from the surface PAR of MAREL buoy along with the light extinction coefficient.

2.3 Chemical parameters

After return to the lab, water samples for dissolved inorganic phosphate (DIP) and silicate (DSi) analysis were immediately filtered by Nuclepore membrane filters (47 mm) and DIN by pre-combusted Whatman GF/F filters (25 mm). Samples for nutrient measurements were taken from the surface, middle and bottom layers of the sampling site. Samples for dissolved inorganic nitrogen (DIN) and DIP were then frozen, whereas samples for DSi were kept at 4°C in the dark. DSi and DIN concentrations were later measured by the colorimetric method on a Technicon automatic Analyser II and semi-automatic analyser respectively (Tréguer and

Le Corre, 1975). Phosphate was measured by the colorimetric method of Murphy and Riley (1962).

2.4 Particulate matter

The water samples obtained from the plates were used for the study of particulate matters of MPB, while water samples from the surface of the sampling site were used for phytoplankton particulate matters.

For Chlorophyll (Chl-*a*) analysis, water samples were filtered onto glass-fiber filters (GF/F Whatman). Chl-*a* was extracted in 6 ml of 90% acetone and kept in the dark at 4° C for 12 hours. Samples were then centrifuged and fluorescence was measured with a Turner Design fluorometer. Equation of Lorenzen (1966) was used to calculate Chl-*a* concentration. Seasonality index was calculated by the equation of Berger and Wafer (1990) which is $\alpha = 260 - \beta$, where β is required number of days to obtain half of the integrated biomass for a period of 266 days (1st February, 2011 to 24th October, 2011).

For particulate organic carbon (POC) and particulate organic nitrogen (PON) analysis, samples were filtered onto pre-combusted (450°C for 4 hours) Whatman GF/F filters and placed in a stove at 60°C for desiccation. Filter samples were then analysed by combustion method (Strickland and Parsons, 1972), using a CHN elemental analyzer (Thermo Fischer Flash EA 1112).

Biogenic silica (BSi) was determined from particulate matter collected by filtration of water samples through 0.6 µm polycarbonate membrane filters. Analyses were performed by the double alkaline leaching technique, using the Si/Al ratio to correct for the mineral interference (Ragueneau et al., 2005).

2.5. Numerical analysis:

In order to draw a parallel between the environmental and biological parameters, Principal Component Analyses (PCA) were performed upon data for each compartment (pelagic and benthic) using XLSTAT 2012 software. Biological variables (such as chl-*a* and POC) were added as supplementary variables to the PCA, and were thus correlated with the canonical axis (which is a linear combination of environmental parameters) on the plot. For the

analysis, PAR for both surface and bottom were considered in µmol photons m^{-2} s^{-1}, where the surface PAR was taken from Marel buoy and bottom PAR was calculated from k.

3. Results:

3.1 Physical parameters

The temperature pattern of the surface of Bay of Brest exhibited a typical seasonal pattern of temperate area with a lowest of 8.7°C in February and a highest of 17.4°C in August (Table 1). CTD profiles evidenced a well-mixed water column most of the time, with no more than 0.7°C difference between the surface and the bottom water over the whole year.

Salinity was always higher than 32 and evidenced low variations increasing from 33 in February to 35 in June and remained stable till October. This range of variation is a characteristic of coastal ecosystem.

	Surface			Bottom		
	Min.	Max.	Average	Min.	Max.	Average
Temperature (°C)	8.6	17.3	13.7	8.7	17.3	13.6
PAR (mol m^{-2} day^{-1})	3.2	58.3	28.8	0.81	18.0	5.3
Salinity	32.0	35.5	34.5	32.0	35.5	34.6
DIN (µmol L^{-1})	Below detection	33.2	6.7	Below detection	25.9	6.2
DIP (µmol L^{-1})	Below detection	0.70	0.16	Below detection	0.60	0.17
DSi (µmol L^{-1})	Below detection	14.82	5.09	Below detection	17.24	5.10

Table 1 Ranges of physico-chemical parameters of surface and bottom water along the study

As expected sea surface irradiance followed a clear seasonal pattern with the minimum being recorded in February (3.2 moles m^{-2} day^{-1}) and the maximum in May (58.3 moles m^{-2} day^{-1}) (Table 1). The surface PAR declined from May till the first week of July, when it reached the maximum again with a value of 58.2 moles m^{-2} $day^{-}1$. Henceforth, the irradiance at the surface declined with some episodic peaks. For the entire seasonal scale, high variability of

the daily solar radiation was observed. Values as high as 37.3 moles m^{-2} day^{-1} was observed in late winter (beginning of March), while summer (June) observed values as low as 17.7 moles m^{-2} day^{-1}. The daily high variations of incident PAR were in relation to the cloud status.

Daily solar radiation at the bottom was highly fluctuating. The first peak after winter was observed in the middle of March and the bottom PAR increased with fluctuations till the middle of April. Henceforth, the irradiance at the bottom showed a decreasing trend till the middle of May, after which the peak for maximum bottom PAR was observed in the end of May. After the maximum peak was observed in the bottom, the irradiance started to decline with fluctuations till the middle of September from when the bottom PAR rapidly dipped down till the end of October. The lowest average PAR for a day at the bottom was observed in February as 0.81 moles m^{-2} day^{-1} and the highest being 18 moles m^{-2} day^{-1} on 9th May (Table 1). The extinction coefficients (k) in the water column, ranged from 0.32 to 0.14 m^{-1} over the year, showing no clear seasonal variation. As a result 12% of surface irradiance in average reaches the seafloor at the study site (at 9 m depth).

3.2. Chemical environment:

Nutrient concentrations of the three vertical compartments (surface, middle and bottom) of the sampling site were observed to be almost the same for all the three nutrients along the entire time scale of our study. During our study period high nutrient concentrations were observed until late February, early March (Fig. 2). Maximum concentrations reached 33.18 µmol L^{-1} for DIN, 0.70 µmol L^{-1} for DIP, and 14.82 µmol L^{-1} for DSi (Table 1).

From early March, all nutrients concentrations gradually decreased and became successively completely depleted. The DIP first reached depletion at the end of April. After that, DIP concentrations rose to 0.15 µmol L^{-1} in May before falling to minima again. From there on DIP concentration gradually increased along with fluctuations till October.

After DIP, DSi concentration became exhausted at the beginning of May but in a week´s time DSi concentration started rising again and continued till October.

Finally, DIN depleted steeply from March till mid-May and remained low until the end of August.

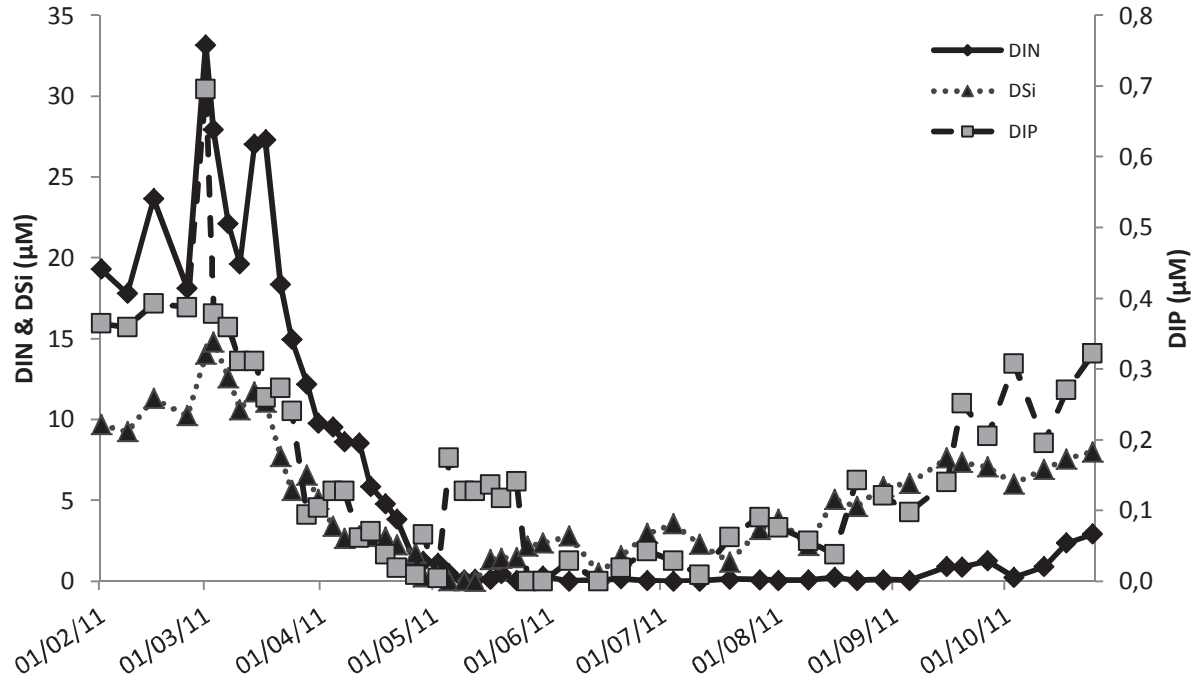


Fig. 2 Temporal variations of the nutrients (dissolved inorganic nitrogen, dissolved inorganic phosphate and dissolved silica) at the surface layer of the studied site from February 2011 to October 2011.

3.3 Particulate matter:

3.3.1 Chlorophyll-*a*

Surface Chl-*a* concentration ranged from 0.69 – 5.1 µg L^{-1} and from 5.2 – 45.2 mg m^{-2} when integrated over depth (Fig. 3a). The phytoplankton biomass started to increase gradually from February, bloomed from middle of April and reached its peak in the first week of May. The concentration started declining hence forth and continued till the end of May. With subsequent fluctuations the biomass remained constant till the end of August. From the middle of August the biomass rose again and had three consecutive peaks in the end of August, middle of September and beginning of October with concentrations around 30 mg m^{-2}. After these three peaks the biomass of phytoplankton decreased to reach lower concentrations characteristic of winter (around 5 mg m^{-2}).

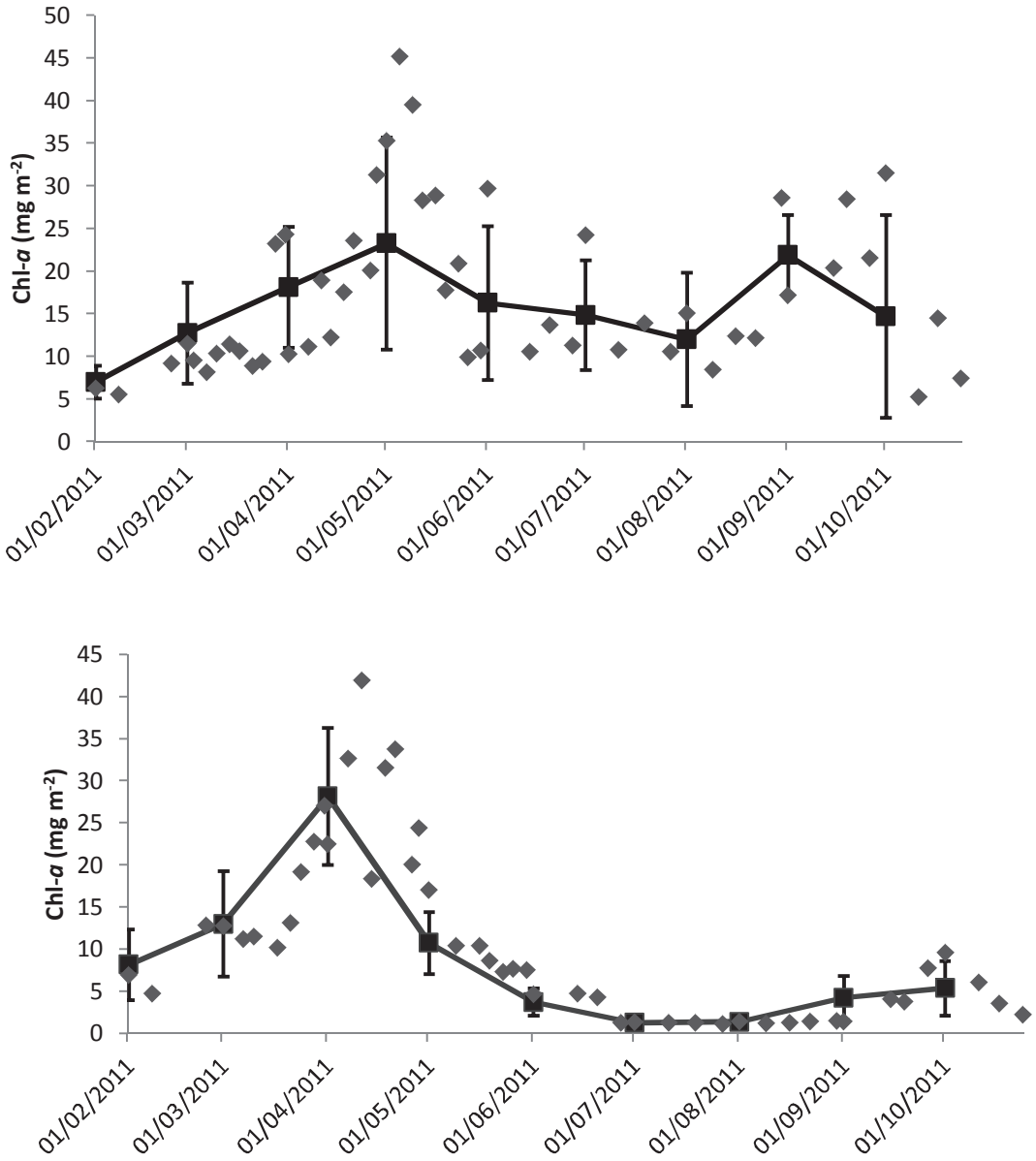


Fig. 3. Patterns of seasonal Chl-a variations of (a) phytoplankton in the water column and (b) MPB. Dots: original data; line: monthly means

Variation of benthic Chl-*a* was completely different from that of phytoplankton (Fig. 3b). In February the minima was 4.8 mg m^{-2} (Table 2). From there on the biomass started rising to its peak in the second week of April with a concentration of 41.9 mg m^{-2} (Table 2). Then the biomass started subsiding down from the end of April to end of June. From the end of June to the end of August, the Chl-*a* concentration remained at its lowest (< of 1.2 mg m^{-2}). The Chl-*a* concentration of biomass slightly rose again in fall, after the peaks in the water column were observed. The biomass reached 9.6 mg m^{-2} in the first week of September and declined in October.

	Water column			Bottom (Plates)		
	Min.	Max.	Average	Min.	Max.	Average
POC (mg m^{-2})	789	4634.1	1997.2	292.6	1617.7	903.5
PON (mg m^{-2})	106.6	689.4	326.7	43.2	290.4	143.6
Chl-*a* (mg m^{-2})	5.2	45.2	17.2	1.2	41.9	10.7
BSi (mmol m^{-2})	2.6	22.3	7.1	0.0	11.8	3.2
POC/PON	4.4	11.1	6.3	4.9	8.2	6.5
POC/Chl-*a*	57.1	230.8	132.8	25.5	1065.6	245.1
BSi/Chl-*a*	3.0	37.3	13.2	0.10	50.39	12.0
BSi/POC	0.01	0.08	0.04	0.0002	0.16	0.04

Table 2 Ranges of biological parameters of depth integrated water column and bottom samples (plates) along the study period.

3.3.2 Particulate organic carbon and nitrogen

POC in surface waters ranged from 7.4 to 40.3 µmol L^{-1}, with maximum concentrations in the second week of May. The vertical concentration profiles of POC from surface to bottom of the water column were most of the time equivalent along the study period.

When integrated over depth (9 m) (Fig. 4a), POC concentrations in the water column started rising from February (min 789 mg-C m^{-2}) along with fluctuations, reaching its peak on 9th May (max 4624 mg-C m^{-2}) and subsiding down in the end of May. After that the POC concentration had occasional peaks in June, July, August and September before declining in October. POC, in MPB samples reached the highest concentration by the end of April, two weeks earlier than that of water column with a value of 1617 mg-C m^{-2} (Fig. 4a). The concentration gradually dipped down by middle of July and rose again by the end of July. Henceforth, the concentration fluctuated till the first week of October, before declining after that. Average POC of water column was 1997 mg-C m^{-2} while average POC for benthic samples was 903 mg-C m^{-2}. In surface water, PON ranged from 0.8 to 4.9 µmol L^{-1}, with the maximum concentrations reaching during the second week of May.

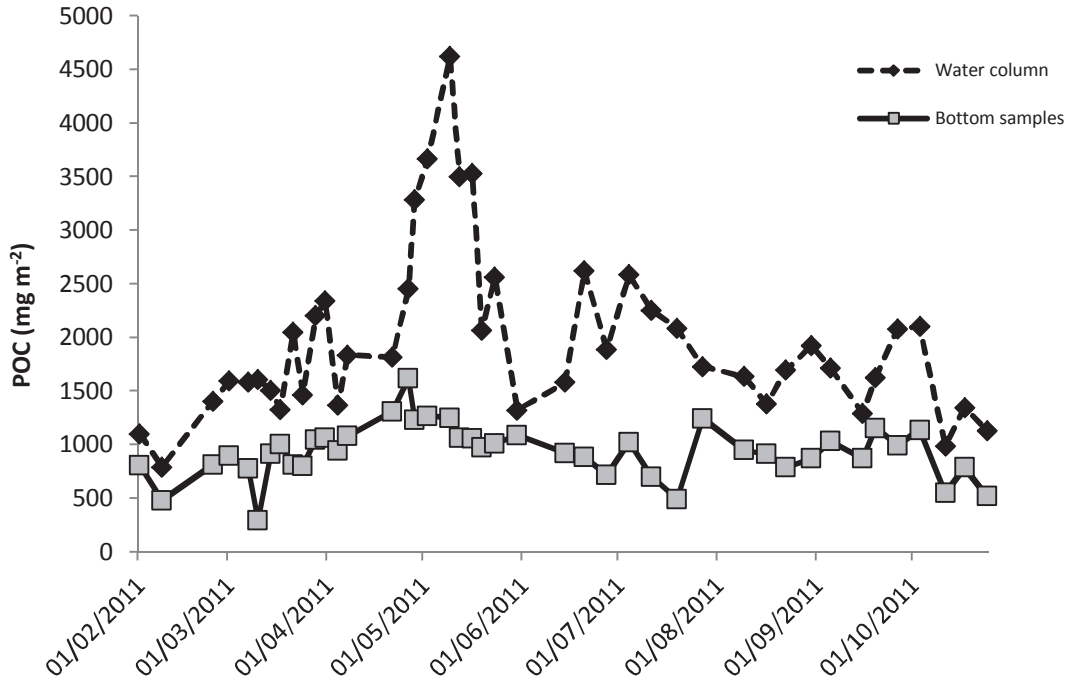


Fig. 4 (a) Seasonal variations of particulate organic carbon in bottom samples and in the water column in mg–m^{-2} from February 2011 to October 2011.

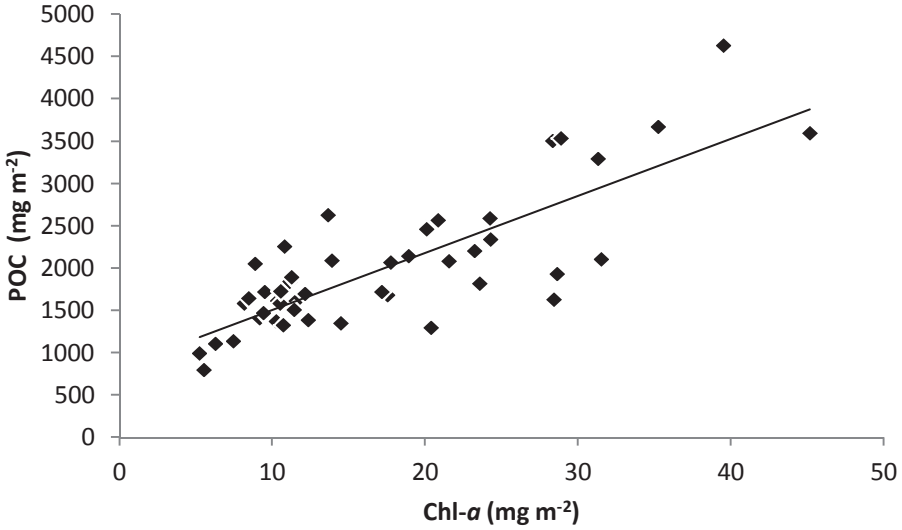


Fig. 4 (b) Relationship between Chl-a and POC in the water column

The PON concentration in the water column was observed to be at its lowest in February with a value of 106.6 mg m^{-2}, from when the concentration increased to reach its peak to 689.4 mg m^{-2} in the middle of May (Fig. 4c). Henceforth, the PON concentration in the water column subsided, although having separate peaks from June to September. At the bottom, PON reached its peak by the end of April with a value of 290.4 mg m^{-2}, subsided down during

middle of July and rose again from the end of July to fluctuate till the first week of October before going down (Fig. 4c).

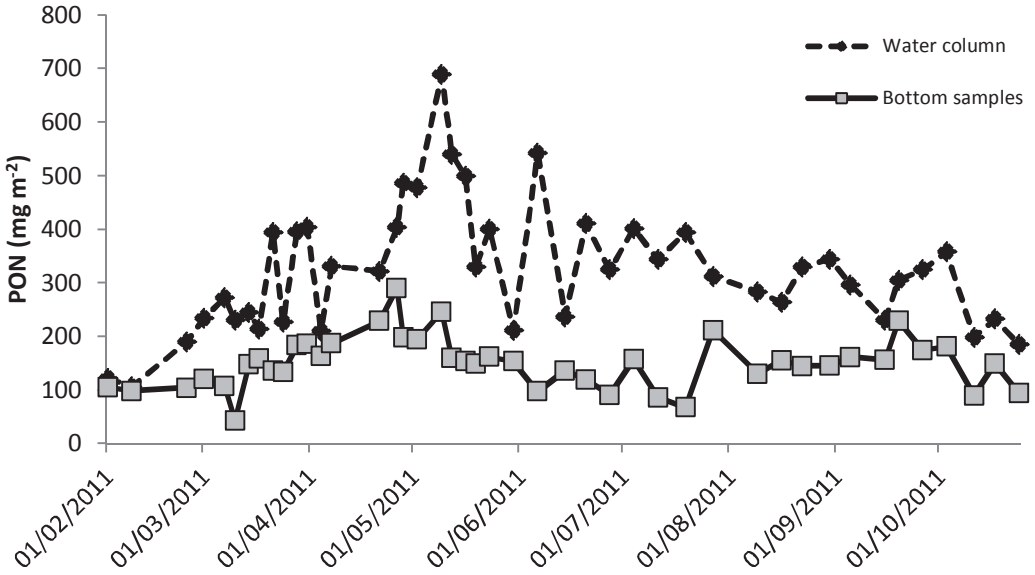


Fig. 4 (c) Seasonal variations of particulate organic nitrogen in bottom samples and in the water column in mg–m^{-2} from February 2011 to October 2011.

3.3.3 Biogenic silica

Biogenic silica of water column and sediment maintained a similar trend till the end of April (Fig. 5). From May, biogenic silica of surface water phytoplankton rose up to its maximum value of 22.3 mmol-Si m^{-2} by early June. After that BSi concentration came down with gradual fluctuations (Fig. 5). On the other hand, benthic biogenic silica started decreasing from May to undetectable levels by the middle of June. After that, BSi maintained a very low concentration for the rest of the study period with the maximum being 2.1 mmol m^{-2}.

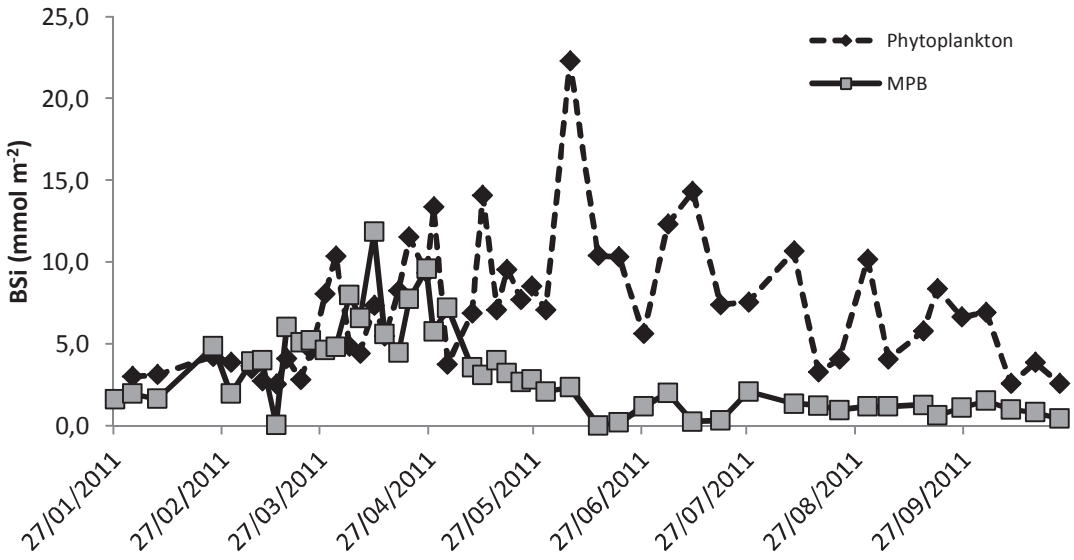


Fig. 5 Seasonal variations of biogenic silica for MPB and depth integrated phytoplankton from February 2011 to October 2011.

BSi/POC was calculated for depth integrated water column and was observed to vary from 0.01 to 0.08 with an average of 0.04. For the bottom samples, BSi/POC ranged from 0 to 0.16 with a mean of 0.04.

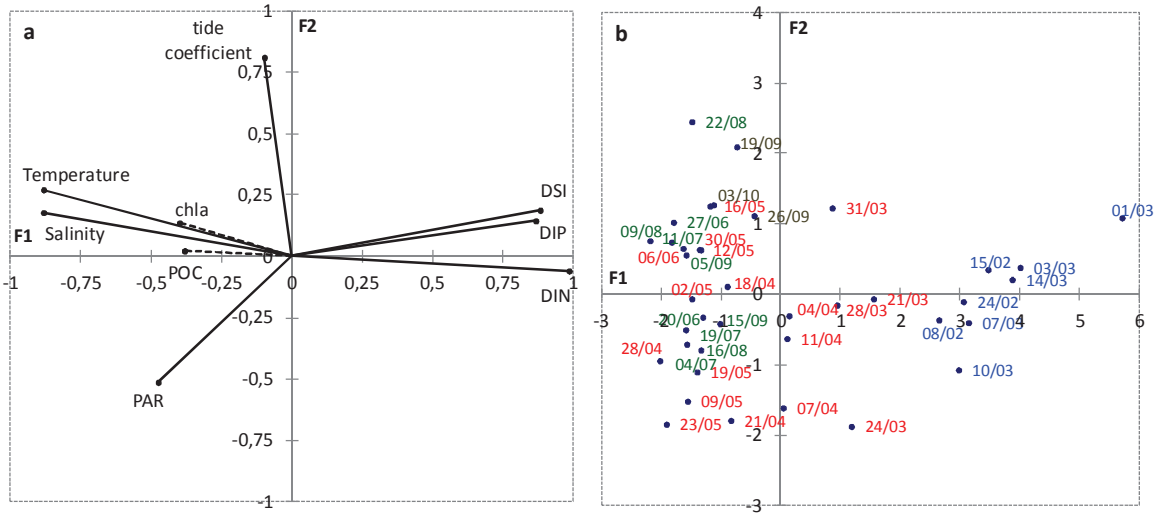
BSi/Chl-*a* for depth integrated water column ranged from 3.0 to 37.3 with an average of 13.2 while BSi/Chl-*a* of MPB varied from 0.10 to 50.39 with a mean value of 12.0 (Table 2).

3.4 Principal component analysis (PCA)

Two PCA were performed, one with pelagic parameters (Fig. 6a) and one with benthic parameters (Fig 6b). For the first PCA (Fig. 6a) Kaiser–Meyer–Olkin (KMO) value of sampling adequacy was 0.75 and for the second PCA (Fig. 6b) it was 0.67. The analysis was observed to be appropriate (Pallant, 2007) as both the KMO values were greater than the recommended value of 0.6. To understand the significance of the analysis, Barlett's Test of Sphericity showed $P < 0.0001$ for both the PCAs. From the first PCA applied to the pelagic parameters, the first axis (F1) accounted 61.3% of the explained variance and the second axis (F2) accounted for 15.5%. The first two axes explained also 76.8% of total variance. F1 described a "seasonality gradient" with high values of temperature and salinity (positively correlated) on the left side and high values of nutrients (DIN, DSi and DPi) for surface and

bottom (positively correlated) on the right side of the factorial plan (Table 3). This opposition linked the seasonality of environmental parameters with high concentrations of nutrients in winter when values of temperature are low. The biological variables (Chl-*a* and POC) are linked with high temperature values and associated with low nutrient concentrations. Also, when temperature values increased, the phytoplankton biomass increased by consuming the nutrients available.

In the second PCA performed with bottom parameters, the first two axes explained 72.2% of the total variance with 51.5% of the explained variance for F1 and 20.6% for F2 (Fig. 6b). As for the PCA performed on pelagic parameters, F1 supported the seasonality gradient (Fig 6a, Table 3). Indeed, high values of temperature and salinity (positively correlated) were on the left side and high value of nutrient concentrations were on the right of the factorial plan. However the biological variables analyzed showed different results. Whereas, the second PCA reveals that in the benthic compartment, Chl-a seemed to be linked with high values of nutrient concentrations and low temperature values, while being unrelated with POC.



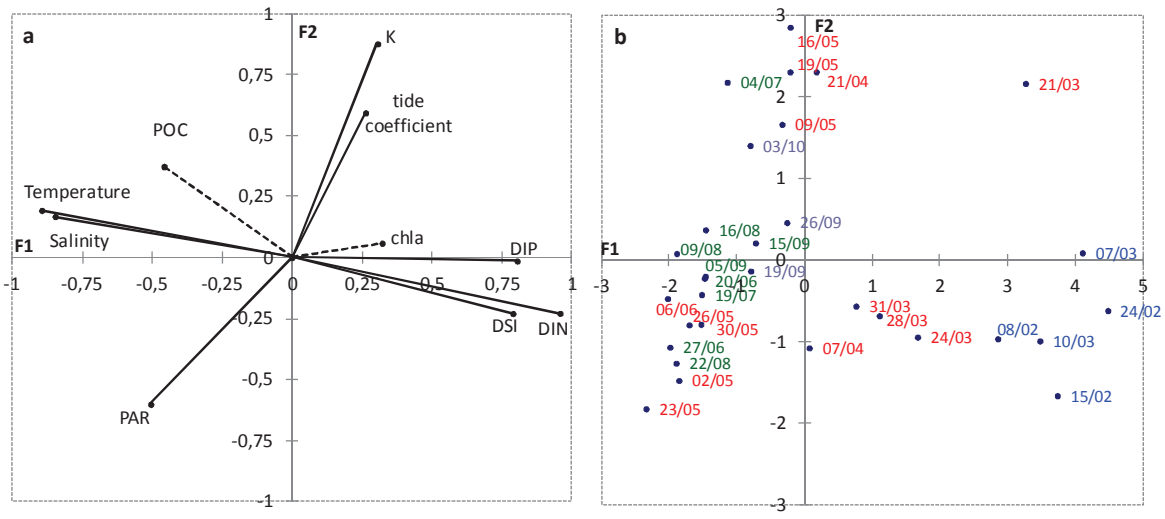


Fig 6. Principal Canonical Analysis showing the relationship between physical, chemical (solid lines) and biological variables (dotted lines) of the pelagic compartment (a) and the benthic compartment (b). Biological variables were included as supplementary variables and sampling dates. Physico-chemical Variables: PAR (µmol photons m^{-2} s^{-1}); temperature (°C); salinity, tidal coefficient, k (m^{-1}), DIN (µmol L^{-1}), DIP (µmol L^{-1}), DSi (µmol L^{-1}). Biological variables : pelagic POC (µg L^{-1}), benthic POC (µg C m^{-2}), pelagic Chl-a (µg L^{-1}), benthic Chl-a (mg m^{-2}).

	Pelagic compartment		Benthic compartment	
	F1	F2	F1	F2
Tide coefficient	-0,098	0,810	0,262	0,593
Temperature	-0,883	0,271	-0,895	0,193
Salinity	-0,883	0,179	-0,848	0,168
PAR	-0,475	-0,512	-0,506	-0,601
K	-	-	0,305	0,876
DIN	0,985	-0,059	0,957	-0,229
DSI	0,882	0,188	0,789	-0,229
DIP	0,866	0,145	0,804	-0,014
POC	-0,379	0,021	-0,458	0,371
chl*a*	-0,395	0,135	0,324	0,058

Table 3 Correlation between parameters and factors (F1 and F2) for both ACP (pelagic compartment and benthic compartment).

4. Discussion:

4.1 General pattern

In the Bay of Brest, the dynamics of phytoplankton in the water column has been quite well described (Ragueneau et al., 1994, Del Amo et al., 1997,) as explained by the PCA performed on the pelagic parameters (Fig. 6a). It exhibits a spring bloom in between mid-April and mid-May, a collapse in summer due to the lack of nutrients and a rise in late summer (Ragueneau et al., 1994, Le Pape et al., 1996, Del Amo et al., 1997). Other than the mentioned features, the Bay of Brest also exhibits secondary spring blooms and long-term observations of pelagic communities (from 1977 to 1996) have evidenced a decrease in the maximum concentrations of Chl-*a* during the first spring bloom (from 14 µg L^{-1} to 6 µg L^{-1}) in contrast to the subsequent spring and summer blooms (Chauvaud et al., 2000). This observed long-term change was evidenced by a decrease in seasonality index (α, as defined in Berger and Wefer, 1990) from 170 days to 125 days over the 20 years of study, whereas the integrated Chl-*a* concentration of the surface layer over the annual scale did not exhibit any change, with a mean around 500 µg L^{-1}. Our study of 2011 reveals that 15 years later, besides a slightly lower Chl-*a* maximum in spring (5.1 µg L^{-1}), the annual integrated biomass in surface water (508 µg L^{-1}) and the seasonality index (133 days) have stayed almost the same.

Our study, with a more frequent sampling, demonstrates a strong seasonality of MPB, with a major peak early in April, followed by a rapid fall of biomass, low concentration all throughout the summer and a small rise in autumn. Though there have been some studies about MPB seasonal dynamics in intertidal zones, for subtidal areas, MPB seasonal pattern is till yet poorly documented. Facca et al. (2002) found a poor seasonal variability at Venice lagoon with a monthly time step, whereas others have described uni-modal peak but with considerable variation in the timing of the peak: April in the Gulf of Mexico (Pinckney et al., 2008), July in Seto Inland Sea, Japan (Yamaguchi et al 2007). In 2004, Ní Longphuirt et al. (2007) have studied the distribution of MPB in the Bay of Brest at three different periods for a single site. The average biomass observed in winter was 4.6 mg-Chl-*a* m^{-2} for mud and 3.1 mg-Chl-*a* m^{-2} for fine sands, while the late summer values showed an average of 5.4 mg-Chl-*a* m^{-2} for mud and 3.7 mg-Chl-*a* m^{-2} for fine sands (Ní Longphuirt et al., 2007). However, the time step did not allow concluding reasonably about seasonal variability from this study.

Our study shows that phytoplankton and MPB do not follow the same dynamics as summarized by the two PCA (Fig. 6a and 6b). MPB is the first to rise in the season. It holds

60% of the total biomass until April and constitutes a large energy input to the system right from the beginning of spring. MPB is already known to contribute a large part to the benthic fauna food source (Grall et al., 2006). However, because this source of organic carbon is available before phytoplankton blooms in the water column, it may also play a primary role in the onset of meiobenthic and macrobenthic life forms. Chauvaud et al. (1996) showed that post-bivalve larvae such those from *Aequipecten opercularis*, *Anomia ephippium*, *Crepidula fornicata* , mytilids and hydroids begin to settle on hard substrates right from the beginning of April Thus the presence of MPB could influence the quality and the success of the early recruitment of these spats. Suspension-feeding animals like *Ficulina ficus* and *Phallusia mammillata* also occurs frequently (Hily, 1991).

Phytoplankton in the water column blooms a month later (in May) and continues more or less throughout the summer while the MPB is then almost nonexistent. During that period (May-October), the phytoplankton comprises most of the biomass, contributing to 70% of the total biomass in summer, and up to 85% in October. So, the system switches from a system where benthic biomass dominates early in the season to a system where planktonic biomass takes over.

Over the year, we calculated that the MPB Chl-*a* biomass (2 g Chl-*a* m^{-2}) contributed for 1/3 of the total biomass at the site of study. This is also close to the previous estimates made by Ní Longphuirt et al., 2007 who showed that MPB contribution lies between 22% and 36% of the overall microalgae biomass. These estimates are rather conservative as MPB biomass is expected to decrease with depth and the depth of the studied site is deeper than the average depth of the ecosystem (8 m). Anyway, it points out that benthic processes are fundamental and benthic-pelagic coupling must be integrated to a thorough understanding of ecosystem dynamics and functions.

Hence, in this regard, we tried to understand the reasons dictating the difference between the phytoplankton and MPB dynamics.

4.2 Light

Several factors may explain the difference in the seasonality of pelagic and benthic microalgae. In the subtidal zone, light is a factor whose role may be critical early in the

season when nutrients are still abundant. In nutrient replete conditions, photosynthetic parameters, and particularly the irradiance saturation parameter (E_k), can give some indication on micro-algae photoacclimation. A study examining Production versus light energy responses of MPB communities in the Bay of Brest (Ní Longphuirt et al., 2007) reported E_k values ranging from 58 in winter to 83 µmol photons m^{-2} sec^{-1} in spring. These values are in the lower range compared to other temperate subtidal MPB communities where E_k ranged from 30 to 265 µmol photons m^{-2} sec^{-1} (Sundback and Jonsson, 1988; Blanchard and Montagna, 1992; Light and Beardall, 2001). On the other hand, Claquin et al. (2010) observed the E_k values for phytoplankton in the Bay of Brest to be ranging from 56 to 266 µmol photons m^{-2} sec^{-1} in autumn, while general E_k values for phytoplankton have been reported to be 176 ± 6 µmol photons $m^{-2}sec^{-1}$ at the near shore coastal waters of North Sea (Shaw and Purdie, 2001). Thus E_k reported values for phytoplankton and MPB are approximately in the same order of magnitude and it is impossible from these data to conclude whether the benthic community is better adapted to lower light intensity. However, in our study, the range of light fluctuations is much narrow at the bottom than at the surface (Table 1) and values close to the maximum bottom irradiance (around 200 µmol photons m^{-2} sec^{-1}) are reached much earlier in the season (mid-march), than maximum surface irradiance (around 2500 µmol photons m^{-2} sec^{-1}) at the surface (mid-April) (Fig. 7a). It is to be noted here that, no linear relationship between solar irradiance and biomass was observed, but rather a "threshold" to pass for the effective development of biomass.

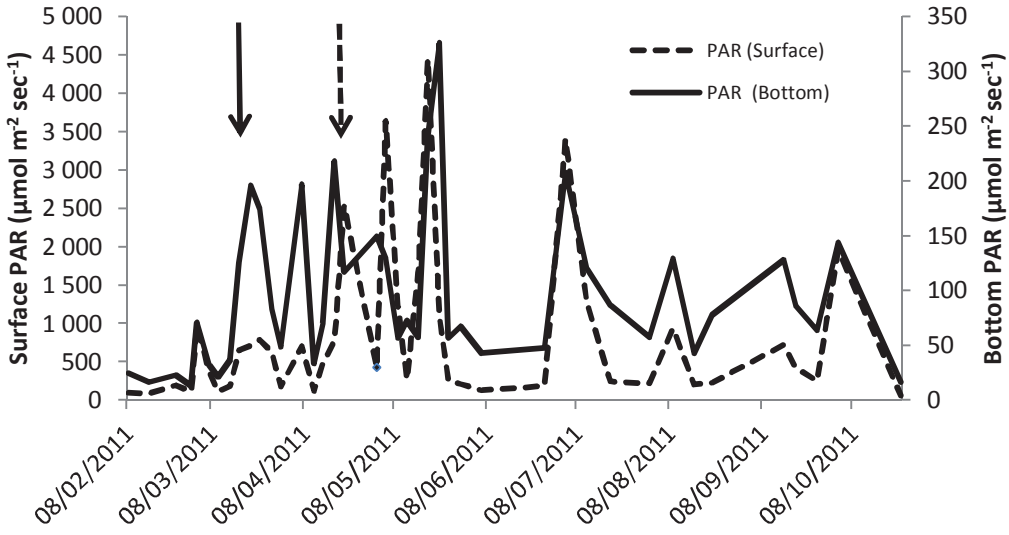


Fig. 7 (a) Seasonal variations of solar irradiance at the surface and the bottom of the study site from February, 2011 to October, 2011. Arrows indicating the timing of maximum bottom and surface irradiance at the beginning of the season

Why this different light threshold if there is no apparent difference in light acclimation? In conjunction with light; tidal energy and vertical mixing are key factors in triggering micro algae blooms. Though phytoplankton has direct access to light, it has to face turbulent mixing in the water column and has to adapt rapidly to the changing light conditions. For these reasons, phytoplankton growth often occurs during periods of neap tides (Del Amo et al., 1997). Meanwhile, MBP receives much lower light, but to its advantage, it is attached to a substrate, can avoid advective processes and its residence time is much longer, allowing it to adapt to the ambient light. This could help to explain the different light threshold observed for phytoplankton and microphytobenthos development and the delay observed between phytoplankton bloom in the water column and MPB bloom at the water-sediment interface. Further study should take into account the influence of mixing processes in photosynthetic capacities to better understand the growth dynamic of both communities.

Our objective was also to better understand how both communities share the same light resource, and more specifically determine if the high biomass of phytoplankton observed in spring reduces the light penetration down to the sediment to the point of limiting MPB growth as it has already been shown to occur in other environments (Sundback 1984, Jahnke et al., 2000). It has been noticed that in shallower waters (estuaries and tidal flats) where water is turbid ($k > 1\ m^{-1}$), the phytoplankton biomass fluctuations do not impact k (the light attenuation coefficient) (MacIntyre and Cullen 1996, Yamaguchi et al., 2007). But less turbid subtidal zones are known for the contribution of phytoplankton biomass into k (Smith and Baker 1978, Yagamuchi et al., 2007). The range of k in our study was 0.15 to 0.32 m^{-1} which suggests low turbidity for the subtidal zone of Bay of Brest.

The attenuation of light due to Chl-*a* (k′) in the water column can be estimated by the equation of Riley (1956) which is $k' = 0.040 + 0.0088\ (Chl) + 0.054\ (Chl)^{2/3}$. This equation is generally applied when the absorbance of irradiance is mostly due to the water and chlorophyll (e.g. Parsons et al., 1977, Smith and Nelson 1991). According to this equation, we calculated that phytoplankton contributed to more than 50% of the global light extinction (k) in most of the cases (where 34% was the minimum on 3rd of March). When the k′ was plotted against the biomass of MPB, k′ did not seem to control MPB biomass considering the whole year. But, during spring it was noted that MPB biomass gradually came down as the k′ increased (Fig. 7b). This indicates that the biomass fluctuation of MPB is partially influenced by the k′ of phytoplankton (Fig. 7c). These results indicate that in May, when the

phytoplankton grows in the water column, it overshadows the microphytobenthos by increasing the attenuation of light in the water column by a factor of 2. This shade created by phytoplankton during spring certainly plays a role in the collapse of MPB bloom.

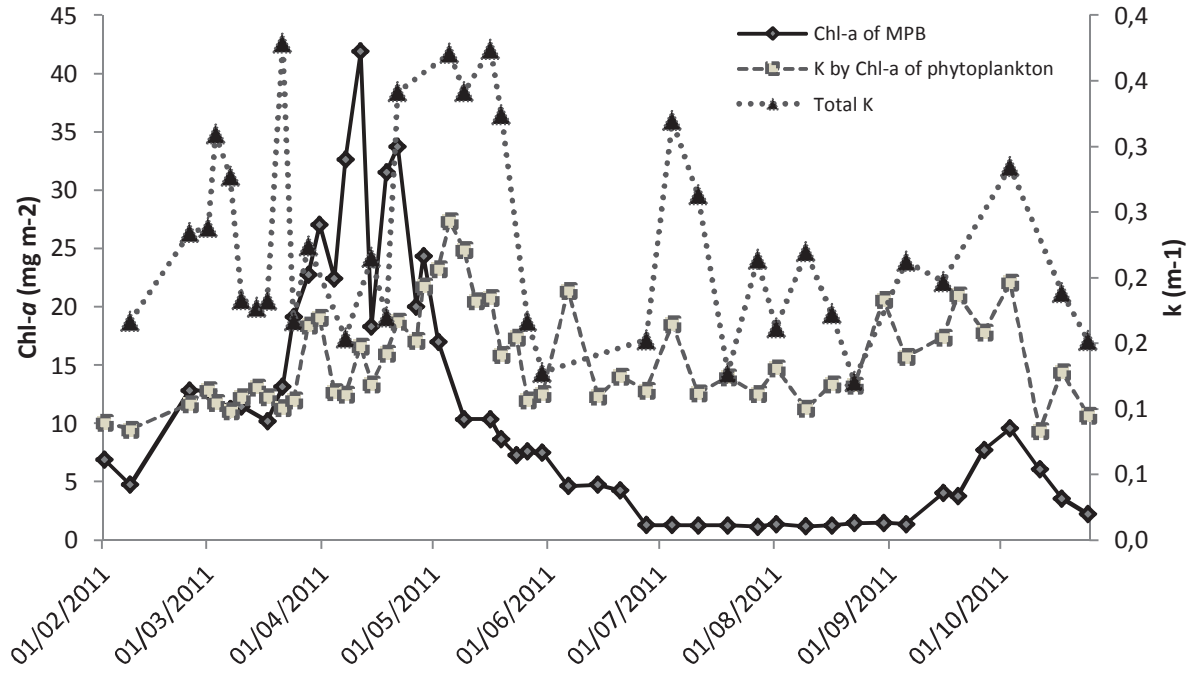


Fig. 7 (b) Temporal variation of the attenuation of light coefficient (k), attenuation of light coefficient due to Chl-a in the water column and Chl-a biomass of MPB from February, 2011 to October, 2011.

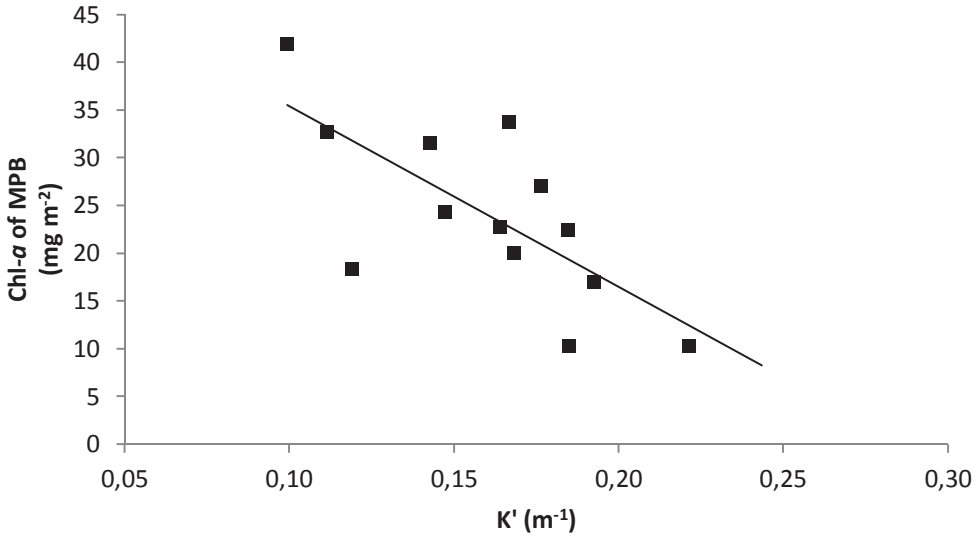


Fig. 7 (c) Relationship between k by the Chl-a of water column and Chl-a biomass of MPB from 11th April, 2011 to 16th May, 2011.

4.3 Nutrients

Nutrients (essentially, DIN, DSi and DIP) are necessary for microalgae growth. Depending on their inputs to the system (quantitatively, but as well relatively to each other), they can lead to changes in the species composition of the communities with an increase or a decline in the overall biomass (Munn et al., 2010).

Although it can vary according to the nutrient load (Glibert and Burkholder, 2011), the microalgae nutrient requirement for growth is species specific (Lagus et al., 2004). Both pelagic and benthic algae have to share the resources in a shallow coastal ecosystem. Generally, the benthic algae have access to higher nutrient concentrations from subsurface sediment and are less effective in their ability to uptake nutrients at low concentrations (Leynaert et al., 2009).

Temperate estuaries and bays are known to show seasonal shifts of nutrient limitations due the large seasonal inflow of fresh water (McComb et al., 1981). The nutrient condition at the Bay of Brest has been well documented for the past few years. Like many other macrotidal ecosystems of Western Europe, which receives nutrient inputs from adjoining rivers, the Bay of Brest is affected by dramatic nutrient alterations (Del Amo et al., 1997). For the past three decades increasing agricultural and industrial activities have caused extensive discharge of DIN and DIP compounds in the Bay (Cann 1995). Generally, the coastal waters of most developed countries face 3 potential consequences in relation to the long term deposition of anthropogenic wastes of nitrogen and phosphorous (Howarth et al., 1996, Del Amo et al., 1997). Firstly, it can lead to severe eutrophication by the phytoplankton population which were previously nitrogen or phosphorous limited (Meybeck and Helmer, 1989; Smayda, 1990). Secondly, the diatom dominated population may suffer from silicic acid limitation due to the lowered Si:N ratio (Officer and Ryther, 1980; Smayda, 1990; Conley et al; 1993). Thirdly, due to the Si limitation, a shift from siliceous to non-siliceous population of phytoplankton may occur resulting in the disturbance of the typical pattern of succession (Ragueneau et al., 2002). In the Bay of Brest, the DSi/DIN ratio during winter has decreased by a factor of 6 from 1975 to 1993 (Le Pape et al 1996), which could have led to a shift in

phytoplankton communities (Ragueneau et al., 2002) with a greater likelihood of harmful algal blooms. However, the benthic flux of DSi in summer prevents nutrient limitation and allows diatom dominance to be maintained all throughout the season.

Although there have been studies about phytoplankton, the dynamics of MPB in relation to nutrients and the relative comparison with phytoplankton have been completely ignored till date. In order to better assess the role of nutrients in the observed shift between the pelagic and benthic seasonal dynamics of microalgae in the Bay of Brest, we examined in situ nutrient concentrations and their ratios (DSi/DIN/DIP), and compared them to the reference Redfield (1934) and Brzezinski (1985) ratios to determine the potentially limiting nutrient during our period of study (Fig. 8). We are aware of the fact that Redfield ratios and remaining nutrient concentrations in the water column are just indicative of nutrient limitation. Thus, one must indeed be cautious with the assumptions that are implied, but at least they give some ideas to deepen.

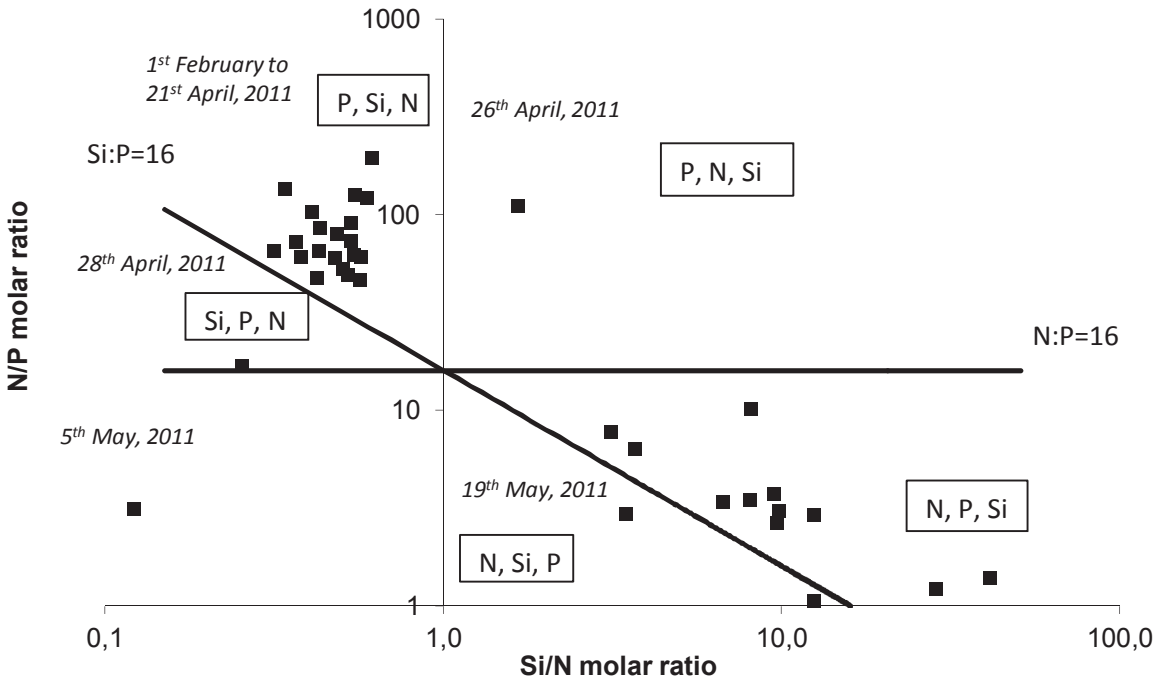


Fig. 8 Representation of Si:N:P molar ratios in the water column of the study site from February 2011 to October 2011. Each area is delimited by Brezinski ratio (1985) and Redfield et al. (1934) ratio of Si:N:P = 16:16:1. Order of priority is maintained for the potentially limiting nutrients.

DIP appears to be potentially the main limiting nutrient early in the year. On one hand, the ratios (DIN/DIP and DSi/DIP) are high and largely over the reference ratio of 16/1 (>50 and >20 respectively, from January till May), and on the other hand, DIP concentrations are low (< 0.1 µM) falling below the range for half-saturation constants for PO_4 uptake (Smith & Kalff 1982) at the end of March. DSi is completely depleted only during the first week of May (below detection limit) and thus became the primarily potentially limiting nutrient during that short period of time. Then DIN appears to be the main limiting nutrient later in the season (from mid-May until October), with DIP of secondary importance.

Thus the lack of DIP could be put forward to explain the decline of MPB biomass at the beginning of April, whereas the phytoplankton decline in the first week of May coincides to the DSi deficiency. Indirect and direct DSi limitation has been already reported in previous studies in the Bay of Brest (Ragueneau et al. 1994, 2002, Del Amo et al., 1997), though the role of DIP has been understudied.

Martin (2005) showed that DIP benthic fluxes are at their lowest or non-existent in winter, whereas riverine discharges and DIP loads are still important by the end of March (Czamanski, pers. com., ECOFLUX). Similar results were observed in the Tomales Bay, California, where the lowest benthic flux was observed in winter and the maximum was observed in late summer (July/August) over the annual cycle (Dollar et al., 1991).These data support the idea that at the water-sediment interface, the MPB could be DIP starving, while in the water column the phytoplankton can bloom, fed by river inputs. This also highlights the need to study the role of phosphorus in the functioning of coastal waters more closely as along with its importance, phosphate is possibly the most difficult to assess amongst the three nutrients (Del Amo et al., 1997) because of its fast biological (Admiraal and Werner, 1983) and geochemical (Lean et al., 1983, Conley at al., 1988) turnover and the fast reactivity of phosphorous with suspended matter (e.g. Carrit and Goodgal, 1954).

4.4 Elemental composition

Particulate matter was investigated to examine the differences of elemental composition between phytoplankton and MPB biomass. The POC fluctuations of water column maintained a correlation with that of the Chl-*a* of water column with R^2=0.66 (Fig. 4b).
On the other hand, POC and Chl-*a* of MPB did not show any relation, and also, the high concentrations of POC observed in bottom samples all along the time scale, as compared to

the Chl-*a* concentrations, gave rise to a higher POC/Chl-*a* ratio in benthic samples (with an average of 245 ± 250) than POC/Chl-*a* in the water column (average 132 ± 41) (Table 2). Deducing from the study of Del Amo et al. (1997), the maximum POC/Chl-*a* of phytoplankton in the Bay of Brest during the spring bloom of 1994 was approximately 87. Compared to that, our study represents a POC/Chl-*a* value of 123 during spring bloom in May, while the maximum was observed to be 230 on 21st March. In the Bay of Seine, another macrotidal ecosystem in France, POC/Chl-*a* value as high as 612 has been observed with a Chl-*a* concentration of 10 µg L^{-1} at the end of June (Savoye et al., 2003). Values ranging from 200 upwards for POC/Chl-*a* ratio generally indicate considerable amount of heterotrophs, macroalgae or detritus in the particulate matter (Pena et al., 1991), whereas lower ratios relate to healthy phytoplankton (Tulaskar et al., 1992). The PCA also indicated that MPB Chl-*a* and MPB POC were totally unrelated with each other (Fig. 6b), while phytoplankton POC was related with the concentrations of phytoplankton Chl-*a* (Fig. 6a). But interestingly, the large discrepancy observed in POC/Chl-*a* ratio between pelagic and benthic samples was not reflected in POC/PON ratios. POC/PON in water column averages 6.3 (± 1.1) only slightly lower than in the benthic samples (average 6.5 ± 0.8), and were both of them quite close to Redfield's ratio of 6.6. Among particles that constitute the bulk samples and influence elemental signature, macroalgae, seagrass and detritus have generally a lower PON content in comparison to phytoplankton and Redfield ratio (Nielsen et al., 1996). Thus the presence of detritus and probably heterotrophs in benthic samples would explain, at least in part, the observed variations in particulate matter stoichiometry, essentially in summer, when the Chl-*a* concentrations are so low as compared to POC.

We also looked at the particulate biogenic silica (BSi) content of both compartments. The BSi/Chl-*a* or BSi/POC ratios can give indications on the contribution of diatoms to the particulate matter and on their degree of silicification. Sigmon and Cahoon (1997) showed that benthic diatoms are more silicified in terms of silica content per unit of Chl-*a* (14.3 ± 3), than their pelagic counterpart (2.8 ±1.6). The average BSi/Chl-*a* ratio in the Bay in our study was observed to be almost the same for water column (13 ± 7) and the MPB (12 ± 10). Therefore, in the subtidal zone of Bay of Brest, the trend of Sigmon and Cahoon (1997) was not observed as BSi/Chl-*a* ratio was similar for benthic and pelagic communities. BSi/POC molar ratio averaged 0.04 (± 0.02) for phytoplankton and also 0.04 (± 0.02) for benthic samples, significantly lower than the reference ratio of 0.13 given by Brezinski (1985) for diatom growth in nutrient repleted conditions. The BSi/ POC ratio of phytoplankton conformed with that of Ragueneau et al (1994) where they observed it to be 0.05.

4.5 Other factors

Other factors which can be responsible for the disparate temporal dynamics of MPB and phytoplankton are the presence of macroalgae and grazing at the bottom. Macroalgae concentration in the Bay of Brest has been observed to reach its highest in summer (Grall et al, 2006), which coincides with the minima of the MPB biomass in our study, which was also attained in summer. For grazing, it is well known that the effect of nutrient supply on phytoplankton biomass and species composition can be strongly modified by the top-down control exerted by the grazing community (e.g. Reynolds 1984, Sterner 1989, Cottingham et al., 2004) and it has already been noticed that the benthic suspension feeders partially influence phytoplankton dynamics in the Bay of Brest ecosystem (Le Pape et al., 1999). Presence of filter feeders (molluscs and crustaceans) have been detected in the Bay of Brest which Grall et al, (2006) hypothesized that they either feed on MPB or particulate organic matter (POM). But the comparative analogy between the temporal dynamics of benthic fauna and MPB in the Bay of Brest could not be achieved because the study of benthic fauna dynamics in the Bay is yet to be established. However, annual cycle of benthic fauna in the Bay of Morlaix (Chardy and Dauvin, 1992) has been studied, which is another temperate subtidal zone in the same region. They observed that the population of meiobenthos started increasing from mid-May and reached a peak in late June. The peak sustained till the end of September before coming down. Now, in our study we observed that Chl-*a* biomass of MPB depleted down to minima from mid-May to the last week of June and stayed there till the first week of September. Although the two sets of data do not match precisely, but relating our study with that of Chardy and Dauvin (1992), and considering the factor that MPB are a major source for secondary production (Peterson and Howarth, 1987; Sullivan and Moncreiff, 1990; Currin et al., 1995) by being more nutritious and labile than vascular plants (Miller et al., 1996); it can be said that grazing as an important environmental parameter can definitely be expected to influence the MPB dynamics and composition of the subtidal zone of the Bay of Brest

5. Conclusion

This study showed the dynamics of MPB and phytoplankton in the subtidal zone to be quite different from one another. Amongst the investigated variables, the potential limitation of DIN and DIP might be responsible for the depletion of benthic microalgae because of the high specific uptake rates and half saturation constants of MPB. On the other hand, availability of light at the bottom during spring might well have partially contributed to the initiation of MPB bloom. Unaccounted possible factors for the disparate course of phytoplankton and MPB seasonal dynamics include competition of MPB and macroalgae at the bottom and grazing of MPB. Further investigations are needed in order to have a more detailed picture on the controlling factors of MPB dynamics. Study of photosynthetic parameters and biodiversity of MPB could provide insight in this regard.

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Chapter 3

Primary production and photosynthetic performance of subtidal benthic microalgae in a North Atlantic coastal ecosystem

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REGIONAL INDEX TERMS: France, Brittany, Bay of Brest

Abstract:

We conducted a whole year survey to study the seasonal dynamics of the microphytobenthos (MPB) population in the subtidal zone of the Bay of Brest. Pulse amplitude modulation (PAM) was used to determine photosynthetic parameters and primary production was measured by C14 isotope techniques. Maximum primary production of MPB was found in summer to be around 100 mgC m^{-2} day^{-1}. The primary production of MPB reached its peak in early May right after the Chl-*a* bloom subsided. After its peak the production of MPB declined and roughly followed the dynamics of Chl-*a* biomass. Previous studies have shown that temperature has a large effect on the production of MPB. In our study the specific production (production/biomass) of MPB reached its maximum through fluctuations in the middle of August, when the temperature also reached its peak, which in turn explained a partial dependence of MPB production on temperature. Potential nutrient limitation was not observed to be an inhibiting factor as specific production of MPB showed its increment in the months of potential DIN and DIP limitation. The effect of light on the MPB communities was studied through the photosynthetic characteristics. The *P-I* parameters as such showed no seasonal patterns with values fluctuating all along the study period. Ek (light saturation parameter) dependent variation was observed since no relationship was found between the

photosynthetic transport rate (rETRmax) and the light utilization efficiency parameter α. rETRmax was also observed to be unmatched with Chl-*a*, suggesting a top down control for MPB. Rise of rETRmax and α during mid-March suggested light to be the triggering factor for spring bloom. Ek ranged on a higher scale from 59 to 355.3 µmol quanta m^{-2} s^{-1}, and also, was observed to be greater than PAR on a few occasions with the maximum ratio of E/E_k reaching 2.5, which in turn suggested poor photoacclimation for MPB.

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1. Introduction:

Coastal zones bear tremendous ecological importance considering the fact that nearly half of human population of earth resides near the coasts (Pandolfi., 2003). Humans depend on the ocean for food to livelihood to recreational activities (Halpern et al., 2008). However, human pressure emerging directly from leisure activity, boat traffic, and indirectly from industry and agriculture is reshaping the state and functioning of marine coastal ecosystems. The shallow coastal areas of Western Europe are being subjected to remarkable levels of climate forcing and anthropogenic stress (Goberville, 2010). On top of that temperate coastal zones are significant for shellfish and fish farming because of their biological productivity (Pannard et al., 2008). The high spatiotemporal variability of physicochemical parameters in the temporal coastal ecosystems necessitates localized ecological studies to understand the coastal dynamics and to uncover the impact of human activities and climactic forces.

The most important primary producer groups of the coastal zones are pelagic and benthic micro algae (MPB) ((Pannard et al, 2008, Woelfel et al., 2010). In these regions, phytoplankton and benthic microalgae are both recognized as being principal components of the diet for economically important suspension-feeding fauna (Gillespie et al., 2000). In some shallow and intertidal systems MPB can be equally or even more contributing to primary production compared to phytoplankton (Underwood et al., 1998) because sufficient light for photosynthesis reaches the bottom and enough nutrients are available. (Cahoon & Safi, 2002). For example in the arctic coastal ecosystem of Norway, benthic microalgae are

known to be major primary producers (Woelfel, 2010). In shallow water regions (2-40m depth) benthic production can even surpass pelagic contribution (Underwood and kromkamp, 1999). With their ability of high primary production benthic microalgal communities can profoundly influence the flux, transformation and turnover of carbon and nutrients in coastal areas. Benthic primary producers contribute to the availability of energy and matter for benthic and pelagic food webs and define benthic and pelagic energy budgets, which affect the chemistry at the sediment-water interface, and regulate sediment stability. Models investigating the consequences of human pressure on coastal zones and coastal ecosystem dynamics have therefore to include knowledge about the dynamics of benthic primary producers and their contribution to the flux of energy and matter. Especially the control of benthic production by resource availability is a major task to be able to predict consequences of human impacts on benthic primary production.

However, while global and local estimates of phytoplankton productivity have been analyzed comprehensively (Gazeau, 2004; Longhurst, 1995), few studies have so far been carried out the assessment of benthic primary production in coastal areas especially in the subtidal zones(Longphuirt, 2007),. In the subtidal zones of temperate climactic areas, the global benthic production ranges from 0-211 mg C m^{-2} day^{-1} (Cahoon, 1999), while specifically in Europe the average comes as 18 mg C m^{-2} day^{-1} (Gazeau, 2004). According to Nelson et al. (1999), 42% of the marine benthic primary production is contributed by subtidal MPB. In previous studies of Bay of Brest, benthic production were calculated to be between ~57-111 mg C m^{-2} day^{-1} which summed up to be around 12-20% of the total primary production in the bay contributed by the benthic microalgae (Longphuirt, 2007).

However, despite the potential importance of microphytobenthos for coastal ecosystem dynamics, there are very few studies which quantified the productivity and photosynthetic dynamics of benthic microalgae in coastal areas. This is crucial for a mechanistic understanding of the importance of benthic primary production for food web dynamics and the parameterization of coastal zone ecosystem models. One such study has been performed by Light and Beardall, (2001), where the photosynthetic parameters of subtidal MPB were studied on an annual scale in Southern Australia. However, none such investigative measures have been taken till now in the temperate coastal zones of the North Atlantic. We found already a clear seasonal pattern in phytoplankton and MPB dynamics in the Bay of Brest (Chatterjee et al, in press). Both primary producer communities were showing distinct seasonal dynamics including a spring bloom which was earlier in MPB and a subsequent

sudden biomass decline. Whereas the seasonal dynamics of phytoplankton and the mechanistic base of these patterns are already well investigated (Sommer et al. 2012), no clear testable concept is available for MPB. Especially the role of resource limitation is a crucial aspect that could be different between substrate bound MBP and suspended phytoplankton usually constantly mixed within a gradient of light and nutrients.

Here we analyzed for the first time the primary production and photosynthetic performance of MBP communities during a seasonal succession pattern from early spring to autumn, following in detail the spring bloom and the subsequent biomass decline with physiological measurements.

2. Materials and methods:

2.1 Sampling

The sampling site (Fig. 1) is located in the Bay of Brest at Lanveoc (48 ° 17'41 .23 "N - 4 ° 27'12 .63" W). Freshwater influx into the Bay is provided by the rivers Penfeld, Aulne and Elorn, while fast mixing exchanges with Atlantic water happens through a narrow strait (1.8 km) that remains connected with the Iroise Sea (Le Pape et al., 1996). The maximal tidal amplitude at the Bay reaches over 8 m in spring and almost 2.6 m/s is the maximal tidal current (Chauvaud, 2000).

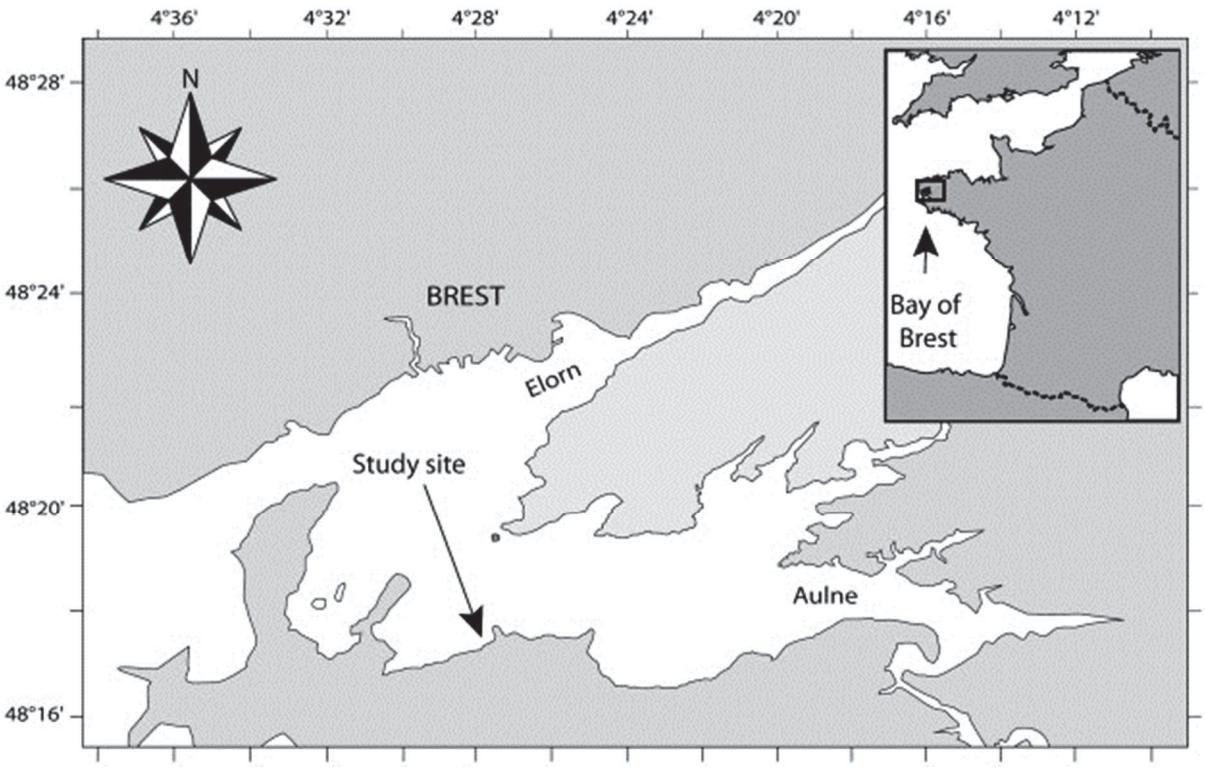

Fig. 1 Sampling site of Bay of Brest

Sampling started in 2011 from the beginning of February to the end October. Sampling was performed through the LEMAR/IUEM research vessel Hesione or Albert Lucas, sampling intervals were once a week in general and twice a week during the spring bloom (March to May). Care was taken to perform the sampling as close as possible to medium tidal coefficient and mid-tide. Water samples were collected from the surface, middle and bottom (9m) layers of the water column by a 12 L Niskin bottle.

To overcome the high spatial variability of MPB populations in the sediment, plexiglass plates (12x15 cm) were exposed on the sediment surface in June, 2010 to simulate hard surface substrat. Cattaneo and Kalff (1978) showed that such plates can be used successfully to mimic natural substrate. For the entire study period, one plate was sampled each week; two plates per week were taken out during the spring bloom period. The biomass on the plates was brushed off right after the sampling and was suspended in filtered (0.6 μm) bottom sea water before taking out subsamples for further investigations.

2.2 Physical parameters

Salinity, temperature and PAR (µmol photons m^{-2} s^{-1}) was measured by a CTD profiler Sea-Bird SBE-911, equipped with a photosynthetically active radiation (PAR) sensor. The PAR profiles collected from CTD were used to calculate the light extinction coefficient "k". Along with that, a PAR sensor at MAREL buoy also continuously recorded the surface PAR (http://www.ifremer.fr/mareliroise/index.html). From the light extinction coefficient "k", the bottom PAR at 9m depth was then calculated from the surface PAR of MAREL buoy.

2.3 Chemical parameters

After return to the laboratory water samples were immediately filtered for dissolved inorganic phosphate (DIP) and silicate (DSi) by Nucleopore membrane filters and for dissolved inorganic nitrogen (DIN) by Whatman glass fibre GF/F filters. Samples for DSi were kept in dark at 4°C and samples for DIN and DIP were frozen subsequently. A Technicon automatic Analyser II and semi-automatic analyser were used to measure DSi and DIN concentrations respectively by the colorimetric method (Tréguer and Le Corre, 1975), while the colorimetric method of Murphy and Riley, (1962) was used to measure DIP concentrations.

2.4 Particulate matter

Glass-fiber filters (GF/F Whatman) were used for the filtration of water samples for Chl-*a* analysis. 6 ml of 90% acetone was used to extract Chl-*a* and henceforth stored in the dark at 4° C for 12 hours. After centrifugation, fluorescence was measured by a Turner Design fluorometer. Chl-*a* concentration was calculated according to the equation given in Lorenzen (1966).

Samples were filtered on pre-combusted (450°C for 4 hours) Whatman GF/F filters for particulate organic carbon (POC) and particulate organic nitrogen (PON) analysis and kept in a stove at 60°C for desiccation. A CHN elemental analyzer (Thermo Fischer Flash EA 1112) was used to analyse the filtered samples by using the combustion method of Strickland and Parsons, (1972).

2.5 Primary Production

250 ml of water samples were filled into polycarbonate bottles in duplicates. 2µCi of C14 was added as sodium bicarbonate to each of these bottles. For each bottle, 100 µl was immediately sampled in triplicate and put in scintillation vials containing 50 µl of ethanolamine to measure activity at time zero (To). 5 ml of scintillation cocktail (Hionic Fluor, Perkin Elmer Life Sciences) was added to the samples and activity was measured with a scintillation counter (Wallac Guardian model 1414).

Polycarbonate bottles were then incubated in sunlight for 24 hours under 11.4% light reduction nickel screens to simulate in situ light conditions for and the MPB community. Two further subsamples of the initial samples were also incubated under controlled laboratory conditions with light intensities of 200 µmol m^{-2} sec^{-1} for 4 hours.

At the end of the incubation, samples were filtered onto 0.6 µm Nucleopore filters. Filters were placed in 20 ml scintillation vials. 1 ml of HCL was added to each of the filters to… and later 15 ml of scintillation cocktail was added for analysis. The samples were then measured in the scintillation counter. Primary production was measured in mg C m^{-3} day^{-1} by the equation:

$PP = 1.05*(Tf/ T_0)*24000/d*24,$

where d is the duration of the incubation, in hours, T_f is the activity on the filter at the end of the incubation and T_0 is the activity on the filter at the start of the incubation. The primary production was converted in mg-C m^{-2} day^{-1} by taking into account the surface of the plates from which the MPB was scratched off and the volume of water in which it was. By dividing production by the Chl-*a* concentrations of a sample we got the specific productivity for MPB in mg-C mg-Chl-a^{-1} day^{-1}.

2.6 Photosynthetic parameters

Measurements of fluorescence were performed with an underwater fluorometer diving PAM (Heinz Walz, Effeltrich, Germany) soon after sampling the plates. Photosynthesis – Irradiance (P vs I) analyses were carried out in triplicates after 10 min of dark adaption of samples with 8 sequential irradiance steps from 37 to 1389 µmol-quanta m^{-2} s^{-1}. The measurements were transferred to computer via Win control software and processed further by Sigmaplot. The model of Webb (1974) or the Eillers and Peeters model (1988) were used to fit the data and calculate photosynthesis parameters.

The Webb model was used for non photoinhibiting curves. In this model, a is representing rETRmax and b is the slope of the curve representing the light utilization efficiency (α)

In the Eillers and Peeters model (1988), for photoinhibition curves, the relative electron transport rate (rETRmax) is derived by the following equation:

$$rETRmax = ([b+\{2*(a*c)^{0.5}\}])^{-1}$$

While α, the slope of the curve is calculated as:

$$\alpha = 1/c$$

The light saturation parameter (Ek) was obtained by the equation:

$$Ek = rETR_{max}/\alpha$$

2.7 Numerical analysis:

XLSTAT 2012 software was used for Principal Component Analyses (PCA) to analyse environmental and biological parameters of the benthic compartment. The supplementary variables to the PCA comprised of the biological variables like Chl-*a*, POC, ETRmax, E/Ek, α and Fv/Fm. The linear combination of the environmental parameters, which is the canonical axis on the plot were correlated with the supplementary variables.

3. Results

3.1 Physical parameters

Minimum irradiance on the sea surface was observed to be 2.8 moles m^{-2} day^{-1} or 167 µmoles m^{-2} s^{-1} in February and the maximum observed in May was 58.3 moles m^{-2} day^{-1} or 1012 µmoles m^{-2} s^{-1} (Fig. 2). On average 12% of surface irradiance was reaching the seafloor (at 9 m depth). No clear seasonal variation was observed for the extinction coefficient (k) in the water column which ranged from 0.32 to 0.14 m^{-1} over the year The lowest average PAR

for a day at the bottom was observed in February with 0.8 moles m^{-2} day^{-1} or 20 µmoles m^{-2} s^{-1} and the highest being 18.0 moles m^{-2} day^{-1} or 299 µmoles m^{-2} s^{-1} in May (Fig. 2)..

Temperature, exhibited a typical seasonal pattern of temperate area with the lowest being 8.7°C in February and the highest at 17.4°C in August (Fig. 2).

CTD profiles evidenced a well-mixed water column most of the time, with no more than 0.7°C difference between the surface and the bottom water over the whole year.

Salinity evidenced the typical characteristic of a coastal ecosystem where it was always higher than 32 PSUand low variations were recorded increasing from 33 PSU in February to 35 PSU in June and remained stable till October.

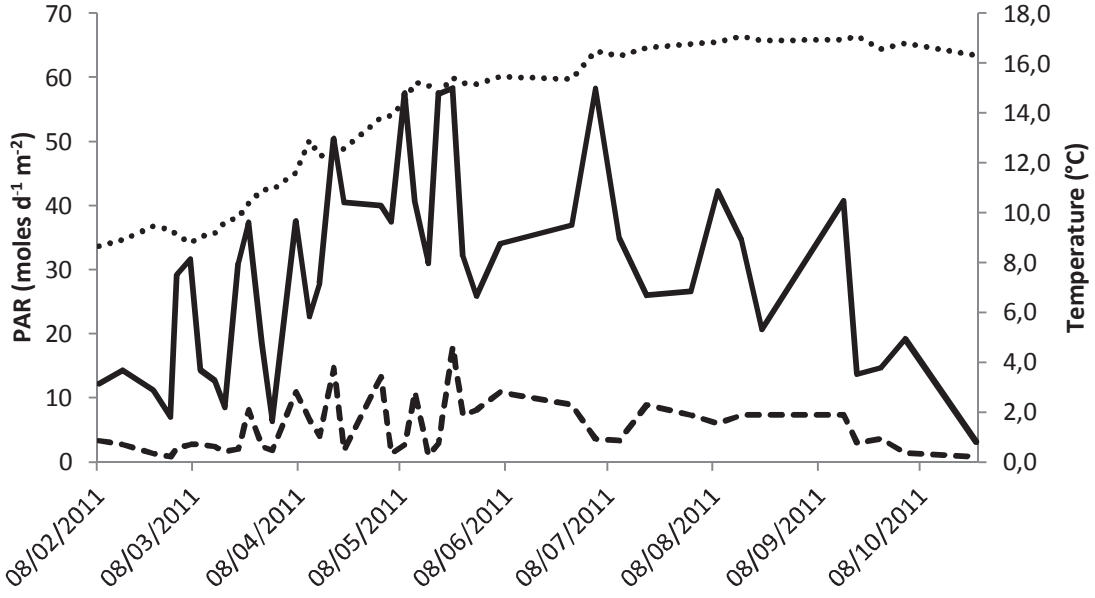

Fig. 2 Temperature and light variation for the study period of 8th Feb. 2011 to 24th October 2011 Data measured from Marel buoy on the days of sampling.

3.2 Chemical parameters

High nutrient concentrations were observed in the water column till late February and early March. DIN reached its peak with 33.18 µmol L^{-1}, DIP with 0.70 µmol L^{-1}, and DSi with 14.82 µmol L^{-1} (Table 1). The nutrient concentrations started decreasing from early March and completed depleted thereafter.

	Min.	Max.	Average
Chl-*a* (mg m^{-2})	1.2	41.9	10.7
POC (mg m^{-2})	292.6	1617.7	903.5
DIN (µmol L^{-1})	Below detection	25.9	6.2
DIP (µmol L^{-1})	Below Detection	0.60	0.17
DSi (µmol L^{-1})	Below detection	17.24	5.10

Table 1. Ranges of nutrient parameters from bottom water (DIN, DPI and DSi) and biomass parameters in terms of POC (bottom water) and Chl-a (MPB) along the study period

By the end of April, DIP was the first to be completely exhausted. Though DIP concentrations rose up to 0.15 µmol L^{-1} in May, it again fell to its minima. Henceforth till October, the concentration of DIP gradually rose with fluctuations.

At the beginning of May, DSi concentration was the next to become depleted. However, DSi concentrations started to rise again and increased till October.

DIN concentrations declined steeply from the middle of March to the end of April. The low DIN concentrations remained till the end of August.

3.3 Particulate matter

3.3.1 Chl-*a*

The Chl-*a* biomass of MPB started rising from February when the biomass was at around 4.8 mg m^{-2} (Fig. 3). The biomass reached its peak in the second week of April with a concentration of 41.9 mg m^{-2} (Table 1). After that the biomass followed a decreasing trend from the end of April to end of June. The minimum Chl-a concentration of MPB (< 1.2 mg m^{-2}) was recorded from the end of June until the end of August. The biomass slightly recovered in fall, reaching 9.6 mg m^{-2} in the first week of September but declined thereafter in October.

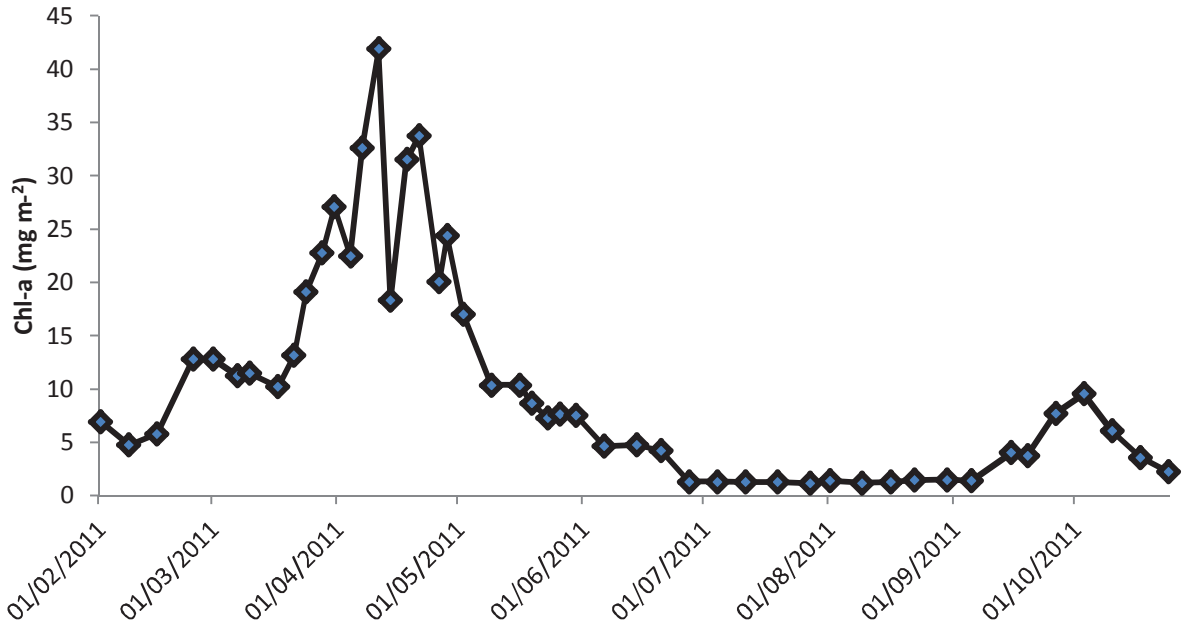

Fig. 3 Seasonal dynamics of Chl-a of MPB from 1st Feb. 2011 to 24th October 2011. (Adapted from Chatterjee et al., in press)

3.3.2 Particulate organic carbon

POC concentrations for the MPB samples reached a peak (1617 mg-C m^{-2}) at the end of April (Table 1). In the middle of July the concentration decreased before rising again at the end of July. From there on, concentrations fluctuated around 900 mg-C m^{-2} till October and declined after that.

3.4 Production

3.4.1 Primary production

Benthic primary production under in situ simulated conditions reached its peak (699 mgC m^{-2} d^{-1}) on 19th April, while production under ambient light peaked (107 mgC m^{-2} $d^{-}1$) on 3rd May (Fig. 4a). The production of MPB under ambient light conditions reached its maximum by the time Chl-*a* biomass already started declining. However, after 3rd May, the primary production under ambient light of MPB started decreasing following the trend of Chl-*a* biomass. It increased a little in July, August and September, but overall the production remained low.

Primary production under full light, after its peak on 19th April, reached a smaller peak (376 mgC m^{-2} d^{-1}) on 3rd May as well and maintained almost a similar pattern as ambient light conditions.

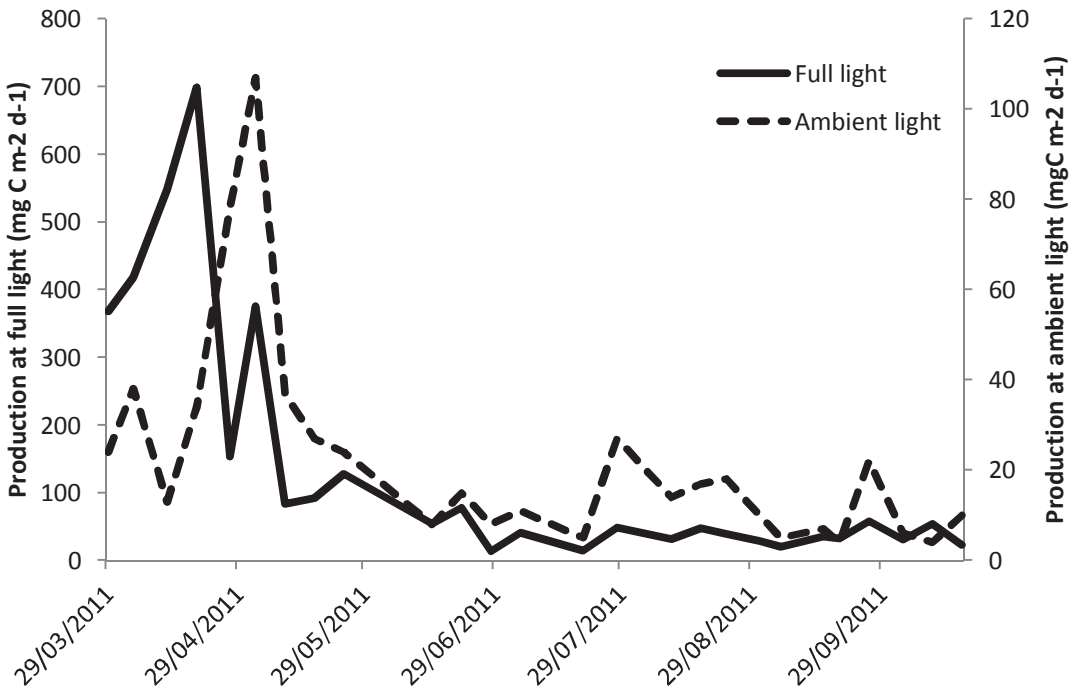

Fig. 4(a) Primary production of MPB in full and ambient light (11.4% filter) from 29th March 2011 to 17th October 2011

3.4.2 Specific production

Specific production of MPB under full light reached its maximum (49 mgC $mgChl^{-1}$ d^{-1}) on 21st June (Fig. 4b). From the middle of July to the end of August, the specific production was high before subsiding down to its minima (3 mg-C $mg\text{-}Chl^{-1}$ d^{-1}) in October. For ambient light conditions (Fig. 4b), the specific production slowly started increasing with peaks every month from 4th April until it reached its maximum (23 mgC $mgChl^{-1}$ d^{-1}) on 28th July. The specific production was high till the end of August and then it declined to its minima (1 mgC $mgChl^{-1}$ d^{-1}) and remained low for the rest of the period.

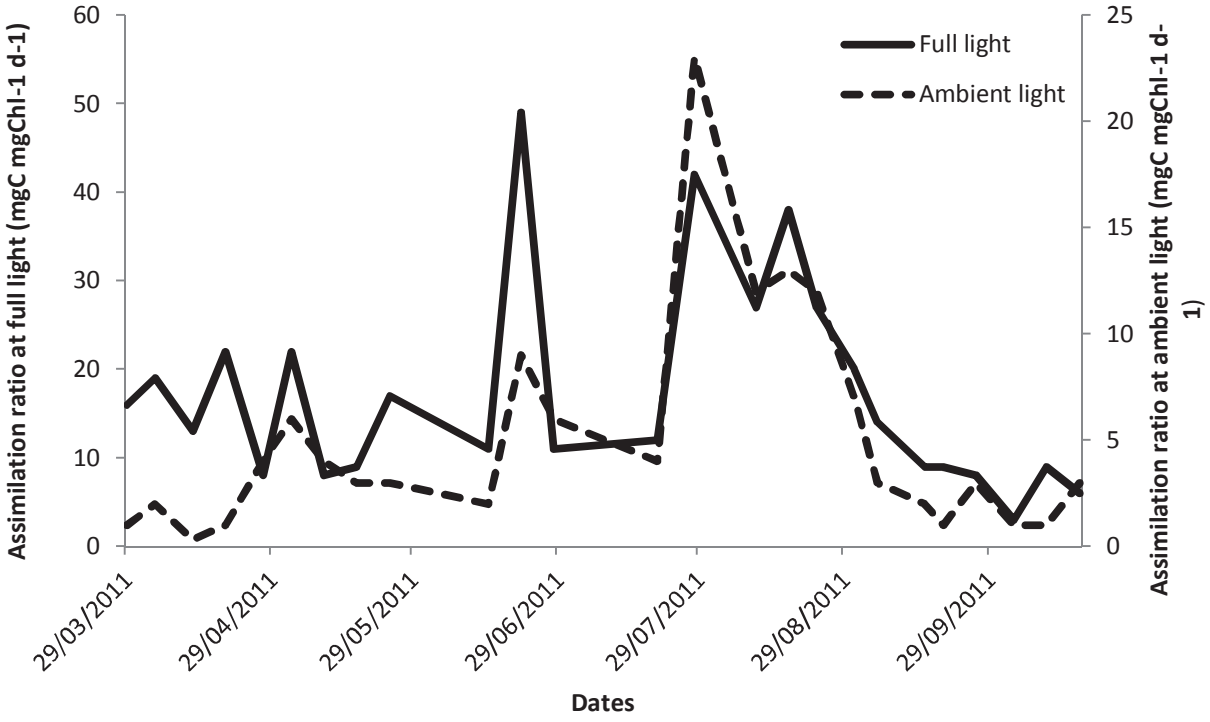

Fig. 4(b) Specific production of MPB in full and ambient light (11.4% filter) from 29th March 2011 to 17th October 2011

An index of light limitation (Fig. 4c) was calculated (ambient/full light) which showed varied fluctuations with the lowest being 0.17 on 20th June and the highest was observed to be 0.58 on 9th May. The average was noted to be 0.37.

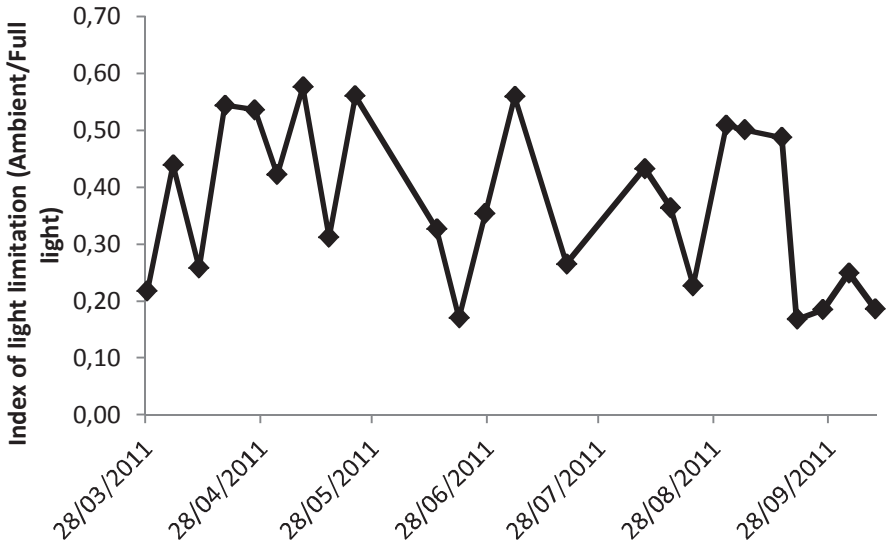

Fig. 4(c) Index of light limitation (ambient/full light) from 29th March 2011 to 17th October 2011.

3.5 Photosynthetic parameters

3.5.1 Maximum relative electron transport rate (rETRmax)

rETRmax of MPB was highly variable over time. The rETRmax started rising from 27th January from 34.3 (Fig. 5). From the first week of April the rETRmax increased and remained around 100 until the first week of May. On 27th June rETRmax reached its highest value of 190. rETRmax had two more peaks in middle of August and middle-end of September. On 24th October rETRmax reached again low values of 35.4.

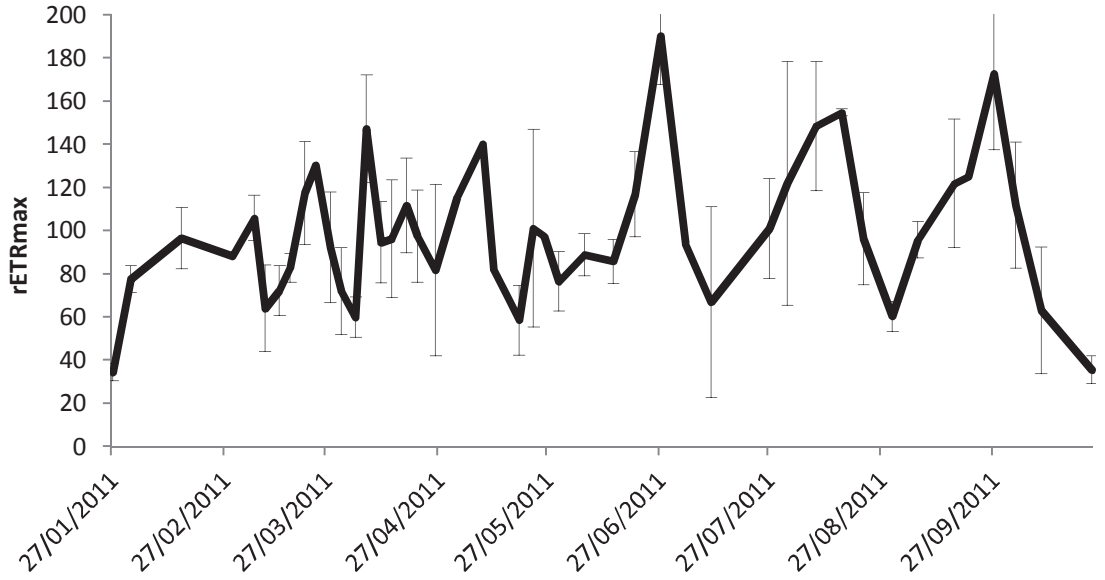

Fig. 5 Seasonal dynamics of rETRmax of MPB from 27th January 2011 to 24th October 2011

3.5.2 Light utilization efficiency (α)

The light utilization efficiency parameter (α) varied between 0.4 and 0.7 (Fig. 6). Within this range α was highly variable over time. The lowest values of 0.4 were observed on 2nd May and 16th August, while the highest values of 0.7 were observed on 15th February, 10th March and 21st March.

3.5.3 Quantum yield (Fv/Fm)

Fv/Fm values ranged between 0.54 and 0.7 (Fig. 6). The maximum values of 0.7 were observed on 15th February and 10th October. Values remained on the higher side during February, early March, September and October and get lower in the months of April, May, June and July. The minimum value of 0.54 was observed on 23rd May.

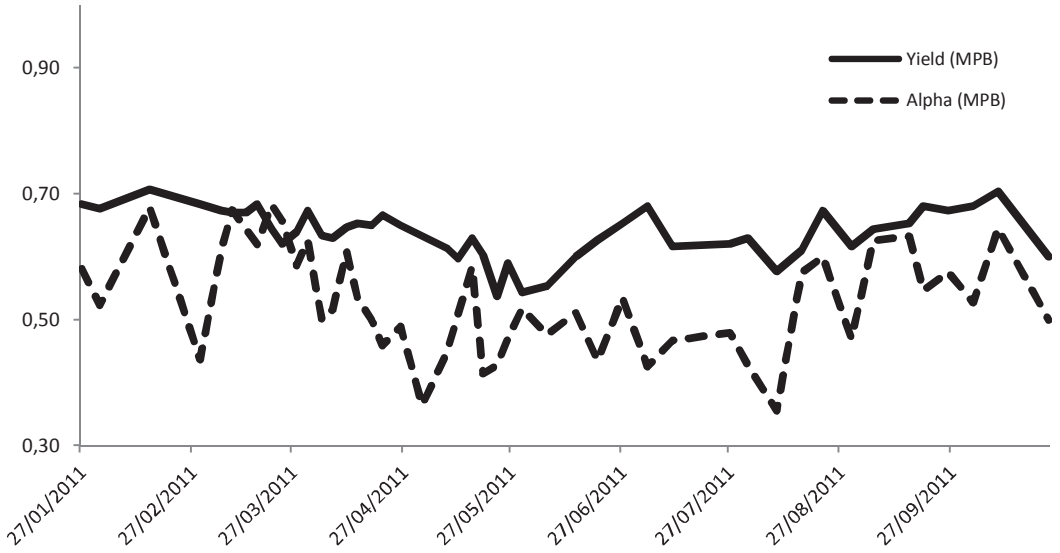

Fig. 6 Seasonal dynamics of Fv/Fm (yield) and α of MPB from 27th January 2011 to 24th October 2011

3.5.4 Light saturation (E_k)

E_k showed similar range of variability as rETRmax. Before reaching its peak (355 µmoles m^{-2} s^{-1}) on 27th June, E_k showed a gradual trend of increment from March till June along with fluctuations (Fig. 7). Two large peaks of E_k were also observed on 9th August (297 µmoles m^{-2} s^{-1}) and 26th September (300 µmoles m^{-2} s^{-1}). The lowest value was noted on 4th April (54 µmoles m^{-2} s^{-1}) and 30th August (55 µmoles m^{-2} s^{-1}).

E/E_k, the photoacclimation parameter ranged from 0.1 (1st March) to 2.4 (18th April). The E was calculated from the surface radiation as measured by the MAREL buyoy. The values fluctuated with peaks higher than 0.5 in March and April (Fig. 7). In May high values of E/E_k were also reported with E/E_k being 1.3 on 23rd. After 6th June (E/E_k = 1.0), the values descended and remained low till the first week of August. On 22nd August another peak was observed showing a value of 2.3. After the end of August, E/E_k descended steeply and reached a minimal value of 0.2 in the first week of October.

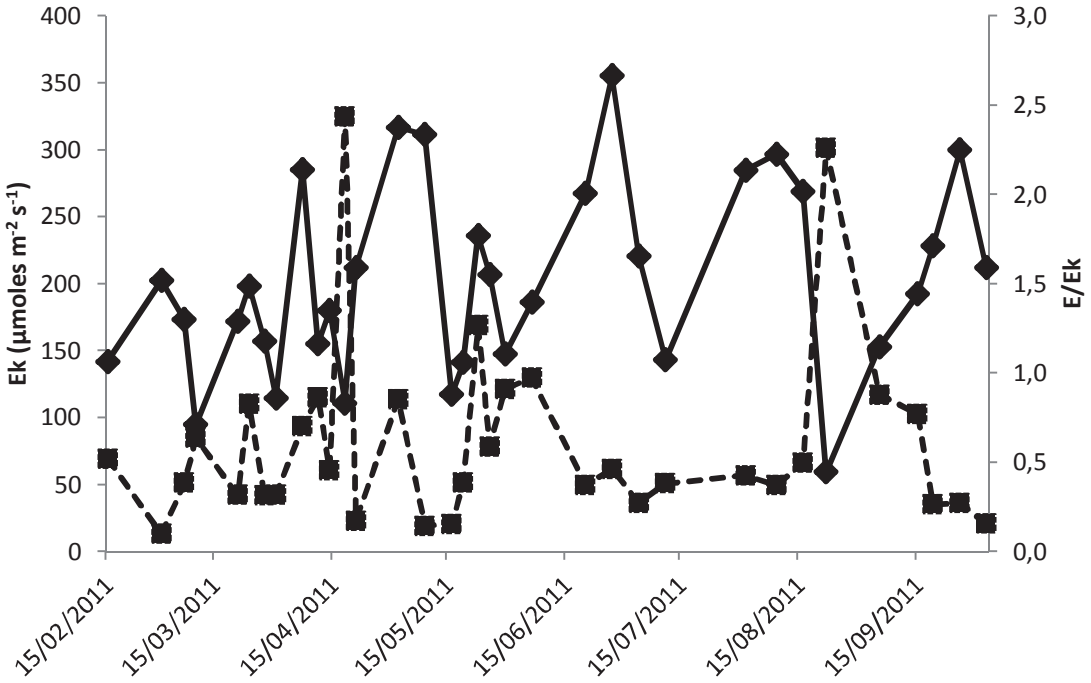

Fig. 7 Seasonal dynamics of Ek and E/Ek of MPB from 15th February 2011 to 3rd October 2011

3.6 Principal component analysis

The first two axes of the PCA (Fig. 8) explained 69.97% of the total variance, with the first axis (F1) explaining 48.60% and the second axis (F2) explaining 21.37% of the (explained) variance. A seasonality gradient was suggested by F1 as on the left side were the high values of temperature and salinity (positively correlated) and the right side of the factorial plane explained high values of nutrient concentrations. Chl-*a* biomass of MPB was positively related with the nutrients and unrelated with salinity. POC and photosynthetic rate rETRmax of MPB had no relationship with the Chl-*a* biomass of MPB. Photosynthetic yield Fv/Fm was found to be unrelated with photosynthetic efficiency parameter α and also with nutrients (DIN, DSI and DIP). (! Police character)

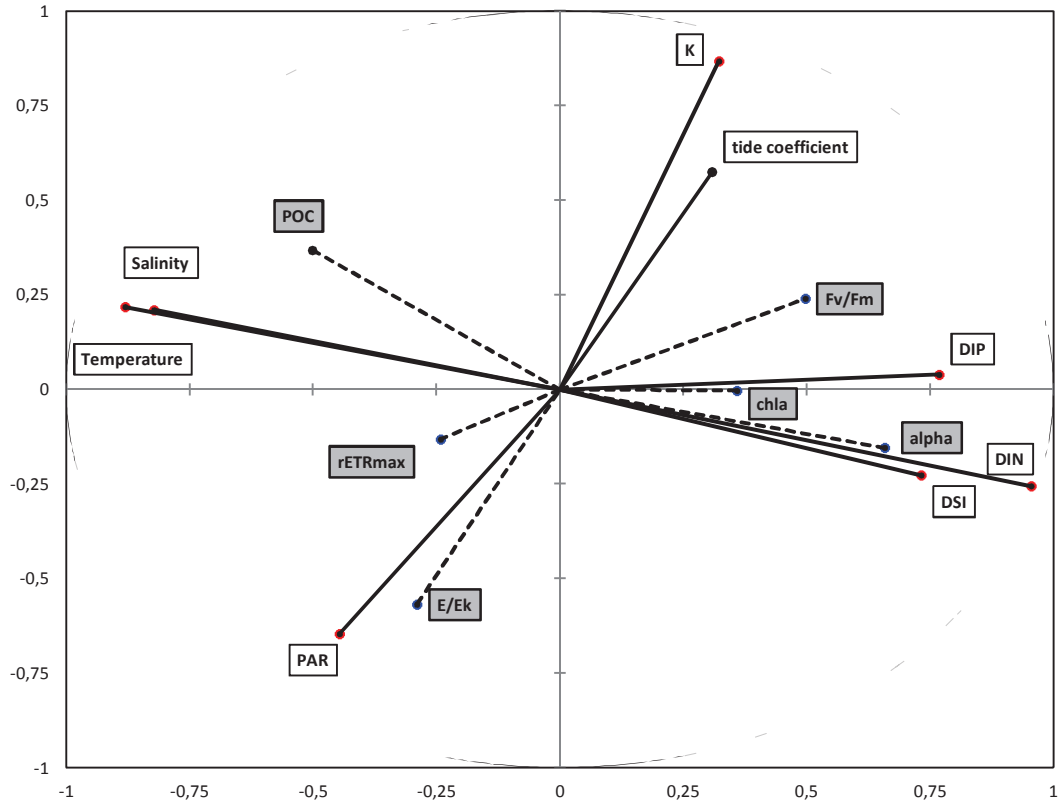

Fig. 8 Principal Canonical Analysis showing the relationship between physical, chemical and biological variables of the MPB community studied from 27th January 2011 to 24th October 2011. Biological variables were included as supplementary variables (dotted lines). Physico-chemical Variables: PAR (µmol photons m^{-2} s^{-1}); temperature (°C); salinity, tidal coefficient, k (m^{-1}), DIN (µmol L^{-1}), DIP (µmol L^{-1}), DSi (µmol L^{-1}). Biological variables : POC (µg C m^{-2}), benthic Chl-a (mg m^{-2}), rETRmax , E/Ek, α and Fv/Fm

4. Discussion:

The aim of our study was to analyze the importance and dynamics of resources, especially light, for benthic primary production by microphytobenthos in a North Atlantic coastal ecosystem. Our study combined for the first time the combined seasonal measurements of benthic microalgal biomass, primary production and photosynthetic performance. The Chl-a bloom of MPB in our study period might well have been initiated by the bottom PAR and after the bloom the reason for the decline of MPB biomass can be attributed to potential DIN and DIP limitation or unaccountable factors like grazing (Chatterjee et al., in press). To probe further we investigated the potential effects of abiotic and biotic drivers on the observed benthic primary production.

4.1 General pattern of MPB primary production :

The maximum production estimate of MPB in the Bay of Brest was previously observed to be around 100mg C m^{-2} day^{-1} (Ni Longphuirt et al., 2007). It closely matches with our observed peak production of MPB which is 107 mg C m^{-2} day^{-1}. However, in our study the peak was observed in early May compared to the study of Ni Longphuirt et al. (2007), where the maximum production was observed in August/September

The only previous estimates of the contribution of MPB to total primary production were around 12-20% on an annual scale (Ni Longphuirt et al., 2007)., In our study on average the contribution of MPB to total primary production was around 32% (Phytoplankton data, unpublished) for the entire study period. Our data show that MPB can contribute significantly to total primary production and is therefore an important parameter which has to be taken into account for estimates of fluxes of energy and matter in the Bay of Brest. Our observed MPB contribution does not however reach such high values as in studies where MPB production equal or even surpass pelagic production (Underwood and Kromkamp., 1999) or reach high absolute values as high as 892 g C m^{-2} $year^{-1}$ or 800 mg C m^{-2} $hour^{-1}$ (Grontved 1962, Hargrave et al., 1983). Compared to these values the annual productivity of MPB in the subtidal zone of Bay of Brest is minimal with an average value of 8.03 mg C m^{-2} $year^{-1}$. However, in terms of subtidal MPB production (although there are very few studies), the value from our study can be taken into perspective. For example, at the coast of Chukchi Sea,

the annual MPB production was observed to be 5 g C m^{-2} $year^{-1}$ (Matheke and Horner, 1974), which is well below the estimate observed in our study.

MPB Chl-a biomass was observed to be 1/3 of the total biomass (phytoplankton and MPB combined) in our study period of 2011, whereas, specific production of MPB contributed on average around 20% of the combined specific production (phytoplankton data, unpublished), which is lower than the contribution of total primary production by MPB. A striking observation was that, the seasonal pattern of biomass specific production of MPB showed an inverse pattern to the total primary production by MPB. Some of the important contributing factors such as temperature, nutrient limitation, grazing and light limitation are discussed in the following in order to understand the disparate seasonal pattern of biomass specific and total primary production by MPB.

4.1.1 Temperature:

Temperature is known to profoundly influence the production of both phytoplankton and MPB and it has been already shown that water temperature casts its greatest influence on the photosynthetic efficiency of MPB populations (Light & Bardall 2001). In our study, total benthic primary production strongly declined after a production peak in late April and early May and stayed low in the later months. However, although no direct relationship was found between specific production and temperature, a seasonal increasing gradient was indeed observed. From April, 2011 to July, 2011, specific production under ambient light conditions was observed to gradually increase along with temperature, showing however some fluctuations. This indicates a potential indirect influence of seasonal temperature on the specific production of MPB. However, it is not possible to separate direct physiological effects of temperature from indirect temperature effects on food web interactions, such as for example a higher grazer activity at higher temperatures. This would result in a stronger removal of MPB biomass and thereby a release of resource competion increasing specific production.

4.1.2 Nutrient limitation:

Diatoms with their need for silicate (Si) dominate MPB in general. Dissolved Si:N ratios decreased during the last decades in the Bay of Brest (Ragueneau et al. 1994, Le Pape et al. 1996, Del Amo et al 1997) as increasing agricultural production has caused extensive discharge of N compounds in the bay (Cann 1995). From 1975 to 1993 the ratio decreased about 6 fold (Le Pape et al 1996). We used established dissolved nutrient ratios of (Redfield 1934, Brzezinski 1985) to identify potential nutrient limitation patterns of MPB.We linked the dissolved nutrient concentration ratios to the measured primary production patterns.

In the early spring DIP concentrations were in a range that indicated potential nutrient limitation because the ratios of DIN/DIP and DSi/DIP were higher than 16:1 (Chatterjee et al., in press), but also, by the end of March, the absolute DIP concentrations did not satisfy the range for half-saturation constants for PO_4 uptake (Smith & Kalff 1982). DSi was observed to be below detection limit in the first week of May making it potentially limiting for diatoms during that period of time. Lastly, DIN was found to be potentially limiting from middle of May till October , surpassing most probably the effects of DIP on nutrient limitation effects (Chatterjee et al., in press).

The Chl-*a* biomass of MPB started to decline after a peak from end of April. Total primary production of MPB therefore also subsided during May and stayed low until October. Potential limitations of the nutrients might be responsible for such a biomass decline and most available nutrients could have been removed during the biomass peak. However, if serious resource limitation would limit biomass production leading to a decline, then specific primary production would also come down limited by nutrient availability. However, specific production gradually increased especially in the months in which DIN and DIP could be potentially limiting production as indicated by nutrient concentration ratios. Specific production reached its peak in July when DIN was primarily potentially limiting primary production. Our findings indicate that nutrient limitation per se was not a reason for the observed strong decline in MPB in late spring .

4.2 Light limitation and photosynthetic parameters:

A second essential resource that affects MPB production is light. Light availability would generally increase with increasing season in temperate regions. However, increasing spring phytoplankton biomass production would result in a strong consumption of light within the water column and thereby less availability of light for MPB. The question arises whether phytoplankton light consumption leading to light limitation is resulting in the observed MPB patterns. It has been observed that over 50% of the light extinction in the water column has been contributed by phytoplankton biomass in our study period (Chatterjee et al., in press). On the other hand, the light extinction coefficient k at the Bay for our study period ranged from 0.15 to 0.32 which indicates low turbidity within the Bay. To understand the effect of solar irradiance on the MPB community, we investigated the physiological parameters..

4.2.1 Photosynthetic capacity (rETRmax) :

Light has a strong influence on the photosynthetic capacity of subtidal MPB (Blanchard and Montana, 1992; Light and Beardall, 2001). In our study, no direct relationship was observed between the daily light variations at the bottom and the daily variations of rETRmax. However, in early spring, when the first distinct peak of rETRmax was observed, rETRmax and PAR were tightly coupled and the Chl-*a* amount of MPB also started to bloom. Therefore, the coupling of the first peaks of bottom PAR and rETRmax at the beginning of the season can explain the initiation of the MPB spring bloom, indicating a bottom-up regulation of algal biomass during this time (Caraco et al., 2006; Sommer and Sommer, 2006; Sommer and Stibor, 2002). This argument gets further support from the fact that the high nutrient concentrations at the bottom gradually diminished and were being used up by the MPB community as the Chl-*a* concentration of MPB started rising during the bloom. The MPB spring bloom seems to have the same physical drivers (increasing light and temperature) than phytoplankton spring blooms in temperate regions.

However, a strong uncoupling was noticed between rETRmax and the Chl-*a* biomass of MPB for the majority of the study period past early spring. Several factors might be responsible for this. After the initial spring algal bloom was over, dissolved nutrients (DIN and DIP) went potentially limiting and along with that the MPB Chl-*a* biomass crashed. Although biomass specific production data do not directly point towards severe nutrient limitation as a reason

for the biomass crash of MPB, but after the initial spring algal bloom, dissolved nutrients (DIN and DIP) went potentially limiting along with the MPB Chl-*a* biomass crash. On the other hand, the strong peaks of rETRmax that were observed in summer can potentially be attributed to the high seasonal temperature recorded during that period of time (Claquin et al., 2012). None the less, the low nutrient concentrations required for growth generally causes an imbalance between the utilization rates of produced organic compounds and their production rates (Claquin et al., 2012). In our study, this can be seen not only for the high rETRmax peaks in summer, but also, for the specific production of MPB which had its maximum peak in July with gradual increment through the summer; although the variations of rETRmax and specific production did not well match with each other. As a result of this imbalance, the excess organic compound would be excreted as organic carbon (Dubinsky and Berman-Fran, 2001., Staats et al., 2001), resulting in a high rate of carbon excretion (Klein et al., 2011, Claquin et al., 2010). In our study, POC concentrations at the bottom were quite high compared to the Chl-a concentration of the MPB community. Especially during summer, when the Chl-a concentration were minimal, the POC concentration maintained a mean level of around 1000 mg m^{-2}. Thus, the detachment of rETRmax and Chl-*a* of MPB in summer together with a potential nutrient limitation of algal production could have resulted in excessive carbon excretion by the MPB community resulting in high POC concentrations.

However, most probably also a strong top – down control by higher trophic levels contributed to the observed MPB dynamics and the uncoupling of rETRmax and Chl-*a* of MPB. Grazers which feed on MPB are present in the Bay of Brest (Grall et al., 2006). Although the seasonal dynamics of grazers are yet to be known in the Bay of Brest, observation from another subtidal system in near vicinity of the study site (Bay of Morlaix, Chardy and Dauvin (1992))shows that algal grazing meiobenthos populations starts increasing from mid-May and peaks in late June. This coincides with the timing of the crash of the Chl- *a* bloom of MPB in our study and points towards a grazer controlled algal bloom development, similar to the so called “clear water phase” which refers to a grazer determined phase of low phytoplankton concentration after a spring peak in pelagic ecosystems (Sommer et al 2012) .

4.2.2 Light utilization efficiency (α) :

The light utilization efficiency α ranged from 0.4 to 0.7 in our study, which indicates that the range falls within the range of values given for α in different aquatic ecosystems as reported in the literature. However, the range of α in our study is rather narrow compared to other

studies where the range of α for MPB has been observed to be much wider, e.g. 0.013 to 0.8 in the intertidal zone of Netarts Bay (45°N) (Davis and McIntire, 1983). Other studies dealing with subtidal zones reported values from 0.045 to 0.506 (Blanchard and Montagna, 1992) or 0.012 to 0.540 (Light and Beardall, 2001). It has been observed that during light limitation, α generally remains high (Behrenfeld et al. 2004; Claquin et al. 2010; Mangoni et al. 2009). In contrast to the narrow range of variation of α, the rETRmax of the MPB community was highly fluctuating for the entire study period and also was entirely decoupled from α over time. However, having high α values together with low photosynthetic rate values is not uncommon for microalgae (Beardall and Morris, 1976; Richardson et al., 1983). This indicates an increment of the light harvesting capability due to lowered photon flux density but a decline in the total carbon assimilation capability (Light and Beardall, 2001). This is a strategy often taken up by microalgae for photoacclimation in low light levels which happens by the increment of the photosynthetic unit (PSU) size when there is a decrement of photosynthetic rate and the resulting changes of α remains minimal. (Prezelin, 1981; Richarson et al., 1983). Therefore, from our study, where the α values were observed to be a bit on the higher range with narrow degrees of fluctuation and the rETRmax values were found to be fluctuating and dipping quite frequently, it can be said that the MPB community suffered from insufficient light quite frequently.

4.2.3 Index of photoacclimation (E_k) :

Ek, the light saturation parameter, describes the conformity between the capture of photosynthetic energy and photosynthetic system capacity for the processing of this energy by reflecting the optimum PAR intensity required for cells (Falkowski and Raven, 1997). E_k is a photosynthetic parameter which is considered to be independent of the Chl-a biomass and is able to give a clearer picture of photoacclimation compared to rETRmax or α (Light and Beardall 2001). In this study, the observed declines in E_k were mostly accompanied by declines in rETRmax as well; together with minimal change of α which indicates that low light photoacclimation was primarily controlled by the increase of PSU size (Prezelin, 1981; Richardson et al.,1983). This strategy has been described as an indicator of diatom dominated populations and has been previously observed for phytoplankton communities (Falkowski, 1981; Gallagher et al., 1984). On the other hand, the high fluctuations of E_k and the absence of any any specific seasonal pattern over time explains the absence of long term

photoacclimation strategy by the MPB community (Light and Beardall 2001). This finding is in contrast to the studies of Gargas, 1971, Blanchard and Cariou-Le Gall, 1994 and Light and Beardall 2001, where both, unimodality of E_k on the seasonal scale and long-term photoacclimation were inferred from the E_k values of MPB communities of subtidal zones and intertidal zones.

In contrast to subtidal zones, intertidal zones generally have higher values of the light saturation parameter for MPB because PAR values are usually considerably higher, e.g. literature values of E_k range from around 170 to 800 µmol quanta m^{-2} s^{-1} (Mills and Wilkinson, 1986, Davis and McIntire, 1983, Pinckney and Zingmark, 1993b) It has been observed that Ek values decrease usually with depth because of shade adaptation (Gargas,1971; Sundback and Jonsson, 1988; Light and Beardall 2001). Therefore, E_k values reported from subtidal zones (having a depth range of usually 9-13 m), are lower in comparison to that of intertidal zones, observed values ranging from e.g. 35-250 µmol quanta m^{-2} s^{-1} (Sundback and Jonsson, 1988, Light and Beardall 2001). However, the range of values in our study (59 to 355.3 µmol quanta m^{-2} s^{-1}) was found to be slightly on the higher end compared to other subtidal zones of similar depth. The E_k values of the MPB community at Bay of Brest has been measured previously by Ni Longphuirt et al., 2007 and was observed to be ranging from 57.8 to 83.4 µmol quanta m^{-2} s^{-1} (Ni Longphuirt et al., 2007). However, the study in 2007 was conducted on three distinct temporal points rather than covering a seasonal gradient which our study did. In our study, except for just four sampling dates, all the E_k values were observed to be higher than the bottom PAR for almost the entire study period and the mean ratio between available light and Ek (E/E_k) was observed to be 60%. Our data indicate Therefore our data indicate that the MPB community at the subtidal zone of Bay of Brest was subjected to a constant but weak light limitation, although the light limitation alone is not sufficient to describe the observed MPB pattern.

4.2.4 Quantum yield (Fv/Fm):

The quantum yield explains the maximum possible light utilization efficiency of PSII or the photosynthetic efficiency known as the Genty parameter and is denoted by Fv/Fm (Genty et al., 1989). 0.8 has been observed to be the maximum photosynthetic efficiency as yet measured (Magnuson, 1997). The Fv/Fm ratio of our study maintained a mean of 0.64 which

falls within the optimal range for algal cells further indicating no serious limitation of MPB photochemistry during our study period. The minimal fluctuations of quantum yield for the entire study period describes no sudden stress factors acting on the photosynthetic efficiency of the MPB community, even during the period of the crash of MPB biomass from summer till October. This further supports grazing as the main reason for the observed decline in MPB biomass. However, as Fo is known as an indicator of biomass (Serodio et al., 1997, Honeywill et al., 2002, Kromkamp and Forster 2003) and also is primarily deduced by the concentration of Chl-*a* (Kiefer et al., 1989, Kolber and Falkowski 1993, Serodio et al., 1997, Honeywill et al., 2002, Sylvan et al., 2007), we tried to observe the specific quantum yield of the MPB community by dividing the quantum yield by the Chl-a concentration of MPB. As the quantum yield had minimal fluctuations for the entire season, the specific quantum yield was observed to be the reverse in pattern of the Chl-a dynamics. On the other hand, the specific production in our study also showed a peak in summer during the time of the MPB crash. Although, the variations of specific quantum yield and the specific production did not match with each other, the increment of specific photosynthetic efficiency during the time of algal crash suggests a better utilization of light and nutrients, possibly because reducing biomass by grazers would release the remaining algal community from strong competition for light and nutrients. However, the use of Fv/Fm ratios to explain the algal nutrient status has been severely criticised (Kruskopf and Flynn 2006). Additionally, low light levels as typical for subtidal systems can also result in higher specific quantum yield (Pinilla et al., 2006)

4.3 Grazing:

The seasonal pattern and dynamics of the benthic fauna at the Bay of Brest is not yet known in detail. However there have been some studies describing the activity of several grazers at the Bay (Chauvaud et al.,1996, Grall et al, 2006). The Bay is known for suspension feeders like *Ficulina ficus* and *Phallusia mammillata* and filter feeders like molluscs and crustaceans (Hily, 1991, Grall et al., 2006) which likes to feed on MPB and particulate matter. It has been observed that from April on the post-bivalve larvae of *Aequipecten opercularis*, *Anomia ephippium*, *Crepidula fornicata* , mytilids and hydroids begin to settle on hard substrates (Chauvaud et al.,1996). On the other hand, the total primary production of MPB started to decline during May. The decrease in total production combined with the simultaneous increase in specific production, as observed during this observation period, strongly suggests

persistent grazing on the MPB community, indicating a strong top down control on phytobenthos biomass.

5. Conclusion:

In summary our study allows to draw some conclusions about the seasonal dynamics of MPB in the subtidal zone of a temperate North Atlantic coastal ecosystem. The observed seasonal pattern seem to follow general patterns that are also observed in seasonal phytoplankton dynamics of temperate pelagic ecosystems (Sommer PEG model). A spring peak of algal production and biomass, - which is initiated by the increasing light availability together with high dissolved nutrient concentrations - is followed by a situation where grazing is reducing biomass but thereby also releasing algae from severe competition for resources. Our photosynthetic measures, together with the analyses of specific production clearly point towards grazing and not resource limitation, as a main reason for the decline of algal biomass after the spring bloom. Our findings support the statement by Banse and English, 2012 that top down effects of predation are definitely an overlooked factor structuring dynamics and composition of marine micro algal communities. Grazing would not only affect resource availability and thereby photosynthetic parameters but also community structure and composition. Future studies have therefore to include grazing measurements as an important parameter to follow seasonal dynamics of MPB communities, especially as MPB can contribute considerably to total primary production in coastal ecosystems. .

6. Acknowledgement:

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Chapter 4

Temporal distribution of pelagic and benthic microalgae in a temperate coastal ecosystem

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Abstract :

Like phytoplankton, microphytobenthos (MPB) contributes significantly to primary production of coastal ecosystems. However, compared to phytoplankton, not much is known on temporal distribution and diversity of MPB, especially in the subtidal zones. In this study, we have parallely characterized the seasonal diversity of both pelagic and benthic microalgae in a subtidal zone of the Bay of Brest. Samples were collected from January, 2011 to October, 2011 and the analysis of microalgal biomass and diversity were performed accordingly. Phytoplankton community comprised of 74 species of which 35 belonged to dinoflagellates and 32 belonged to diatoms along with other functional groups, whereas the MPB community comprised of 22 diatom species. The individual cell biovolume of phytoplankton varied from 42 μm^3 to 15.10^7 μm^3 and that of the MPB varied from 79 μm^3 to $3\ 10^3$ μm^3 throughou the season. For the phytoplankton, *Chaetoceros* sp. dominated amongst diatoms and *Gymnodium* sp. amongst dinoflagellates, whereas for the MPB, *Navicula* sp. dominated mostly for the study period. *Chaetoceros debilis* and *Chaetoceros didymus* were both observed in the phytoplankton and the MPB communities. The Chl-*a* of the phytoplankton- and MPB community were correlated with their respective taxon richness until the bloom in early spring. Taxon richness of the pelagic diatoms strongly correlated with the Chl-*a* biomass of water column for the entire study period. The phytoplankton in community composition changed during major peaks shifting from high to low average cell biovolume and community similarity and low species evenness indicating strong dominance of a species. On the other hand, the diversity indices of MPB explained the Chl-a dynamics until the bloom, by taxon richness being correlated with Chl-a biomass and shifts of community similarity, species evenness and average cell biovolume before the bloom., After

the bloom the biomass declined and remained minimal till September. *Navicula* sp. being a preferred food item for meiobenthos and the absence of any specific grazing resistant diatom species in the MPB community might explain the inability of the community to sustain its biomass after the bloom.

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1. Introduction

The high frequency of species extinction and the future impact of anthropogenic pressure have already been a concern for biodiversity loss and its possible functional consequenses (Sala et al., 2000). About 40% of human population around the world inhabit within 100 km bordering the coast (Cohen et al., 1997) and as a result of which, a considerable amount of this population explore the ocean for economic reasons, food and other factors related to their well-being (Solan et al., 2006). Just like terrestrial ecosystems, both direct and indirect human interference considerably affect the diversity and composition of the communities in the ocean, and that too at almost every trophic level (Puly et al., 1998, Solan et al., 2006).

One of the preliminary biological elements in the trophic food chain through which energy transfer occurs to the higher organisms is the phytoplankton (Rajesh et al., 2002; Ananthan et al., 2004; Tiwari & Chauhan, 2006; Tas & Gonulal, 2007; Saravanakumar et al., 2008). Water quality is often evaluated by the density and diversity of phytoplankton as they are being used as biological indicators (Adoni et al., 1985; Chaturvedi et al., 1999; Ponmanickam et al., 2007; Shekhar et al.,2008). In the coastal ecosystems, the mixing of fresh and marine water along with the discharge of industrial and urban effluents can change the physico-chemical and biological processes and in the process can significantly impact the planktonic communities both structurally and functionally (Rochelle-Newall et al., 2011). Shifts in community diversity affects the biogeochemical processes and the carbon fluxes (Rochelle-Newall et al., 2011), and for coastal ecosystems this becomes even more important as they are considerably responsible for the aquatic carbon cycle although comprising relatively less total area (e.g. Borges et al., 2005). Therefore as Borges et al. (2006) stated, the biological diversity of the planktonic communities is very closely linked to the estuarine metabolic balance.

On the other hand, microphytobenthos (MPB) is instrumental in implementing nutrient fluxes at sediment water interface which in turn regulates the nitrogen and oxygen budgets of the sediment (Sundbaeck et al., 1991; Wiltshire, 1993; Wiltshire et al., 1996). Not only that, but also, the functional role of MPB as primary producers and also in the benthic food web has been stressed upon in many studies (Daehnick et al.,1992; Underwood & Thomas, 1990; Hillebrand et al., 2002). As a result of this, in the last two decades the study of diversity and functional role of MPB has gained some importance (Sundbaeck & Joensson, 1988;

Blanchard, 1990; Blanchard, 1991; Montagna et al., 1995;). Like phytoplankton, MPB communities can also act as sensitive indicators of water quality as the taxonomic composition of MPB assemblages can vary as per different nutrient levels (Lange-Bertalot, 1979; Kann, 1986). However, although the importance of MPB assemblages and distribution have been emphasized on intertidal zones (Pinckney & Zingmark, 1993; Colijn & De Jonge, 1984; Herman et al., 2000), the subtidal zones have generally been ignored till yet on this regard. As a result of this, not much is known about the composition or seasonal variation of MPB communities in the subtidal zones.

In this study, we have for the first time simultaneously analysed the comparative dynamics of distribution, composition and seasonal variation of phytoplankton and MPB assemblages in the subtidal zone of a temperate coastal ecosystem, the Bay of Brest.

2. Materials and Methods :

2.1 Sampling

The sampling site of the Bay of Brest can be considered as a typical temperate, subtidal, semi-enclosed marine ecosystem. The average depth of the Bay is about 8 m and the main rivers Aulne and Elorn merge into the Bay to bring in freshwater inputs while the adjoining Iroise sea pours in Atlantic water into the Bay by remaining connected through a 1.8 km strait.

The research vessel “Hesione” or “Albert Lucas” was used for sampling, which started from February, 2011 to October, 2011. In general sampling was performed once a week and during spring bloom (March to May) the frequency increased to twice a week. Priority was given to be as close as possible to medium tidal coefficient and mid-tide chosen to facilitate comparisons between the cruises.

A 12 L Niskin bottle was used to collect water samples for phytoplankton from the surface layer of the sampling site. Samples for MPB were collected from plexiglass plates (12 x 15 cm) which were placed on the sediment in June, 2010. Plexiglass plates were used to simulate artificial hard surface substrat to overcome the spatial heterogeneity of the sediment as they

have been observed to be good mimics of the natural substrate (Cattaneo and Kalff, 1978). Each week one plate was sampled out in general and two plates per week were sampled out in spring (March to May). A medium brush was used to scrap off the biomass immediately after sampling and suspend in filtered (0.6 µm) bottom sea water. Subsamples were taken for further analysis.

2.2 Chl-a biomass

The biomass suspended filtered sea water for MPB and the water collected from the surface layer fr phytoplankton were filtered on Glass-fiber filters (GF/F Whatman). Chl-*a* was extracted by 6 ml of 90% acetone and then kept in the dark at 4° C for 12 hours. The extract was centrifuged and a Turner Design fluorometer was used to measure the fluorescence. The equation given in Lorenzen (1966) was applied to calculate the concentration of Chl-*a*.

2.3 Biodiversity:

The subsamples for phytoplankton and MPB were fixed with Lugol for subsequent analyses. Cells were identified and counted to the lowest possible taxonomic level by the Utermöhl method under 10X and 40X magnifications. At minimum, 300 cells were counted. Number of cells were first calculated in Litres^{-1} and then converted into m^{-2}.

Individual cell biovolume was calculated based on geometrical models and equations reported for microalgae in Hillerbrand et al. (1999) .

Total biovolume was calculated in µm^3 by multiplying the number of cells with the calculated biovolume of each species.

Average cellbiovolume was calculated as X = Total biovolume/ Total number of cells for one sampling date.

Diversity was calculated as per Shannon-Weaver index and Pilou's evenness index was considered for species evenness.

Community similarity between two sampling dates was also measured by using the xy Index S = Σmin. (p1+ p2+...), where p1, p2 are the minimum proportion of each species which was present at the two sampling dates (Krebs, 1998) .

3. Results

Gliding average between two sampling dates was considered for all the data for smoothening of the data and better understanding of the seasonal gradient. A detailed representation of the Chla - biomass dynamics is represented in Chatterjee et al (in press).

3.1 Chl-a:

From February, the Chl-a biomass of phytoplankton gradually started to increase and started to bloom from the middle of April till it reached its peak on 5th May with a concentration of 40.2 mg m^{-2} (Fig. 1a). The bloom subsided at the end of May. At the end of August the Chl-a concentration increased again and concentrations around 30 mg m^{-2} were observed in September and October. However, by the end of October, the concentration declined to a lower level (around 5 mg m^{-2}) which is typically characteristic of winter.

Chl-a dynamic of the MPB was different from that of the phytoplankton. The biomass started to increase from February and reached its peak on 18th April with a concentration of 32.6 mg m^{-2} (Fig. 1c). From the end of April the biomass started to decline till the end of June. The lowest concentration of Chl-a was observed from the end of June to the end of August. The biomass increased a little in September before declining again in October.

3.2 Biovolume and Taxonomic composition:

A total of 74 species of phytoplankton was recorded during the study period, of which 32 belong to diatoms and 35 belong to dinoflagellates. Along with that, parasinophytes, chlorophytes, chrysophytes, cryptophytes, coccolithophores and Euglena were also observed.

The number of cells of the phytoplankton community varied from 80 cells L^{-1} in February to 4*10^{7} cells L^{-1} in June. The individual biovolume varied from 42 µm^3 to 1.5*10^{6} µm^3) throughout the season (Table 1). The biovolume of Coscinodiscus was observed to be 1.3*10^{5} µm^3. The total biovolume ranged from 5.10^{5} µm^3 in February to 13 10^{10} µm^3 in March (Table 2). The largest average cell biovolume (9*10^{3} µm^3) was observed on 11th April (Fig. 1a). . There was a shift in phytoplankton average cell biovolume right before the bloom

started. The phytoplankton average cell biovolume declined to lower values from its highest peak right before the bloom. Although the average cell biovolume remained low after the bloom, during the Chl-a peak in September, the average cell biovolume faced another decline. For the diatoms of the phytoplankton community, the average cell biovolume increased to its maximum on 18th April ($5*10^3 \mu m^3$) and then came down to as low as $2*10^4$ μm^3 (Fig. 1b). For diatoms too, there was steep shift of average cell biovolume from high to low right before the Chl-a bloom. The phytoplankton community in the water column was chiefly composed of diatoms with an annual average of 26% in cells numbers and 56% in biovolume. The dinoflagellates accounted for 11% in cell numbers and 17% in biovolume.

Microphytobenthos	Individual Biovolume (µm^3)
A. Diatoms	
Achnanthes sp. (>20 µm)	**510**
Achnanthes sp. (<20 µm)	**1029**
Amphora spp.	**30069**
Amphora vc	**1980**
Amphora sp. (>20 µm)	**1086**
Bacillaria paradoxa	**856**
Caloneis sp.	**11299**
Cocconeis sp. (>20 µm)	**628**
Cocconeis sp. (<20 µm)	**8327**
Diatoma sp.	**468**
Diploneis sp.	**2088**
Fragillaria sp. (>20 µm)	**1313**
Fragillaria sp. (<20 µm)	**318**
Licmophora sp. (>20 µm)	**18467**
Licmophora sp.	**12908**
Navicula sp. (8-10 µm)	**79**
Navicula sp. (25-30 µm)	**1060**
Nitzschia longissima	**294**
Pleurosigma sp. (>20 µm)	**18555**
Pleurosigma sp. (<20 µm)	**3951**
Roicosphaenia sp.	**840**
Toxarium undulatum	**34015**

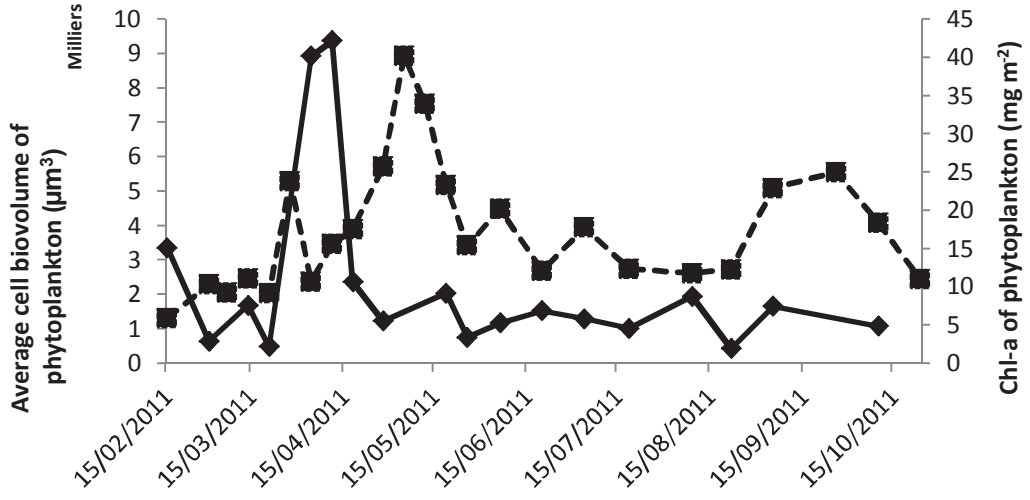
Phytoplankton	Individual biovolume (µm^3)
A. Diatoms	
Bacteriastrum delicatulum	**3,973**
Cerataulina pelagica	**27,814**
Chaetoceros curvisetus	**2,925**
Chaetoceros debilis	**2,513**
Chaetoceros decipiens	**1,971**
Chaetoceros didymus	**1,980**
Chaetoceros gracilis	**816**
Chaetoceros laciniosus	**654**
Chaetoceros pseudobrevis	**2,190**
Chaetoceros socialis	**49**
Chaetoceros sp.	**1,066**
Coscinodiscus wailesii	**13,203,700**
Cyclotella sp.	**422**
Dactyliosolen fragilissimus	**2,037**
Dactyliosolen phuketensis	**13,150**
Ditylum brigthwellii	**7,845**
Eucampia zodiacus	**10,254**
Guinardia delicatula	**10,207**
Guinardia flaccida	**38,477**
Guinardia striata	**15,814**
Haslea wawrickae	**1,125**
Leptocylindrus danicus	**5,332**
Meuniera membranacea	**6,798**
Paralia sulcata	**636**
Proboscia alata	**27,214**
Pseudo-nitzschia seriata	**915**
Pseudo-nitzschia delicatissima	**2,640**
Pseudo-nitzschia pungens	**1,752**
Rhizosolenia hebetata	**23,300**
Rhizosolenia mbricata	**54,733**
Rhizosolenia pungens	**14,099**
Rhizosolenia setigera	**15,100**
Rhizosolenia styliformis	**14,099**
Skeletonema sp.	**331**
Thalassionema nitzschioides	**565**
Thalassiosira spp.	**3,933**
B. Dinoflagellates	
Akashiwo sanguinea	**35,168**
Amphidinium crassum	**1,358**
Amylax triacantha	**23,280**
Cochlodinium sp.	**12,414**
Dinophysis acuminata	**23,550**
Diplopsalis spp.	**5,571**
Gymnodinium chlorophorum	**2,438**
Gymnodinium sp.	**1,219**
Gyrodinium spp.	**4,639**
Heterocapsa minima	**125**
Heterocapsa triqueta	**1,354**
Neoceratium furca	**35,128**
Neoceratium fusus	**23,026**
Neoceratium kofoidii	**10,110**
Neoceratium lineatum	**9,460**
Noctiluca scintillans	**15,586,213**
Phalacroma rotundatum	**4,042**
Polykrikos schwarzii	**39,741**

Prorocentrum micans	**8,836**
Prorocentrum balticum	**905**
Prorocentrum triestinum	**1,658**
Protoperidinium bipes	**3,713**
Protoperidinium conicoïdes	**9,063**
Protoperidinium conicum	**26,236**
Protoperidinium crassipes	**18,745**
Protoperidinium depressum	**19,660**
Protoperidinium diabolus	**62,360**
Protoperidinium divergens	**26,098**
Protoperidinium oblongum	**31,761**
Protoperidinium sp.	**3,713**
Pyrocystis noctiluca	**32,500**
Pyrophacus sp.	**25,011**
Scrippssiella sp.	**3,640**
Torodinium sp.	**4,836**
Warnowia polyphemus	**9936**
C. *Euglena* sp.	**9090**
D. Prasinophytes	**569**
E. *Chlamidomonas* sp.	**1172**
F. Chrysophytes	**687**
G. Cryptophytes	**368**
H. Haptophytes	**153**
I. Flagellates	**42**
J. Coccolithophores	**115**

Table 1. Individual biovolume of the microphytobenthos and phytoplankton community measured during the entire study period of February, 2011 to October, 2011

During the start of the season (February to the first week of May), the phytoplankton community was chiefly dominated by *Chaetoceros* sp. and *Thalassiosira* sp. for diatoms and *Gymnosinium* sp., *Prorocentrum balticum* and *Scrippssiella* sp for dinoflagellates, in terms of both cell numbers and biovolume. During the bloom, diatom species like *Dactyliosolen fragilissimus* and *Cerataulina pelagica* started dominating with *Chateoceros sp.* to be the most dominant one, while for dinoflagellates, *Heterocapsa minima* began to dominate in cell number and biovolume. After the bloom, diatom species like *Guinardia delicatula* and *Thalassiosira* sp. started to increase in concentration and biovolume and reached their highest in September-October. For dinoflagellates *Gymonodinium* sp. dominate again after bloom until it was taken over by *Heterocapsa minima* in September-October. Phytoplankton species like *Leptocylindrus danicus* and *Pseudonitzschia* sp. were observed intermittently from spring to the end of the season.

On the other hand, for the MPB community, a total of 22 benthic species was recorded during the study period. Along with the benthic ones, occasional presence of the pelagic species *Chatoceros debilis* and *Chaetoceros didymus* was also observed. However, the presence of the pelagic species amongst the benthic ones was quite negligible in proportion. The number of cells varied from 5.10^7 cells m^{-2} in August to 2.10^9 cells m^{-2} in April and the total biovolume varied from 10^8 μm^3 in August to $19*10^9$ µm3 in April. The individual biovolume varied from 79 μm^3 to $3*10^4 \mu m^3$ throughout the season (Table 1). Average cell biovolume of MPB were generally 1 to 2 orders of magnitude smaller than for phytoplankton. It varied from 306 μm^3 to 1450 μm^3 (Fig. 1c). Larger peaks were observed very early in the season, by the last week of March, but declined by the second week of April. The average cell biovolume increased again on 20th June which again declined by the second week of July. The largest peak of average cell biovolume for MPB was observed on 16th August (10^3 μm^3). The average cell biovolume remained on the larger scale till 26th of September after which the average cell biovolume declined again. Just before the bloom the average cell biovolume of MPB decreased from high to low as well.



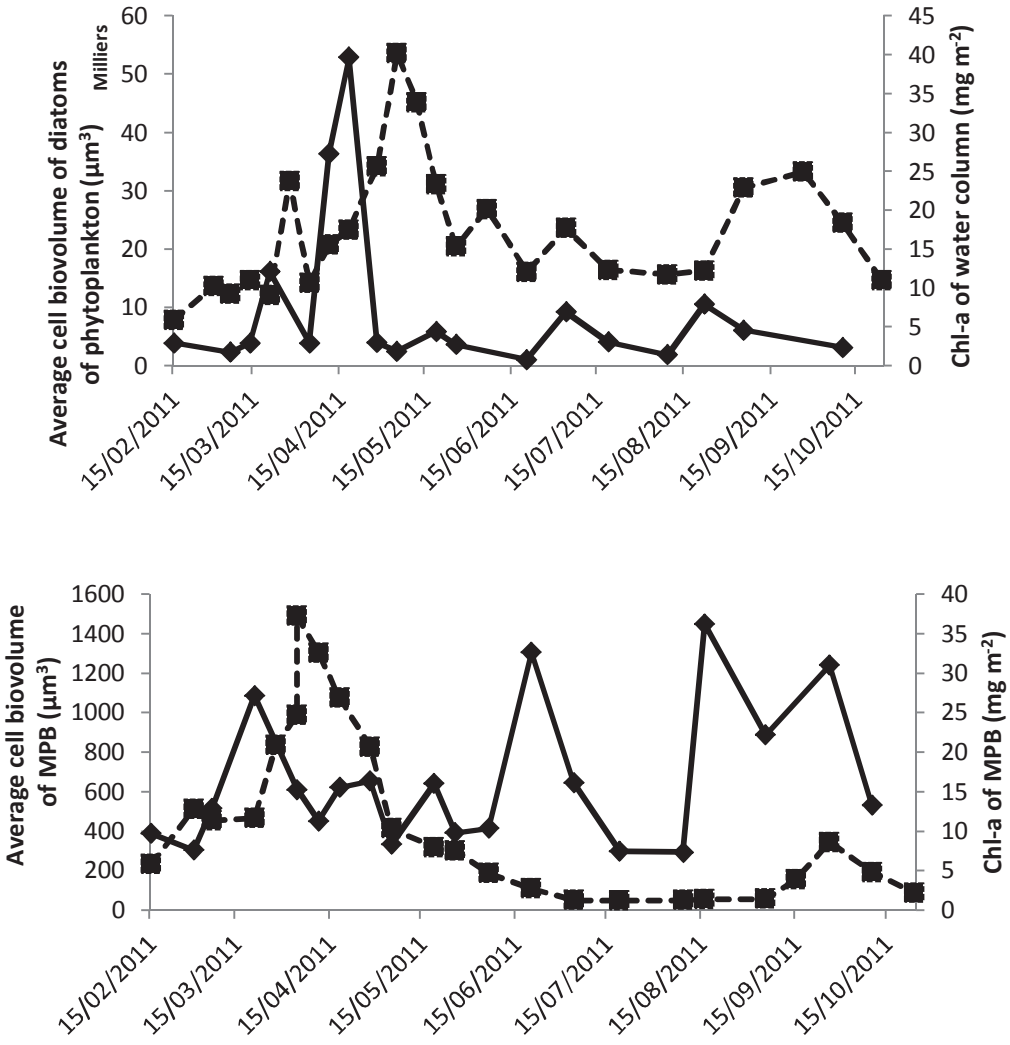


Fig. 1 Comparison for the entire study period of Chl-a biomass (dotted lines) and average cell biovolume (solid lines) (a) of phytoplankton (b) of diatoms of the phytoplankton community (c) of the MPB community

Right from the start of the season, species like *Fragillaria* sp. and *Navicula* sp. seemed to dominate the benthic community both in terms of cell number and biovolume. In the early part of the study period (February to April), species like *Cocconeis* sp., *Pleurosigma* sp., *Roicosphaenia* sp., *Toxarium* sp. were also observed. During the bloom, *Navicula* sp. was observed to be the most dominant one followed by *Fragillaria* sp. and *Achnanthes* sp. Smaller species of *Amphora* sp., *Licmophora* sp., *Achnanthes* sp., also comprised the benthic community during bloom. After the bloom, only *Navicula* sp., *Fragillaria* sp., and *Cocconeis* sp. appeared frequently, while species like *Nitzschia* sp., *Pleurosigma* sp., *Amphora* sp. and *Achnanthes* sp. appeared occasionally until their frequency increased in September-October.

Other species like *Caloneis* sp. appeared in the benthic community intermittently all throughout the time scale.

Column1	Phytoplankton	Column2	MPB	Column3
	Minimum	Maximum	Minimum	Maximum
Individual biovolume (μm^3)	42	$1.5*10^5$	79	$3*10^4$
Total biovulme(µm3)	$5*10^5$	$13*10^{10}$	108	$19*10^9$
Average cell biovolume (µm3)	423.2	9372	306	1430
Taxon richness	8	28	5	12
Evenness	0.1	0.4	0.3	0.7
Shannon-Weaver diversity	0	2.5	0.4	1.9
Community similarity (%)	5.7	96.7	10.2	81.3

Table 2. Range of the diversity indices and the individual, total and average cell biovolume of the microphytobenthos and the phytoplankton community.

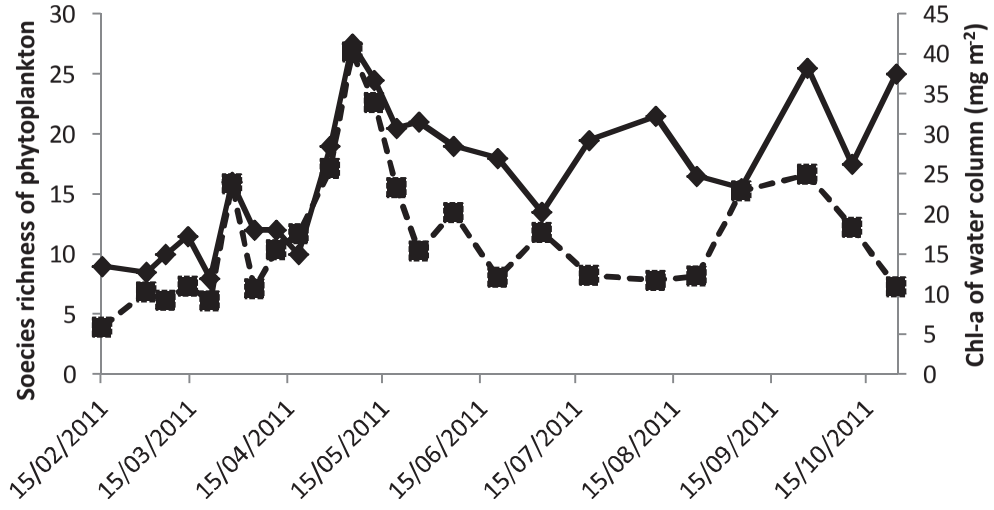
3.3 Diversity indices:

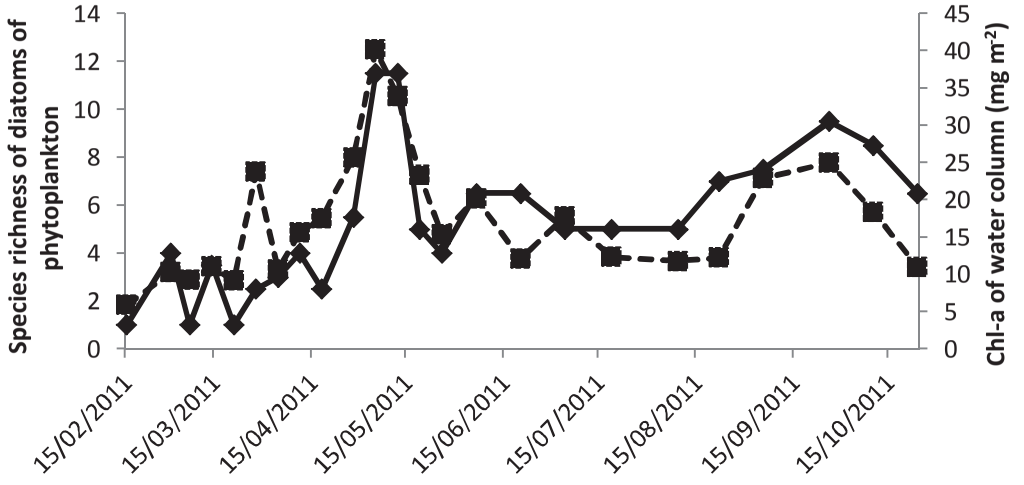
3.3.1 Taxon richness:

Taxon (species) richness of phytoplankton increased gradually till the bloom (May) where it reached its highest with a value of 28 (Fig. 2a). After that the taxon richness gradually declined to 14 at the first week of July and then recovered fluctuating between 22 and 25 with three separate peaks at the end of August, September and October.

The number of diatom species in the water column was maximum at the beginning of May , with a value of 12 and then subsided along with the bloom to 4, at the end of the month (Fig. 2b). The taxon richness increased again at the end of the summer, up to 10 in the end of September, and then declined in the end of October.

The number of species in the MPB was much lower in general than in the pelagic community. A maximum of 12 species was observed at the end of March, during the bloom (Fig. 2c). After the bloom taxa richness declined, fluctuating between 6 and 9 during the rest of the year, with three main peaks in June, August and October.


Soecies richness of phytoplankton
Chl-a of water column (mg m-2)
0
5
10
15
20
25
30
35
40
45
15/02/2011
15/03/2011
15/04/2011
15/05/2011
15/06/2011
15/07/2011
15/08/2011
15/09/2011
15/10/2011


Species richness of diatoms of phytoplankton
Chl-a of water column (mg m-2)
0
2
4
6
8
10
12
14
0
5
10
15
20
25
30
35
40
45
15/02/2011
15/03/2011
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15/09/2011
15/10/2011

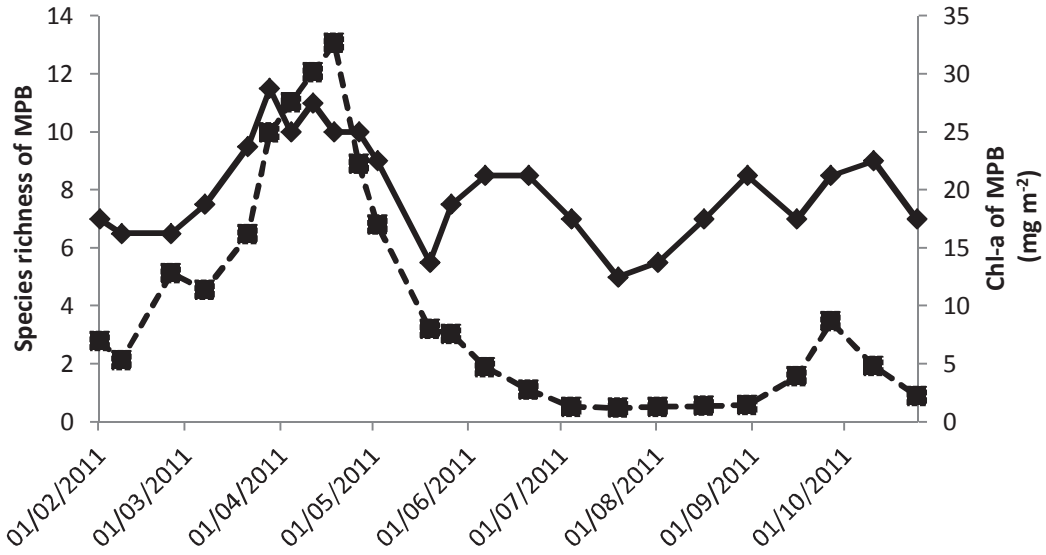


Fig. 2 Comparison for the entire study period of (a) taxon richness and Chl-a biomass of phytoplankton (b) taxon richness and Chl-a biomass of pelagic diatoms and (c) taxon richness and Chl-a biomass of MPB (dotted lines represent the Chl-a biomass, solid lines are taxon richness)

3.3.2 Shannon-Weaver diversity

The Shannon-Weaver diversity of the phytoplankton community varied from 0 to 2.5 (Table 2). The diversity started to increase from January with frequent fluctuations till the spring. During spring the diversity increased steeply and showed its highest values with the maximum on 23rd May. After the spring the diversity maintained an average of 1.5 for the rest of the period with occasional fluctuating declines.

The Shannon weaver diversity of the MPB community fluctuated heavily over the time scale. During spring the fluctuations were more severe with diversity varying from 0.7 to 1.7. The lowest in terms of Shannon-weaver diversity was observed on 9th August with a value of 0.4, while the highest was observed on 30th August with a value of 1.9.

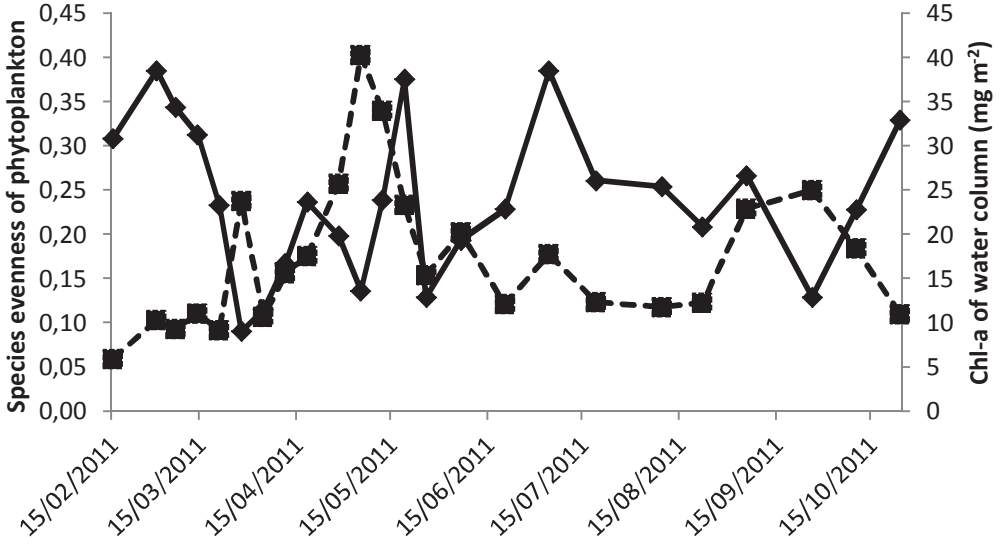
3.3.3 Species evenness:

The species evenness refers to how close in numbers each species in an environment are. For phytoplankton, the range of evenness varied from 0.1 to 0.4 (Table 2). It started format the beginning of March with a value of 0.39 and decline to 0.09 at the end of the month (Fig. 3a). The evenness recovered with a small peak and then had two subsequent large peaks on 19th

May (0.38) and 4th July (0.38). After that, it declined and remained at an average of 0.25 from the middle of July till the first week of September. The species evenness declined henceforth to 0.13 on 26th September before increasing again in October. The evenness of phytoplankton reached lower values during the Chl-*a* bloom and also during the end of September when the biomass values of phytoplankton increased.

The species evenness of diatoms of the phytoplankton community started with high degrees of fluctuations before declining from 21st March with a value of 1.0 to 0.30 on 11th April (Fig. 3b). The evenness increased with a peak of 0.72 on 18th April and continued with fluctuations till the middle of July when it reached another peak of 0.65 on 19th July. From the last week of August the evenness of diatoms of the water column reached its lowest point of 0.16 on 10th October from which it recovered to 0.33 in the last week of October. The evenness of diatoms was also observed to be low during the Chl-a bloom and also during periods of higher biomass and vice versa.

The species evenness of MPB reached its lowest point during the time of the bloom. It decreased from 0.64 the 24th of February to 0.25 on 28th March (Fig. 3c). From there on, it increased to a large peak of 0.69 on 19th May and had three subsequent peaks on 19th July (0.64), the largest on 16th August (0.72) and the final on 24th October (0.64).



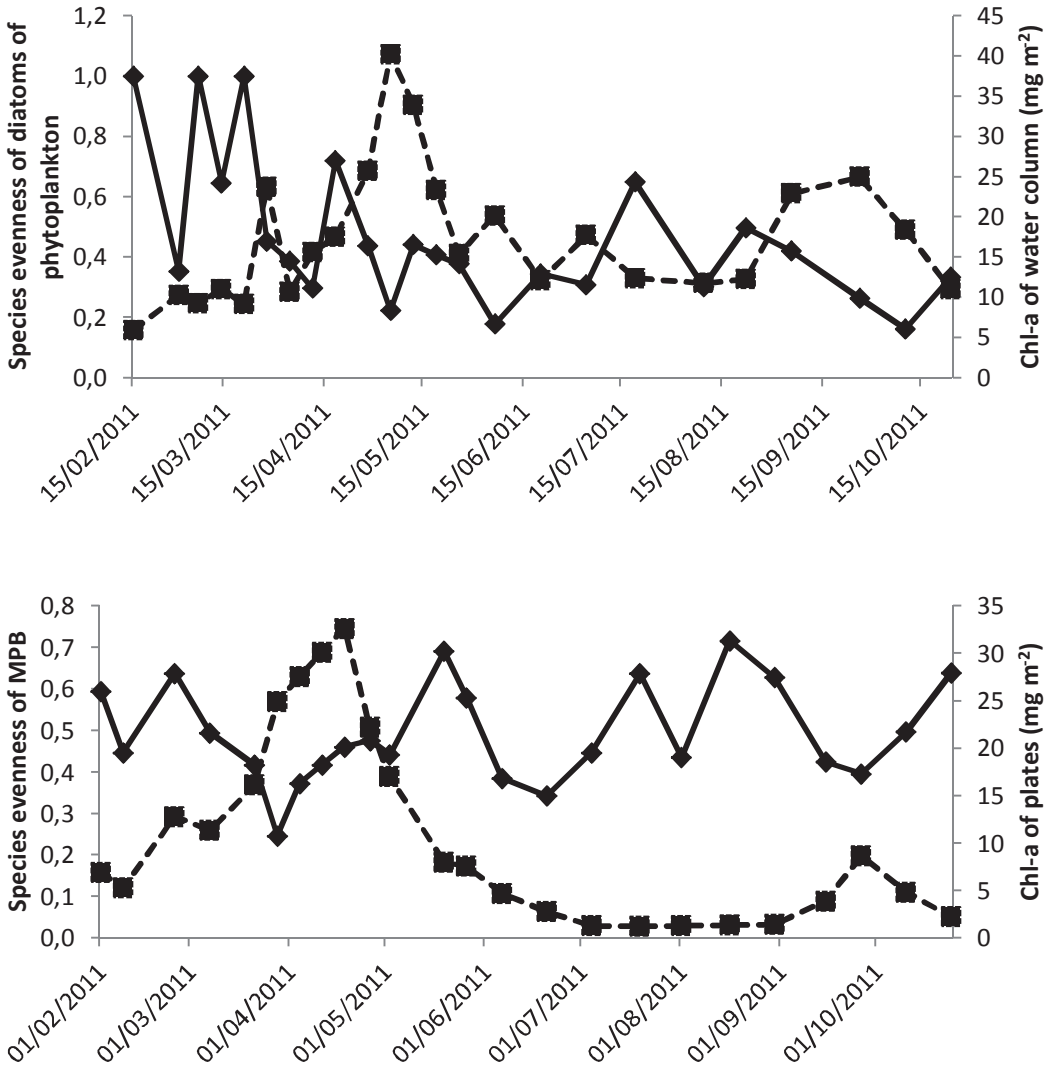


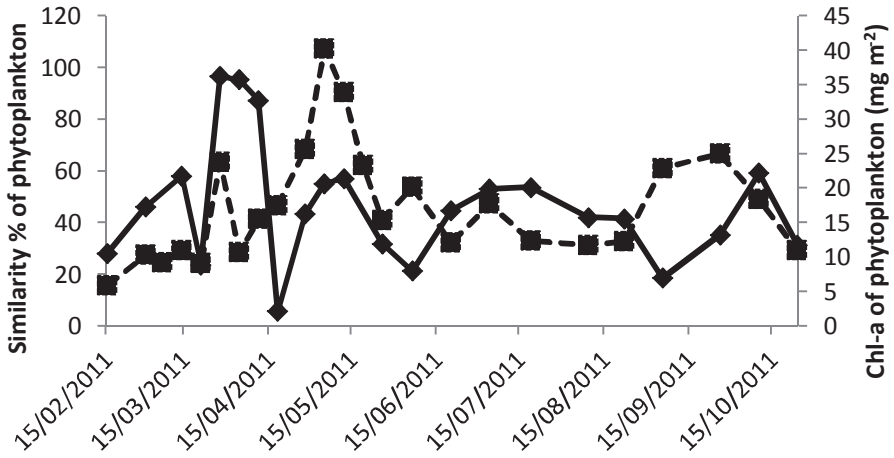
Fig. 3 Comparison of (a) Chl-a biomass and species evenness of phytoplankton for the entire study period (b) Chl-a biomass and species evenness of the diatoms of the phytoplankton community for the entire study period and (c) Chl-a biomass and species evenness of the MPB community for the entire study period. (Dotted lines represent the Chl-a biomass, solid lines are evenness)

3.3.4 Community similarity:

Although, community similarity indices are mostly used to compare communities from different places or to study the resilience of a community after a perturbation compared to a reference community, such indices can also be used as simple quantitative measures of seasonal changes in community composition between sampling dates, helping to identify periods of strong community composition shifts. The phytoplankton community was very similar between sampling dates during March with a similarity of 97% and the similarity

remained high till the second week of April (11th April). However, right after that, there was a massive drop in similarity on 18th April with just 6 % similarity, the lowest point in the phytoplankton dynamics (Fig. 4a). After that the similarity increased to 55% during the first week of May, but dropped again by the last week of May. The similarity recovered henceforth and remained at an average of 45 % from the middle of June till the end of August. A drastic fall was again observed in the first week of September with a value of 19% and then a steep peak on the first week of October with a value of 59%. The community similarity again came down to 10% by the second week of October. The community similarity, just like the average cell biovolume of phytoplankton community, declined right before the bloom and during the bloom followed a similar pattern as the Chl-a biomass of the phytoplankton community. The community similarity again dropped down during the Chl-a peak of September and slowly started increasing as the biomass peak started subsiding.

The community similarity of MPB also started with a huge decline from 81% on 24th February to 10.2% on 21st March (Fig. 4b). The similarity recovered by the end of March to 54% and kept on fluctuating till another peak was observed on 19th May with a value of 75.2%. The peak subsided to 22% by the end of June. However, two subsequent peaks were observed on 19th July and 16th August with values of 71% and 54% respectively, after which the community similarity declined again to 13%. By the end of the season, the similarity percentage of MPB managed to recover to 41%. For MPB as well, there was a massive shift of community similarity right before the bloom, where the community similarity declined from its highest point to its lowest point.



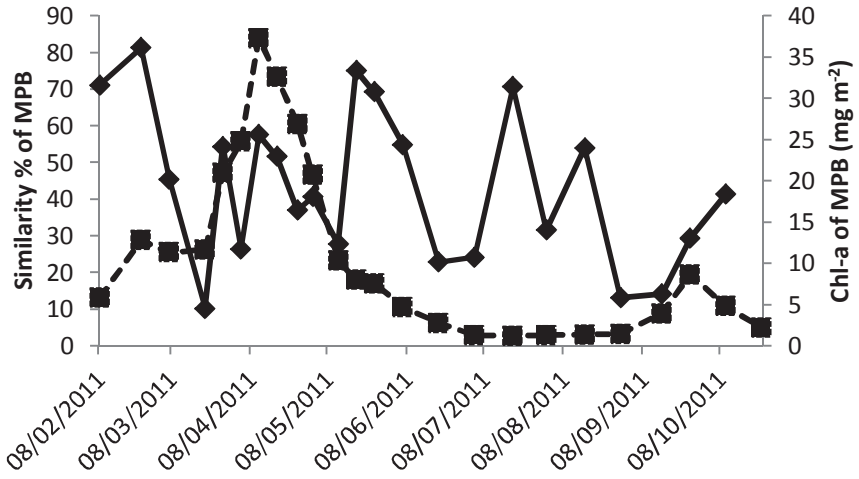


Fig. 4 Comparison between (a) Chl-a of water column and the community similarity of phytoplankton and (b) Chl-a biomass of MPB and the community similarity of MPB community. (Dotted line represents the Chl-a biomass)

4. Discussion

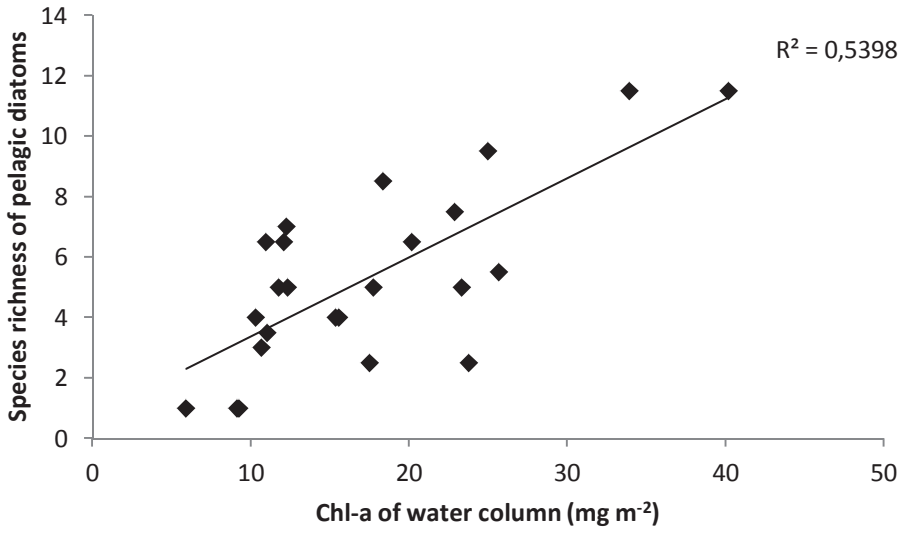
The phytoplankton and microphytobenthos communities that we studied are living in an environment where temperature and salinity are the same, but light, nutrient availability and hydrodynamic conditions are completely different (Chatterjee et al, in press). We were thus expecting a different trend in the diversity patterns of these two communities, with potential important implications for the ecosystem structure and functions.

4.1 Species diversity:

We clearly observed that the microalgal taxon richness, and also the total number of species in the entire study period, were much higher in the pelagic community (74) than in the benthic community (22). What is interesting is that the number of diatom species of both the phytoplankton community (32) and MPB community (22) are comparatively closer to each other ,while species themselves are all different in each environment (except: *Chaetoceros debilis* and *Chaetoceros didymus*). The number of diatom species for the MPB community for the entire year was moderately high compared to other ecosystems where the number of diatoms have been observed to be approximately 16-20 in lakes and intertidal zones. The

closeness on the abundance of MPB diatoms with that of the water column might possibly be due to the independence of benthic microalgae on nutrients from the water column (Kann, 1993), as they can effectively access nutrients from the sediment-water interface (Wiltshire, 1993; Hillebrand & Kahlert; 2002). On top of that, the diel rhythms of vertical migration of the diatoms can also play a part.

Available studies about the relationship between the variability of community biomass with taxon richness lead to divergent predictions (Cottingham et al. 2001, Morin and McGrady-Steed 2004, Shurin et al. 2007). In our study, a strong correlation was observed between the taxon richness of phytoplankton and its biomass during the bloom period only (Fig. 5a), whereas it was observed all along the seasonal scale for the diatom community of the phytoplankton (Fig. 5b). Similar pattern of correlation till the bloom was also observed for MPB biomass and taxon richness (Fig. 5c) In all the cases increasing taxon richness contributed to high temporal variability resulting in the bloom.



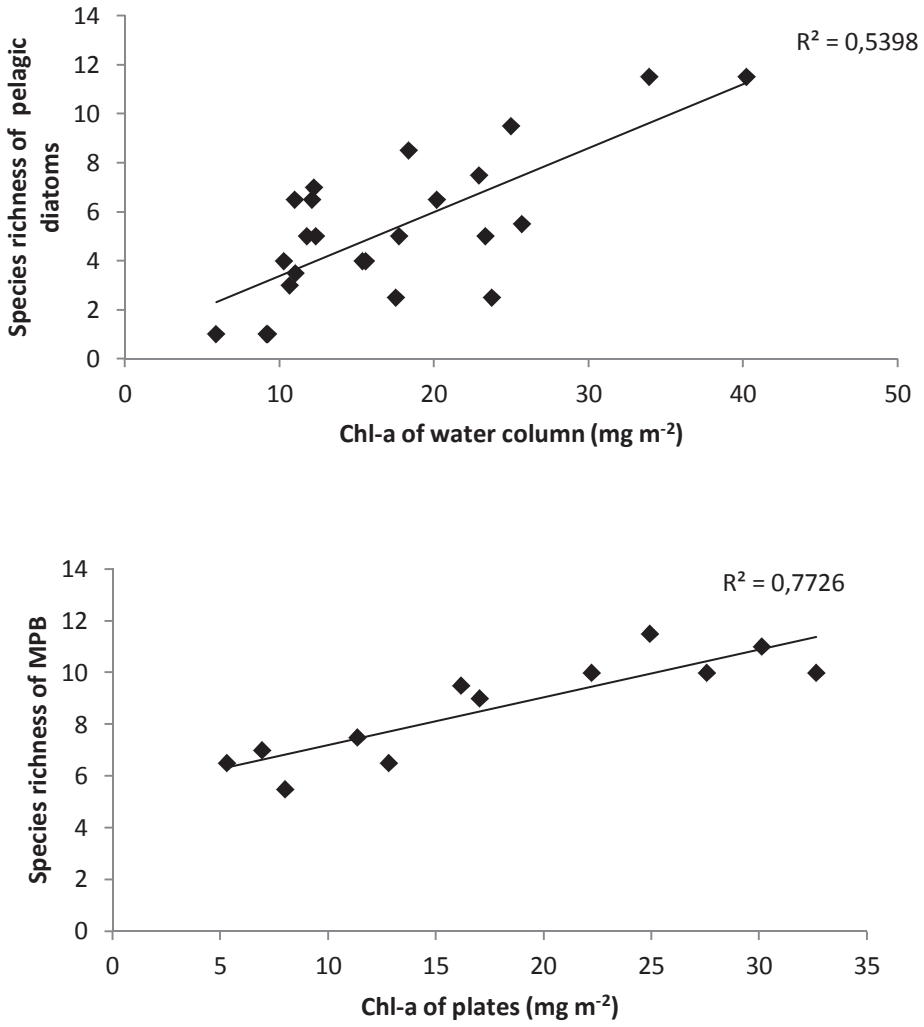


Fig 5 Regression analysis between (a) taxon richness and Chl-a biomass of phytoplankton till 19th May, 2011 (b) between taxon richness and Chl-a biomass of diatoms of the phytoplankton community for the entire study period and (c) taxon richness and Chl-a biomass of MPB till 19th May, 2011. (Dotted lines represent the Chl-a biomass)

However to better comprehend this pattern, evenness must also be looked at, as evenness generally complements the information provided by the richness data (Stirling and Wilsey 2001, Wilsey et al. 2005). In our study, the evenness of the phytoplankton, and the MPB were observed to decline right during the bloom in May (Fig. 3). The evenness of both the phytoplankton and MPB community increased immediately after the bloom and for phytoplankton the evenness was again observed to be dipping down during the biomass peak of September-October. This clearly suggests the dominance of a single species during the abundance Chl-a biomass for both the phytoplankton and the MPB community.

A strong correlation was observed between taxon richness of phytoplankton and the biomass of phytoplankton during the bloom period only (Fig. 5a), whereas it was observed all along the seasonal scale for the diatom community of the phytoplankton (Fig. 5b). Similar pattern of correlation till the bloom was also observed for MPB biomass and taxon richness (Fig. 5c). This is common for other ecosystems, especially during the period of bloom, as the abundance of nutrients and light supports growth of different species for both the phytoplankton and the MPB community.

Richness and evenness have been previously documented to be negatively correlated (Buzas and Hayek 1996, Stirling and Wilsey 2001). However, in our study no relation was observed between the richness and evenness of the phytoplankton or the MPB communities. None the less, the temporal variability of a community can reach a stable state with high richness, only when the dominance is low (Doak et al. 1998). High dominance drives the community biomass to such an extent, that the variability across the community cannot be reduced by the averaging effect (Cottingham et al. 2001). The pelagictaxon richness was observed to be increasing during September-October. On the other hand, for MPB, after the bloom, the biomass declined to minima while the evenness and richness fluctuated for the rest of the period. Therefore, especially during the bloom, the communities of phytoplankton and MPB can be regarded as unstable as the stabilizing effect of richness is reduced by dominance (Hillebrand et al., 2008). For the rest of the year, although the MPB community seemed stabler than that of the pelagic community, the minimal biomass of the benthic microalgae questions the idea of stability of the community.

4.2 Strategy of composition:

Gaillerd et al., (2003) proposed that for phytoplankton diversity, the geographical topology is more related to the hydrodynamic properties of each area than local influences like differences in nutrient input. On a previous study on the Atlantic coast, it has been observed that diatoms dominated the phytoplankton community of the English Channel while dinoflagellates were more abundant in the Bay of Biscay (Gaillerd et al., 2003). Historically, the dominance of diatoms/dinoflagellates had mainly been attributed to the physical properties of water column (Estrada et al., 1999; Kaneta et al., 1985; David et al., 2012) as per the “Margalef Mandala” model. The model relates diatoms to mixing and high nutrient

concentrations, while dinoflagellates are related to oligotrophic and stratified conditions (Margalef 1978, Thomas and Gibson, 1990). However in our study, although the diatoms dominated in the number of cells, we also observed a diverse distribution of dinoflagellates in the phytoplankton community. In terms of taxon richness, the dinoflagellates often outnumbered the diatom population, as it has been observed that diatoms albeit dominating may have low species rich pool and generally exhibit mono-specific blooms (Samyda and Reynolds, 2003). On the other hand, the MPB community remained devoid of any dinoflagellates. Therefore, to better understand the compositional dynamics, our study was also corroborated with the C-S-R model as proposed by Reynolds et al. (2002) which is based on the species tolerances of mixing and nutrient availability.

The C strategists thrive in stratified and high nutrient concentrations and are small and fast growing; the S strategists survive in oligotrophic waters vertically migrating for nutrients and are slow growing and large and the R strategists generally survive under high mixing and high nutrient levels because of their large surface/volume ratio (David et al., 2012). Although, the dinoflagellates can be categorized into the C, S and R stategists, the diatoms are generally considered to be R strategists except for *Coscinodiscus* spp. (Smayda and Reynolds, 2001; Smayda and Reynolds, 2003; Alves-de-Souza et al., 2008; David et al., 2012). In our study, the diatom/dinoflagellate ratio of the phytoplankton community (in terms of number of cells and biovolume) was observed to be high in spring (Fig.6). After spring the ratio declined to below 1.0 and then increased again in September/October. The Bay of Brest is characterised by strong tidal currents and high vertical mixing (Ni Longphuirt et al., 2007) which is generally preferred by the R strategist diatoms. For example, *Pseudonitzschia* sp., which was observed in our study intermittently along the entire seasonal scale, is one of the diatoms species and a R strategist which prefers high mixing (Alves-de-Souza et al., 2008). This is a common species for high mixing coastal regions of northern Brittany (David et al., 2012). Anyway, during the spring with high nutrient concentrations (Chatterjee et al., in press) and strong vertical mixing, the diatoms thickly populated the phytoplankton community as is the requirement for the R strategists. Diatom dominated bloom has also been previously reported in the Bay (Ragueneau et al., 2005) as well. However, after the spring as the water column became more stratified and the nutrient concentrations decreased, the dinoflagellates took over the diatoms, both in cell number and biovolume. The C-S-R model of Reynolds et al., (2002), further explains the dynamics when the nutrient concentrations increased again in September/October (Chatterjee et al., in press)

and along with that an increment of diatom dominance was observed again during this time. Also, no specific diatom species was observed in the Bay of Brest which could otherwise be not found in the other coasts of Brittany (David et al., 2012).

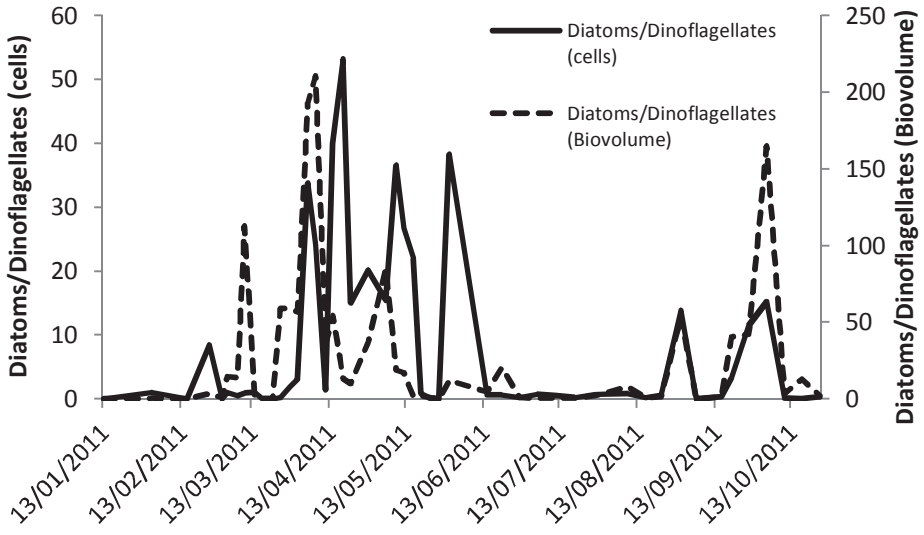


Fig.6 Diatom/dinoflagellate ratio obtained from cell numbers and biovolume of the phytoplankton community for the entire study period.

On the other hand, the MPB community was highly dominated by diatoms, which is typical for benthic microalgae. The dynamics of cell number and biovolume showed similar trends like the phytoplankton community, where the highest population was observed in spring, after which the diatom concentration declined and a resurgence was observed in September/October. However, unlike the phytoplankton community, the low diatom population after spring was not overtaken by dinoflagellates for the MPB. Although, no proper explanation has yet been noted for such a pattern, but, this observation can possibly be a reminiscent of the "Margalef Mandala" model where the strong vertical mixing might have inhibited the growth of dinoflagellates and have allowed the diatoms to dominate and occupy the community.

4.3 Community dynamics:

Just before the bloom, the average cell biovolume of the MPB community was observed to decline (Fig. 3 c) and small sized diatom species such as *Navicula* and *Fragillaria* were found to be abundant. During the bloom, not only did the number of small sized diatom species increase, but also, large diatom species of *Amphora* or *Achnanthes* also started to populate, thereby increasing the resultant average cell biovolume. However, *Navicula* sp. was noted to be the most abundant in terms of cells and total biovolume in the entire time scale. This is a feature which is commonly observed in MPB communities (Gaetje, 1992; Mitbavkar & Anil, 2002; Hagerthey et al., 2002). Amongst other diatom species, *Navicula* sp. is greatly appreciated by several meiobenthic organisms (Admiraal et al., 1983). Under high grazing pressure of a particular species, a grazing resistant species can outcompete and take its dominance in the community contributing significantly to the biomass content of the community. For example, C. *closterium* has been observed to outnumber *Navicula* sp. during high grazing pressure as the larger size and the needle shaped morphology of C. *closterium* apparently favours it to be grazing resistant (Gaetje, 1992). However, in our study no such grazing resistant diatom species was observed throughout the time period. Also, after the spring bloom, the Chl-a biomass and the cell number of *Navicula* sp. along with the other observed species rapidly declined, which gives a strong indication towards grazing without compensation for biomass with grazing resistant species. It has been observed in Bay of Morlaix, a subtidal zone near to the study site of Bay of Brest that meiobenthos population starts increasing from mid-May and sustains till the end of September (Chardy and Dauvin, 1992). This matches with our data of Chl-a growth (Chatterjee et al., in press), where the Chl-*a* of MPB declines at around middle of May and stays at a minimal concentration until September. The resurgence of cell numbers of *Navicula* sp. along with the other observed species happens only after September. So, it can be said that, the spring bloom of MPB possibly declined due to heavy grazing pressure and the lack of any grazing resistant diatom species in the community might have further hindered the growth of Chl-*a* biomass post bloom.

For the phytoplankton community, the increment in average cell biovolume during the bloom was greatly influenced by the dominance of a few species (in cell number and in biovolume) such as *Chaetoceros* sp. and *Gymnodium* sp. which is apparent from the low evenness during the bloom (Fig. 3a) and the decline of community similarity before the bloom (Fig. 4a). The

phytoplankton bloom was followed by a “clear water phase”. suggesting grazing as per the PEG model (Sommer et al., 2012) or mass sedimentation. *Chaetoceros* sp. was not only present and dominating during the bloom, but has persisted to do so, , although in smaller numbers during the entire time scale suggesting it has particular ability to face the changes with time of environmental conditions.

On the other hand, *Gymnodium* sp. was outnumbered by *Heterocapsa minima* before the bloom and during the peaks of Chl-*a* biomass in September and October, 2011. This suggests that the dinoflagellates of the phytoplankton community have faced efficient and selective grazing, where *Gymnodium* sp. being grazed upon had been taken over by *Heterocapsa minima*.

5. Conclusion

In this study, although the community composition and species identity and density vastly varied between the phytoplankton and the MPB community, the diversity indices showed more or less similar temporal trends for both the communities, especially just before and during the spring bloom. This suggests that the dynamics and mechanism of community build up and succession might be similar for both the communities. However, the large discrepancy of Chl-*a* biomass of MPB and their diversity indices after the bloom indicates strongly towards heavy grazing from which the MPB community could not recover resulting in the low observed biomass and algal cell numbers. For future studies, it would be interesting to study biodiversity in relation to productivity across different sampling sites, potentially varying in diversity. As long as reasons and mechanisms of seasonal shifts of algal diversity - and how these mechanisms interact with factors affecting productivity - are not known in more detail, it is very difficult to argue about causes and consequences of potential diversity – productivity relationship originating from seasonal trends. On top of that, the temporal variations of diversity and productivity have not yet been established to be directly inter-dependent on each other as factors like physico-chemical parameters of the bay or any other biological factor might also influence the variations of productivity.

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Chapter 5

General Conclusion:

The interface between continents, oceans and atmosphere are frequently subjected to high anthropogenic pressure. In this context, the question arises how this pressure affects the ecological functioning and ecosystem services of coastal systems. Understanding the response and resilience/resistance of coastal ecosystems is generally challenging which must be also followed by conservation efforts and ensuring sustainable development of the territory. The overall structure and functioning of coastal ecosystems are strongly influenced by the dynamics of the lower food web, and in particular the main primary producers, micro - algae which grow in the water column and sediments or hard substrates of the shallow coastal regions. This first link, producing organic biomass from inorganic sources, is essential to the food chain but too often only the pelagic component of the water column is taken into account. To understand and model the response of coastal ecosystems with respect to global change and future increasing anthropogenic pressure, there is an urgent need to incorporate also the dynamics of the micro-algae in the benthic compartments of coastal ecosystems into such models. . In the presented project, we have studied seasonal dynamics, production and biodiversity of these microalgae and we have also compared the growth, physico-chemical parameters and biodiversity of MPB with that of the phytoplankton of the overlying water column. This thesis has been intended upon understanding the role and importance of benthic algae, mainly diatoms for coastal ecosystems along with providing the basis for the development of biological indicators of water quality in the coastal zone. The study has been conducted in the Bay of Brest, one of the most studied model coastal ecosystems in France.

In this thesis, it has been shown that phytoplankton and MPB do not follow the same dynamics at all. MPB rises first in the season and contributes around 60% of the total micro-algal biomass until April. The system then moves from a system dominated by benthic biomass in early spring to a system where the pelagic biomass takes over with probable large consequences for coastal food web dynamics. In the overall distribution of the entire season, MPB ultimately contributed just 33% of the total biomass due to the decline of MPB biomass after the spring bloom. However, the interesting point to be noted was that, the MPB and the phytoplankton communitieshad same range of concentration in the seasonal scale, although the dynamics for the two communities was observed to be different from each other.

The irradiance at the bottom was observed to be quite infrequent in fluctuations and low in concentration compared to that of surface where the surface irradiance followed a typical seasonal trend with higher range of concentration. Having said that light seems to have triggered the initial MPB bloom as the maximum bottom irradiance at the bottom was observed during the initiation of spring bloom. A similar trend was also observed for the phytoplankton community where the maximum surface irradiance matched with the initiation of the phytoplankton spring bloom. On the other hand, it was observed that the k' (light attenuation contributed by phytoplankton biomass) during the increment of the phytoplankton bloom was directy correlated with the decline of the MPB bloom. Therefore, it can be said that the phytoplankton biomass might have cast its shadow at the bottom of the study site and thus hindering the growth of MPB after the spring bloom. This makes light an important parameter which might have been responsible for both the initiation and the decline of the MPB biomass. On top of that, the photoacclimation parameter (E_k) was observed to be fluctuating in the seasonal scale. The range of fluctuation was observed to be similar to that of the phytoplankton of the Bay as noted from a previous study. Therefore, the degree of photoacclimation of MPB was almost impossible to render for our study. The E/E_k ratio was observed to be greater than 1.0 on a few occasions which highlights that the MPB community might have suffered from occasional light limitation. Howver, as the PAM readings were taken directly from the plates, the heterogeneity of the plates were not taken into account and thus the E_k values of the MPB community should only be considered as a suggestion.

The nutrient concentration along the vertical depth of the water column was observed to be equivalent in fluctuations and similar in concentration for the entire time period. So, the surface concentration of nutrients was considered for both the phytoplankton and the MPB communities. The nutrient dynamics of DIN, DIP and DSi showed a typical trend where high concentrations were observed in winter and then the concentrations decreased during the period of spring bloom. Because of this, nutrients were not able to explain the comparative delay of MPB bloom as all the nutrients were equally high in concentration in the beginning of the season. However, to better understand the role of nutrients in the decline of the MPB biomass Redfield and Brezinski ratio was conducted for potential nutrient limitation. DSi was observed to be potentially limiting during the first week of May and DIP and DIN from May till the end of season. The concentration of the nutrients when compared with the biomasses of MPB and phytoplankton on the seasonal scale, and along with the derivations from the redfield ratio, it can be said that the decline of MPB biomass might have been triggered by

the potential limitation of DIN and DIP while, potential limitation of DSI might be responsible for the phytoplankton biomass decline during spring bloom.

The average annual primary production was observed to be 8.03 mg C m^{-2} $year^{-1}$ which is relatively on the higher scale when compared to other subtidal ecosystems. The primary production under laboratory controlled and the in situ simulated light condition showed similar trends throughout the season. However, in the beginning during spring bloom, the laboratory controlled showed higher range of primary production than the in situ simulated. This indicates towards liht limitation in the beginning of the season for the MPB community. The specific production also showed similar trends which indicate towards early light limitation on the MPB community.On the other hand, interestingly, specific production increased considerably during summer in the months June, July and August than what it was during the spring bloom. Biomass specific production of MPB showed its largest values in the months of potential DIN and DIP limitation. This strongly suggests towards grazing and not resource limitation, as the most probable reason for the decline of benthic algal biomass after the spring bloom and its maintenance of minimal biomass henceforth.

In terms of taxonomic composition, the MPB community was solely comprised by diatoms and the genus Navicula dominated it, while the phytoplankton community consisted of diatoms, dinoflagellates, euglena and other functional groups, where *Chaetoceros* sp. dominated amongst diatoms and *Gymnodium* sp. amongst dinoflagellates. The total number of species for phytoplankton contributed to 74 amongst which 32 were diatom species. The total number of species for MPB contributed to 22 which were in parity with other subtidal ecosystems. The phytoplankton cells were observed to be larger in size and range compared to the MPB cells as per the average cell biovolume. Although, the range of evenness for the phytoplankton community and the MPB community were different, they both showed a sharp decline during the spring bloom, which clearly points out towards the dominance of one species in the respective communities during the spring bloom. The Shannon-Weiner diversity index showed higher range of diversity for phytoplankton compared to that of MPB. However, the diversity indices showed more or less similar trends for both the phytoplankton and the MPB community, especially just before and during the spring bloom. This indicates that the underlying dynamics of community build up and succession are more or less similar between both micro-algal communities. As per the size distribution of the MPB community, it was observed that it was the medium and the very large cxells which contributed mostly to the MPB community. Throughout the time period, large cells like *Licmophora* sp., *Amphora*

sp. and *Cocconeis* sp. Were always present in the community, whereas *Navicula* sp. And *Fragilaria* sp. Represent the samller cells which were observed all year round. Other than that, species like *Caloneis* sp., *Pleurosigma* sp. and *Toxarium* sp. were also observed to be abundant in the MPB community. The phytoplankton community indicated selective grazing after the bloom which might have helped them in the sustenance of their biomass, though the MPB community showed no such pattern due to the lack of any grazing resistant diatom species in the MPB community. *Navicula* sp. being a preferred food item for meiobenthos and the absence of any specific grazing resistant diatom species in the MPB community might explain heavy grazing losses and the inability of the community to sustain its biomass after the bloom.

In summary, for a concise understanding of the research, the thesis can be broken down into the following conclusive points:

1) *Dynamics of phytoplankton and MPB are totally different*
2) *Solar irradiance plays an important role in the delay of phytoplankton bloom and the decline of MPB and phytoplankton biomass*
3) *Potential limitation of nutrients might contribute to the decline of the MPB and phytoplankton community*
4) *Primary and specific production indicated light limitation during the beginning of the season*
5) *MPB community contained fewer number of species.*
6) *Smaller cells were dominant in number through out the seasonal cycle*

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For a deeper understanding of MPB dynamics in subtidal zones of coastal systems, further investigative accounts in different departments are urgently required. To name a few, simultaneous comparison of photosynthetic parameters of the phytoplankton and MPB community of the study site would give more clarity in estimating the role of light not only on the physiology of the MPB community, but also, would allow a fair comparison between the two communities. In our study, the heterogeneity of the plates was not considered for PAM measurements which might have led to highly fluctuating parameters throughout the season. So, it would be very necessary to develop a different method to understand the photosynthetic parameters, which could either be done by using imaging PAM or by the study of individual or specific species of the community. Unfortunately, in our study we

could not come around to measure the diversity-productivity relationship of the MPB community. Bit, it would be very interesting and enlightening to know and study this relationship. Therefore, instead of a temporal scale, the study of diversity-productivity relationship across different sampling sites in the Bay would lead us to a better understanding. This study strongly indicates that grazing by mesozoobenthos may be crucial for the observed MBP community patterns.. Hence, for a deeper understanding of MPB dynamics in the subtidal zones, detailed accounts of the temporal patterns and the activity of benthic grazers are immediately needed, which would allow to further elevate the importance of benthic food web dynamics for coastal ecosystems. And along with that, to put further insight into the community structure of the MPB community, molecular fingerprinting can be used to study diversity, as there can be cryptic and pseudocryptic species present in the MPB community which can otherwise be not found through morphoecological studies and which can considerably influence the diversity patterns of the community.

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