

MATHEMATICAL MODELS FOR AQUATIC POPULATIONS

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ABSTRACT

High inherent spatial and temporal variability in the abundance of marine populations does not allow for the simple concept of a natural steady state with populations close to a more or less constant carrying capacity. On the contrary, a variable carrying capacity which induces fluctuations in population number often seems to be the rule in marine pelagic environments. The effects of human impact are often superimposed upon this natural variability, and by means of traditional monitoring and statistical analyses it is non-trivial to discriminate between natural variability and human influence even if the latter may be severe. The situation is improved if the mechanisms causing the natural variability are known. Through realistic mathematical modelling of human influence and of the mechanisms behind natural variability, we may provide scientific answers about the role of human impacts in specific situations. Mathematical models for marine pelagic organisms range from simple analytical equations to complex simulation models, which include three-dimensional water movement. While simple analytical equations may demonstrate the general impact of human actions in an idealized environment, more complex simulation models may be appropriate when it is necessary to take fluctuating environmental conditions into consideration. Examples of both categories of models, dealing with enhancement and marine eutrophication, are provided.

INTRODUCTION

Can mathematical models help us to assess human impacts on self-recruiting populations? While Stenseth (1993) concentrated on the terrestrial biota, I will restrict myself to the aquatic, or more correctly, to the marine pelagic environment. A further restriction is that number of individuals will be the important variable. Hence, I will discuss models of human impact affecting the numbers of animals or their biomass in the marine environment. Mathematical models of marine populations range from simple analytical equations to complex simulation models which include three-dimensional water movement. As will be demonstrated later, both these extremes of model categories are useful in order to analyze the dynamic nature of marine populations. While simple analytical equations may demonstrate the general impact of human actions in an idealized environment, the simulation models may be more appropriate when it is necessary to take a fluctuating environment into consideration. I will begin with some rather basic ecological models and make some comments on the important concepts of "maximum sustainable yield" and "carrying capacity". Then I will review some of my own research dealing with marine modelling and human impacts before presenting my conclusions about the role of modelling in the assessment of human impacts on natural populations.

MODELS FOR POPULATION GROWTH

Mathematical models of marine pelagic populations are, of course, no different in principal from those of terrestrial populations. As given in most introductory text books in ecology (e.g., Begon et al. 1986) the fundamental equation for animal or plant numbers is expressed as:

$$N_{t+1} = N_t + B - D + I - E \quad (1)$$

where N_t is the number of individuals at time t , while B , D , I and E are the number of births, deaths, immigrants and emigrants during the time between t and $t + 1$. This equation, however, is rather descriptive and does not serve as a very valuable predictive tool. Most predictive models are based on the simple fact that the number of births in a population depends on the number of individuals in the population. This is commonly expressed for a closed population as:

$$dN/dt = rN \quad (2)$$

which simply states that the increase in population number depends on both the number N itself and the growth rate r , the instantaneous birth rate minus the death rate. Under environmental restriction, such as space or resource limitations, r tends to decrease because of an increased number of deaths and a decreased number of births. The classical, and very instructive, way to account for this is simply to assume that the realized population growth rate r decreases linearly as the population size approaches K , a “carrying capacity”:

$$dN/dt = rN = r_{\max} (1 - N/K) N \quad (3)$$

where r_{\max} is the maximum growth rate that can be approached only at a population size well below the carrying capacity. The carrying capacity has the same unit as N and represents the number of individuals that the environment can sustain. Consequently, population sizes above the carrying capacity make the number of deaths higher than the births which results in a population decline (negative r). In resource management the idea of a carrying capacity has led to the concept of a “maximum sustainable yield”. This concept relies on the assumption that the maximum absolute growth dN/dt , which often is applied also to growth in biomass instead of individuals, is reached at some intermediate population size (or mass) between 0 and K (Fig. 1). Hence, the highest long term sustainable

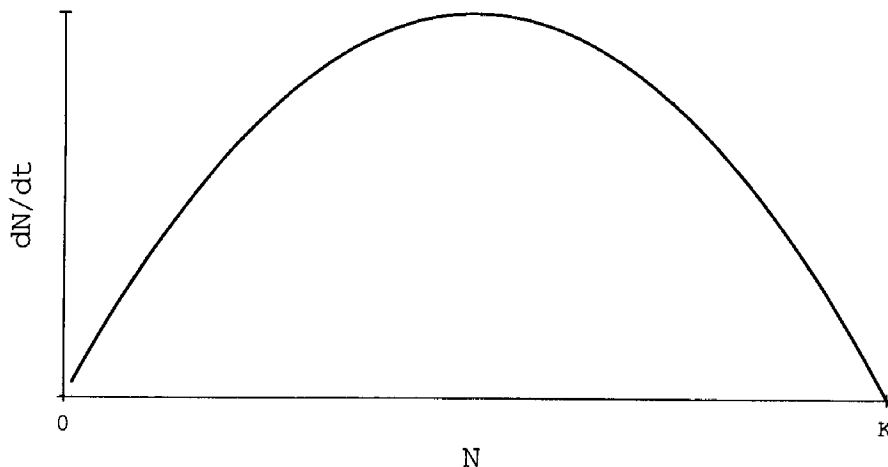


Fig. 1. The concept of carrying capacity K and maximum sustainable yield (see Equation 3). The population increase dN/dt is at a maximum at a population level N below the carrying capacity ($N = K/2$ in the present illustration). Hence the sustainable yield is maximized by keeping the population at this level.

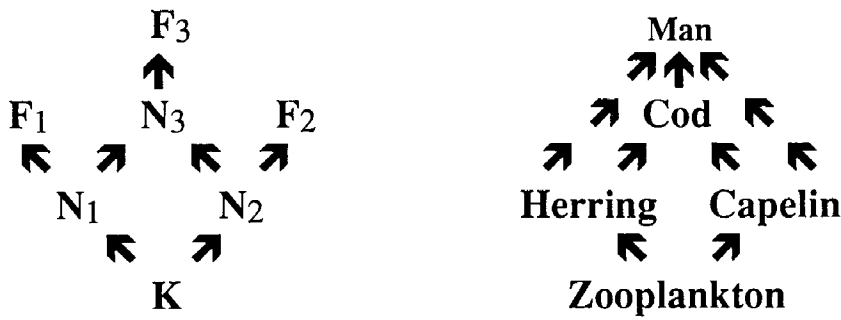


Fig. 2. The multispecies system. Fishery on, or enhancement of, one population is likely to influence the other populations. Furthermore, variability in a “common” carrying capacity is likely to propagate into the food web. Equations representing such systems (see Equation 4) become complex and tend to be unrealistic due to missing knowledge about the processes linking the different populations.

yield may be obtained by keeping the population size at this “optimum”. Apparently this gives a straightforward and sound rationale for the management of populations. A population size above the optimum calls for more intensive exploitation, while a size below the optimum calls for reduced exploitation or enhancement. However resource managers are faced with the problem of estimating the optimum population size. Equation (3) suggests that this size amounts to 50% of the carrying capacity (Fig. 1), but this result is based on the *assumption* that density dependent processes lead to a linear decrease in r as population size approaches K . Furthermore, in the multispecies situation several species may be constrained with a common carrying capacity in addition to predator-prey relationships, which means that exploitation or enhancement of one population influences the other populations (Fig. 2). Of course, such a system also may be represented mathematically, for example (see Fig. 2 for definition of the food web):

$$\begin{aligned}
 dN_1/dt &= r_{\max 1} [(K - N_1 - kN_2) / K] N_1 - a_1 N_1 N_3 - F_1 \\
 dN_2/dt &= r_{\max 2} [(K - N_1 - kN_2) / K] N_2 - a_2 N_2 N_3 - F_2 \\
 dN_3/dt &= a_3 a_1 N_1 N_3 + a_3 a_2 N_2 N_3 - F_3
 \end{aligned}
 \tag{4}$$

Such multispecies models may be quite complex, but their realism increases with complexity as long as the mechanisms in the model are well-understood and can have a realistic mathematical description. Unfortunately, above this level the realism and predictability of ecologi-

cal models tends to decrease as the complexity increases. As will be argued later, this decrease is not linked to the complexity itself, but rather is a consequence of missing knowledge about the detailed ecological and biological processes governing the dynamics of the different populations. Hence, state-of-the-art knowledge in ecology puts strong limits on the possibility of applying models in order to simulate real situations, as the detailed mechanisms are essentially unknown or not adequately described mathematically. Nevertheless, such models may be extremely useful as analytical tools. In the following I will not focus on complex multispecies models, but rather return to the simple concept of a carrying capacity as defined in Equation (3).

VARIABILITY IN CARRYING CAPACITY

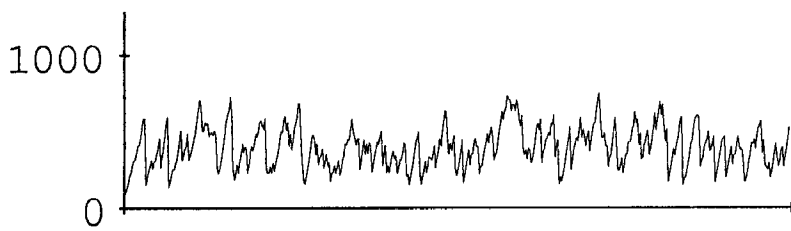
The hope of ensuring a maximum sustainable yield in the exploitation of wild populations rests on a basic assumption that there is a certain degree of constancy in the carrying capacity for the populations considered. However, this might not be a tenable assumption. Let us define a simple model, frequently encountered in text books, for a population which recruits at discrete intervals (one year), but in which the carrying capacity fluctuates from one year to another:

$$N_{t+1} = N_t e^{(1 - N_t/K)r_{\max}} \quad (5a)$$

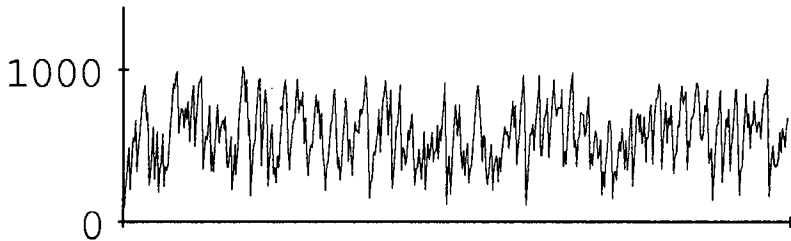
and

$$K = K_{\min} + \sigma \quad (5b)$$

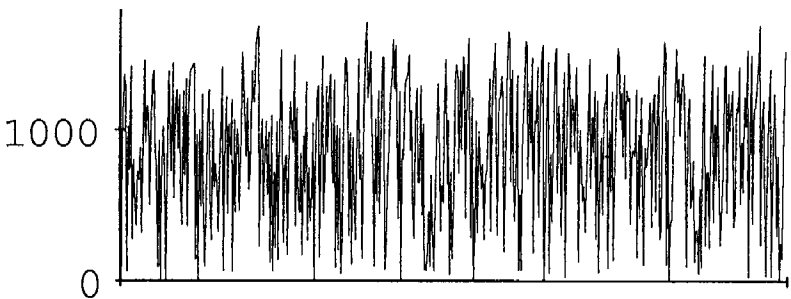
where K_{\min} is a minimal carrying capacity and σ is a random contribution. A variable carrying capacity leads to fluctuations in population abundance such as depicted in the 500 years simulation in the upper panel of Figure 3. As demonstrated by Hylan (1993), abundance indices of marine fish populations (especially at high latitudes) suggest large natural fluctuations which cannot be due to human influence (e.g., the variability in the Norwegian herring stock during the last two centuries). Such fluctuations may be interpreted as a result of a variable carrying capacity. If this is the case, then in enhancement programs where the release of individuals is thought to be a way to stabilize the fluctuations in the populations by turning a "bad" year into "good" year, the opposite may occur (Fig. 3). With releases of low numbers of animals the average stock size is increased, but the fluctuations are also increased. Increasing the size of the enhancement increases the oscillations and, not surprisingly, with a



Impact of enhancement:



low



medium

Fig. 3. Simulated population development over 500 years when carrying capacity fluctuates randomly between 100 and 1000 individuals (Equation 5). The two lower graphs simulate the effects of enhancing the population with a constant number of released individuals each year, either low, 100 individuals, or medium, 1000 individuals. Although this simple model illustrates that the average yield may be increased by enhancement, the population fluctuations are likely to increase which is often the opposite of the goals of enhancement programs.

high degree of enhancement the average stock size is actually decreased as a result of the magnification of density dependent processes.

The increased oscillations resulting from both release sizes can be intuitively explained. Release of individuals in a year when the carrying capacity decreases below the population level results in worse conditions for the already existing population through increased intraspecific compe-

tition. On the other hand, in a year with high carrying capacity, additional releases will obviously tend to strengthen population growth. Although the above model (Equation 5) is highly simplified, and neglects age structure, maturation, etc., it illustrates the importance of considering variability in the carrying capacity. The question is then: How variable is the carrying capacity for marine populations?

The dominant herbivore *Calanus finmarchicus* is a main prey item for planktivorous fish, such as herring and capelin, in the North Atlantic, Norwegian Sea and the Barents Sea. In the northernmost regions the standing stock of this copepod is dominated by individuals produced during the spring phytoplankton bloom and a yearly generation time is the prevailing situation. Egg number is on the order of 10^3 per female, and hence the reproductive potential of the copepod is rather low compared to one of its predators, the capelin, which has a generation time of two years and an egg number of 10^4 . The adult cod, preying on capelin, although the early life stages feed on *Calanus finmarchicus*, has an even higher egg number of 10^6 , is iteroparous, and has a generation time of years. Hence, contrary to many terrestrial systems the reproductive potential is quite high for the large carnivores. On the other hand, the relatively low reproductive potential in *Calanus finmarchicus* means that the population cannot readily compensate for reductions due to changes in the physical oceanic environment or to increases in predation pressure. In the Norwegian Sea, Barents Sea and along the coast of Norway the physical environment may fluctuate considerably from one year to another due to variable influxes of warm Atlantic Water and variable meteorology (Skjoldal et al. 1993). The predation pressure on *Calanus finmarchicus* is also likely to fluctuate as for example the herring stock undergoes large fluctuations (in the range of 10^5 to 10^7 metric tons) both in periods with and without intensive fishing.

Given this background, natural variability at the herbivore level, and hence in the carrying capacity for the higher levels in the food chain, should be the rule rather than the exception at high latitudes. Actually, realization of the possible role of *Calanus finmarchicus* as a bottleneck has led to the initiation of a Norwegian multidisciplinary research program in the Norwegian Sea, with the goal of providing increased predictability concerning fish resources through increased knowledge about the fundamental processes responsible for the large natural fluctuations (Skjoldal et al. 1993).

A research program on cod enhancement along the western coast of Norway has revealed several important characteristics about the impact of

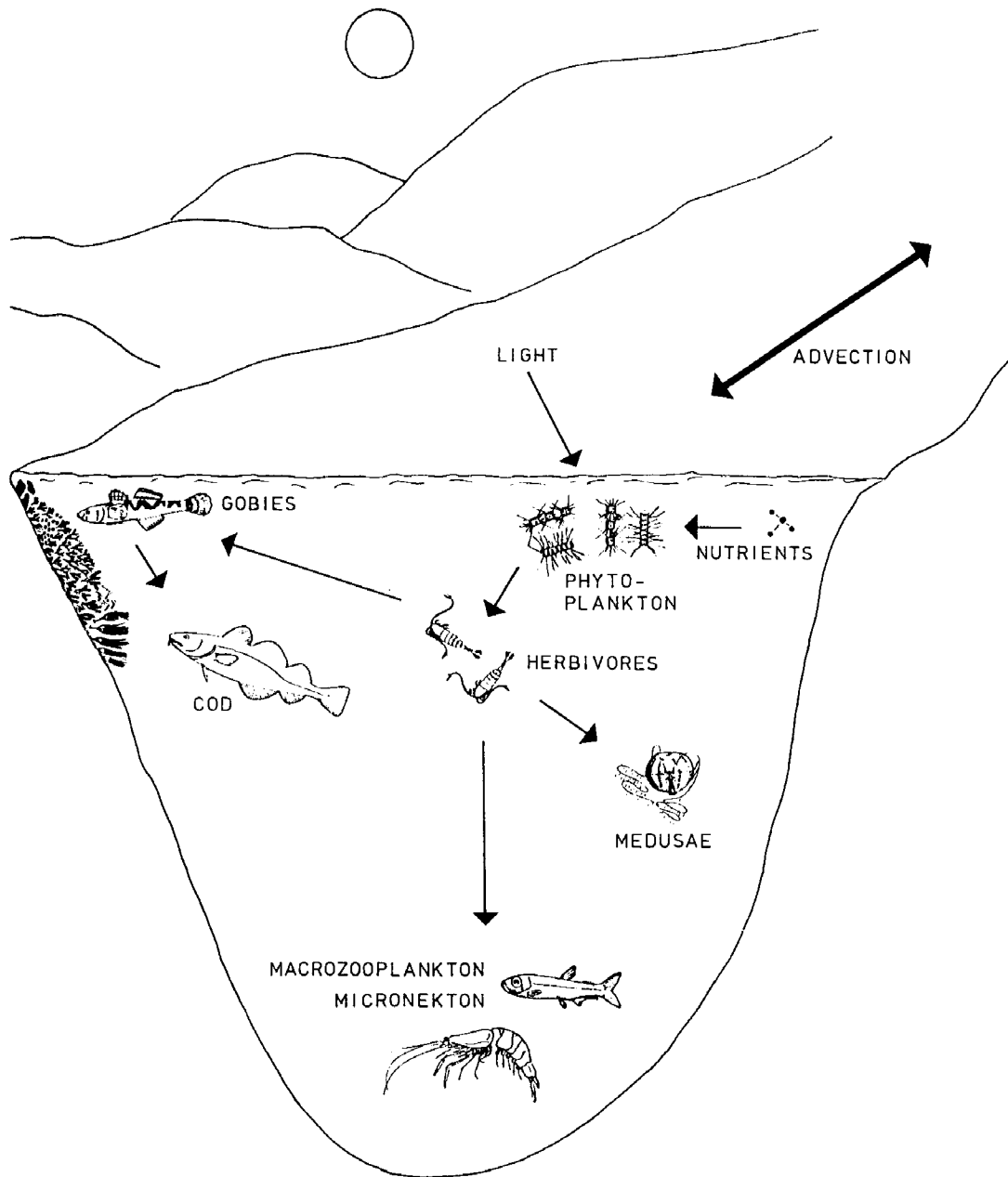


Fig. 4. A simple representation of the food web in a fjord on the west coast of Norway. Juvenile cod eat gobies hiding in the sublittoral macrovegetation. The gobies, and thereby the cod, depend on the supply of zooplankton advected into the fjord and into their restricted nearshore habitat. Similarly, large numbers of mesopelagic fishes hiding in the deep dark during daytime predate upon the advected zooplankton. The advection of zooplankton is highly variable and is likely to propagate into the stocks of stationary fish populations (see text). (From Giske et al. 1991 with permission.)

a fluctuating carrying capacity on population dynamics (Aksnes et al. 1989, Giske et al. 1991, Salvanes et al. 1992, Fosså et al. 1993). Here, planktivorous gobies were found to be a main prey item for juvenile cod (Fosså 1991). Gobies find shelter in the macrovegetation which is restricted to a narrow sublittoral zone along the shoreline (Fig. 4). The goby population, and thereby the juvenile cod, depend on zooplankton availability in this sublittoral habitat which is rather small compared to the pelagic habitat. The local production of zooplankton in the sublittoral habitat is negligible, and goby biomass is sustained on zooplankton advected from the pelagic habitat. Hence, the carrying capacity of the gobies and juvenile cod is essentially determined by this advective supply. Both the advective input and the standing stock of zooplankton in the coastal areas, however, depends heavily on the wind direction as southerly winds along the Norwegian coast in summer cause a transport of water and zooplankton in the upper 20 m towards the coast, while northerly winds result in transport of plankton away from the coast (Aksnes et al. 1989). Furthermore, the net transport of zooplankton depends on the standing stock in the oceanic water outside the coast, which again is influenced by large scale fluctuations as previously mentioned. To summarize, we may define a system with stationary predators (goby, cod) and advected prey (Aksnes et al. 1989). For the prey the equation is

$$dB/dt = r(1 - B/K)B - aBC + \beta(B_b - B) \quad (6a)$$

and for the predator,

$$dC/dt = aeBC - dC \quad (6b)$$

where B is local plankton abundance, $r(1 - B/K)$ is local growth rate of zooplankton, β is the advective rate at the boundary of the system, B_b is the boundary prey abundance, C is the local predator abundance while a , e and d are coefficients concerning predation, assimilation and mortality. In Norwegian coastal areas the advective term rather than local zooplankton growth is likely to dominate (Fig. 5) the formation of biomass of the planktivores and of the predators relying on the planktivores (Aksnes et al. 1989, Giske et al. 1991, Salvanes et al. 1992). Measurements indicate that the advective input of zooplankton is highly variable (Aksnes et al. 1989, Giske et al. 1991), and observations indicate that both goby production and cod growth are enhanced several fold in the years with high zooplankton availability (Fosså 1991). Such variability in the carrying capacity seems not to be restricted to coastal areas, but may apply to oceanic systems also. As such, variability in the advective input of *Calanus fin-*

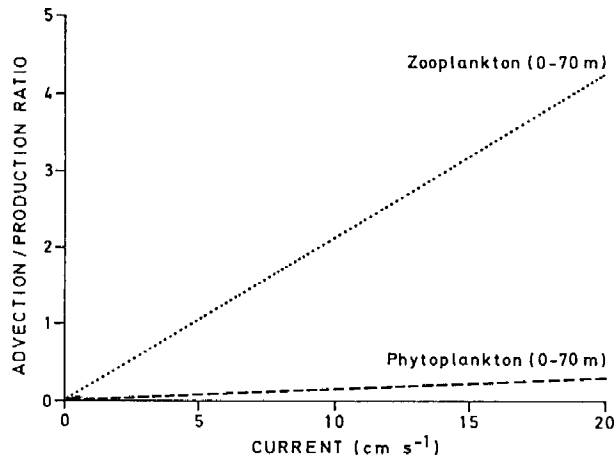


Fig. 5. Scale analysis of the role of advection relative to production for the availability of zooplankton in a fjord (on the basis of Equation 6). Y-values above 1 indicate that advection dominates over local production in the renewal of the plankton biomass in the fjord. Such analyses indicate that zooplankton in coastal areas, and hence the carrying capacity of the planktivores, is often dominated by advection rather than local production. (Modified after Aksnes et al. 1989.)

marchicus into the Barents Sea from the Norwegian Sea probably affects severely the herring, capelin and cod production in this area.

As the above example makes clear, analysis of advective systems should not be restricted to an analysis of the biological mechanisms, but has to be based also upon models encompassing the processes responsible for the variability in the advective terms themselves. Here, meteorology and oceanography are as fundamental as predator-prey interactions. Fortunately, compared to biology, these scientific disciplines are well understood and can readily be included quantitatively in explanatory models. Nevertheless, integrative modelling approaches are often refuted by ecologists because such attempts are often claimed to involve ignorance of the biological complexity. Of course, physical realism in a model can not substitute for missing biological realism, but neither can biological realism substitute for physical realism.

MODELS OF PHYTOPLANKTON DYNAMICS

For four major reasons phytoplankton production is attractive for ecological modelling. First, growth is well represented by the equation $dN/dt = \mu N$ where N is the number of individuals, t is time and μ is the instantaneous growth rate (in the absence of mortality). This equation describes a continuous process whereas production is made up of discrete events. However, for phytoplankton, the number of individuals is high, the generation time is short and unsynchronized, and the assumption about continuity seems adequate. Second, because phytoplankton divide by binary fission, fecundity is constant. Hence, the instantaneous growth rate μ depends only on generation time T_g according to the relationship $\mu = \ln 2/T_g$. Third, phytoplankton growth potential is generally much higher than is the growth potential of their predators. Thus, when favorable conditions occur in terms of light and nutrients, numbers of phytoplankton are likely to increase exponentially until resource limitation occurs. Fourth, mobility at least horizontally is dominated by water movements rather than by the behavior of individuals. Stated somewhat provocatively, phytoplankton modelling is essentially a question of correct representation of generation time or growth rate, whereas at the higher levels of the food-chain the modeler is faced with such complexities as age classes (N becomes a vector), maturation times, variable fecundity including density dependent mechanisms, predators with similar growth potential as the prey, and mobility dominated by behavior. Of course, as in higher animals, phytoplankton growth is also regulated by complex processes at the cellular and biochemical levels. Furthermore, phytoplankton consist of an unmanageable number of species (at least to the modeler), each having different growth characteristics. Nevertheless, I believe that it is within the area of primary production and nutrient dynamics that ecology is closest to its goal of providing predictive models through integration with physics, i.e., physical oceanography and meteorology. The exponential decrease in computing costs is likely to accelerate this development in the near future. Current research on ocean-climate relations and eutrophication also is stimulating development of more realistic primary production models.

Realistic biology requires realistic physics, and this is especially true for primary production modelling where water movement is a most important forcing function for nutrient and phytoplankton dynamics. The local change in phytoplankton biomass is commonly expressed:

$$\frac{\delta P}{\delta t} = -(w + s) \frac{\delta P}{\delta z} - u \frac{\delta P}{\delta x} - v \frac{\delta P}{\delta y} + \frac{\delta}{\delta z} K_v \frac{\delta P}{\delta z} + \frac{\delta}{\delta x} K_H \frac{\delta P}{\delta x} + \frac{\delta}{\delta y} K_H \frac{\delta P}{\delta y} + (\mu - m) P \quad (7)$$

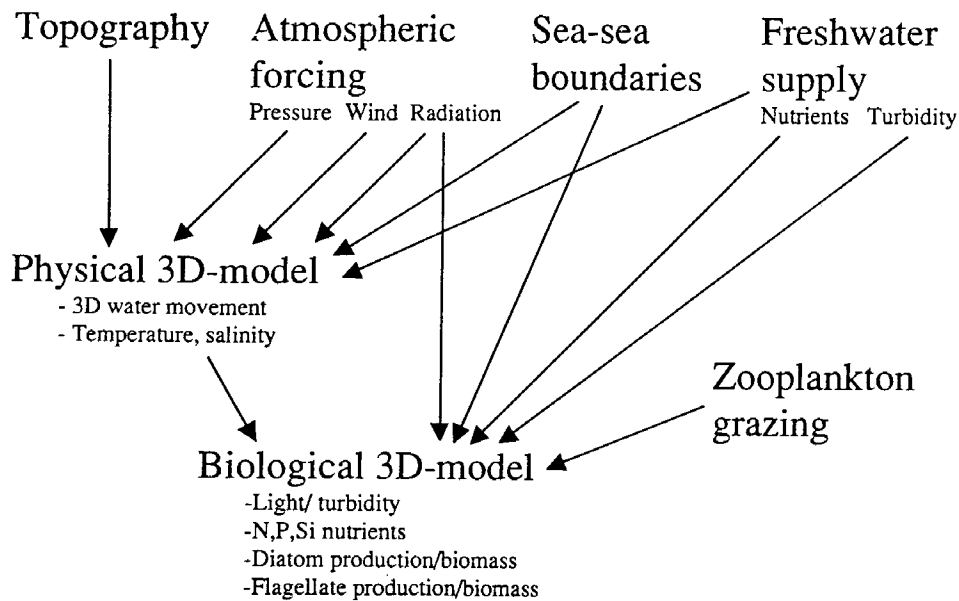


Fig. 6. Main components of a coupled physical-biological three-dimensional simulation model of phytoplankton.

where B is phytoplankton biomass and t , z , x and y are time and spatial dimensions. Phytoplankton sinking is denoted s , while transport due to water movement is denoted w , u and v . K_v and K_H are the coefficients of turbulent mixing in the vertical and horizontal. Finally μ and m represent local phytoplankton growth and mortality, respectively. Hence, a primary production model is likely to be dominated by the physical rather than the biological terms. Furthermore, realistic representation of the two kinds of transports, laminar and turbulent flow, requires realistic topographic and atmospheric representation (Fig. 6). Such coupled models may become quite complex especially at the physical level. The realism of ecological models is likely to decrease at high complexity levels, but as earlier emphasized, complexity is not a threat as long as the mechanisms are well known.

I will give two examples to illustrate the potential use of coupled physical-biological models at the phytoplankton level. The first deals with a fjord system in Lindåspollene, western Norway, where the impact of nutrients supplied with the freshwater was investigated (Aksnes and Lie 1990). Measurements indicated nutrient depletion in the uppermost 15 m during summer. Furthermore, the primary production (measured as ^{14}C uptake) was highest in the uppermost five meters. The water column was highly stratified which effectively prevented supply of new nutrients from

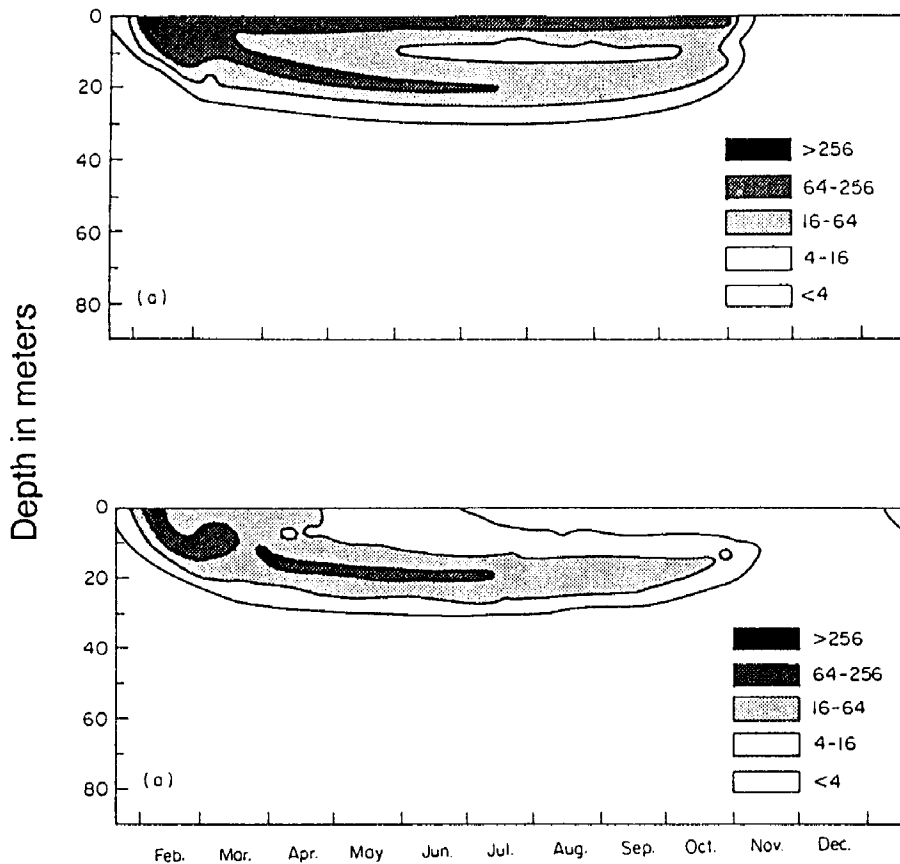


Fig. 7. Simulated phytoplankton production ($\text{mg C/m}^3/\text{d}$) in a fjord when nutrients are supplied with the freshwater runoff (upper panel), and when they are removed (lower panel). Such sensitivity analyses are extremely valuable in the assessment of human impact related to eutrophication problems. (Modified after Aksnes and Lie 1990.)

the deep, nutrient rich water. The high primary production in the uppermost meters was measured also in water columns that were trapped in plastic enclosures for several weeks. On the basis of these observations it was concluded that the elevated production close to the surface was due to high local remineralization of nutrients which gave rise to “regenerated” production, rather than to the new nutrients which may give rise to “new” production, supplied with the freshwater, as the enclosures were not supplied with such nutrients during the experiments. The simulations gave the same picture as the observations; namely, a highly stratified nutrient depleted water column with elevated production in the surface layer during summer (Fig. 7). The importance of remineralization of

nutrients was also substantiated as the model indicated that 61% of the total annual primary production was due to local remineralization. Removal of the freshwater nutrients, however, significantly affected the primary production as the surface production during summer was significantly lowered (Fig. 7). Thus, a hypothesis drawn from the simulation was that remineralization of nutrients are important for the *magnitude* of the production maximum in the surface layer, but that the *existence* of the maximum is due to nutrients supplied with the freshwater. This hypothesis assumes that the rate of remineralization depends on the standing stock of the herbivores in the surface layer, which again depends on the freshwater nutrients that have been supplied within the *lifetime* of the herbivores. Therefore, a cessation in the supply of new nutrients would result in a gradual decrease in herbivores, followed by a decline in remineralized production and total primary production. Actually, the measurements made in the enclosures (Skjoldal et al. 1983) support this hypothesis as the primary production close to the surface decreased with the duration of the experiments. Hence this example clearly demonstrates how simple sensitivity analyses (in this case the sensitivity of primary production to alternation in freshwater nutrients) may generate hypotheses about human influence (increased nutrient supply) that are difficult to assess on the basis of measurements alone.

The second example deals with a simulation model developed for the North Sea (Svendsen et al. in preparation, Ulvestad et al. in preparation), which was used to analyze possible influence of human impacts on the development of a toxic phytoplankton bloom, composed of *Chrysochromulina polylepis*, during the spring of 1988 (Fig. 8). Observations before and after the bloom are summarized in Maestrini and Graneli (1991) and Skjoldal and Dundas (1991). The first indications of the bloom were unusual behavior of the fish, and then death, in a fish farm in the Gullmar Fjord, Sweden, on 9 May 1988. During the next week the lethal phenomenon moved to the north. On 17 May, fish mortality was attributed to the presence of the microalga *Chrysochromulina polylepis*. An alga front spread along the coast of Norway, up to the Bokna Fjord just north of Stavanger. By the end of the third week, the bloom was also observed in the southern part of the Kattegat, in the Belt and the Sound, at the entrance of the Baltic Sea. The density of the alga was frequently higher than 10^7 cells per liter. It was speculated early on that the massive exceptional bloom was stimulated by nutrients released from the large rivers flowing into the southern part of the North Sea during the winter and early spring of 1988 (Aksnes et al. 1989). Water with a high nutrient

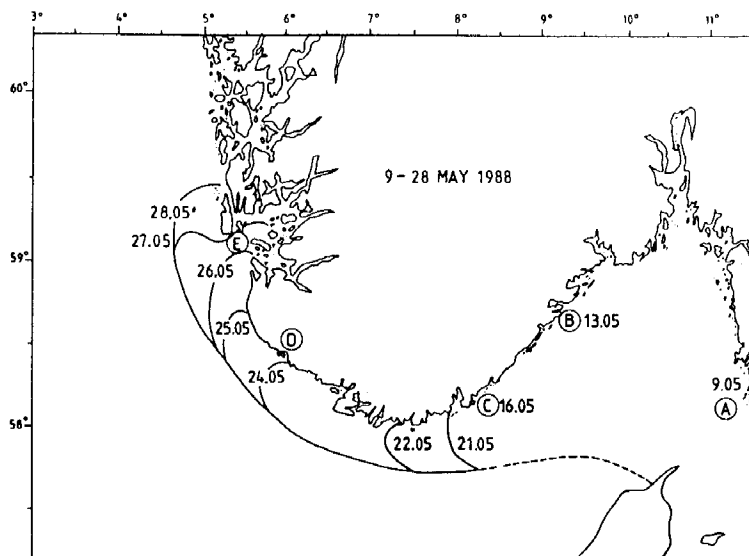


Fig. 8. Spreading of the *Chrysochromulina polylepis* bloom along the Norwegian coast during May 1988. The numbers refer to the dates for the position of the algal front. (From Aksnes et al. 1989.)

content and with distorted N:P:Si ratios, i.e., high in N and low in Si, was advected by the Jutland Current from the southern North Sea into the Skagerrak/Kattegat area during the winter of 1987/1988 (Aksnes et al. 1989, Skjoldal and Dundas 1991). Precipitation during that winter was higher than normal, causing increased input of nutrients by land runoff into the Skagerrak/Kattegat area. A spring bloom of diatoms depleted the silicate, leaving a still high nitrate level and a high N:P ratio in the deeper water. The outflow of brackish water from the Baltic Sea was considerably greater than normal, resulting in a high entrainment of the underlying water in the Kattegat. Calculations indicate that 1000-2000 tons nitrogen per day were entrained into the surface layer. Because of this entrainment, *Chrysochromulina polylepis* was fed with nutrients possibly of an anthropogenic origin. Also it was likely that the high N:P ratio of the underlying water resulted in P-deficiency during the *Chrysochromulina polylepis* bloom. This is significant because experimental evidence exists that P-deficiency results in increased toxicity of this and related species (see Skjoldal and Dundas 1991 for references).

This example emphasizes the role of anthropogenic nutrients in the development of the exceptional bloom. Other authors such as Maestrini and Graneli (1991), however, have questioned the role of anthropogenic

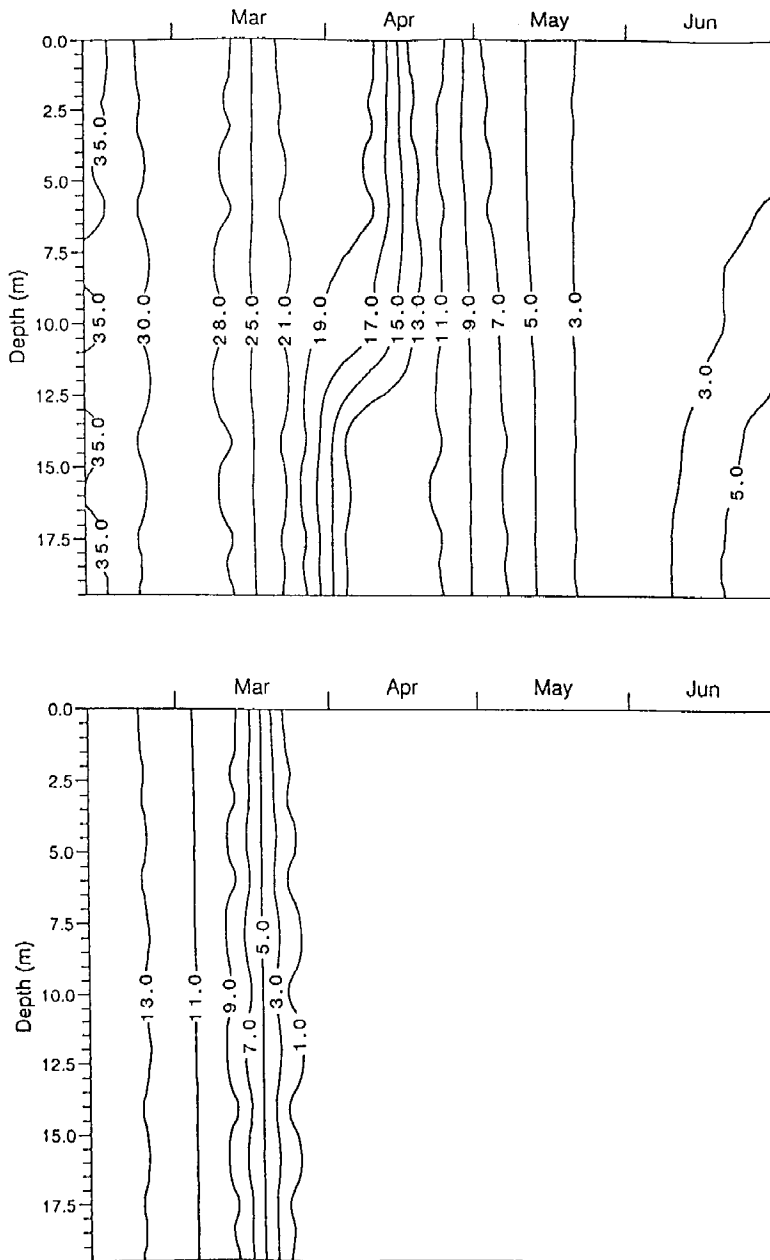


Fig. 9. Simulated nitrate and silicate distribution in the shallow coastal areas west of Denmark during the spring 1988. It is demonstrated clearly that high concentrations of nitrate are left after the silicate is depleted during the simulated diatom bloom in March. (After Ulvestad et al. in preparation.)

nutrients. Hence, although the North Sea is one of the most monitored marine waters in the world, the important question whether anthropogenic nutrients affect the phytoplankton community and production, or more specifically affected this particular *Chrysochromulina polylepis* bloom, remains unclear. Unfortunately, such debates, regardless of whether they deal with eutrophication, fisheries or stock enhancement, are the rule rather than the exception in marine environmental research, where the common problem is to discriminate between the effects of human impacts and of the natural variability in the system.

I hope to show that models incorporating both the major natural sources for variability and the effects of human impact may help this situation. Recently we (Ulvestad et al., in preparation) developed for the North Sea a three-dimensional phytoplankton model which included diatoms and flagellates. The elements of the model are shown in Figure 6. The period from February to June 1988 was simulated with realistic meteorological data, both wind and barometric pressure, available from the hindcast archive at the Norwegian Meteorological Institute, realistic solar radiation, volume and nutrient concentrations for the runoff of all major European rivers entering the North Sea, and data on the outflow from the Baltic Sea. Measured initial nutrient concentrations (N, P, and Si) for the North Sea in February were supplied by the International Council for the Exploration of the Sea. A detailed presentation of the simulation results will be presented elsewhere (Ulvestad et al., in preparation), and here I will emphasize only two aspects. First, the simulated nutrient development west of Denmark clearly indicates the presence of anthropogenic nitrogen originating from the southern part of the North Sea (Fig. 9) during February, March and April, because water of marine origin at this location cannot contain nitrate concentrations higher than $15 \mu\text{M}$. After the silicate depletion, caused by a simulated diatom bloom in March, considerable amounts of nitrogen are still present. The nutrient rich water west of Denmark was then advected northward and entered the Skagerrak area during winter and spring as described above. The simulated nutrient distributions are in good agreement (both vertically and horizontally) with the observations reported by Aksnes et al. (1989) and Skjoldal and Dundas (1991). Second, the simulation produced a large flagellate bloom in the Kattegat area during May (Fig. 10). Both the timing and the biomass of this bloom corresponds with the *Chrysochromulina polylepis* bloom. Thus a model essentially based on the simple, but powerful, principle of mass balance seems to reproduce quite realistically the main features of the phytoplankton and nutrient development during the spring of 1988.

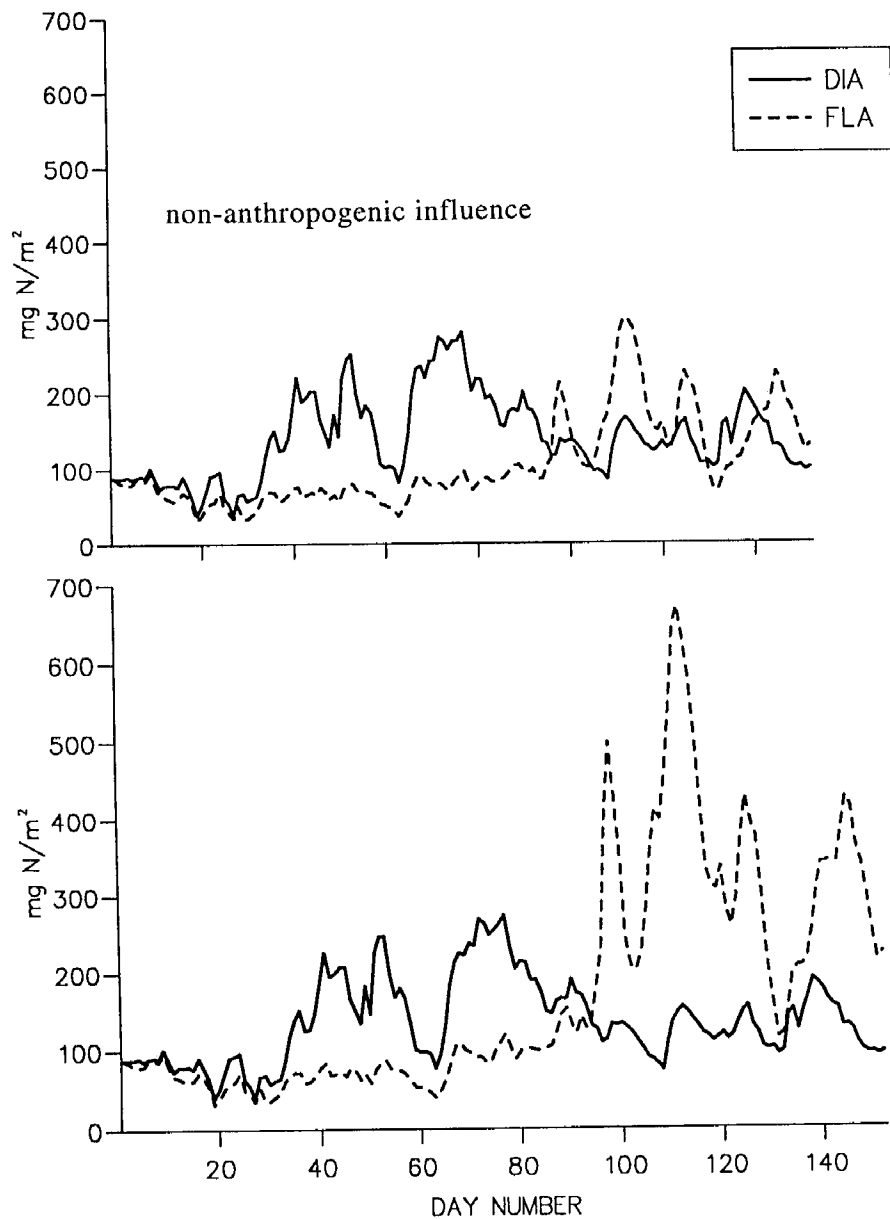


Fig. 10. Simulated phytoplankton biomass (mg N/m^2) in the Kattegat area in 1988 (lower panel). Day one refers to the beginning of the simulated period (1 February). The simulation shows that diatom blooms occurred during March and April while a large flagellate bloom was generated in May. In a run where anthropogenic nutrients were removed from the initial nutrient field and from the rivers entering the North Sea, the May flagellate bloom was depressed (upper panel).

The strength of the modelling approach is its ability to manipulate natural variability and/or human impacts on the system. Thus, in the next run we removed all anthropogenic nutrients, both in the initial values and in the rivers entering the North Sea, but kept all the other factors as in the previous run, that is, we kept the natural factors present that particular spring: the wind, radiation, river runoff, etc. Then the flagellate bloom in the Kattegat area decreased, while the diatom development was similar to the previous run (Fig. 10). Hence, the model supports the idea that the rather strong flagellate bloom in the Kattegat-Skagerrak area in May 1988 was stimulated by anthropogenic nutrients. But, of course, the model cannot tell us why the actual species happened to be *Chrysochromulina poly-lepis*, although it can explain why it could not be a diatom. Of course, the model may be as erroneous as human thoughts and can hardly *prove* the role of human impacts in this specific bloom. The modelling approach, however, allows for a more systematic and objective use of available data than do subjective analyses, which are in any case difficult to perform when the observed system is acted upon by several, quite different, environmental factors over several time and spatial scales.

CONCLUSION

Generally, it is not trivial to assess the effect of human impact on marine pelagic populations even in cases where human impact is severe. The problem is to define *the* "natural" situation on which the effect of human impact should be contrasted. Although several exceptions exist, the high inherent spatial and temporal variability in the abundance of marine populations, especially at high latitudes, does not allow for the simple concept of a natural steady state for those populations close to a more or less constant carrying capacity. Effects of human impact will be superimposed upon the natural variability, and in order to discriminate between the two, the natural variability has to be ascertained. As the fluctuations in the marine environment are governed by changes in climate, in short term meteorology, in advective patterns and by the organisms themselves, single factor explanations are likely to fail. It seems necessary to consider all major factors causing variability no matter to which scientific discipline the factors belong. Here, the modelling approach is not only extremely valuable, but probably also necessary in order to provide scientific answers. Through realistic representation of both the major natural variability of and the human impacts on marine populations, we are more

likely to generate more convincing and conclusive answers about the role of human impacts. The answer to the question raised in the Introduction: "Can mathematical models help us to assess human impact on self-recruiting populations?" is therefore not only "yes", but also that mathematical models seem necessary in the assessment of human impacts on marine populations.

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Discussion – Aksnes' paper

Fleming: *The use of complex models to make predictions requires, at least from a physical point of view, parameter values that are arriving constantly. I wonder if we will ever have enough biological parameters for realism. The farther we go up the food chain, the more difficult it is for us to make predictions about what is happening to populations of large sized fish or mammals.*

Aksnes: *This model can not be applied to the higher trophic levels in the coming years. We can use it to calculate the variability and the carrying capacity of the higher trophic levels at least when it comes to the primary productivity of the oceans. We know that this productivity in the Norwegian Sea and the Barents Sea is changing and such models will be strong tools to analyze such variability. I don't think this model will be used for predictions in the near future but rather to analyze the causal relationships in the system. One limitation is that the meteorologists can provide us with forecasts for only one week.*

Stenseth: *I agree that if you know the processes in detail, then complex equations are not necessarily a problem. But I am uncertain if we know as much as we think we know. This concerns me in the sense of making*

predictions. Meteorology is monitored very well in both time and space. Nevertheless, we know now that weather can not be predicted because of its complexity and its non-linearity. It follows that you can not interpolate between two points. When the system is complex, there is no unique set of parameters that can be fitted to the data.

Aksnes: *I don't think it is relevant to compare the phytoplankton model with meteorological models because meteorological models are very sensitive to the initial state.*

Stenseth: *That is true but this is also with regard to the dynamics.*

Aksnes: *The model I have shown here is not sensitive to the initial stock of phytoplankton. Their development is sensitive to the strong forcing which is rather predictable or, if it is not predictable, at least we have data. The purpose of this model is to represent the strong physical forcing on the biology of a system not to make a model that is sensitive to the initial state. In contrast, if the initial air pressure in meteorology is not correct, the predictions will suffer severely from this.*

Hedgecock: *I have a question about your decision to ignore zooplankton. The Joint Global Ocean Flux Study to model global carbon flux through phytoplankton found that zooplankton could not be ignored because they crop a significant amount of phytoplankton and therefore are a major component in regulating that element in the system. You have to include the higher trophic levels in models.*

Aksnes: *Zooplankton may be important and are not ignored. We ignored their dynamic behavior. Their impact is represented by a non-dynamic grazing rate.*

Hedgecock: *Can you do that?*

Aksnes: *Yes, it is the only way we can do it because it introduces non-trivial problems when zooplankton are included as a dynamic variable. Then, we also have to include the mortality of the zooplankton, and that raises the problem of representing their predators, etc. When it comes to phytoplankton blooms, often there is an exponential increase for three or four weeks and then a decrease. The zooplankton may delay this development for some days, but very seldom do we see an impact of zooplankton*

in a way that phytoplankton can not utilize the nutrients. Usually if we have plenty of sun and nutrients, we get an algal bloom.

Bottomley: *Have other workers used your model in other parts of the world to see if the same kinds of conditions are conducive to these blooms?*

Aksnes: *Similar models have been made for many parts of the world. I don't think the meteorology has been presented as realistically as in our models. We read in realistic meteorology every six hours for a very fine scale model. This is not commonly done. Because meteorologists store these data for the entire globe, in theory our model could be used all over the world.*

Bottomley: *What is the other possible fate of the nitrate?*

Aksnes: *There is denitrification going on that is not represented here. Or, the nitrate is dispersing with the water.*

Bottomley: *The combination of conditions kept the nitrate concentrated in a pocket.*

Aksnes: *In the rivers it was 400-500 mM and then when it arrived in the Kattegat-Skagerrak area it was about 20 mM and then conditions moved it back out of the Skagerrak area.*

Bottomley: *But nutrients must come from Europe into this area all the time.*

Aksnes: *That is correct but the special thing this year was the very high levels of precipitation in Europe which resulted in large amounts of nitrogen entering the ocean. But the model can not explain why that particular species bloomed, it is just a mass balance model of nitrogen, silicon and phosphorus). The model can explain why diatoms didn't occur because there was no silicate in the anthropogenic nutrients. When humans increase the nitrogen and decrease the silicate, then flagellates bloom and not diatoms.*

Fleming: *If the same weather conditions repeated, would we see a similar bloom of a different species of phytoplankton? I am not sure about the dynamics.*

Aksnes: *We used the same weather conditions when we removed the anthropogenic nutrients from the simulation, but the model can not explain the bloom of a particular species.*

Fleming: *I wonder if we can predict the conditions needed for another bloom of the same species?*

Aksnes: *It is possible to do so with an associated probability level.*

Bottomley: *Were those conditions very unusual?*

Aksnes: *The unusual conditions were a combination of the high level of nutrients, the difference in the water level between the Baltic and the North Sea, and the very sunny weather during May. If May had been cloudy, it might have been a different story.*