Chapter 9

Eutrophication, primary production and vertical export

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9.1 Introduction

The effects of global and local changes are most prominent at the land-sea margins where presently population growth is greatest. For example, the population of coastal counties of the USA has roughly doubled since 1960 (Eos, 1992). This gives rise to increased pressure on natural resources and a large number of disturbances to coastal regions. Presently, eutrophication of coastal waters is probably the most important environmental effect (Gesamp, 1991). The effects of nutrient enrichment thoroughly change coastal ecosystems and occur virtually worldwide. Nutrients move across the land-sea margins at such high rates that coastal waters and estuaries are the most fertilized ecosystems on earth (Figure 9.1).

The discharge of nutrients to the coastal zone increased strongly during the last centennial. The increase in human population, the use of fertilizers, increased intensity in agriculture, logging and increased atmospheric deposition are the main cause for this intensification. However, significant periods of eutrophication took place much earlier. Already during pre-Roman time significant amounts of the mixed woods in the Mediter-
ranean disappeared. During pre-Viking times natural woods disappeared in Denmark, during the Middle Ages most of the original woods from central and northern Europe. Europe developed into the cultural landscape that we encounter today, unrecognisable and widely different compared to the pristine state. The removal of woods and the introduction of agriculture had a strong impact on the leaching of nutrients all over Europe and periodically eutrophication in the Baltic and North Seas must have been significant over the last 1000 years. Cultural eutrophication, intense as it may be at present, is thus nothing new, but a close and well-known companion of human civilisation, mainly through the introduction of agriculture that paved the road for human development and population explosion.

Coastal ecosystems can accommodate large amounts of nutrients, but there is certainly the danger that increased loading gives rise to increases in suspended biomass, far beyond the range of natural concentrations. For scientists and managers alike the question arises how much nutrient discharge a specific recipient can accommodate per unit time before undesirable consequences occur. Can we determine the primary production rates where excessive biogenic matter is exported to the bottom water and the sediment that result in bottom fauna changes and ultimately anoxia?

9.2 Eutrophication

The term eutrophication derives from the Greek roots eu (‘well’) and trope (‘nourishment’) and could thus be translated into well-fed, well-nourished. With the term eutrophication we imply that the ecosystem, not an individual, is well-nourished and that nutrients or biomass are supplied to a particular recipient. Eutrophication is not a clearly defined term and there are various definitions such as:

1. The process of changing the nutritional status of a given water body by increasing the nutrient resources (Richardson & Jørgensen, 1996)

2. An increase in the rate of organic carbon production in an ecosystem (Nixon, 1995)

In most cases we use definition 1 and this will also be the case in the present text. Thus we focus upon the supply to and the dynamics of nutrient resources in a water body. Eutrophication can entail either the process or the result. One has further to distinguish between natural eutrophication that is caused by winter accumulation, precipitation, vertical mixing, upwelling, river run-off and entrainment of nutrients. Climatic variability obviously influences and modulates the nutrient availability of a recipient and natural eutrophication thus varies over time. The natural variability in eutrophication is often poorly known, in particular because it may be camouflaged by cultural eutrophication, which is any type of nutrient discharge caused by anthropogenic activity, e.g agriculture run-off (see Sections 3), sewage, atmospheric deposition (see Sections 1), changes in water discharge etc.

9.3 Primary production and vertical export: Background considerations

Primary production consists of new production (PN) that is based on allochthonous, i.e. externally supplied nutrients, and regenerated production (PR), which is based on autochthonous, i.e. internally recycled nutrients (Dugdale & Goering, 1967). Hence total primary production (PT) is the sum of PN and PR. The amount of carbon that enters the aphotic zone is entitled export production (PE) (Figure 9.2).

The concept of new production is of utmost importance for understanding natural and eutrophicated ecosystems because the fraction f = PN/PT represents the upper limit of organic matter and energy which can be removed or extracted from the surface waters of the system without de-
Figure 9.2: New and regenerated production are based on (a) the supply of the limiting (allochthonous) nutrients from the aphotic zone, by advection, run-off or from the atmosphere (straight arrows) and (b) the recycled (autochthonous) nutrients in the euphotic zone (circular arrows), respectively. New and regenerated production comprise total primary production. Export production is the amount of sinking organic carbon at the bottom of the euphotic zone.

Given the practical difficulties in estimating $P_N$ for lengthy periods of time, sediment traps can be used to estimate $P_N$. $P_E$ estimates as measured by sediment traps come close to $P_N$, but are always smaller because it comprises only the particulate fraction and some transformation takes place from ammonium to nitrate even in the upper layers. Calculations of the productivity index $f$ by applying $P_E$ give, therefore, rise to underestimates (Wassmann, 1993). As a consequence, the term $e = P_E/P_T$ can be applied and used as an approximation of $f$. In boreal, coastal areas where steady state, if at all, cannot be assumed for intervals of less than the length of the productive period, $e$ is meaningful as a base for estimating $f$ for lengthy periods only (e.g. > 6 months). Therefore, the term $< e >$, representing $e$ for lengthy periods of time will be applied.

### 9.4 Nutrient supply, primary production, retention and vertical export

Increased supply of nutrients to the euphotic zone gives rise to increased production of algae which sooner or later sink to deeper water and the sediment, resulting in increased sediment-water exchange rates, at times in mass mortality of macrofauna and fish eggs (Rosenberg & Loo, 1988; Morrison et al., 1991) and finally in anoxia (Rosenberg, 1985; Graf, 1987). During the last decades widespread occurrence of low oxygen concentrations or anoxia in bottom waters, decreased catches of fish and blooms of toxic algae threatening aquaculture as well as stocks of wild animals have been reported with increasing frequency (Rosenberg & Loo, 1988). These changes seem to be caused by increased inputs of nutrients to aquatic areas from sewage, agricultural run-off and atmospheric fallout, giving rise to various degrees of eutrophication of fresh-water as well as marine, coastal environments (e.g. Wulff et al., 1990).

Figure 9.3 shows the principle processes of atmospheric CO$_2$ uptake and release, primary production, suspended biomass and vertical export to
the bottom. Seawater takes up CO$_2$ from the atmosphere that is either taken up by phytoplankton or released again to the atmosphere. The phytoplankton uptake of CO$_2$ is caused by primary production and first and foremost dependent on photosynthetic active radiation and nutrients. In addition it is influenced by the residence time of phytoplankton in the euphotic layer (determined by vertical mixing and stratification). Phytoplankton accumulates in the upper layers if grazing and degradation rates are lower than primary production, i.e. a bloom takes shape. A part of the suspended biomass, consisting of phytoplankton cells and detritus will inevitably escape grazing and degradation and sink into the aphotic zone and further to the bottom. The export of biogenic matter to the bottom is a complex function of the total amount of suspended matter, the sinking velocity of the sinking particles and the degradation impact of the pelagic heterotrophs. For example, low suspended biomass, low pelagic degradation and high sinking rates give result in a similar sedimentation rate at depth than high suspended biomass, high pelagic degradation and low sinking rates. Degradation of organic matter in the water column or the sediment results in nutrients that sooner or later can be taken up by phytoplankton.

If the limiting nutrient is nitrogen the new primary production depends on the allochthonous nutrient nitrate while the remaining primary production is based upon the autochthonous nutrient ammonium that derives from internal recycling by heterotrophic organisms. The basic principle to use nitrogen species to determine how much of the total primary production comprises new production (in case nitrogen is the limiting element) is difficult to apply in shallow water where the cycle of nutrients is rapid and where particulate nitrogen supplied to the bottom can be recycled to nitrate that is available for primary production. In this case nitrate is not new, but regenerated. Thus some of the nitrate is not ‘new’ and does not comply with the basic assumption of new production. In countless eutrophicated regions ammonium and urea are supplied as allochthonous nutrients. Also

Figure 9.3: Primary production, vertical flux and regeneration of nutrients in a coastal marine ecosystem. Also shown are some of the involved organisms such as phytoplankton, zooplankton, higher trophic levels and benthic organisms. The massive and narrow vertical arrows indicate scenarios of substantial and insignificant vertical flux. (Illustration courtesy: dr. Alexander Keck.)
in this case the traditional method to distinguish new from regenerated production is not possible because some of the per definition autochthonous nutrients are allochthonous. New production is thus impossible to measure in eutrophicated waters.

The state of an ecosystem during a transient bloom is basically characterised by export food chains with high vertical export. The amount of regenerated production increases, as the planktonic system develops and becomes more complex during the post bloom phase. Sedimentation of organic material is low and the ecosystem is characterised by retention food chains. In the non-eutrophicated coastal zone export chains are based upon new production and represent episodic events on the background of a continuous, seasonally variable recycled production based on the recycled nutrients from retention chains. If eutrophication continues, i.e. nutrients are supplied in a steady manner, a new steady state with a mixture of export and retention food chains will develop.

In conclusion, an estimate of new/net/harvestable production as a consequence of eutrophication in coastal zones is difficult to measure, among other reason because our terminology and measuring techniques are inadequate.

9.5 Algorithms of primary production versus vertical carbon export

An overview on algorithms predicting export production on the base of total primary production in marine environments on an annual scale has been presented by Wassmann (1990b; 1993) (Figure 9.4). Significant variability with regard to the $P_E$ versus $P_T$ relationship was detected. What algorithm should be selected for a global or coastal eutrophication carbon flux model? Obviously, there is no universal algorithm that would fit all ecosystems. Does the variability of the algorithms reflect real difference in the $P_E$ vs. $P_T$ relation-


ships in the various ecosystems from which they were derived (Figure 9.5)? If so, then different algorithms should be applied in different regions.

In particular data from the boreal coastal zone from the North Atlantic were investigated. The data used was mainly selected from simultaneous, time-integrated measurements derived over intervals covering most of the productive season (>6 months). Through a regression analysis $P_E$ was positively and nonlinearly correlated with total production $P_T$ (Figure 9.5). Best fit ($r^2 = 0.94$) was found by a power model calculated by the equation:

$$P_E = 0.049P_T^{1.41} \quad (9.1)$$

The $< e >$ ratio was also calculated and both $< e >$ and $P_R$ were found to be positively, nonlinearly correlated with $P_T$. The upper limit for $< f >$ was calculated to be about 0.5 in boreal coastal environments, i.e. at most about 50% of $P_T$ may be exported through sedimentation to below the euphotic zone. The curvilinear nature of the relationship implies that vertical export of biogenic matter increases relatively more than total primary production.

The results of the model of Aksnes & Wass-
Meso-zooplankton species composition obviously influences the pelagic-benthic coupling: for example, copepods and cladocerans have different reproductive strategies (hence different grazing pressure), and cladocerans do not produce distinct faecal pellets. A comparison of retention and export food chains, and vertical flux in lakes dominated by copepods (e.g. Lake Baikal) or marine environments strongly influenced by cladocerans (e.g. the eastern Baltic Sea), would be advantageous to analyse in greater detail the contrasting scenarios of copepod and cladoceran dominance for pelagic-benthic coupling.

In case the algorithms depicted in Figure 9.5 are truly predicting annual $P_E$ on the base of $P_T$, why are there significant differences? In the case of subalpine lakes and boreal coastal areas we have already recognised that differences in the zooplankton community species composition result in the observed variance. The question can be raised if the results presented in Figures 9.4 and 9.6 suggest that various types of top-down regulation are the base for the observed variability? The few data which do exist from non-boreal environments outside the North Atlantic suggest that coastal areas and tropical bays in the North Pacific Ocean experience more efficient retention in the upper layers and less vertical export (Figure 9.5). This interpretation is in consistency with the notion that tropical environments are characterised by effective retention food chains. This may also be true for the North Pacific Ocean where at least the open ocean is characterised by extensive micro-zooplankton grazing which prevents major accumulation of phytoplankton biomass (Frost, 1991; Dagg, 1993). $P_E$ as a function of $P_T$ in miscellaneous ecosystems with different production, recycling and export regimes could fall onto a suite of lines falling between maximum export (steep angle, straight line = bottom-up regulation) and high retention (flat angle, curved line = top-down regulation) efficiencies (Figure 9.6). The
9.6 Increases in primary and export production: Examples from the Gullmaren Fjord and the Kattegat

Two cases studies illustrate that a ‘threshold interval’ in primary production exists where vertical export increases strongly. The pelagic ecosystem of the Gullmar fjord situated on the west coast of Sweden and adjacent waters has been studied since the late 1970s, principally in relation to oceanographic variability in the Skagerrak and the possible influence of climatic forcing on this area (Lindahl and Hernroth, 1983; Andersson and Rydberg, 1993; Heilmann et al., 1994; Lindahl et al., 1998; Belgrano et al., 1999). Primary phytoplankton productivity has been a part of these studies and a measuring program in the mouth area of the Gullmar Fjord is ongoing since 1985. An evaluation of this time series was carried out in 1994 (Lindahl, 1995), suggesting that even when elevated values of primary production are observed during the spring period (March-April), the main contribution to the annual production was found during the period May-September.

More recently a first attempt was carried out to study the effect of weather/climatic forcing on the physical-chemical processes related to the primary productivity. These results suggested the presence of an indirect link between the North Atlantic Oscillation index (NAO), the supply of nutrients to Kattegat, wind direction and the primary production (Lindahl et al., 1998; Belgrano et al., 1999). The development of primary production was reconstructed by combining measurements in the Gullmaren fjord with older measure-
9.6. GULLMAREN FJORD AND KATTEGAT EXAMPLES

Figure 9.7: Unpublished results from a physically-biologically coupled 3D model presenting primary production versus export production in 4 different regions in the Barents Sea (pers. com., D. Slagstad). The scattered line is the daily variability in the phase diagram while the loops are the 5 day running average.

Figure 9.8: Development of primary production in the Gullmaren fjord over the last 30 years.

ments from the Kattegat (Figure 9.8). The striking increase in the 70s and 80s seems caused by eutrophication, while the slight rise is interpreted as a function of climate change. Applying the relationship suggested by Wassmann (1990b), the export production in the 1950/60 period was about 30 g C m\(^{-2}\) year\(^{-1}\) (\(P_T = 100\) g C m\(^{-2}\) year\(^{-1}\)) while at present it is about 120 g C m\(^{-2}\) year\(^{-1}\) (\(P_T = 240\) g C m\(^{-2}\) year\(^{-1}\)). If the assumptions behind these calculations are true, they imply the vertical C export increased four times over a time interval of 50 years! The carbon loading of the basin water of the fjord is obviously far greater today then during the more ‘pristine’ times prior to 1960.

But even over the recent period significant increases in the organic load to the deep part of Gullmaren Fjord below the euphotic zone can be calculated. \(P_E\) has increased from approximately 105 g C m\(^{-2}\) year\(^{-1}\) in 1985 to almost 123 g C m\(^{-2}\) year\(^{-1}\) in 2000, corresponding to an increase of the organic load of about 17% over 15 years. One possible result of this process may be the observed decrease in oxygen content of the deep water (>60 m) the beginning of the 1980s. However, it should be pointed out that the decrease in oxygen may be explained by other processes as well, e.g. a change over time in deep-water exchange. Finally, it should be mentioned that the relationship between \(P_T\) and \(P_E\) in the fjord reflects both eutrophication (which has not increased significantly in recent years due to increased effluent control) and climate changes (variations in NAO, global warming etc.). However, to differentiate between natural and anthropogenic variability is difficult.

Applying again the \(P_T\) and \(P_E\) relationship of Wassmann (1990b), the vertical export from the upper layers in the Kattegat region appears to
Table 9.1: Increase in primary production in the southern Kattegat over time. Also shown the calculated change in export production (from Wassmann, 1990a).

<table>
<thead>
<tr>
<th>Area</th>
<th>Time interval covered (years)</th>
<th>Change $P_T$ (g C m$^{-2}$ y$^{-1}$)</th>
<th>Change $P_E$ (g C m$^{-2}$ y$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Storebelt</td>
<td>24</td>
<td>+63</td>
<td>+29</td>
</tr>
<tr>
<td>Øresund</td>
<td>44</td>
<td>+58</td>
<td>+22</td>
</tr>
</tbody>
</table>

have increased 130–250% over a time interval of 20–40 years (Table 9.1; Wassmann, 1990a). This fundamental increase should be adequate to explain the frequently observed oxygen deficiencies in the region (Rosenberg & Loo, 1988), although, as mentioned above, stratification and lack of exchange of bottom water results in anoxic conditions. The curvilinear nature of the $P_T$ versus $P_E$ relationship implies that the linear increase in $P_T$ causes an exponential type of increase in $P_E$, in particular at $P_T$ rates $>150$ g C m$^{-2}$ y$^{-1}$. It would be advantageous to determine the primary production threshold intervals for various coastal regions where $P_E$ turns out to be greater than oxygen content of or supply to the benthic boundary layer and where undesirable effects (hypoxia, anoxia) develop in the bottom layers.

### 9.7 Variability of vertical export in the pelagic zone

All investigations of export of biogenic matter indicate that the export flux decreases more or less exponentially with depth in the upper part of the ocean, with minor decreases below 200–500 m depth (for algorithms predicting the depth variation of vertical carbon flux see Berger et al. 1989). Resuspension and protrusion of advective, particle rich layers or vertical differences in current direction may alter this general feature of vertical flux. The degradation rate of organic matter in the water column and, in particular for fast sinking particles is of pivotal importance for the quantitative regulation of pelagic-benthic coupling. Depend-
9.8 SEASONAL VARIATION IN VERTICAL EXPORT

...ing on the degradation rate of fast sinking particles in the water column, the absolute vertical export of organic matter at a certain depth could be small or large, irrespective the size of the new production from which it derives.

The current lack of adequate investigations of the vertical export above the depth of 200–500 m where the majority of long-term sediment traps have been deployed, results in difficulties to understand and model vertical carbon flux. There exists a black box of several hundred metres between the surface layers where measurements and algorithms of primary production exists and where data on the carbon export to the ocean interior are available. In this black box, the twilight zone, we face a lack of basic understanding on how vertical export of biogenic matter in general is regulated, let alone in eutrophic regions. In order to guide future investigations of vertical flux attenuation in eutrophicated regions we present an idealised, conceptual model of vertical carbon export and focus upon the ‘pelagic mill’ and vertical flux regulation in the upper 200 m (Figures 9.3 and 9.9). An adequate understanding of carbon cycling demands not only adequate investigations of primary production, but also concomitant research on the functional biodiversity of the pelagic zone, plankton dynamics, vertical flux and its regulation in the twilight zone.

9.8 Seasonal variation in vertical export in eutrophicated coastal areas

Considering the seasonal flux of organic matter in various coastal settings three major modes can be distinguished: one-pulse, multi-pulse and in eutrophicated regions ‘buffered’ systems (Wassmann, 1991). As an example, we present data from west-Norwegian fjords (Figure 9.10). Non-eutrophicated land-locked fjords represent simple one-pulse systems, where new production, suspended biomass and sedimentation give rise to one major, annual pulse during spring. The relative amplitude of the seasonal signal in flux of organic matter is large, but the average sedimentation rate is low.

Eutrophicated land-locked fjords show also seasonal variability in organic matter flux, but the relative amplitude of new production, suspended matter and sedimentation is lower (Figure 9.10). The average sedimentation rate, however, is high. The variability in such ecosystems is ‘buffered’ by the continuous supply of allochthonous nutrients. Eutrophicated land-locked fjords are mainly one-pulse systems, but depending on the supply of nutrients from fresh water run-off, sewage etc. and climatic conditions, several minor summer and autumn blooms may develop. They may thus turn into two- or multi-pulse systems (Figure 9.10).

Open fjords are complicated multi-pulse systems. Pulses in spring and autumn are normally found. However, upwelling of nutrient rich deep water can introduce additional pulses to the system at any time, but normally during late spring and early summer (Figure 9.10). Also, accumulated biomass can be removed from the fjord by large-scale exchange of water. In multi-pulse systems advection represents the most significant element.

Comparing the dynamics of primary production and sedimentation in fjords renders, therefore, difficult because of the differences in time and space scales of these processes.
Primary production is usually estimated in terms of litres and hours, sedimentation, however, integrates the vertical flux at a given depth over the time of trap deployment and is expressed in terms of square meters and days. While the produced biomass can stay in the fjord or is dispersed in adjacent bodies of water, sediment traps might catch organic particles that have been produced and altered throughout the coastal zone. If advection is significant in fjords, the locally measured primary production and sedimentation rates might have little in common, but rather reflect the general productivity and vertical flux regime in all parts of the coastal zones, from the innermost reaches to the open shelf. This has also implications for eutrophication. Eutrophication-derived suspended biomass may be introduced into a non-polluted region from outside or local eutrophication signals may be exported to unpolluted regions.

Ecosystems that receive nutrients continuously or pulsed differ with regard to the pelagic-benthic coupling. Pulsed nutrient addition may cause a higher build-up of phytoplankton biomass, a larger temporal mismatch between herbivores and phytoplankton biomass and a higher sedimentation rate of biogenic matter. This was tested in enclosures (Svensen et al., 2002). Each enclosure received the same total amount of nutrients, but the nutrients were supplied at four different intervals ranging from one single load to continuous additions. Spring bloom-like systems developed where nutrients were added in one or two pulses as they were characterised by high primary production, high suspended biomass of chlorophyll a (Chl a) and particulate organic carbon (POC) and high sedimentation rates. In contrast, the seawater enclosures receiving nutrients about every third day or in a continuous supply resembled regenerated systems with low concentrations of suspended Chl a and POC and with low and stable loss rates. The frequency of nutrient additions had a strong influence on the development of the phytoplankton and vertical flux of biogenic matter as pulsed nutrient addition resulted in the highest vertical export.

9.9 Eutrophication and phytoplankton biomass accumulation

The influence of top-down control is obviously important for the flow of nutrients through the food chain or food web. In lakes the cascading effects through the food web by manipulating the top-down regulation is well known (Mazumder et al., 1988). Top-down effects have less-known effects on marine coastal eutrophication. As most of the eutrophicated regions are in the shallow coastal zone some of the peculiarities of these ecosystems have become mixed up into the term eutrophication that is almost analogue with green or brown waters. Do green or brown waters indicate marked increases in marine productivity or eutrophication? In most cases in the coastal zone this is the case, but it could also just reflect the lack of important grazers such as copepods that are excluded from overwintering in shallow waters, resulting in decreased grazing pressure on large-celled bloom phytoplankton. Primarily brown and green waters do not suggest that there is less grazing than phytoplankton production: a mismatch between producers and consumers. Do blue water indicate that marine productivity is low? In some cases this is true, in others not. Blue water reflects a balance between producers and consumers: biomass accumulation does not take place. Production could be high or low. Contradicting to common belief, some blue waters are highly eutrophic (e.g. the north Norwegian shelf; Wassmann et al., 1999) while others are oligotrophic (e.g. the central and eastern Mediterranean Sea). These findings have obvious implications for the interpretation of pigment data and remotely sensed pigments concentrations that traditionally have been applied to construct P_T fields over regions where P_T measurements were unavailable. There cannot exist a constant pigment/P_T.
ratio, analogous to that no constant $P_T/P_E$ ratio exists. The top-down regulation of phytoplankton biomass is thus important to keep in mind when the eutrophic status of a region is established. Blue water can produce large amounts of detritus and result in large-scale vertical export of biogenic matter, resulting in large supply to the benthos and oxygen deficiency in bottom waters.

The cascading effect of top-down manipulation influenced the plankton community and results in different functional response in the various regions exposed to eutrophication. During the process of eutrophication, the food web structure, timing of fertilisation and alternative grazing/predation strategies of the planktonic heterotrophs have a crucial impact on the retention and loss of nutrients from the pelagic zone (Heiskanen et al., 1996; Svensen et al., 2002).

References


