

Chapter 9

Eutrophication, primary production and vertical export



Paul Wassmann
Norwegian College of Fishery Science
University of Tromsø
N-9037 Tromsø, NORWAY
paulw@nfh.uit.no

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

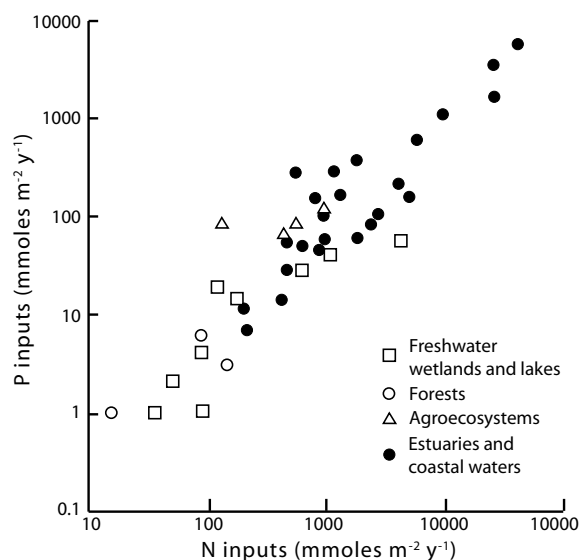


Figure 9.1: Nitrogen and phosphorous loadings to different types of ecosystems (redrawn from Eos, 1992).

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 fertilisers, 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 *trophe* ('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* (P_N) that is based on allochthonous, i.e. externally supplied nutrients, and *regenerated production* (P_R), which is based on autochthonous, i.e. internally recycled nutrients (Dugdale & Goering, 1967). Hence total primary production (P_T) is the sum of P_N and P_R . The amount of carbon that enters the aphotic zone is entitled *export production* (P_E) (Figure 9.2).

The concept of new production is of utmost importance for understanding natural and eutrophicated ecosystems because the fraction $f = P_N/P_T$ represents the upper limit of organic matter and energy which can be removed or extracted from the surface waters of the system without de-

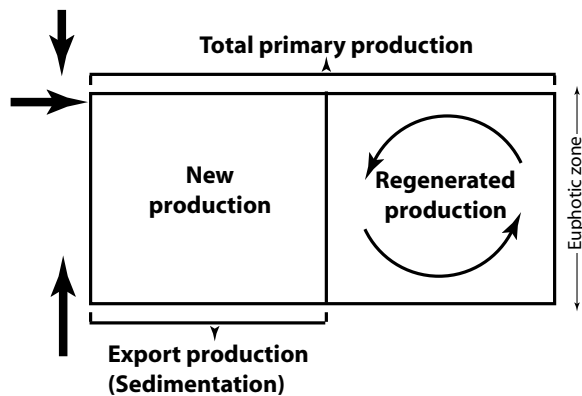


Figure 9.2: New and regenerated production are based on (a) the supply of the limiting (allochthonous) nutrients from the aphotic zone, by advection, run-off or from the atmosphere (straight arrows) and (b) the recycled (autochthonous) nutrients in the euphotic zone (circular arrows), respectively. New and regenerated production comprise total primary production. Export production is the amount of sinking organic carbon at the bottom of the euphotic zone.

stroying the long-term integrity of pelagic systems (Vezina & Platt, 1987; Iverson, 1990; Legendre, 1990). P_N represents thus the biomass that has to be handled by an eutrophicated recipient (e.g. mineralization, accumulation, harvestable biomass and export of biomass to adjacent recipients). Given the importance of P_N for the overall cycling of organic matter, considerable emphasis has recently been given to estimating P_N in coastal (e.g. Wassmann, 1990b) as well as oceanic environments (e.g. Knauer et al. 1990). New production represents the *carrying capacity* of a marine ecosystem. New production represents the *maximum production* capacity of an ecosystem or the *harvestable production*. New production is a *critical component* of marine primary production that limits the supply of food to the benthos, zooplankton, fish, and extensive aquaculture as well as the removal rate of atmospheric CO_2 by the marine biota. New production estimates are of great interest for understanding eutrophication. Increased new production results in additional biomass that the ecosystem has to deal with in terms of grazing, vertical export to the bottom and pelagic and benthic degradation.

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 $\langle e \rangle$, 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 fall-out, 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

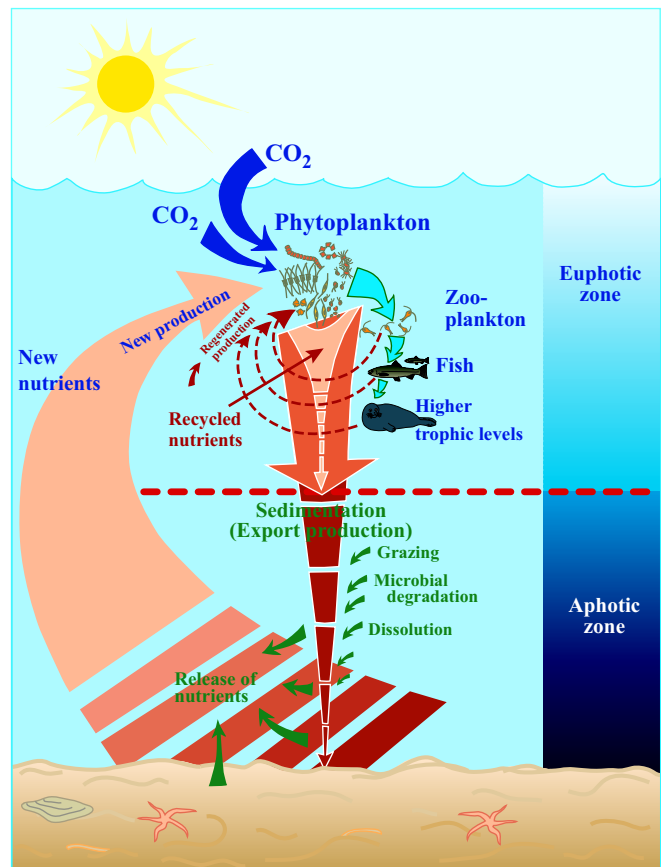


Figure 9.3: Primary production, vertical flux and regeneration of nutrients in a coastal marine ecosystem. Also shown are some of the involved organisms such as phytoplankton, zooplankton, higher trophic levels and benthic organisms. The massive and narrow vertical arrows indicate scenarios of substantial 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 regenerated 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-

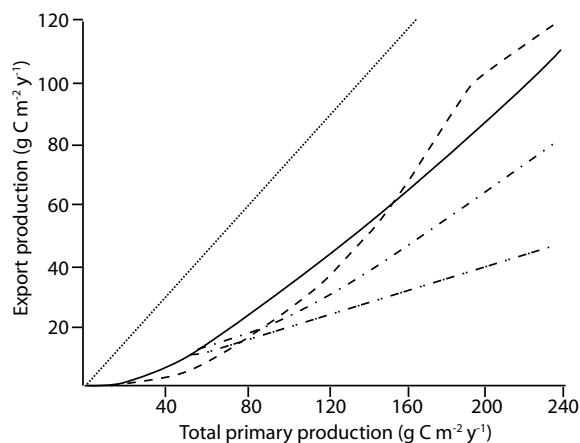


Figure 9.4: Export production as a function of total primary production on an annual scale in marine ecosystems. Algorithms from various publications are presented. Suess (1980) (.....), Eppley & Petersen (1979) (- - - - -), Betzer et al. (1984) (-.-.-.-.), Pace et al. (1987) (-.-.-.-.-) and Wassmann (1990) (—). Source: Wassmann (1990b, 1993).

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 $\langle e \rangle$ ratio was also calculated and both $\langle e \rangle$ and P_R were found to be positively, nonlinearly correlated with P_T . The upper limit for $\langle f \rangle$ 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-

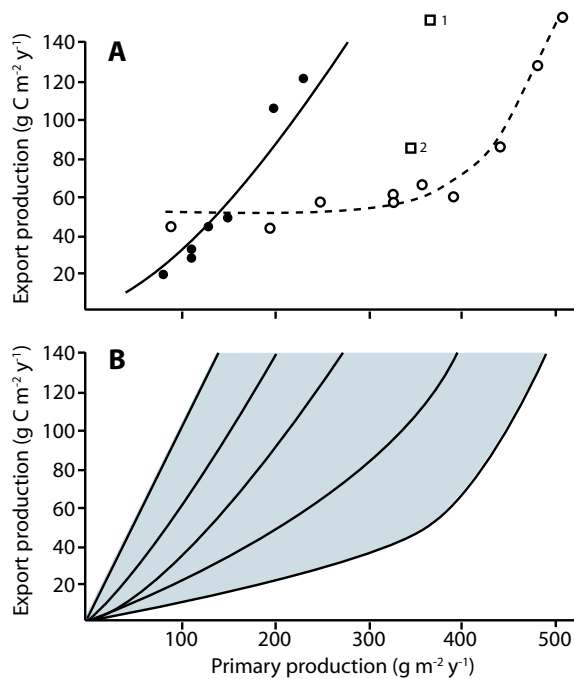


Figure 9.5: (A) Export production as a function of total primary production from the North Atlantic, boreal coast (Wassmann, 1990; full line) and subalpine lakes (Aksnes & Wassmann, 1993; broken line) on an annual scale. The zooplankton of the former ecosystems is often dominated by copepods, the latter one by cladocerans. Also shown are two data points from Dabob Bay, a boreal, North Pacific fjord, and a tropical lagoon, Kaneohe Bay on Hawaii (open squares, 1 and 2, respectively). (B) Schematic diagram on the conceivable relationship between annual export production and total primary production in miscellaneous ecosystems with different production, recycling and export regimes. The functional lines of the various ecosystems could be spread in the shaded area. The relationships could fall onto a suite of lines contrasting between maximum export (steep angle, straight relationship) and high retention (flat angle, strong curvature) efficiencies.

mann (1993) indicate that domination by copepods in the marine and cladocerans in lakes can give rise to very different relationships between primary versus export production (Figure 9.5). 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

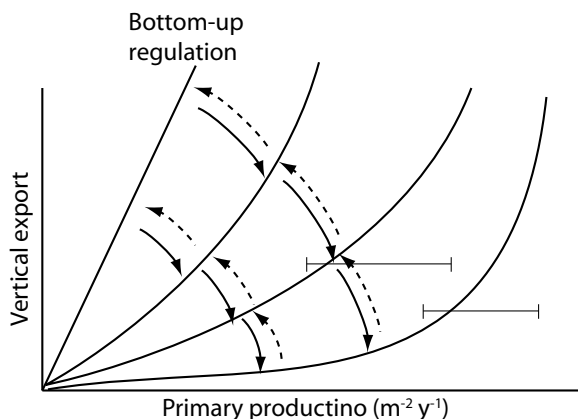


Figure 9.6: Schematic representation of annual primary production and vertical export during a phytoplankton bloom. Increased new production drives the relationship along the linear relationship total primary production = new production = export production. Planktonic heterotrophs reduce vertical export. As the grazing capacity of the planktonic heterotrophs increases with increasing primary production (full arrows), a curvilinear relationship emerges. Note the horizontal bars that indicate threshold intervals where the curvature of the primary production vs. vertical export relationship increases rapidly. Carnivory (stippled arrows) counteracts the retention of suspended biomass by the herbivores and detritivores.

balance between bottom-up and top-down regulation shapes the curvilinear nature of the P_T vs. P_E relationship. Not only P_T varies as a function of climate variability and eutrophication, also the P_T/P_E ratio is not constant, but varies in accordance with the composition and dynamics of the heterotrophic plankton community. ‘The’ P_T vs. P_E relationship does that not exist.

On a daily scale the P_T vs. P_E relationship is characterised by irregularities (Figure 9.7). Primary production varies greatly between days and contributes to in different degrees to the suspended pool of biogenic matter (a function of total production, the f -ratio, grazing etc.) that may sink. *Although short-term variability in vertical flux takes place, that of primary production is greater.* The phase plot in Figure 9.7 illustrates the spiky nature of primary production as compared to the buffered rates of vertical export. The 5 days running average plot indicates the loop-type relationship between daily P_T and P_E , as pre-

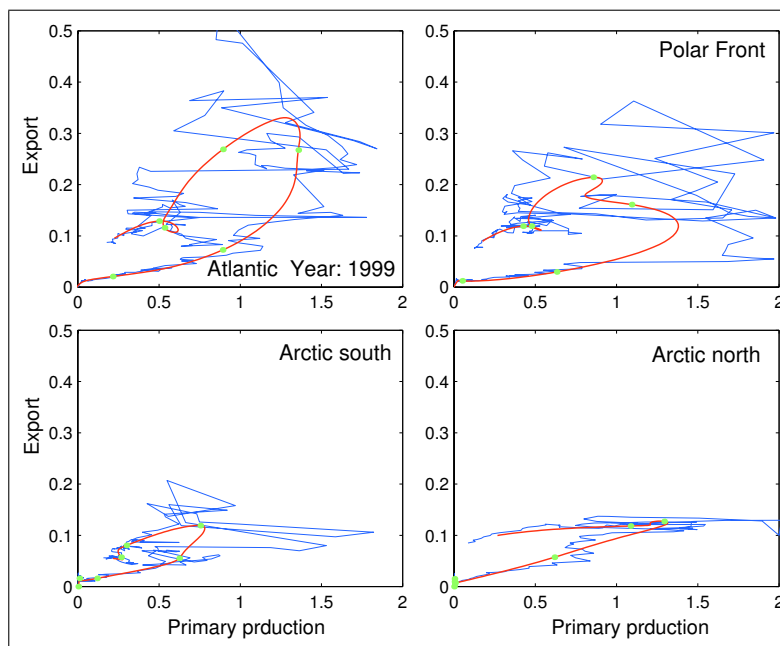
dicted by Wassmann (1998). Increased bottom-up regulation by eutrophication will increase the ‘loopy’ nature of the P_T vs. P_E relationship. In contrast, increased top-down regulation will decrease the loop size. Increased top-down regulation will eventually force the loop onto a retention line and remove excessive vertical export.

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-

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.



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 $30 \text{ g C m}^{-2} \text{ year}^{-1}$ ($P_T = 100 \text{ g C m}^{-2} \text{ year}^{-1}$) while at present it is about $120 \text{ g C m}^{-2} \text{ year}^{-1}$ ($P_T = 240 \text{ g C m}^{-2} \text{ year}^{-1}$). 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 than 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 $105 \text{ g C m}^{-2} \text{ y}^{-1}$ in 1985 to almost $123 \text{ g C m}^{-2} \text{ y}^{-1}$ 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

Development of primary production in the Gullmaren fjord

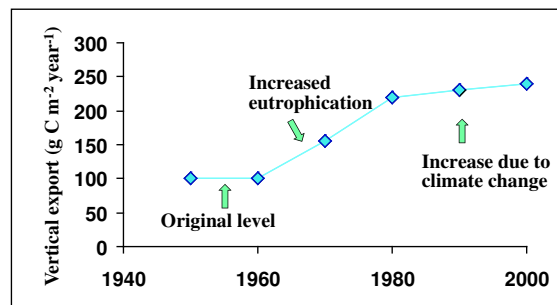


Figure 9.8: Development of primary production in the Gullmaren fjord over the last 30 years.

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).

Area	Time interval covered (years)	Change P_T ($\text{g C m}^{-2} \text{y}^{-1}$)	Change P_E ($\text{g C m}^{-2} \text{y}^{-1}$)
Storebelt	24	+63	+29
Øresund	44	+58	+22

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 $>150 \text{ g C m}^{-2} \text{y}^{-1}$.* 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-*

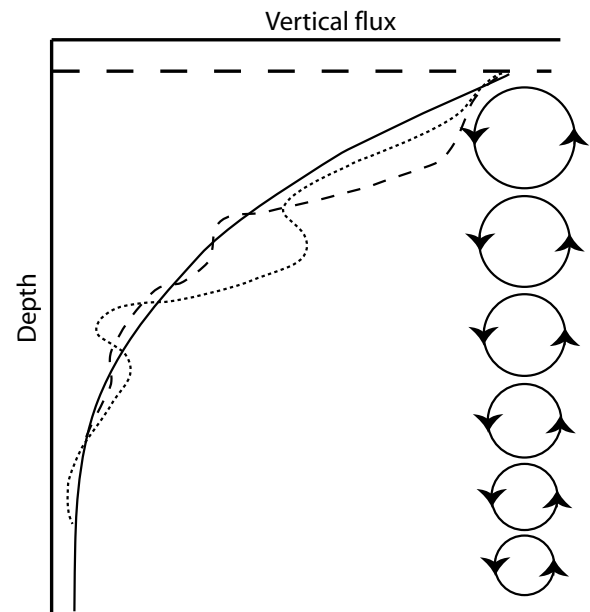


Figure 9.9: Schematic presentation of the ‘pelagic mill’ in the upper part of the ocean and its regulation of biogenic vertical flux. The full line assumes a continuous mineralisation of export production, giving rise to a decline in flux that follows a power function. The broken line indicates a step-wise decrease in vertical flux caused by extensive grazing at certain depth horizons. The stippled line indicates that vertical flux can increase intermittently due to repackaging. The recycling by the zooplankton community is schematically indicated to the right.

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 of 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 exist 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

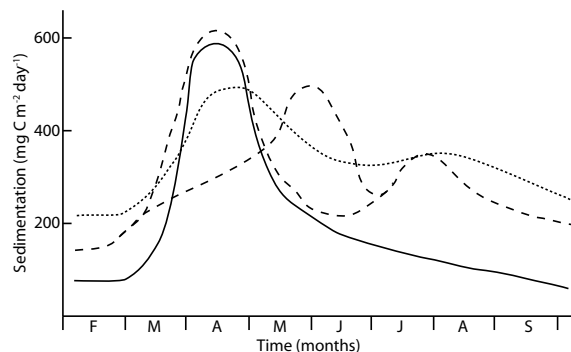


Figure 9.10: Semiquantitative diagram of annual variation of sedimentation of particulate organic carbon (POC) in fjords, eutrophicated as well as non-eutrophicated fjords. One-, two- or multi-pulse systems can be distinguished. The characteristic line for eutrophicated fjords is the dotted line (increased average, reduced seasonal variability).

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 phytoplank-

ton 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 believe, 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

- AKSNES, D. L., & WASSMANN, P. 1993. Modelling the significance of zooplankton grazing for export production. *Limnology and Oceanography*, **38**, 978–985.
- BERGER, M. H., SMETACEK, V. S., & WEGER, G. 1989. Ocean productivity and paleoproductivity - an overview. Pages 1–34 of: BERGER, W. H., SMETACEK, V. S., & WEFER, G. (eds), *Productivity of the ocean: present and past*. New York: John Wiley & Sons.
- DAGG, M. 1993. Grazing by the copepod community does not control phytoplankton production in the Subarctic Pacific Ocean. *Progress in Oceanography*, **32**, 163–183.
- DUGDALE, R. C., & GOERING, J. J. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography*, **12**, 196–206.
- EOS. 1992. Understanding changes in coastal environments: the LMER Program. *Eos*, **73**, 481–485.
- FROST, B. W. 1991. The role of grazing in nutrient-rich areas of the open sea. *Limnology and Oceanography*, **36**, 1616–1630.
- GESAMP. 1991. *The state of the marine environment*. Oxford: Blackwell.
- GRAF, G. 1987. Benthic response to annual sedimentation pattern. Pages 84–91 of: RUHMOR, J., WALGERT, E., & ZEITZSCHEL, B. (eds), *Seawater-Sediment Interactions in Coastal Waters*. Lecture Notes on Coastal and Estuarine Studies, vol. 13. Berlin: Springer Verlag.
- HEISKANEN, A.-S., TAMMINEN, T., & GUNDERSEN, K. 1996. The impact of planktonic food web structure on nutrient retention and loss from a late summer pelagic system in the coastal northern Baltic Sea. *Marine Ecology Progress Series*, **145**, 195–208.
- IVERSON, R. L. 1990. Control of marine fish production. *Limnology and Oceanography*, **35**, 1593–1604.
- KNAUER, G. A., REDALJE, D. A., HARRISON, W. G., & KARL, D. M. 1990. New production at the VERTEX time series site. *Deep Sea Research*, **37**, 1121–1134.
- LEGENDRE, L. 1990. The significance of microalgal blooms for fisheries and for the export of particulate organic carbon in the ocean. *Journal of Plankton Research*, **12**, 681–699.
- MAZUMDER, A., MCQUEEN, D. J., TAYLOR, W. D., & S., KEABM D. R. 1988. Effects of fertilisation and planktivorous fish (yellow perch) predation on size distribution of particulate phosphorus and assimilated phosphate: Large enclosure experiments. *Limnology and Oceanography*, **33**, 421–430.
- MORRISON, J. A., NAPIER, J. R., & GAMBLE, J. C. 1991. Mass mortality of herring eggs associated with a sedimenting diatom bloom. *ICES Journal of Marine Science*, **48**, 237–245.
- NIXON, S. W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia*, **41**, 199–219.
- RICHARDSON, K., & JØRGENSEN, B. B. 1996. Eutrophication: Definition, history and effects. Pages 1–20 of: *Eutrophication in coastal marine ecosystems*. Coastal and Estuarine Studies, vol. 52. Washington DC: American Geophysical Union.
- ROSENBERG, R. 1985. Eutrophication — the future marine coastal nuisance? *Marine Pollution Bulletin*, **16**, 227–231.
- ROSENBERG, R., & LOO, L. O. 1988. Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, western Sweden. *Ophelia*, **29**, 213–225.
- SVENSEN, C., NEJSTGAARD, J. C., EGGE, J. K., & WASSMANN, P. 2002. Pulsing vs. constant supply of nutrients (N, P and Si): effect on phytoplankton community, mesozooplankton grazing and vertical flux of biogenic matter. *Scientia Marina*, **66**, 189–203.
- VEZINA, A., & PLATT, T. 1987. Small-scale variations of new production and particulate fluxes in the ocean. *Canadian Journal of Fishery and Aquatic Science*, **44**, 198–205.
- WASSMANN, P. 1990a. Calculating the load of organic carbon to the aphotic zone in eutrophicated coastal waters. *Marine Pollution Bulletin*, **21**, 183–187.
- WASSMANN, P. 1990b. Relationship between primary and export production in the boreal coastal zone of the North Atlantic. *Limnology and Oceanography*, **35**, 464–471.

- WASSMANN, P. 1991. Dynamics of primary production and sedimentation in shallow fjords and polls of western Norway. *Oceanography and Marine Biology Annual Review*, **29**, 87–164.
- WASSMANN, P. 1993. Regulation of vertical export of particulate organic matter from the euphotic zone by planktonic heterotrophs in eutrophicated aquatic environments. *Marine Pollution Bulletin*, **26**, 636–643.
- WASSMANN, P. 1998. Retention versus export food chains: processes controlling sinking loss from marine pelagic environment. *Hydrobiologia*, **363**, 29–57.
- WASSMANN, P., ANDREASSEN, I., & REY, F. 1999. Seasonal variation of nutrient and suspended biomass along a transect on Nordvestbanken, north Norwegian shelf, in 1994. *Sarsia*, **84**, 199–212.
- WULFF, F., STIGEBRANDT, A., & RAHM, L. 1990. Nutrient dynamics of the Baltic Sea. *Ambio*, **19**, 126–133.