

Marine Food Webs Under Eutrophic Conditions: Desirable and Undesirable Forms of Nutrient Richness

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Summary

The human attitude towards nutrient richness of waters has undergone a substantial change during this century. Prior to the eutrophication crisis nutrient richness was equated with "fertility", i.e. with a high growth potential for harvestable biological resources. The eutrophication crisis, first noted by limnologists but later also by marine ecologists, completely changed this attitude. Today, eutrophy is considered an undesirable state associated with nuisance algal blooms, deep water oxygen depletion and loss of biodiversity. However, the "fertility"-point of view has persisted as a minority opinion.

Empirical support for the "harmful eutrophication" point of view comes from oxygen depletion and benthic fauna impoverishment in the deep basins of the Baltic Sea and from blooms of various kinds of toxic or nuisance algae from many eutrophic coastal seas. Empirical support for the fertility point of view comes from the upwelling zones which are among the richest fishing grounds of the world. Can the current status of the harmfully eutrophied seas be converted into the more desirable status of the upwelling areas? This question is of vital interest both from an environmental protection and from a fisheries point of view. A recently designed cluster of research projects dedicated to that question (MARICULT) has led to considerable public embarrassment, including an official inquiry in the federal parliament of Germany.

As the first project within the MARICULT framework, COMWEB is just being installed. It is focussed on the response of the lower part of coastal pelagic food webs (phytoplankton, bacteria, protozoa, mesozooplankton) to changes in nutrient conditions. The working hypotheses of COMWEB are:

- Nutrient richness based on upwelling is characterized by high Si:N ratios (0.6 to 1.5 stoichiometrically). Eutrophication by human waste waters, agricultural fertilizers and combustion processes increases N- and P, but not Si-loadings, thereby causing a decline of Si:N ratios.
- Declining Si:N ratios shift the competitive advantage away from diatoms to flagellates (and Cyanobacteria in the Baltic Sea). The non-siliceous taxa contain more toxic species (several dinoflagellates, *Chrysochromulina*, *Nodularia*) or otherwise undesirable species (e.g. *Phaeocystis*).
- A shift from diatoms to other taxa leads to more complex food webs and a less efficient transfer of energy and matter from primary producers to fish.

If these assumptions are correct, a transition from the "harmfully eutrophied" status to the "desirably fertile" status of marine food webs could be brought about by increased silicate loading. A success of such a management strategy would suppress undesirable phytoplankton species, enhance fish production and increase the burial of CO₂ by enhanced sedimentation. However, there may be undesired side effects and risks which need careful evaluation, such as a deterioration of oxygen deficiency in deep waters, a failure of diatoms to grow at suitable Si:N ratios but unsuitable physical conditions, development of the wrong diatom species (toxic *Pseudonitzschia pungens*, inedible *Coscinodiscus wailesii*), an increase of tunicates and coelenterates at the expense of crustacean zooplankton and fish and a loss of diversity.

Introduction

There is a conflict between fighting eutrophication and managing the sea for maximum sustainable harvests of biological resources. In 1995, scientists from several European countries developed the research program MARICULT to address this conflict directly. Within the framework of MARICULT several projects have been submitted to the European Commission. Among them, the project COMWEB was selected for funding while FAPPE has been put on place one of the waiting list. During the first months of 1996 there was considerable excitement in the press about MARICULT. The scientists cooperating within the framework of MARICULT were accused of planning to dump fertilizer into the North Sea and taking the risk of a large environmental disaster. The excitement led to an official inquiry by MdB Ulrike Mehl in the federal parliament of Germany on 17 January 1996. The response by Staatssekretär Walter Hirche clarified that no large scale disposal of fertilizers into the North Sea is planned within the projects COMWEB and FAPPE. The actual amount of nutrients used for laboratory and field experimentation within the different MARICULT-projects is very marginal indeed: For 1996 a total usage of 2-3 kg of nutrients is anticipated, as op-

posed to an annual loading of the North Sea of about 10^9 kg. As was to be expected from these figures, the environmental risk has been assessed to be marginal during the evaluation procedure of the MARICULT-projects. Still there is some concern that MARICULT will challenge one of the supreme goals of contemporary environmental management, the fight against eutrophication. As a partner in COMWEB, I will summarize the philosophy of MARICULT (cf. Saks haug et al. [1995]), the working hypotheses and the scheduled experimental approaches of COMWEB.

Changing attitudes towards eutrophy

Fertility: When first introduced into limnology by Thienemann [1928] and Nauman, the terms “oligotrophy” and “eutrophy” had no value connotation. They simply described a nutrient rich and a nutrient poor status of lake ecosystems. Later, marine ecologists also began to use this terminology, again without regarding “eutrophy” as an undesirable state. It was rather seen as an analogue to the “fertility” of terrestrial soils. Nutrient richer systems support more primary productivity which in turn supports more heterotrophic organisms, particularly fish and other sea food. Today this view persists as a minority opinion, as illustrated by the title of a paper called “eutrophication of the North Sea continental zone: a blessing in disguise” (Boddeke and Hage1 [1991]).

There is ample empirical evidence for the fertility view on eutrophy. The positive relationship between nutrients and primary productivity has been established so frequently that just one citation should stand as an example for many (Berger [1989]). How does fish production relate to primary productivity? Iverson's [1990] analysis of literature data showed a highly significant positive correlation. The data set comprised only seasonally stratified seas and spanned annual primary production rates (PP) from approx. 40 to 250 $g\ C \cdot m^{-2} \cdot y^{-1}$. The regression equation was:

$$FP = -0.472 + 0.012 PP ; r^2 = 0.96; p < 0.001,$$

where FP is fish and squid production in $g\ C \cdot m^{-2} \cdot y^{-1}$ (converted from fresh weight to carbon by a quotient of 7.9). An exponential regression shows a significantly more than linear increase of FP with PP :

$$FP = 0,000308 PP^{1.653}; S. E. \text{ of the exponent: } \pm 0.07; r^2 = 0.985; p < 0.001$$

At the lowest PP -levels FP is approx. 0.3%, at the highest levels it is slightly above 1% (Fig. 1). This finding contrasts with the frequently observed decrease of ecological efficiency (ratio between the production rates of adjacent trophic levels) with increasing primary productivity (e.g. Cushing [1971]). It becomes compatible with Cushing's trend if different food chain lengths are assumed. An estimate of FP as 0.3% of PP is compatible with an efficiency of 14.4% and four trophic levels (e.g. phytoplankton – protozoa – copepods – planktivorous fish) and 1% is compatible with an efficiency of 10% and three trophic levels (phytoplankton – copepods – fish).

Harmful eutrophication. Since the 1960s the process of rapid lake eutrophication has radically changed the attitudes of both scientists and the general public. Eutrophication of surface waters was experienced as one of the most urgent aspects of environmental crisis. The symptoms of harmful eutrophication included decreased water clarity, blooms of nuisance algae, deep water oxygen depletion, fish kills, and an impoverishment of the benthic fauna. Similar symptoms have been observed in coastal seas and have been attributed to eutrophication, among others: blooms of toxic dinoflagellates in European and American coastal seas (Granéli et al. [1989], Smayda [1989, 1990]), a bloom of the toxic flagellate *Chrysochromulina polylepis* in the Kattegatt (Maestrini and Granéli [1991]), blooms of the foam-producing nuisance alga *Phaeocystis* in the southern North Sea (Riegman et al. [1992]), increasing oxygen deficiency in the deep basins of the Baltic Sea (Granéli et al. [1989], Gerlach [1996]), bottom fauna impoverishment in the Baltic Sea (Rumohr [1996]). Justifiably, stopping eutrophication and a return to more oligotrophic conditions has become a prime goal in environmental management.

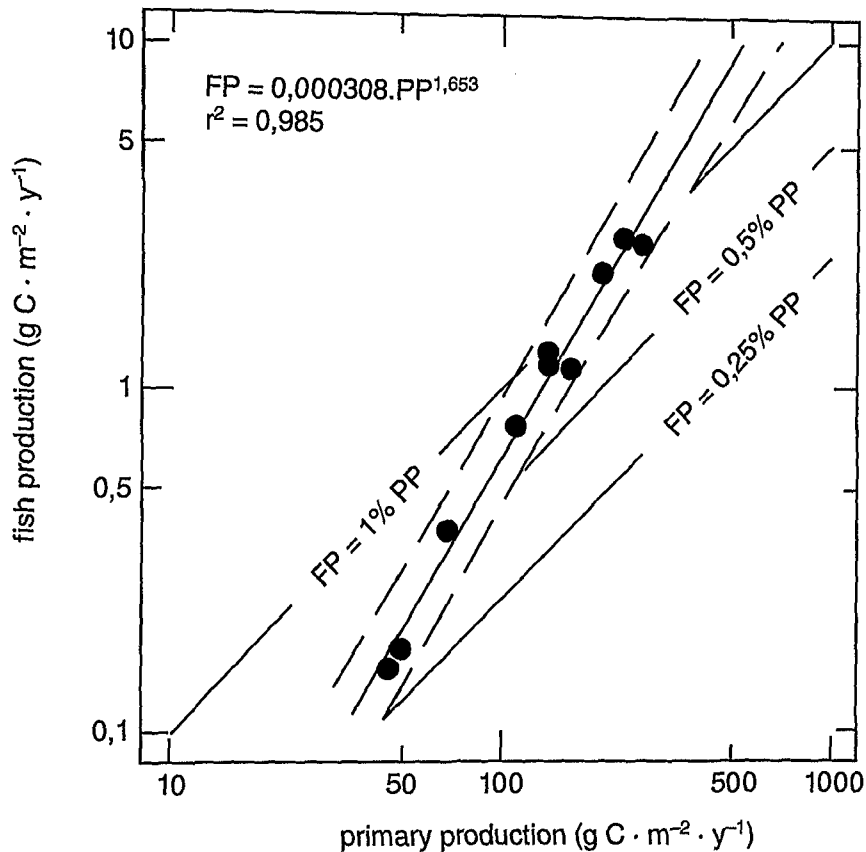


Fig. 1 Log-log plot of fish (and squid) production vs. primary production in different areas of the sea (constructed from data in Iverson [1990])

The biological “CO₂-pump”. Currently a third view on eutrophy is emerging. More phytoplankton production should lead to enhanced sedimentation of organic carbon. If this carbon is transported below the permanent thermocline it will not be recycled for some 10³ years and thus relieve the effect of increasing CO₂-production. An intentional eutrophication by addition of iron has been discussed for those parts of the world oceans where phytoplankton biomass is low in spite of high N and P concentrations (Chisholm and Morel [1991]). Currently, the hypothesis of Fe-limitation (Martin et al. [1990]) seems to be the most plausible explanation of “high-nutrient-low-chlorophyll” area.

Upwelling areas as models for “good” nutrient richness

In contrast to the concern about eutrophication symptoms in the North Sea and Baltic Sea, there is no concern about the eutrophy of upwelling areas, such as the Peru and the Benguela upwelling. The upwelling zones contribute approx. 0.1% to the surface area of the world oceans and about 0.5% to planktonic primary productivity. Their contribution to world fish production and to world fisheries is far out of proportion: Ryther [1969] estimated a 50% contribution to world fish production. Although still cited in many textbooks, this value is almost certainly an overestimate. It is not based on direct measurements but calculated from primary productivity assuming an ecological efficiency of 20% and a food chain length of 2.5 links. This assumption implies that anchovies (*Engraulis spp.*) feed half on phytoplankton and half on herbivorous zooplankton. However, guts analyses of *E. mordax* and *E. capensis* have shown that phytoplankton contribute maximally 20% to the carbon content of the anchovy diet, in spite of high numerical abundances of algae in the gut content (James and Chiappa-Carrara [1990]). Assuming more realistically anchovy on the 3rd trophic level, this would reduce Ryther’s estimate to about 25% of world fish production

at an ecological efficiency of 20% and to 7.5% at an an ecological efficiency of 10%. Even the most conservative estimate implies that the contribution of upwelling areas to world fish production is 25 times higher than their contribution to primary production. This extraordinary efficiency in fish production coincides with an apparent absence of major symptoms of harmful eutrophication (except for reduced water clarity). The absence of deep water deoxygenation problems is an oceanographic feature (permanent advection of water with sufficient O₂-reserves). The absence of nuisance blooms must be attributed to properties of the pelagic food web.

The central question of the pelagic projects within the MARICULT concept is: Can marine food webs elsewhere be managed in order to achieve the desired properties of the upwelling food webs? If yes, how can this goal be achieved and which risks and side effects have to be faced?

The experimental research will be grouped around the following working hypotheses:

- Nutrient richness based on upwelling is characterized by high Si:N ratios (0.7 to 1.5 stoichiometrically). Eutrophication by human waste waters, agricultural fertilisers and combustion processes increases N- and P, but not Si-loading, thereby causing a decline of Si:N ratios.
- Declining Si:N ratios shift the competitive advantage away from diatoms to flagellates (and Cyanobacteria in the Baltic Sea). The non-siliceous taxa contain more toxic species (several dinoflagellates, *Chrysochromulina*, *Nodularia*) or otherwise undesirable species (e. g. *Phaeocystis*).
- Diatom-based food webs are dominated by the short food chain diatoms – crustacean zooplankton – fish. A shift from diatoms to other taxa leads to more complex food webs and a less efficient transfer of energy and matter from primary producers to fish.

If these assumptions are correct a transition from the “harmfully eutrophied” status to the “desirably fertile” status of marine food webs could be brought about by increased silicate loading. A success of such a management strategy would have three desirable effects:

- Suppression of undesirable phytoplankton species
- Enhanced fish yields
- Enhanced CO₂-burial by enhanced sedimentation

Diatoms and the Si:N-ratio

Field evidence. Anthropogenic eutrophication of coastal seas such as the southern North Sea has induced biomass increases and compositional changes of phytoplankton (Cadée [1986], Radach et al. [1990]). The most typical compositional change is a decrease in the relative importance of diatoms in favour of non-silicified algae, particularly flagellates (Cadée and Hegeman [1991]). Some of these flagellates, e. g. *Phaeocystis* (Riegman et al. [1992]) and *Chrysochromulina polylepis* (Maestrini and Granéli [1991]) can form nuisance blooms. An increasing frequency and magnitude of such blooms has been observed worldwide with increasing eutrophication (Granéli et al. [1989], Smayda [1989, 1990]).

Among others, Riegman [1991] and Smayda [1989, 1990] offered decreasing Si:N and/or Si:P ratios as a working hypothesis to explain the shifts from diatom dominance to an increased importance of flagellates. There is ample evidence for an increase in N- and P-inputs into coastal seas, but not for a similar increase in Si-loading (Andersson and Rydberg [1988], Radach et al. [1990]). Atomic Si:N ratios in the German Bight (Helgoland Reede) prior to the spring bloom ranged between 0.5 and 1:1 in the 1960s and range from 0.12 to 0.15 at present. In the Peru upwelling, Si:N ratios range from 0.6:1 to 1:1 (Barber and Smith [1981], Codispoti et al. [1982]). It is assumed that with decreasing Si:N and/or Si:P ratios, more N and P remain available for the growth of non-diatom biomass because silicate sets a limit to diatom growth. This hypothesis requires that diatoms are superior competitors for non-silicate nutrients under silicate sufficiency.

Experimental evidence. The above hypothesis is perfectly consistent with Tilman's [1982] theory of resource competition and has been frequently tested in continuous culture competition experiments with freshwater phytoplankton (summarized in Sommer 1989). There have also been several successful attempts

to apply the resource ratio hypothesis to species shifts in freshwater phytoplankton (Makulla and Sommer [1993], Sommer [1993], Sommer et al. [1993]). The first experimental application of Tilman's competition theory to marine phytoplankton was performed with phytoplankton from the Antarctic Sea (Sommer [1986]). In a first series of competition experiments with mixed cultures of North Sea phytoplankton (4 diatoms, 6 flagellates from various taxa, one cyanobacterium) algal assemblages were exposed to different Si:N ratios at different light intensities (Sommer [1994a]) and at different combinations of light intensity and daylength (Sommer [1994b]). The diatoms in those experiments (*Pseudonitzschia pungens*, *Stephanopyxis palmeriana*, *Neostreptotheica subindica*, *Lauderia anulata*) had particularly high Si-requirements. Therefore, the transition from flagellate to diatom dominance took place at the extremely high Si:N ratio of 25:1. The light climate was decisive for the competitive success of particular species (both among diatoms and flagellates), but not for the flagellate-diatom transition along the Si:N gradient. In a later series of experiments (Sommer [1995, 1996]), the taxonomic basis had been broadened by using six species of diatoms (Table 1). Nitrogen was supplied as ammonium and as nitrate. Here, the transition from flagellate to diatom dominance took place between 0.3:1 and 0.6:1, irrespective of the N-source (Fig. 2). This transition is much more in agreement with the field observations.

Table 1
Phytoplankton species used in the competition experiments shown in Fig. 2

species	higher taxon	dominant at Si:N
<i>Chaetoceros sociale</i>	Bacillariophyceae, centrales	0.6:1
<i>Stephanopyxis palmeriana</i>	Bacillariophyceae, centrales	>27:1
<i>Thalassiosira rotula</i>	Bacillariophyceae, centrales	
<i>Asterionella glacialis</i>	Bacillariophyceae, pennaes	3:1, 9:1
<i>Nitzschia closterium</i>	Bacillariophyceae, pennaes	1:1
<i>Pseudonitzschia pungens</i>	Bacillariophyceae, pennaes	
<i>Dunaliella tertiolecta</i>	Chlorophyta	<0.3:1
<i>Chrysochromulina polylepis</i>	Prymnesiophyceae	
<i>Pleurochrysis carterae</i>	Prymnesiophyceae	
<i>Prymnesium parvum</i>	Prymnesiophyceae	
<i>Scropsiella trochoidea</i>	Dinophyta	
<i>Rhodomonas sp.</i>	Cryptophyta	
<i>Synechococcus sp.</i>	Cyanobacteria	

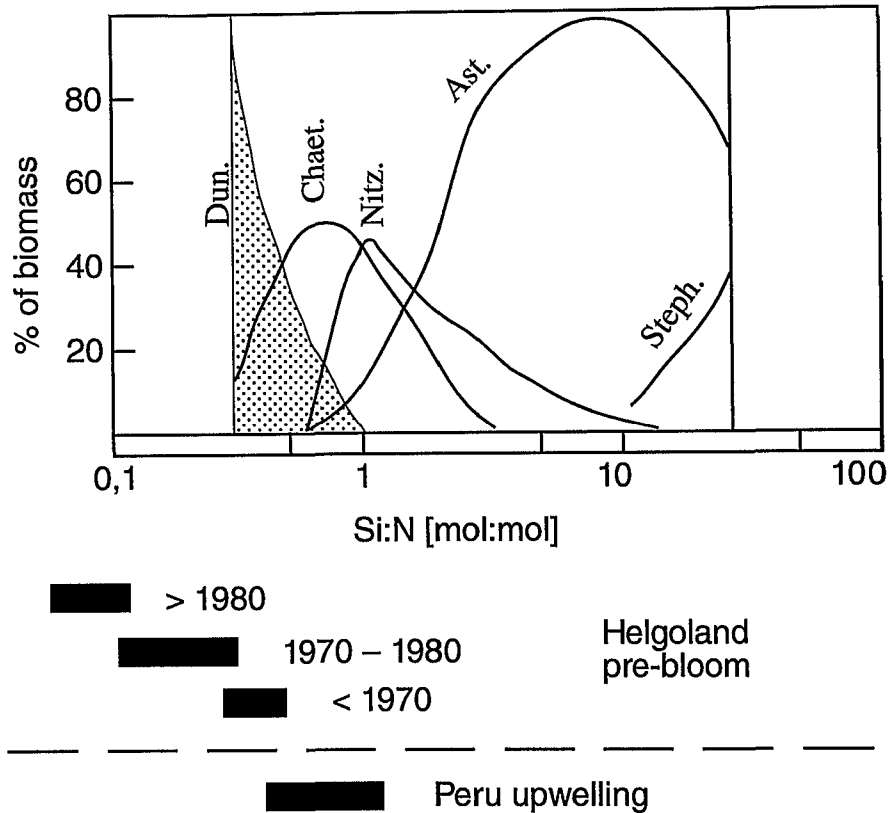


Fig. 2 The competitive success expressed as % of biomass in the final equilibrium community of the diatoms *Stephanopyxis palmeriana*, *Asterionella glacialis*, *Nitzschia closterium*, and *Chaetoceros sociale* and the flagellate *Dunaliella tertiolecta* in competition experiments at Si:N ratios from 0.3 to 27:1, at light intensities of $145 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a photoperiod of 16:8 h (after data in Sommer [1995, 1996]). Comparison to Si:N ratios in the German Bight prior to the spring bloom (after data in Radach et al. [1990]) and Si:N ratios in the Peru upwelling (after data in Barber et al. [1991]; Codispoti et al. [1982]).

Food web structure

Fig. 3 gives a simplified scheme of a the pelagic food web. The relative importance of the different pathways of matter and energy flow have important managerial consequences. From a fisheries point of view it is desirable that as much as possible of the energy and matter flow is channelized through the “classic” food chain: Autotrophic nanoflagellates plus diatoms – herbivorous, crustacean zooplankton (copepods and krill) – planktivorous fish. This food chain is short and most of the phytoplankton species at its base cause little water quality problems. Any kind of detour from this food chain increases the chain length (protozoa as primary herbivores, carnivorous zooplankton) or produces zooplankton which are poor food for fish (tunicates, coelenterates) or even competitors for fish (coelenterates). At present, a good quantitative description is available for some local food webs (e. g. Roff et al. [1990]) but little is known about the causal mechanisms responsible for the particular structure of individual food webs. Filling this gap will be one of the central contributions of MARICULT to biological oceanography. The following explanations are either quite descriptive (e. g. the predominance of picoplankton in oligotrophic waters) or they are untested hypotheses which will be tested experimentally within the MARICULT projects.

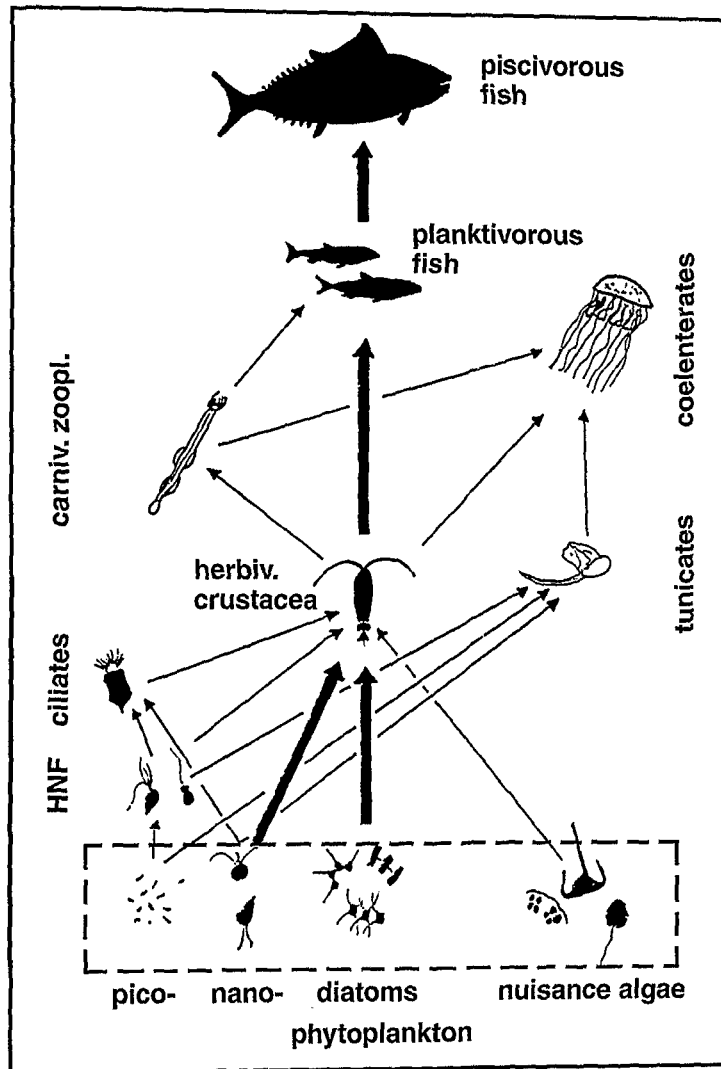


Fig. 3 A generalised scheme of the pelagic food web. The thick arrows indicate the pathways considered "desirable" from a fish production point of view.

Phytoplankton and zooplankton nutrition. Primary productivity of oligotrophic waters is dominated by picoplankton, e. g. the cyanobacterium *Synechococcus spp.* (Stockner and Antia [1986]). They are the primary food source of protozoa, especially heterotrophic nanoflagellates (HNF). A predominance of picoplankton channelizes the energy flow through the "microbial loop" (Azam et al. [1983]) and contributes little to the direct nutrition of herbivorous crustaceans. A mix of autotrophic nanoflagellates and diatoms dominates phytoplankton in the upwelling zones throughout the year and during the spring bloom of stratifying, nutrient rich waters. Those algae are directly available as food source for herbivorous crustaceans. There is some recent evidence that some copepod species cannot grow or reproduce on a diet composed of some single diatom species (Uye [1996]) but this seems to be no problem with the natural mix of phytoplankton species. Blooms of large, "nuisance" algae are typical of the stratified summer period in waters which receive elevated inputs of N and P by anthropogenic eutrophication. They form "red tides" (dinoflagellates), foams (*Phaeocystis*) and surface scums (filamentous cyanobacteria). Many of them are toxic and make seafood toxic for men. Because of their size they are a poor food source at least for the smaller crustaceans, the largest colonies and some of the toxic species may be inedible for most zooplankton species.

Herbivorous zooplankton. There are three major groups of herbivorous zooplankton: protozoa, crustaceans, and tunicates. Protozoa are favoured by a predominance of small (pico-) phytoplankton and are too small to be a suitable food for fish. Crustaceans are the classic food for planktivorous fish. Their bio-

mass is rich in protein because their muscular bodies are adapted to rapid flight from predators (Verity and Smetacek [1996]). Tunicates have a suitable size for fish but they are a particularly poor food because of their high water content. This implies that fish cannot retrieve much carbon and energy even from completely filled guts. As fine-particle filtrators, tunicates seem to have a competitive advantage over crustaceans when the phytoplankton size spectrum is skewed towards the small size classes. High predation rates by planktivorous fish should give them a selective advantage over crustaceans.

Carnivorous zooplankton. Carnivorous zooplankton compete with planktivorous fish for food and at least some of them are prey for the fish as well. Because of their large body size the muscular among them are even preferred prey items. Generally, fish predation will keep them in check and minimize this detour from the direct food chain. However, gelatinous megazooplankton (coelenterates) are avoided by most pelagic fish (exception: *Mola mola*) and are predators on juvenile fish. There is some concern that coelenterates are currently expanding at the expense of fish (Legovic [1987]). Because of a shortage of reliable reference data from earlier times it is not clear whether this is a real trend. Its causal explanation is even less clear: Environmental deterioration or relief from competition by overfishing?

The MARICULT-perspective

If the working hypotheses of MARICULT are right, there is a possibility in principle of fertilizing parts of the sea in order to harvest more without producing too many harmful eutrophication effects. Without touching the oligotrophic oceans two management schemes seem possible:

- Additional supply of Si where N and P loadings have been increased by eutrophication and further efforts to revert eutrophication are not feasible or cost-effective any more.
- Additional nutrient supply at the appropriate Si:N and Si:P ratios where the spring blooms start under eutrophic conditions and summer stratification leads to a loss of nutrients and a subsequent summer depression of phytoplankton production, e. g. in the waters off Norway.

Risks and side effects. At present, our understanding of marine pelagic community ecology is not sufficient to evaluate the risks and side-effects of such strategies. Conceivable risks are:

- Diatom growth might fail under stratified summer conditions even if Si:P and Si:N ratios are adequate.
- Even if diatoms develop, it might be the wrong species. Some planktonic diatom species are toxic, e. g. *Pseudonitzschia pungens* (Bates et al. [1991]) which can cause amnesic shellfish poisoning by domoic acid.
- Some diatom species might be unwelcome because they are not well usable by copepods. *Coscinodiscus wailesii* is too large to be edible, some other species (e. g. *Phaeodactylum tricornutum*) can produce repellants against copepods (Shaw et al. [1995]).
- Oxygen deficiency in deep waters might increase because an increased production of diatoms will also increase the sedimentation of organic matter. This increase of sedimentation also has a positive side effect by speeding up the biological pump of CO₂.
- Possible side effects at higher trophic levels include the increase of coelenterates at the expense of fish and the increase of tunicates at the expense of planktonic crustacea.
- A loss of diversity is an almost inevitable consequence of managing food webs in the proposed way because a complex food web will be reduced to simple food chains.

Scheduled experiments within COMWEB. Several levels of experimentation will be combined in order to analyse nutrient effects on the lower part of the pelagic food web. The combination of several scales is necessary because of the inevitable trade-off between the rigour of experimental control (maximal in laboratory experiments) and the avoidance of artifacts because of unnatural experimental conditions (maximal in comparative field observations). **Microcosm experiments** (at Kiel, D) in the laboratory will use two-chamber flow-through cultures to study the bottom-up propagation of the impact of changed nutrient ratios and concentrations on phytoplankton species composition and its effect on zooplankton. **Mesocosm experiments** (near Tvärminne, SF and Blanes, E) will use enclosures in the sea of several m³ to study the impact on nutrient regimes. In a **fjord experiment** (near Trondheim, N) a small fjord of about 27 ha surface

area will first be studied in its present, unmanipulated state and then its nutrient regime will be manipulated according to the MARICULT philosophy. The response of plankton communities to the **natural variability** of nutrient supply will be analysed by a long-term data series from a standard station off Belgium. The data from all levels of experiments will be used to construct a model of matter and energy flow in pelagic food-webs.

Environmental risks and long-term perspectives. The total use of nutrient salts for the COMWEB experiments is estimated to be about 2–3 kg · y⁻¹ which compares with an annual loading of the North Sea by terrestrial sources in the order of 10⁶ tons. The actual hazard caused by the COMWEB experiments is therefore absolutely insignificant, even the local risk during the fjord experiment will be less than in the classic eutrophication experiments in the Canadian Experimental Lake Area (Schindler [1988]). While not causing any significant direct risk for the environment, the results of the projects within MARICULT might eventually shake the central paradigm of environmental management of aquatic ecosystems: the unconditional fight against eutrophication, at any cost and anywhere. COMWEB will certainly not end up in the recommendation to give up eutrophication control efforts or to fertilize the sea. COMWEB and its companion project FAPPE are too much concentrated on the “lower” food web (up to the copepods) to end up in such a recommendation.

The next generation of MARICULT projects, however, will directly face that issue. There seems to be no big chance that a growth of human the population to 10 billion by the middle of the next century can be avoided. Food supply will become a problem of production, not only of distribution. The agricultural pressure on terrestrial ecosystems cannot be expanded much more. On the contrary, a loss of arable land is to be expected. Therefore, the sea will have to share some part of the burden which so far has been carried by the terrestrial systems. The increased demand on marine biological resources cannot be met by traditional fisheries which are still at the level of hunters and gatherers. There will be a pressure towards a “marine agriculture” extending far beyond local fish farming in net cages. MARICULT is an effort of the scientific community to know about the risks and perspectives of marine agriculture before there are urgent economic and political demands to start it on a large scale.

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