PROTECTING AN ESTUARY FROM FLOODS — A POLICY ANALYSIS OF THE OOSTERSCHELDE

VOL. IV, ASSESSMENT OF ALGAE BLOOMS, A POTENTIAL ECOLOGICAL DISTURBANCE

PREPARED FOR THE NETHERLANDS RIJKSWATERSTAAT

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PREFACE

In February 1953, a severe storm from the North Sea flooded much of the Delta region of the Netherlands, inundating 130 thousand hectares and killing several thousand people. After this disaster, the Dutch government decided to greatly increase the region's protection from floods by constructing a system of dams and dikes, called the Delta Works, in all the Delta estuaries. By the mid-1970s, this protective construction had been completed, or was well under way, in every Delta estuary except the largest—the Oosterschelde. In the Oosterschelde, the construction work had barely begun before it was interrupted by controversy.

The original plan for protecting the Oosterschelde had been to construct an impermeable dam across the nearly 9-km-wide mouth of the estuary, thereby closing off the estuary from the sea, and then to turn the resulting basin into a freshwater lake. This, however, threatened the Oosterschelde's extremely rich and rare ecology and its thriving oyster and mussel fishing industry. As the time approached when the construction in the Oosterschelde would cause major changes, the original plan provoked strong opposition among people with a special interest in protecting the fishing industry or preserving the natural environment. For people primarily interested in safety, however, the original plan continued to receive strong support.

In 1974, in response to the growing controversy, the Dutch Cabinet directed the Rijkswaterstaat, the government agency responsible for water control and public works, to study an alternative approach—the construction, in the mouth of the Oosterschelde, of a special kind of dam called a *storm-surge barrier*. Basically, the storm-surge barrier was to be a flow-through dam containing many large gates. In a severe storm, these gates would be closed. Under normal conditions, they would be open to allow a reduced tide—somewhat smaller than the original—to pass into the Oosterschelde basin from the sea. The size of the reduced tide is governed by the size of the aperture in the barrier.

The Cabinet specified two conditions for accepting any plan for a storm-surge barrier: First, as in the original plan, the storm-surge barrier was to provide protection against a storm so severe that it might be expected to occur only once in 4000 years.[1] Second, it had to be possible to complete the barrier by no later than 1985 for no more than a stipulated cost. If these conditions could not be met, the original plan would, supposedly, be implemented.

Some opponents of the original plan were fearful that the storm-surge barrier, with its reduced tide, might also seriously damage the fishing or the ecology, even though it met the specified conditions. They pressed for yet another alternative—an open plan, where the mouth of the Oosterschelde would be left open to maintain the original tide and a system of large dikes would be built around its perimeter to protect the land.

In effect, three alternative approaches were proposed, either formally or informally, for protecting the Oosterschelde: closing it off completely, as in the original

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[1] Such a storm is called a 1/4000 exceedance frequency (or excess frequency) storm, because the frequency with which it might occur would not exceed 1/4000 per year.

plan; leaving it open and building large new dikes; or constructing a storm-surge barrier. Each approach, of course, had many possible variations; the storm-surge barrier, for example, could be built with different aperture sizes, each size producing a different reduction in the tide and hence a potentially different effect on the Oosterschelde's ecology.

It soon became clear that the process of comparison and choice among the Oosterschelde alternatives would be very difficult, for their potential consequences were many, varied, and hard to assess. To aid the decisionmaking process, the *Policy Analysis of the Oosterschelde (POLANO) Project* was established, in April 1975, as a joint research project between Rand (a nonprofit corporation) and the Rijkswaterstaat.[2]

The project began with one year of analysis, during which each organization spent about eight man-years of effort on joint research, concentrating on different but complementary tasks. Rand's primary task was to help develop and then apply a methodological framework for predicting the many possible consequences of the alternatives; most of these consequences were expressed in disparate units (e.g., money versus ecology) and some were impossible to quantify (e.g., aesthetics).[3] The Rijkswaterstaat's primary tasks were, on the basis of special engineering and scientific studies, to develop a specific design for each alternative approach, to analyze the consequences of the designs in which they had special expertise (e.g., the effects on salinity), and to provide data, as well as assistance, for the methodology being developed with Rand.[4]

The Rijkswaterstaat developed three alternative cases to analyze in the POLANO project: the closed, open, and storm-surge barrier cases. These cases embody the three alternative approaches for protecting the Oosterschelde but specify several additional features—the most important being the *compartment design,* which gives the location of the compartment dams.

Two compartment dams are incorporated in each case to aid water management and to provide tide-free navigation (required by treaty with Belgium) for the *ship canal passing through the rear of the Oosterschelde.* One dam merely blocks off the Oosterschelde from the Volkerak Krammer, and has the same location in all three cases. The other dam separates the Oosterschelde into two basins: a *Western Basin located close to the mouth and an Eastern Basin located close to the* other end. Different locations for this second dam produce different compartment designs and different Eastern Basin sizes. In *compartment C-4,* the dam is located near Wemeldinge, where it produces a larger Eastern Basin than that in compartment C-3. In *compartment C-3,* the dam is located considerably closer to the rear of the Oosterschelde, where it produces a smaller Eastern Basin.[5] In both compart-

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[2] Rand had had extensive experience with similar kinds of analysis and had been working with the Rijkswaterstaat for several years on other problems.

[3] Other Rand tasks were to help the Rijkswaterstaat staff coordinate their various study activities on the Oosterschelde by showing interrelations and identifying data problems, and by making them *familiar with policy analysis techniques by participating in joint research.*

[4] The Rand contract was officially with the Delta Service of the Rijkswaterstaat, which had direct responsibility for the Oosterschelde protection. The Rijkswaterstaat members of the POLANO project came from the Delta Service, the Information Processing Service, and the Economics Department of Rijkswaterstaat Headquarters. Other Rijkswaterstaat services and directorates provided data, consultation, and suggestions.

[5] The name of the dam that produces the Eastern Basin depends on its location. In compartment C-4 it is called the Wemeldingedam and in C-3 the Oesterdam.

ments, the Western Basin remains salt water while the Eastern Basin becomes fresh water.

In the *closed case,* the mouth of the Oosterschelde is completely closed with a dam, while the existing dikes are left basically unchanged. Compartment C-4 produces the larger Eastern Basin, which, in contrast with the original plan, is the only part of the Oosterschelde that becomes a fresh-water lake.

In the *open case,* the mouth of the Oosterschelde is left open, but its perimeter is surrounded by large new dikes, similar to those designed by the Province of Zeeland to withstand a 1/4000 excess frequency storm. Compartment C-3 produces the smaller Eastern Basin.

In the *storm-surge barrier case,* a storm-surge barrier[6] with an aperture of 11,500 sq m is constructed across the mouth of the Oosterschelde; this aperture reduces the tide to about two-thirds of its original value. To increase the protection during the period before the barrier can be completed, the height of the existing dikes is raised to a level that the Rijkswaterstaat believes adequate to resist a 1/500 excess frequency storm while the mouth of the Oosterschelde remains open. Compartment C-3 produces the smaller Eastern Basin.

For the alternative cases, POLANO analyzed and compared many different consequences. Indeed, even the categories for these consequences, which we shall henceforth call "impacts," are very numerous. They include the *security* of people and property from flooding; the *financial costs* to the government from the construction and operation of the works; the changes in the kinds and populations of species that constitute the *ecology* of the region; the additional employment and other *economic* impacts that occur not only in industries directly involved in the construction of the barrier but also indirectly in other interrelated industries; the quantity and quality of the *water supply* available in various locations; and various *social* impacts, including the displacement of households and the disproportionate effects on the Zeeland economy.

In addition, POLANO performed a number of sensitivity analyses to see how the impacts would change with variations in the design of the cases and in certain assumptions. These variations included different aperture sizes for the storm-surge barrier and different assumptions about the recreational investment policy for the Oosterschelde region.

On April 5.1976, one year after POLANO began, Rand presented a final report in the form of an all-day briefing at the Rijkswaterstaat Headquarters; this briefing described the methodological framework that had been developed and summarized the results of the POLANO analysis. After this, Rand helped the Dutch members of the POLANO team synthesize the jointly obtained POLANO results with the results of several special Rijkswaterstaat studies. This work became the foundation of the Rijkswaterstaat's May 1976 report, *Analysis of Oosterschelde Alternatives,* that was presented first to the Cabinet and then to Parliament, along with the Cabinet's recommendation for a decision. Based on the Rijkswaterstaat report, the Cabinet recommended the storm-surge barrier case to Parliament, which accepted it in June 1976. (The Parliament also requested additional analysis by the Rijkswaterstaat to establish the best aperture size for the barrier.)

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[6] In the design concept selected by the Rijkswaterstaat, the barrier receives its vertical support from large pillars founded on top of pits, a kind of piling driven deep into the Oosterschelde bottom. This barrier concept has been called "pillars on pits."

The methodology and results of the POLANO project are described in a series of Rand reports entitled *Protecting an Estuary from Floods—A Policy Analysis of the Oosterschelde.*

Volume I, *Summary Report* (R-2121/1), describes the approach and summarizes the results of the complete analysis. It presents and compares, in a common framework, the many impacts of the different cases. It also shows how these impacts vary with changes in the designs of the alternatives and in certain assumptions.

Volume II, *Assessment of Security from Flooding* (R-2121/2), describes the methodology that was developed to estimate the likelihood and severity of flood damage in the Oosterschelde region. It also presents a detailed analysis of the security offered by the three cases in both the long-run and the construction period, showing how security varies with changes in the alternatives and assumptions.

Volume III, *Assessment of Long-Run Ecological Balances* (R-2121/3), describes how the abundances of the Oosterschelde's different species would change in the long run with variations in the alternatives and certain assumptions; the variations include different apertures for the storm-surge barrier, different sizes for the Western (salt) Basin, and different rates for fishing and detritus import. The report also discusses in detail the ecology model that was developed using mathematical concepts new to ecology. In addition, the report presents the results of our attempt to validate the model: For Grevelingen, an estuary adjacent and similar to the Oosterschelde, the model's abundance estimates were compared with observations made both before and after Grevelingen's tide was reduced to zero by its 1971 transformation to a salt-water lake.[7]

Volume IV, *Assessment of Algae Blooms, A Potential Ecological Disturbance* (R-2121/4), describes a mathematical model that was developed to estimate the risk of algae blooms and presents the results that were obtained by applying the model to the present Oosterschelde and the different cases. When algae have a large population increase, from favorable conditions, the resulting bloom may seriously reduce the dissolved oxygen levels in the water. This, in turn, can cause the death of desirable fish and also produce bad odor. Because an upper bound on the risk of algae blooms is desired, the model uses linear programming techniques to predict the maximum algae biomass that could occur, subject to various constraints on growth (such as the availability of several nutrients).

Volume V, *Anaerobic Conditions and Related Ecological Disturbances* (R-2121/5), describes a mathematical model that was developed for estimating the potential for anaerobic conditions in an Eastern Basin and applied to the different cases. Oxygen-free (anaerobic) water is created in the Eastern Basin during its conversion from salt water to fresh water. By interfering with the normal action of certain bacteria, this oxygen-free water causes bad odors and murky water. Using the model, this report shows that the large and small Eastern basins—and thus the cases that contain them—differ greatly in their potential for anaerobic conditions and related disturbances.

Volume VI, *Selected Social and Economic Aspects* (R-2121/6), considers a variety of impacts for the different cases. These include the effect on jobs and value

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[7] An *Addendum* to Vol. III, published subsequently, will present the raw data on species abundances that were used to calibrate the model.

added in the fishing industry; the changes in recreational opportunities and demand; the savings to the carriers and customers of the canal shipping industry; the total (direct plus indirect) changes in production, jobs, and imports for the 35 industrial sectors of the national economy; and, finally, as social impacts, the displacement of households and activities, and the disproportionate effects on the Zeeland economy.

Several comments about this series of reports should be noted. First, although formally published by Rand, the series is a joint Rand/Rijkswaterstaat research effort; whereas only a few of the reports list Dutch coauthors, all have Dutch contributors, as can be seen from the acknowledgment pages.

Second, the methodology and results described therein are expanded and refined versions of those presented in the April 1976 final-report briefing. The improvements in methodology and results have come not only from the leisure to experiment and reflect, but also from exposure to Rand's rigorous review process; each report has been reviewed by at least two, often three, technical reviewers who are unaffiliated with the POLANO project.

The present report, Vol. IV in the POLANO series, considers the risk of algae blooms in the Oosterschelde. Algae blooms can cause the death of desirable fish and shellfish and also produce bad odor and appearance. There is some risk of algae blooms in the Oosterschelde because the construction activities associated with the alternatives and the resulting division of the present Oosterschelde into several smaller basins may create conditions particularly favorable for algae. Subsequent growth in regional population and industry—and their attendant discharges—could further aggravate the problem.

This report describes the mathematical model that was developed for the assessment of algae blooms, evaluates its performance, and makes recommendations for further research. After investigating the possibility of algae blooms in the present Oosterschelde and determining the sensitivity of algae blooms to variations in environmental conditions, the report presents several policy conclusions about the likelihood of basin-wide fish-killing algae blooms and the conditions conducive to local problem spots.

SUMMARY

S.1. PROBLEM CONTEXT

Algae are generally aquatic, mostly unicellular, photosynthetic organisms that require a variety of nutrients (e.g., nitrogen compounds, phosphate, CO_2, and sometimes silicon) and solar radiation for their survival and growth. When the supply of these factors is abundant, and other conditions are favorable, the algae reproduce rapidly. If the algae population increase is particularly large, the resulting phenomenon is called a bloom.

Algae blooms are objectionable for a number of reasons. They can cause the death of plants on the bottoms of water basins by shielding them from the necessary solar radiation. They often produce substances that are toxic to other species (e.g., fish and shellfish), and can clog filters in water systems. The most important problem, particularly in the Oosterschelde region, is that large blooms may seriously reduce the dissolved oxygen levels in the water. This can cause the death of many types of desirable fish and shellfish and also produce bad odor and appearance.

There is some danger that constructing any of the Oosterschelde alternatives could lead to excessive algae blooms in the Oosterschelde region. The construction activities themselves and the subdivision of the estuary into several smaller basins may cause local conditions that are particularly favorable for algae production. Subsequent growth in regional population or an increase in industrial or recreational activity could further aggravate the problem.

It would be useful to have a model that could predict, for any given abiotic conditions (i.e., those that describe the environment for the algae), how large an algae bloom might occur. This would make it possible to determine what the favorable conditions are for such blooms and when these conditions are possible. With this information, preventative or remedial action might be more easily planned or executed in many situations. It would also be possible to investigate the potential consequences (with respect to blooms) of various activities in open or closed basins. Such activities would include changes in thermal or waste discharges, barrier construction, or alterations in any other areas that could affect the abiotic conditions in the water.

S.2. PURPOSE AND GENERAL APPROACH

In studying algae blooms in the Oosterschelde area, our purpose has been to develop an algae bloom model capable of meeting certain objectives and then to use the model for investigating several important questions. There were four primary objectives the algae bloom model was supposed to meet:

1. To indicate the conditions that can result in the development of objectionable algae blooms.
2. To relate physical conditions to biological production.

3. To provide primary production information for the general ecomodel that predicts changes in long-run ecological balances.
4. To provide a management tool for warning about bloom conditions, investigating control measures, and guiding nutrient and thermal discharge plans.

After developing and testing the model, we wanted to use it to investigate two general questions:

1. What is the sensitivity of blooms to changes in nutrient levels, incident solar radiation, temperature, and mixing depth?
2. What are the critical times for algae blooms to occur?

Our investigation has included studying the sensitivity of algae bloom timing and other characteristics to both external conditions and internal model parameters. There has been no attempt to study extensively the effects of the different Oosterschelde design cases (i.e., the risk of future objectionable algae blooms under the alternative barrier and compartment combinations). This was because of the lack of sufficient data about the nutrient, temperature, and visibility conditions to be expected in the future basins. However, some preliminary work was attempted, and the answers to the first two questions also give insight into what conditions, if they occurred in a particular Oosterschelde case, could lead to excessive algae blooms. In addition, the model, because of its general nature, can easily be applied to any basin where the abiotic conditions are either known or can be estimated. Thus it meets the management tool objective 4 specified above.

S.3. THE LINEAR PROGRAMMING MODEL

In accomplishing the objectives of the study, we constructed a mathematical model of algae (phytoplankton) and their essential relations with the environment. In particular, a linear programming model was developed to predict the *maximum* algae biomass that *could* occur, subject to various constraints on growth: the availability of several nutrients, the effective amount of solar radiation, and the individual species tolerance for water temperature. (Other constraints could have been included but were not, because of the lack of necessary data.)

The italicized words emphasize an important feature of the linear programming approach, namely, that the model's predictions of algae biomass are *upper bounds* on the algae biomass that might actually occur under the specified constraints. Significantly, the introduction of additional constraints can only reduce (or, in some instances, leave unchanged) the degree by which the model's biomass predictions are an upper bound. If, under specified constraints, the biomass predicted by the model is not objectionably large, the actual biomass cannot be objectionable. In such instances, the model's predictions would be directly useful for policy evaluation; moreover, they would obviate the need to introduce additional constraints into the model.

The model predicts many aspects of algae blooms in salt water, including orders present, species and total biomass, total chlorophyll concentration, limiting constraints on further growth, and the concentrations of dissolved forms of nutrients remaining in the water. Phytoplankton orders and species that may be present are characterized by their chemical composition and by their photosynthetic efficiency as a function of the temperature and the solar radiation intensity. The solar energy actually available to the algae is computed as a function of the incident solar energy, the background turbidity in the water, the shading from the algae themselves (self-shading), and the effective mixing depth of the water.

The bloom magnitude predicted is the one that maximizes the total primary biomass present while meeting all of the constraints that have been included in the model. It is assumed that, at this bloom peak, all of the available energy will go to algae respiration; that there will be no self-inhibition except for self-shading; and that grazing (the rate at which algae are eaten by other creatures, primarily zooplankton) is unimportant during the periods of greatest danger to the environment. Nominal values for all necessary parameters were determined from the literature or estimated from data and physical processes when there was no available literature or a particularly wide range of values. The sensitivity of the model outputs to the parameter values and the assumptions mentioned earlier was tested as a part of the analysis.

In the present model, only salt water species of algae have been included. Thus, the model can be used only for salt water environments. Although it can be extended to fresh water environments, this will require the introduction of fresh water species and corresponding changes in the various parameters and compositions.

S.4. RESULTS AND POLICY CONCLUSIONS

The analysis using the model centered on two questions: investigating the possibility of objectionable blooms in the present Oosterschelde and determining the sensitivity of algae blooms to possible future changes in abiotic conditions in the area. In this latter work, we chose to look at the timing and magnitude of blooms as a function of variations in one or more of the environmental conditions (e.g., solar radiation, nutrient levels, or water temperature). Such variations could arise from construction activities, increased waste discharges, or other developments in the Oosterschelde area.

The type of fish and shellfish now living in the Oosterschelde, and whose presence is considered desirable by the Dutch, requires at least 50 percent oxygen saturation in the water. To avoid undesirable conditions, therefore, the amount of algae biomass should not increase to the point where, through algae death and subsequent remineralization, it causes the dissolved oxygen concentration to fall below this 50 percent saturation level. We used the model to calculate maximum algae blooms and resulting oxygen concentration levels under conservative assumptions about death rates, reaeration, and stratification. Based on this analysis, we reached several policy conclusions, as discussed below.

Policy Conclusion One: In general, no basin-wide fish-killing algae blooms are likely to occur in an unchanged Oosterschelde.

Policy Conclusion Two: For an Oosterschelde that has been divided into separate Western (salt) and Eastern (fresh) basins by one of the Oosterschelde alternatives (closed, open, or storm-surge barrier), no basin-wide fish-killing algae blooms are apt to occur in the Western (salt) Basin during the spring months. The present insufficient knowledge of algae death rates restricts this conclusion to the early part of the year; it may be true in general, but this will have to await further research.

The analysis indicated that increases in available nutrient levels in the water would, as expected, cause algae biomass to grow proportionally with nutrient concentrations. This continues until nutrients are exhausted or until solar radiation becomes a limiting constraint. When blooms do not occur in the model, it is because they are constrained by solar radiation or water temperature. Thus, increasing the amount of available nutrients cannot increase the frequency of algae blooms, only their size, and then only if they are nutrient-limited.

In a similar manner, increases in solar energy may result in moderate increases in bloom size, but only when solar energy is limiting. If it is not limiting, there will be no effect. Although increased solar radiation can cause blooms to occur both earlier and later in the year, it was not found to have a particularly strong influence. In general, large increases in incident solar radiation were necessary to produce any significant changes in bloom occurrence.

Water temperature appears to be significant, in some cases, in determining the size and frequency of blooms, especially where waters are shallow or poorly mixed. When combined with simultaneous increases in either solar radiation or nutrient *concentrations, temperature increases (in certain ranges) can lead to shifts in* species present and large changes in the magnitude of blooms early in the year. This combination of circumstances may not be that unlikely, for water temperature changes can be caused either by spells of warm sunny weather or thermal discharges. Thus, they could easily be associated with increases in solar radiation or nutrient discharge.

In general, the mixing characteristics of the water are very important. Where the water is shallow and mixing poor (as in a small closed basin with little wind), solar radiation is effectively much more abundant than under other circumstances. It may no longer be a limiting constraint on algae growth, and nutrient concentrations will generally become the most important factor.

When this critical result is combined with those mentioned above, several other policy conclusions emerge.

Policy Conclusion Three: Although there is little likelihood of basin-wide fish-killing algae blooms in the unchanged Oosterschelde or in the Western (salt) basins for any of the Oosterschelde alternatives, there may be some local problem spots under certain conditions of changing solar radiation, mixing depth, and nutrient *discharges. If areas of the basins are effectively isolated by poor horizontal mixing,* they could at times develop objectionable blooms.

Policy Conclusion Four: Although controlling nutrient discharges may not always be important for limiting objectionable blooms, it is very necessary in areas and at times when solar radiation is effectively abundant. These include the shallow basins and regions with poor mixing, especially during extended periods of sunny windless weather.

Policy Conclusion Five: Future sources of thermal pollution should be carefully investigated to determine their probable effect on algae blooms in the Oosterschelde, particularly in present and future closed basins. This is especially important if there will also be a significant increase in nutrient discharges at the same time.

Comments on Eastern Basin Blooms: Although we were not able to analyze the Eastern Basin of the future Oosterschelde with the available data and the present model, we can nevertheless make some comments about its risk of objectionable algae blooms. First, although the Eastern Basin is still salt, in the period shortly after it has been closed off, the risk of algae blooms would probably be larger than before closure; this is because nutrient concentrations are expected to increase. The size of the risk depends on the increase in nutrients, which remains uncertain. This risk, which should receive future analysis, could be further exacerbated by the factors mentioned in Policy Conclusions Three through Five.

During the transitional period when the Eastern Basin is becoming brackish, there is little danger of objectionable blooms. This is because the duration and extent of brackish water should be limited, and the few algae species that can survive under these conditions will not have enough time to become adapted and bloom.

When the basin eventually becomes fresh, it will again face the threat of algae blooms. However, as we have said before, our model is not currently constructed to deal with blooms in fresh water, and the necessary data are lacking to estimate accurately the nutrient concentrations that may be present. For these reasons, we cannot at this time draw any conclusions about the possibility of objectionable blooms in a fresh Eastern Basin.

S.5. MODEL PERFORMANCE

The performance of the model is best gauged by comparison of its predictions with observed data. Unfortunately, this is difficult to do, because of the limited availability of appropriate information for the Oosterschelde area; there are only a few measurements of chlorophyll concentrations and phytoplankton species in the region, and these were not made inside the estuary, but rather directly outside it in the North Sea. Nevertheless, when the available data are compared with the model predictions for relevant time periods, the results are favorable. There is good correspondence between the types of algae present in the blooms and between the total biomass figures (proxied by chlorophyll concentrations) for the blooms during the spring months.

There are, however, periods when the model does not accurately predict the observed algae abundances. During the winter months, the model appears to underpredict. But this is a time of low algae abundances, and hence not of policy importance. The apparent underprediction may result from problems with the reliability and accuracy of the measurements. Alternatively, the measurements may be accurate but the algae may be in a dormant or nonblooming state. Under these conditions, one would not expect the model to predict the observed abundances, because it is not currently designed to reproduce this situation.

In the summer, the model overpredicts the measured algae abundances. This apparently occurs because the death rates used in the model do not include grazing. Grazing was omitted for lack of satisfactory data in the literature. Thus, the model results should be most accurate for those periods in the spring bloom when grazing would be unimportant because zooplankton are sparse.

There are no available data that can be used to assess the validity of the model's predictions of limiting constraints (i.e., nutrients, water temperature, or solar radiation). Which of these constraints are limiting (and where) has not generally been determined in the region and may prove difficult to establish. The model predicts that solar radiation will be the limiting constraint in the late fall through early spring months. At other times, various nutrients are predicted to be the limiting constraints. More research will be necessary to verify the accuracy of these predictions.

In general, the model proved to be simple and inexpensive to set up and use in practice. A typical run for one year required only 100,000 bytes of core, used less that 7 cpu seconds on an IBM 370/158 computer, and cost less than $2. Besides being easy to operate, the model requires less data than the more conventional differential equation models and provides output information that is useful for many types of policy problems. A wide variety of conditions can be examined by changing only a few input parameters and data values; this setup process may require less than an hour of the researcher's time.

S.6. RECOMMENDATIONS FOR FURTHER RESEARCH

Additional research could improve the model and its predictions in several ways. We need a better description of the present situation, including a census of the phytoplankton species (both abundant and rare) present in the Oosterschelde during all times of the year and a better determination of their chemical compositions and physiological characteristics. Equally important are data about the regional environmental conditions, such as present and future nutrient discharges, water temperatures, water quality, and turbidity.

To analyze the effect of alternative designs on the risk of future algae blooms, we need to obtain better estimates of how the alternatives will affect environmental conditions in the various basins. This estimation is a difficult process, and additional information about the nature of the abiotic processes and interactions would considerably reduce the large estimation uncertainty.

The results from our model also suggest an ecological hypothesis of possible interest, namely, that the number of species of algae in a bloom will be equal to the number of limiting constraints in operation at that time. Although this behavior is always observed in our results because of a property of linear programming, it nevertheless represents a logically plausible hypothesis. Moreover, the hypothesis is supported by the ability of the model to reproduce the measured data reasonably. We have found no observations of this phenomenon mentioned in the literature, but we feel that it is a subject that should be investigated in the future.

ACKNOWLEDGMENTS

This study has benefited immeasurably from reviews by our colleague at Rand, G. M. Carter, and by J. N. Kremer of the Biological Science Department, University of Southern California. Carter, an expert in the mathematical programming methodology used in this study, and Kremer, an authority in marine algae, the subject of the study, provided numerous suggestions for improving the clarity and accuracy of the final report.

We are also indebted to our Dutch colleagues in the Environmental Division of the Rijkswaterstaat's Delta Service: J. C. H. Peeters, B. A. Bannink, and P. Eilers. Peeters brought to our attention the importance of analyzing algae blooms in this context and otherwise advised us on the conduct of the study. Bannink and Eilers aided in collecting and compiling the necessary environmental input data. C. Dzitzer of Rand assisted with the literature survey and the collection of essential biological data. E. T. Gernert of the Rand Publications Department skillfully edited the final version of this report.

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Chapter 1

INTRODUCTION

1.1. THE BEHAVIOR OF ALGAE

Algae are generally waterborne, mostly unicellular photosynthetic organisms.[1] Like all organisms, they require some energy to maintain themselves in the living state, a process called "metabolism" or "respiration." In addition, individual cells may die (mortality) or be eaten (grazing). To replace these losses, a population of algae uses solar energy to combine a variety of nutrients (e.g., CO_2, nitrogen compounds, phosphate, and often silicon) into energy-rich organic molecules and structural components of cells. This process is called "production."

Production does not always balance losses within an algae population. When conditions are poor—for example, when nutrients are in short supply, or there is little available solar energy (as in winter), or when what solar energy there is cannot be used efficiently (as when the temperature is too high or too low)—losses may equal or exceed production. Then the algae population will be static or will decline. Conversely, when conditions are good—when nutrients are plentiful, and solar energy is abundant and efficiently used—production will exceed losses, and the algae population will increase. When the increase is large, this is called an algae bloom.

1.2. ALGAE BLOOMS

Algae blooms can be objectionable for a variety of reasons. The algae can become so numerous that they discolor the water. At lower amounts, they may still block sufficient sunlight from reaching the bottom of the water basin. This will kill off bottom plants in moderately deep water, allowing them to survive only in very shallow places. Or the algae may excrete toxic substances that kill fish and render otherwise edible creatures unfit for consumption.

Algae can also clog filters of all kinds. We usually think of this effect in connection with municipal water treatment plants or industrial plants that use filtered water for cooling, scrubbing, and other purposes. But we also find that the gills of fish, which act as filters, can be clogged by algae.

There are at least two mechanisms by which a heavy algae bloom can deplete the water of oxygen. The first is that during the night, photosynthesis does not take place; hence, oxygen is not produced. Respiration, however, with its attendant oxygen demand, occurs around the clock. Therefore, one observes a dip in oxygen concentration in the water during nighttime hours. If the bloom is large enough, the oxygen concentration can become so low that fish and other organisms are threatened with suffocation.

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[1] Phytoplankton, however, are aquatic, unicellular algae. Although there is a distinction between the two groups (i.e., there exist species of algae that are not strictly aquatic or unicellular), we will tend to use the terms interchangeably in this report.

The second mechanism operates when the bloom dies off. A large bloom occurs because conditions are especially favorable for the algae that make up the bloom. When these conditions change, or when nutrients become depleted, as eventually they must, the massive accumulation of algae may die off very rapidly. The resulting mass of dead organic matter must be decomposed by bacteria, and this process (called mineralization) may deplete the water of oxygen. Again, this will cause fish to suffocate. Furthermore, if the water is entirely depleted of oxygen, decomposition will occur by means of anaerobic processes, creating bad smells.

1.3. FACTORS THAT LIMIT BLOOM SIZE

Fortunately, a bloom is self-limiting. As the algae population grows, more and more of the available nutrients become incorporated in the organisms, leaving less for additional production. Further, solar energy falls upon the body of water containing the algae at a finite rate (with diurnal and seasonal variation). Thus, as the algae become more numerous, each cell receives less solar energy. But respiration and mortality rise in proportion to the algae population. Even if the amounts of the nutrients are unlimited, the limitation on solar energy would bound the ultimate size of the bloom.

We could extend endlessly the list of factors that might under some circumstances limit a bloom. In addition to the major nutrients (nitrogen, phosphate, and silicon), there is a host of minor ones. These include iron, calcium, potassium, and vitamins. Algae may limit their own maximum density by excreting waste products or toxins. And the limitation caused by solar energy is not as simple as we have described it. Different species of algae use different parts of the solar spectrum. Also, different parts of the spectrum are absorbed differentially by the water itself and by its non-algal contents. However, for reasons of data availability, we will limit our attention to the three major nutrients and a single solar energy condition for each species.

A bloom can be controlled by manipulating the factors that limit its size. For example, if a nitrogen-limited spring bloom is likely to occur, nitrogen-rich sewage can be diverted or stored until the critical period has passed. This will make the nitrogen limitation more severe than it would otherwise be, and thereby reduce the size of the bloom.

If solar energy is apt to limit the size of the bloom, steps can be taken to increase the mixing depth. Turbulence will cause each cell to spend time at all depths from the surface down to the mixing depth, but factors such as thermal stratification or the depth of the bottom (when the entire water column is well mixed) prevent algae from penetrating deeper. Less sunlight will penetrate to the deeps than reaches the shallows. Hence, the greater the mixing depth, the less solar energy the average cell will receive. Other things being equal, this should reduce the size of the bloom.

1.4. A MODEL FOR MANAGING ALGAE BLOOMS

There is danger that constructing any of the Oosterschelde alternatives could lead to excessive algae blooms in the area. The construction activities themselves and the subdivision of the estuary into several smaller basins may cause local conditions that are particularly favorable for algae production. Subsequent growth in regional population or an increase in industrial or recreational activity could further aggravate the problem by increasing waste and thermal discharges.

Thus, we will find it useful to predict, for any given conditions, how large an algae bloom might occur. Then we could determine when objectionable blooms are likely to occur, and what factors are apt to limit their size. This information could be of help in designing water systems (canals or reservoirs) to make large blooms less probable, and, when blooms do occur, in suggesting effective means for controlling their size. In particular, it would be possible to investigate the potential consequences (with respect to blooms) of various activities in open or closed Oosterschelde basins. Such activities would include changes in thermal or waste discharges, barrier construction, or alterations in any other areas that could affect the abiotic conditions in the water.

We must stress that our purpose is to estimate how large a phytoplankton bloom can become under specified circumstances. We do not predict what the day-by-day population of phytoplankton will actually be. We feel it necessary to stress this point because most phytoplankton bloom studies (see, for example, Refs. 1, 2, 3, and 4) do attempt to predict the population size at every instant in time. By using our simplified approach to the problem, we have been able to develop a model that (1) requires less data than more conventional models, (2) permits extensive sensitivity analysis of important factors at low cost, and (3) facilitates identification of key parameters and environmental conditions. This is important in determining what information it may be necessary to collect for future policy studies. We have given up the ability to do day-by-day prediction in order to achieve simplicity, low cost, and ease of operation, while maintaining the ability to produce useful policy relevant results.

Because we attempt to predict only the peak of the bloom, we can describe the different species of phytoplankton relatively simply. For example, we need not know how rapidly a species will multiply when neither nutrients nor solar energy are limiting, or how that growth rate depends on the concentrations of the various nutrients. In fact, we only need to know what conditions will limit a species of phytoplankton from further growth, and not how that species behaves when conditions are not limiting. We need not know about conditions that will only briefly limit a bloom and will quickly be relaxed. For example, some species can only use nitrogen in the form of ammonia, and not as nitrates. This factor might temporarily retard the growth of these species. However, bacteria rapidly convert the one form of nitrogen to the other, so that with a delay of a few days at most either form of nitrogen is available to all species of algae.

We realize that it is not possible to predict how large the bloom actually will become. The actual bloom may fall short of the estimated potential bloom for a variety of reasons: Too little time may have elapsed for the bloom to achieve its full potential; a trace nutrient whose need was overlooked may constrain the bloom; or the availability of some nutrient may be overestimated, perhaps because part of it is present in a refractory form. Of course, the usefulness of the model will be greatly reduced if its estimates of the potential bloom too frequently are grossly larger than the actual bloom. But we are willing to be falsely warned of an objectionable bloom from time to time. To repeat, our purpose is to estimate the maximum biomass that may occur during the bloom.[2]

In this report, we describe a model applicable to salt water. Inputs to this model include the availability of nutrients, the intensity of solar radiation, the temperature, and the mixing depth. The model works in much the same way that a bloom limits itself—namely, it seeks the largest mass of algae for which production will exactly balance losses. This is not simply a matter of increasing the mass of algae until one requirement becomes limiting. Rather, our model considers simultaneously several species of algae that have quantitatively different requirements and that may occur together in any proportions.

We consider three orders of salt water algae—diatoms, green algae, and dinoflagellates—and several species within each order. Diatoms are an order with a high requirement for silicon in their extensive skeletal structure and an ability to thrive at low temperatures. Green algae do best at higher temperatures and require little nutrient. Dinoflagellates have generally intermediate requirements. Because of differing requirements, blooms consisting of different combinations of species will occur under different conditions.

Among these different requirements is the need for solar energy. All species of algae need it, of course, but different species need this energy at different intensities. The light can be too dim for one species to survive (i.e., losses exceed production), while at the same time a second species may be successful. Depending on the mixing depth and the rate at which the light intensity decreases in descending to greater depths (the extinction coefficient), different species may be able to take part in a bloom.[3]

Because algae themselves absorb light, they have an influence—sometimes a major influence—on the extinction coefficient. Thus, we cannot know what the extinction coefficient will be before we know how large the bloom will be, and which species will appear in the bloom. And we cannot know this until we know the extinction coefficient.

Our model resolves this dilemma by partitioning the range of the extinction coefficient into intervals, so that each interval corresponds to the range in which a particular species or combination of species can appear in the bloom. A separate linear program is run for each interval of the extinction coefficient. Thus, each program considers a different combination of species, namely, those that can take part in the bloom under the assumption about the extinction coefficient. Each program also contains, for each major nutrient, a constraint that prohibits the algae from using more of that nutrient than is available. The model maximizes the mass

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[2] For this reason we can afford to be less concerned about factors that affect interspecies competition and that alter the competitive advantages of the different species. These factors, some of which were mentioned above, may shift the dominant species in a bloom and thus change the observed biomass. They will not alter the maximum potential biomass, however, so the model predictions will still be valid for policy decisions. The changes in observed biomass may cause a larger or smaller measure of overprediction, but they should not result in underprediction, if we have adequately represented all of the competing species in the model.

[3] We recognize the importance of phytoplankton acclimation to the surrounding environment and the convergence effect that it has on the characteristics of the different species and orders. We have tried to deal with this problem in two ways: (1) by using photosynthesis efficiency curves that should be reasonably representative of the species found in the Oosterschelde area, and (2) by carefully investigating the effect on the model's predictions of variations in the efficiency curves for all species. This is discussed in more detail in App. B.

of algae subject to the constraints of each linear program in turn. Then the largest mass found for any of the linear programs is a limit on the size of the bloom.[4]

1.5. OVERVIEW OF THE REPORT

In what follows, this report describes the development of the model and its application to policy problems in salt water areas of the Oosterschelde region. Chapter 2 discusses the derivation and specification of the nutrient constraint equations. In Chap. 3, the general problem of the death and decomposition of algae is considered. These processes are important to all of the constraints, and they represent an area of some uncertainty in the analysis. The effect of algae on the extinction coefficient and available light is dealt with in Chap. 4, and Chap. 5 considers the basic relationships involved in the determination of primary production functions for phytoplankton. These functions are combined with solar radiation distributions to develop a minimum efficiency criterion for species participation in a bloom. Chapter 6 discusses the general problem of setting up the series of linear programs to solve for maximum biomass in the bloom, and describes the implications of linear programming for the results of the analysis. The study results and conclusions are presented in Chap. 7. Input data and consideration of potential errors and their importance are given in Apps. A and B.

[4] We have chosen to optimize biomass in our model for three reasons: In algae bloom problems, it is the algae biomass that is important. Thus, our model conservatively maximizes the factor that is of most concern to those who make the policy decisions. Second, the linear programming approach lends itself to this choice, thus permitting the formulation of a model that is simple and easy to operate and interpret. Third, there is no consensus in the scientific community about what natural systems tend to optimize, if they do in fact optimize at all. Many alternate viewpoints can be found in the literature [5,6,7,8,9]. In view of this uncertainty, we do not feel that our choice is unreasonable, although it may imply consistent overprediction.

Chapter 2

SPECIFICATION OF NUTRIENT CONSTRAINTS

2.1. MATHEMATICAL DERIVATION OF THE CONSTRAINTS

Nutrients occur in a variety of forms. Some of each nutrient is dissolved in the water. This nutrient pool is directly and immediately available to support further algae growth. Some nutrient is incorporated in the algae themselves. And some is tied up in the remains of dead algae cells or adsorbed on suspended clay particles.

The fraction of each nutrient associated with dead algae is not directly available for further algae growth. However, it can be made available by bacterial action. These bacteria will decompose the dead cells, breaking down the organic molecules that provided them with structure, and releasing nutrients back into the water.

Other pools of nutrients may exist, to which algae may or may not have access. Clay and sand contain important amounts of silicon, but they dissolve slowly. Thus, silicon may limit a bloom even when tons of undissolved silicate lie on the bottom. Other nutrients can be trapped in the bottom sediments and released only under special (e.g., anaerobic) circumstances.

Ordinarily, however, the only nutrients available to blooming algae are those that can be mobilized rapidly (in two to three days or less). Typically, only three forms of nutrients satisfy this criterion: dissolved nutrients, nutrients incorporated in living algae, and nutrients associated with dead algae. These rapidly available forms are the only forms represented in the model.[1]

To begin, let us define the following symbols:

x_j = amount of species j.
$a_{i,j}$ = amount of nutrient i contained in each unit of species j.
y_i = amount of nutrient i temporarily tied up in dead algae, etc.
w_i = amount of dissolved nutrient i, both organic and inorganic forms. This is the nutrient immediately available for further algae growth.
b_i = total amount of nutrient i in the system, in all forms that are rapidly available.

On this basis, we can define

$$b_i = w_i + y_i + \sum_j a_{i,j} x_j \ . \tag{2.1}$$

There are two ways of reading Eq. (2.1). On one hand, it may be considered as a definition of the quantity b_i. In this context, it offers a method for calculating b_i from measurements of the amounts of nutrient i in each of its different forms. On the

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[1] It is important to recognize that nutrient exchanges with the bottom are not entirely excluded from the model. Net shifts between pelagic and benthic forms will be reflected in changes in the measured nutrient concentrations used as input data. This subject is discussed more fully in Sec. 2.2.3.

other hand, if the variables x_j, y_i, and w, change, because, for example, of a change in temperature, they must still satisfy Eq. (2.1). In this interpretation, Eq. (2.1) is a constraint that limits the size a bloom can achieve.

2.2. EVALUATING PARAMETERS IN THE NUTRIENT CONSTRAINTS

2.2.1. Algae Species Selected for Modeling

Inasmuch as there are hundreds of identified species of salt water planktonic algae, we need to limit the selection for our models to those known to occur in waters in the region of the Netherlands under consideration. The most complete census of algae in this region was compiled by Gieskes and Kraay [10]. The important species, listed by these investigators by time period for the coastal area near the Delta, are given in Table 2.1. Also listed in this table are species stated to be generally present in all Dutch coastal waters. We rely on this information to identify species that should appear after the first part of April, because species specific to the Delta area are not listed thereafter in Ref. 10. No species are identified after the end of June. For our modeling purposes, we have assumed that if these listed species exist in the coastal waters, they also exist within the coastal estuaries and sea arms of the region. No specific algae census data are available that are taken within these water basins of interest.

Another factor that limits the orders and species of algae that can be modeled is the nature of the data. Data on relative photosynthesis versus light intensity are available for only three orders of marine phytoplankton—green algae, diatoms, and dinoflagellates. (Most green algae are fresh water species, and hence green algae are rarely if ever important in Dutch marine waters.) The only species not encompassed in these orders in Table 2.1 is *Phaeocystis pouchetti*, a brown phytoflagellate. The relative photosynthesis versus light intensity data for use in our model were taken from Parsons and Takahashi [11] where information of this nature from the literature is summarized. It is stated that this photosynthetic-light relationship is sufficiently homogeneous for various species within an order, for which such measurements were made, and that average values for an order are quite representative of photosynthetic efficiency for species within the order. Details of the assumed relations between algal photosynthesis, intensity of solar energy, and temperature are described in Sec. 5.2.

2.2.2. Ultimate Nutrient Compositions of Algae Species

The ultimate chemical composition of various algae species can vary over a wide range, depending on such factors as season, nutrient composition of the environment, age, size, temperature, etc. In addition, there can be large variations between closely related species and even between "races" of the same species. This presents a difficult problem if we must characterize orders and species by their compositions. Few algae composition measurements have been made and reported. Those available for nitrogen (N), phosphorus (P), silicon (Si), and water content have been compiled with literature references in Ref. 12. From this compilation, we have computed average values for the three orders (diatoms, green algae, and

Table 2.1

ALGAE SPECIES CONTRIBUTING TOGETHER OVER 95 PERCENT OF TOTAL CELL VOLUME IN DELTA AREA AND GENERALLY IN DUTCH COASTAL REGION

Cruise	Delta Area	Generally in Dutch Coastal Waters
18-21 February	*Coscinodiscus*, spp. (diatom) *Biddulphia regia* (diatom)	
25-28 February	*Coscinodiscus*, spp. (diatom) *Biddulphia*, spp. (diatom) *Thalassiosira*, spp. (diatom) *Pennates* (diatom)	
11-14 March	*Biddulphia*, spp. (diatom) *Coscinodiscus*, spp. (diatom) *Streptotheca tamensis* (?) (diatom) *Rhizosolenia hebata* (diatom) *Thalassiosira*, spp. (diatom)	
18-22 March	*Biddulphia sinensis* (diatom) *Biddulphia regia* (diatom) *Coscinodiscus*, spp. (diatom)	
25-28 March	*Chaetoceros socialis* (diatom) *Biddulphia regia* (diatom) *Biddulphia sinensis* (diatom) *Rhizosolenia hebata* (diatom) *Coscinodiscus*, spp. (diatom)	*Chaetoceros socialis* (diatom)
1-4 April	*Biddulphia regia* (diatom) *Chaetoceros socialis* (diatom) *Rhizosolenia hebata* (diatom) *Scenedesmus*, spp. (gr. algae)	*Chaetoceros socialis* (diatom)
8-11 April	*Rhizosolenia imbricata* (diatom) *Coscinodiscus*, spp. (diatom) *Thalassiosira*, spp. (diatom) *Rhizosolenia hebata* (diatom) *Plagiogramma brockmannia* (gr. algae)	
22-26 April		*Phaeocystis pouchetti* (br. phytoflagellate)
May-June		*Phaeocystis pouchetti* (br. phytoflagellate) *Ceratium fusces* (dinoflagellate) *Ceratium tripos* (dinoflagellate) *Ceratium lineatum* (dinoflagellate) *Dinophysis*, spp. (dinoflagellate) *Peridinids*, spp. (dinoflagellate)

SOURCE: Ref. 10.

dinoflagellates) and have used them as one set of values for the fraction of these nutrients associated with the modeled species of algae. The values from the literature are from samples whose characteristics (age, size, etc.) are not usually reported. They are, however, predominantly samples collected from natural marine environments and not from laboratory cultures. They do not, therefore, reflect the high values of N and P that are often noted in well-nourished laboratory cultures, but rather reflect the nutritional and other rigors of the natural state.

This process is an obvious simplification that implies that the compositional differences between orders are greater and more rigid than they are (with the possible exception of the silicon requirement of diatoms). To reflect some of the compositional variation that exists among species within the several orders, we have incorporated additional species in our model that demonstrate these extremes in one or another compositional element. Table 2.2 presents the algae orders and the additional variant species used in the model. Numbers in this table are fractions of dry living material for each category. We use dry living weight instead of ash-free dry weight as a measure of biomass, because substances appearing in the ash, upon analysis, are found to be important to the structure of the living algae and to represent biologically mobilized sinks for the elements. Thus, they are necessary for keeping account of total nutrient stocks.

The appropriateness of the ranges of elemental compositions shown in Table 2.2 may be judged in terms of the following reported observations. In algae cultures, the concentrations of both N and P can decrease by one-half with increasing age of the culture [13]. It is believed that at least a part of this decrease in concentration is caused by increased cellular contents of carbonaceous compounds not incorporating N or P [14,15]. Algae cells also consume and store luxury amounts of N and P when these elements are in excess of the minimum required concentrations in the

Table 2.2

ALGAE SPECIES ULTIMATE COMPOSITIONS (WITH VARIATIONS) AS USED IN BLOOM MODEL

Species Types	Composition (fraction of dry living material)		
	N	P	Si
Diatoms (average)	.0312	.0083	.191
High N and P, low Si (e.g., *Skeletonema costatum*)	.059	.017	.143
Low N and P, average Si (e.g., *Rhizosolenia imbricata*)	.028	.0057	.191
Green algae (average)	.052	.004	.0035
High N (e.g., unicellular chlorophyceae)[a]	.08	.005	.002
Dinoflagellates (average)	.046	.006	.014
High N and Si (e.g., *Ceratium tripos*)	.072	.0057	.03

[a] Values for planktonic green algae are not available.

medium. These excesses can be called upon for metabolism and growth when the medium becomes depleted [13]. When algae are grown in the light in a nonnutrient medium, cells are formed that may contain only one-third of the normal P and one-half of the normal N [16]. These are very stringent laboratory conditions, however, which probably never occur in the waters of interest to us.

Experiments indicate that growth of diatoms in coastal waters is likely to become seriously limited by a shortage of silicate only when most of the silicate originally present in the water has been removed in the course of a diatom bloom [17]. Cell walls in diatoms from a fast-growing population contain more silica than in slow-growing populations [17]. The silicon content is also influenced by the initial concentration of silicate in the culture medium [18].

2.2.3. Total Available Nutrients

To compare the model's predictions with observed bloom sizes, it is necessary to determine the total amount, b_i, of each of the three nutrients (N, P, and Si) available to the phytoplankton at the times and locations of the observed blooms. The sole source of these data is the measurement program of the Environmental Division of the Delta Service. This organization has collected data on the surface water quality in the Delta region since 1971, although there is significant variation in the completeness of the measurements for certain periods and substances. This source of uncertainty in the data will be discussed later.

2.2.3.1. Nitrogen. Nitrogen is most readily available to the phytoplankton in the forms of nitrite, nitrate, and ammonia. Although there may be few species that can use all forms, there are many species that can use more than one form. If there are no species present that can use all forms during the time period selected for the model, the b_i values will overestimate the true amount of nitrogen available to the algae. To counteract this potential problem, there is normal bacterial action that results in the oxidation of ammonia to nitrite to nitrate, so that all forms of nitrogen are present at any time in the natural state. For this reason, we have not assumed that any species will be limited because the proper form of nitrogen is not available to it. Rate constants for these reactions are given in Table 3.2 (see p. 20).

The measurement program of the Delta Service includes all three of these nitrogen components, but it does not consistently determine either the dissolved or suspended organic nitrogen compounds or total nitrogen content of the water. It is therefore necessary to make some assumptions. The total nitrogen available for phytoplankton growth has been taken to be the sum of the dissolved ammonia, nitrite, and nitrate concentrations. Because these values are clearly dependent on the level of phytoplankton growth, their measured, in situ, values vary considerably. For this reason, their maximum winter concentrations have been used throughout the year to reflect the total nitrogen available in one form or another in the system. These maximum concentrations occur generally in February, when the spring bloom has not yet begun, but the mineralization of autumn biomass has been completed. Thus, the amount of nitrogen in other, unmeasured forms should be at a minimum. February values will then be a reasonable measure of the total amount of nitrogen available to the algae.

Unfortunately, there are several uncertainties and potential errors associated with this procedure. First, if organic nitrogen is slow to decay during the low temperatures of winter, there may be an unknown, but significant, amount of this material that will not be included in our inventory. It will be omitted in the measurements but will gradually become available to the phytoplankton as time passes. Also, by confining our data to the winter levels, there is a serious risk of neglecting changes in the various inflows and outflows of nitrogen from the system during the year. Losses from the system may come from sedimentation, bacterial denitrification, or exchange with the North Sea. Additions will occur from municipal and industrial discharges, polder discharges, stream flow, precipitation, release from bottom sediments, direct incorporation of atmospheric nitrogen by algae species, and exchange with the North Sea. In fact, recent work has indicated that the benthos may be an important source of nutrients to the water in some areas during much of the year [19]. Because of our data limitations, we can only take such interactions into account at the beginning of the subsequent year, when again most of the available nitrogen is in the measured, dissolved inorganic forms.

The data indicate that there is no definite trend in nitrogen flows into or out of the Oosterschelde from year to year, but it is not possible to say that the inflows will balance outflows at all times during the year and that there will be no net shifts over periods from a few days to a few months. In fact, there would be some reason to think that the opposite might be true. Nixon et al. [19] have found that the contribution of benthic nutrients is a function of water temperature; hence, it is seasonal. This cannot be determined for the Oosterschelde, however, until better measurements are available. For now, we must assume that the total available amount of nitrogen remains constant throughout the year and that it only circulates between the living organisms and the aqueous environment.

2.2.3.2. Phosphorus. Phosphorus is primarily used by phytoplankton in the orthophosphate form, and measured concentrations of this component show the same characteristic seasonal pattern as nitrogen. The available data include the orthophosphate and total phosphorous concentrations. The latter measures the total amount of phosphorus present, organic and inorganic, dissolved and suspended, in living matter and dead. This total should be a more accurate representation of the phosphorus available to the phytoplankton in all forms. It would be expected that this total concentration would remain relatively stable throughout the year, with variations reflecting shifting patterns in inflows, losses, and exchanges with the North Sea. This does seem to be the case, but there is a variation of almost a factor of two between the high and low extremes over the four-year period from 1971 to 1975.

For these reasons, the measurements of total phosphorus were used for each time period considered by the model. The primary uncertainty in this assumption is the possibility of overestimation. It may be the case that not all of the phosphorus is in a form that phytoplankton can use during the limited time period. However, we feel that it is a reasonable assumption, because of the rapidity with which the nutrient is mineralized in the marine environment, and the probably small fraction of the total that represents inert materials. The fraction in this form will tend to settle out of the water quickly, to be replaced by North Sea exchange or inland sources.

2.2.3.3. Silicon. The situation with respect to silicon is similar to that of nitrogen. Measurements are taken only of the dissolved silicate concentration in the water, not the amount present in all forms. Boney [20] states, however, that evidence indicates this dissolved silicate to be the primary source of the nutrient for phytoplankton. He also asserts that recycling of the nutrient in the marine environment appears to be fairly rapid under most conditions. Consequently, silicon was treated in the same manner as nitrogen. The winter maximum values of the concentration were used throughout the year. The same uncertainties apply to this process as were discussed with respect to nitrogen, except that silicon is not taken up from, or released to, the atmosphere and has a probably higher exchange between the water and the bottom.

2.2.3.4. Uncertainties Common to All Nutrients. Several sources of uncertainty and error are common to all of these procedures. Measurement and analysis errors should be small for all nutrients. These are done using standard procedures and equipment and should not involve very great inaccuracy. There is also roundoff error in the reported concentrations. Most numbers are given to two decimal places, resulting in possible errors of from 0.4 to 50 percent, depending on the magnitude of the concentration. This means that reporting errors will be much larger for phosphorus than for nitrogen or silicon, as phosphorus usually exists in much lower concentrations in the Oosterschelde. In all cases, however, these errors would be expected to be less than 20 percent. It is important to note that the large uncertainties will occur when nutrient concentrations (and therefore bloom magnitudes) are small. When the blooms are large, the significance of these errors will be much less.

There is a potentially larger problem involved with sampling errors and uncertainty. The measurements are taken at varying time periods, with much less frequency during the winter months—when the data are most important. They are also made at a fixed set of sampling points in the Delta area. There has been no determination of how representative the sampling stations are of the total area, and there is a significant variation in the measured concentrations at many points on the same day. This is further complicated by the inconsistent measuring depths between sample stations.

These problems lead to a basic uncertainty in the results of any averaging process used to obtain input data. Our approach has been to average surface and middle depth measurements for each point, and to omit bottom data. Bottom data are frequently not reported and often appear to be anomalous, apparently due to measurement problems. The average values for each sampling point have been combined into a weighted mean for the entire basin. Figure 2.1 illustrates the details of this process. It shows the Oosterschelde basin with each sampling station marked by an ×. Stations with generally similar abiotic conditions were collected into four groups. Each group was given a relative weight, on the basis of the fraction of the surface area of the estuary that it represented. There is obvious uncertainty in determining the values of these weights, but the consistency and regularity of the nutrient concentrations minimize the importance of this uncertainty. The largest variations in measured concentrations usually occur at only a few points that represent small areas (and volumes). For this reason, the errors should not be major, although an accurate assessment of their magnitude will have to await further investigation.

The model input data for available nutrients during the years 1973 and 1974 in the Oosterschelde are given in App. A.

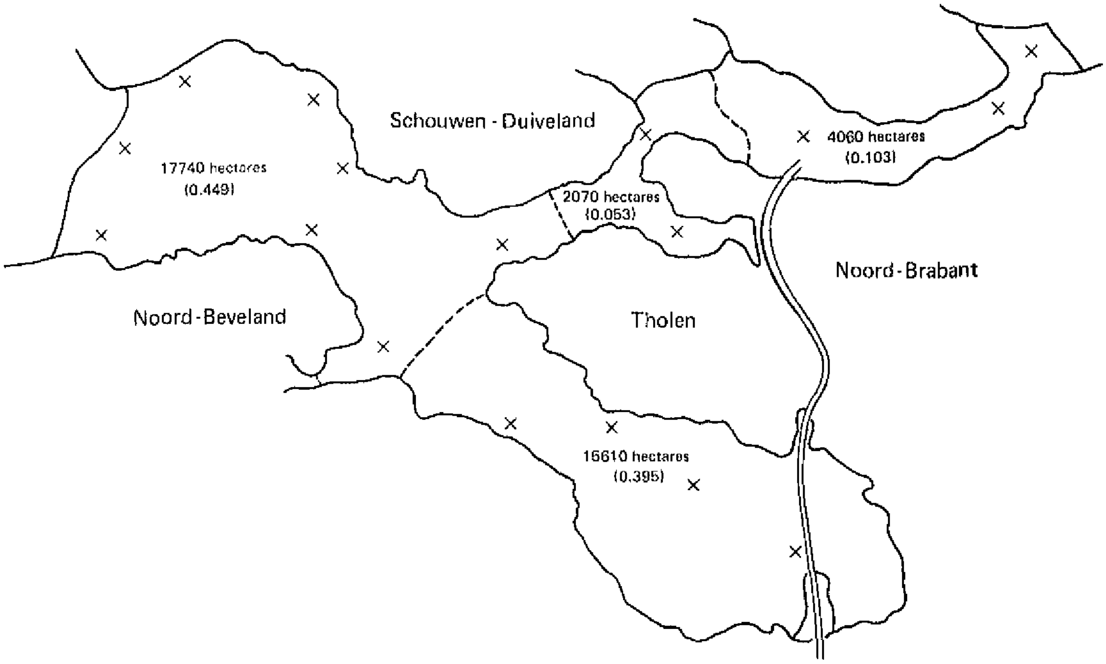

Fig. 2.1 — Surface areas and weighting factors for Oosterschelde divisions
(sampling stations are marked ×)

Chapter 3

DECOMPOSITION OF DEAD ALGAE

3.1. NUTRIENT RELEASE

When an algae cell dies, bacteria begin to decompose it immediately. The organic molecules that gave the cell structure are digested, and smaller, less energy-rich molecules are released into the surrounding water. Among these fragments are the nutrients that the cell incorporated while it was growing.

A similar process occurs if the cell is eaten (i.e., if the death rate includes grazing). In this case, a creature digests the cell and assimilates its fragments. The large organic molecules in the fragments are broken down to provide metabolic energy for the creature, and the breakdown products are excreted as waste. Among the breakdown products are some of the nutrients that the algae cell incorporated while it was growing.

Some of the cells that die sink to the bottom, and much of their nutrient content may be trapped in the sediments. Nutrients released from suspended dead cells may be adsorbed onto suspended clay particles, which then sink to the bottom. By these means, a considerable fraction (up to 60 percent) of the nutrients in dead algae can be made unavailable for further algae growth. (In the Oosterschelde, the nutrient lost this way appears to be replaced almost immediately, probably from land runoff or from the North Sea.) The remainder of the nutrient, however, is recycled, once again becoming dissolved nutrient. In our model, we describe this process as follows.

Define the following symbols:

D_j = death rate constant (mortality plus grazing) of species j.
u_i = rate constant for release of nutrient i from dead algae. Once released, some of this becomes dissolved nutrient and is available for further algae production. The remainder is removed from the rapidly available nutrient pool, either by sedimentation as dead cells, or adsorbed onto particles of clay.

The rate at which nutrient i is being tied up in dead or eaten algae of species j must be the product of the death rate and the amount of nutrient in a unit of live algae. (The death rate is the rate constant D_j multiplied by the amount of algae present.) Each species j contributes such a rate, and the overall rate is the sum of the individual rates. Conversely, the rate at which nutrient i is released is the product of its rate constant u_i and the amount of nutrient that is tied up. (Note that this rate may be different for each nutrient.) Hence we can write

$$\frac{dy_i}{dt} = \sum_j a_{i,j} D_j x_j - u_i y_i \ .$$

We will assume herein that the system has reached a stationary state, in which (by definition) none of the variables is changing. Thus, $dy/dt = 0$, and an equation that relates y_i to the amounts x_j of the various algae species is

$$\sum_j a_{i,j} D_j x_j - u_i y_i = 0 \; . \tag{3.1}$$

We can use Eq. (3.1) to eliminate the variables y_i from our model. Solve Eq. (3.1) for y_i, and substitute the resulting expression into Eq. (2.1). The outcome is a new nutrient balance equation,

$$\sum_j \frac{a_{i,j}(D_j + u_i)}{u_i} x_j + w_i = b_i \; . \tag{3.2}$$

3.2. THE STATIONARITY AND INDEPENDENCE ASSUMPTIONS

3.2.1. The Stationarity Assumption

Our assumption that the system has reached a stationary state is central to the entire model and needs only a few words to justify its importance. As stated above, our model seeks the largest bloom—that is, the largest biomass of algae—that can exist under a specified set of conditions. We consider that if the system has not achieved a stationary state, it is very probable that the biomass variables x_j are among those that are changing. If anything is changing, the biomass will be changing—either increasing or decreasing. In the former case, if we wait a moment the biomass will get larger. In the latter case, the biomass was larger a moment ago. In neither case can the biomass be at its maximum value.

From this assumption, derive all the differences between this model and the more traditional models of algae growth. The traditional models use differential equations to describe the behavior of the system over time, even if we are interested only in the peak biomass. For a discussion and examples of these kinds of models, see Patten [1] and Di Toro et al. [2]. To write these differential equations requires that we know, for example, how the production rate of algae depends on the concentration of nutrients present, or the intensity of sunlight. As data describing these relations are generally unavailable, functional forms are usually assumed as needed.

But our model does not require these types of data. By assuming that the system has reached a stationary state, we do away with all need for differential equations, and hence with the need for these detailed relations. Although we still need data about phenomena that are not well understood, this elimination reduces the difficulty of obtaining the required data, and also reduces our computational burden. In addition, it is easy to include in our model many species of algae, whereas traditional models generally deal with only one.

3.2.2. The Independence Assumption

In addition to stationarity, we make another fundamental assumption in our model—that each time period is independent of the previous time periods. This is clearly contrary to the standard assumption behind differential equation models, which are specifically designed to track the progress of a phytoplankton species through time. Instead, our model looks at a period (the ten-day decade) in terms of its environmental conditions only, and makes its predictions on this basis. It does not consider when these conditions occur during the year or what has occurred previously.

The behavior of phytoplankton indicates that this is not an unreasonable assumption, in view of the nature and purposes of our model. Measured growth rates of phytoplankton species are large enough to produce a bloom in a period of ten days [21,22]. Factors that would reduce these measured values in nature are included in our model in the form of the death rates (discussed in Sec. 3.4). In addition, there should be no time lags for acclimation of the phytoplankton, because the species that will participate in the blooms have presumably been present in the area for some time and should only be adjusting to marginal changes in their environment. For these reasons, we feel that making our predictions independent of the past history of the blooms will not necessarily result in consistent overprediction.

3.3. BIOLOGICAL OXYGEN DEMAND

Consider a mass of algae that has suddenly died. This dead organic matter must now be decomposed by bacteria, a process that will use oxygen if any is present. The biological oxygen demand (BOD) of the mass is the amount of oxygen required to decompose it completely.

The linear program does not make direct use of BOD, as it is not necessary to know this to determine the maximum algae bloom. However, BOD can be important in determining how large the bloom must become to be objectionable. As explained in the introduction, if BOD is too large, and if the bloom dies suddenly, the decomposition process can deplete the water of oxygen. This may cause fish to suffocate. Furthermore, if the water is entirely depleted of oxygen, decomposition will occur by means of anaerobic processes, creating bad smells.

The BOD we are considering is the amount of oxygen that would be required to completely mineralize all of the algae and dead algae fragments present. It is easiest to calculate this in two stages. First, we compute the amount of oxygen that would be required to completely mineralize the algae that are currently alive. This amount has no reference to the respiration by live algae; rather, it anticipates the sudden simultaneous demise of all live algae and their subsequent mineralization. Each species of algae contributes to this part of the BOD in proportion to its abundance. The second part of the BOD is associated with algae that have died but are not yet completely mineralized. We assume that the unmineralized portion of the dead algae use oxygen at a constant rate. Define

p_j = the BOD of a unit amount of species j, when freshly dead.
r = the rate constant for oxygen uptake by bacteria while decomposing algae.
z = the BOD of the unmineralized portion of the dead algae present at the peak of the bloom.

Again, we assume that the bloom has reached a stationary state. This implies that z is constant, so that

$$\frac{dz}{dt} = 0 = \sum_j p_j D_j x_j - rz \ . \tag{3.3}$$

Actually, Eq. (3.3) will only be true if there is no grazing. If the death rate D_j contains a grazing term, the factor D_j in Eq. (3.3) should be replaced by that part of the death rate caused by mortality alone. If there is grazing, and we nevertheless compute z according to Eq. (3.3), we will overestimate the BOD of the dead algae present in the bloom.

We can now calculate the total BOD of the bloom. This equals the sum of the demands by the dead and living fractions:

$$\mathrm{BOD} = z + \sum_j p_j x_j \ .$$

Or, substituting for z from Eq. (3.3), we obtain

$$\mathrm{BOD} = \sum_j \frac{p_j (D_j + r)}{r} x_j \ . \tag{3.4}$$

Accordingly, if there is substantial grazing, Eq. (3.4) will overestimate BOD.

3.4. VALUES FOR DEATH AND REMINERALIZATION RATES

3.4.1. Specific Death Rates

Very few measurements have been made of the specific death rates, or, more generally, of the specific loss rates in either natural algae blooms or in laboratory colonies. Such losses are not usually incorporated in mathematical models of algae blooms. The reason for this dearth of information is the lack of a specific method for direct measurement of death rate or of the other possible sources of losses. As a result, losses must be estimated as a difference between measurements that can involve large uncertainties and thus possibly large errors in the estimation of loss rates and, more explicitly, death rates.

Jassby and Goldman [23] have presented the most careful analysis of this subject that we have located in the literature. Losses defined as the difference between the measured primary productivity and the phytoplankton standing crop can be assigned to any or all of the following phenomena: grazing, sinking and vertical transport, horizontal transport and cell mortality caused by parasitism, and physiological extremes of environment or toxic substances. In their careful study and analysis of these phenomena in Castle Lake, California, Jassby and Goldman eliminated all but the cell mortality factors as being important contributions to losses in these measured natural blooms. They found that total losses have a trend similar to that of primary production and that specific loss rates vary greatly from one part of the year to another, being highest in May and early June.

Although these specific loss rates were measured in a small fresh water lake, they are the most carefully controlled experiments reported and the most complete data available. We believe that they are not inappropriate for use in our models of Dutch waters for the following reasons. Grazing is probably not so important in determining the size of early-peak blooms in which we are interested. It has been suggested, however, that benthic suspension feeders—e.g., cockles and mussels—graze at significant rates (5 to 10 percent daily) even on these early blooms. Good vertical mixing and a small loss from sinking seem assured from the physical characteristics of the basins. Net loss from advection should also be small. Similar but more limited measurements in a more northern latitude (Minnesota) by Megard and Smith [24] yield specific loss rates comparable with those of Jassby and Goldman. These specific loss rates are all averages for mixed communities and are not determined for separate species. We will, therefore, use these same average loss rates for all of the species in our model. Table 3.1 contains these specific loss rates for a year by decades.[1] These values were estimated by fitting a smoothed curve by eye through the data given in Ref. 23. Values for January through April were obtained by interpolation, as no measurements are reported for this period.

3.4.2. Remineralization Rates and Biological Oxygen Demand

As phytoplankton die, the cells may lyse, causing a release of major amounts of their contained organic substance to the aqueous environment. Residual structure is also operated on by chemical and biological processes to yield elemental substances, many of which are available for reuse. Oxygen is involved in a number of these chemical and biological decomposition processes, and because oxygen concentration can be rather easily measured, its rate of change in enclosed laboratory systems has been used for estimating remineralization rates. This technique may underestimate the overall mineralization rate and also lacks the ability to distinguish rates for the various mineralized nutrient types.

Only a very few measurements have been made of the explicit stages of algae decomposition and remineralization. The rates for these processes are known to vary with type of nutrient and temperature. They probably also vary with such factors as salinity, type of algae, and concentration of decomposing bacteria in the water, although little if any quantitative data are available on these effects. Because of the probable influence of these factors, a literature search was undertaken

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[1] In this and all further discussion, a decade will be defined as a ten-day period. For all months that do not have exactly 30 days, the last decade in the month will have the odd number of days necessary to complete the month. Under this system (commonly used by Dutch researchers), all months will have exactly three decades.

Table 3.1

SPECIFIC LOSS RATES FROM A PHYTOPLANKTON COMMUNITY

Decade		Loss Rate, Day^{-1}	Decade		Loss Rate, Day^{-1}
January	I	.18	July	I	.38
	II	.20		II	.35
	III	.23		III	.32
February	I	.26	August	I	.30
	II	.29		II	.27
	III	.32		III	.25
March	I	.35	September	I	.25
	II	.38		II	.29
	III	.42		III	.36
April	I	.46	October	I	.45
	II	.52		II	.55
	III	.57		III	.62
May	I	.65	November	I	.46
	II	.72		II	.38
	III	.84		III	.28
June	I	.55	December	I	.20
	II	.48		II	.12
	III	.42		III	.12

SOURCE: Ref. 23.

to find values for remineralization rate parameters that were measured under conditions as similar as possible to those of the Dutch waters of interest. Table 3.2 lists these published rate parameters for the several nutrients N, P, and Si. The range of values reflects the variation of the phenomena involved in mineralization in the different aqueous environments.

The BOD decay coefficient shown in Table 3.2 provides a linear approximation for the value of this parameter as it changes with temperature. The phenomena involved in determining this rate of BOD are described in our companion report on ecological disturbances arising from anaerobic conditions (R-2121/5). In that report, we use the nonlinear formula for η, the rate constant for oxygen uptake by bacteria, given by Davidson and Bradshaw [29].

$$\eta = (2.35 \times 10^{-7}) \exp (0.0464T) , \qquad (3.5)$$

where T is in degrees Kelvin and η has units of day^{-1}. The BOD per unit of each species, p_j, described in Sec. 3.3, will also vary with a number of factors, including the type and age of the algae colony, the kind of unit used in describing the algae, and the temperature, nutrient, and light conditions under which the colony grew. The unit BOD will also vary with the types of bacteria or other decomposing organisms present during mineralization. An extreme is represented by anaerobic organisms that derive their metabolic energy from the reduction of substances such as SO_3 or NO_3 ions rather than from the direct use of oxygen.

Table 3.2

RATES AND OTHER PARAMETERS FOR ALGAE MINERALIZATION

Parameter Name and Description	Value	Reference Number
Nitrogen		
Organic N-NH hydrolysis rate, $day^{-1}C^{-1}$	.007	3
Organic N-NH hydrolysis rate, $day^{-1}C^{-1}$	.002	4
NH_3-NO_3 nitrification, $day^{-1}C^{-1}$	.01	3
NH_3-NO_3 nitrification, $day^{-1}C^{-1}$	.003	4
NH_3-NO_3 nitrification, $day^{-1}C^{-1}$	.002	25
Constant for preference function, NH_3/NO_3	.95[a]	4
Settling rate for organic N, day^{-1}	.1	3
BOD decay coefficient, $day^{-1}C^{-1}$	.01	3
Phosphorus		
Rate of P release from cells, day^{-1}	.038	26
Bacterial production rate for inorganic P, day^{-1}	.0381	26
Bacterial production rate of refractory organic substance, day^{-1}	.0174	26
Rate of P mineralization, day^{-1}	Very fast	4
Organic P-inorganic P conversion, $day^{-1}C^{-1}$	.007	3
Settling rate for organic and inorganic P, day^{-1}	.10	3
Silicon		
Fraction of Si mineralized as fast as P	.8-.95[b]	4
Excretion		
Percentage of carbon excreted of total C assimilated (natural colonies)	4.5-16[c]	27

[a] This NH_3/NO_3 preference function is

$$P_{NH_3} = aNH_3/aNH_3 + (1 - a)NO_3 \ ,$$

where a is the constant listed in the table, and NH_3 and NO_3 represent their respective concentrations [4].

[b] The remainder of the silicon is believed to be refractory and mineralize at a very slow rate [3].

[c] Excretion of up to 35 to 40 percent of their assimilated organic material during periods of rapid growth has been reported [28]. These excreted materials are subject to mineralization. And in a personal communication to the authors, J. C. H. Peeters reports excretion rates of up to 80 percent in *phaeocystis* in Grevelingen on the southwest coast of the Netherlands.

The units for measuring algae biomass that least distort the differences in BOD for various species are ash-free dry weight, dry organic material, or carbon content. These measures, in contrast with total volume, cell concentration, or dry weight, are more direct indicators of the amounts of organic compounds that the bacteria decompose during mineralization.

As mentioned earlier, mature colonies of algae growing in a low nutrient environment tend to have a cell composition that is fairly low in proteins and fats and high in carbohydrates. When the algae cell contents are used by bacteria as metabolic foods, the respiratory quotient of the bacteria (CO_2 out/O_2 in) will reflect this cellular composition of the algae. In computing the oxygen demand during desalinization of the Oostmeer, Vegter [30] used a value of 1.42 g of O_2 required for each 1 g of ash-free dry weight of organism. Assuming that 1 g ash-free dry weight equals .5 g carbon [31] for algae, this 1.42 g O_2 requirement implies a bacterial respiratory quotient (RQ) of 0.94 (mole basis). Given a theoretical RQ of 1 for pure carbohydrates, 0.71 for fats, and 0.83 for proteins, this O_2 demand estimate appears to be reasonable for use in our model.

Chapter 4

RELATION OF ALGAE AND LIGHT

4.1. THE EXTINCTION COEFFICIENT

The extinction coefficient—the rate at which the light intensity decreases on descending deeper into the water—is a crucial quantity in our model. Algae production depends on the absorption of light energy. Thus, if the extinction coefficient is large, so that little light penetrates to the depths, little algae production will occur there. Because algae absorb light, their presence will increase the extinction coefficient, reducing the production of the algae below them. This can be an important factor in limiting the size of the bloom.

Furthermore, not all species of algae are equally efficient users of light energy at all intensities. Green algae use low-intensity light fairly efficiently, and high intensities less efficiently. Dinoflagellates show the opposite pattern, while diatoms fall between the two. This means that if conditions are otherwise favorable, one species (e.g., a green algae) might dominate another (e.g., a dinoflagellate), driving it out of the bloom through a greater ability to make use of low-intensity light. This process has the characteristic known as positive feedback: The more green algae there are, the greater will be the extinction coefficient and the less intense will be the light at any depth. Thus, the competitive advantage of the green algae will be increased by increases in the green algae's abundance.

This section will discuss how to calculate the extinction coefficient from the abundances of the various species of algae. The next section will show how to determine the conditions on the extinction coefficient that must be satisfied for each species to participate in the bloom.

Define the following symbols:

k_0 = the background extinction coefficient, i.e., the value the extinction coefficient would have if no algae were present but other conditions were unchanged.
K_j = the amount by which adding one more unit of species j would increase the extinction coefficient.
v = the rate constant for eliminating the effect of dead algae fragments on the extinction coefficient.

This last quantity requires some explanation. As dead algae contribute to the BOD, they also affect the extinction coefficient. As they are decomposed, however, their effect diminishes. The rate at which this diminution occurs is v. We realize, of course, that this rate will generally be different for different species, but data limitations have forced us to use a single average value for all species.

In a manner exactly similar to our derivation of BOD (Eq. (3.4)), we can obtain an expression for the extinction coefficient:

$$k = \sum_j \frac{K_j (D_j + v)}{v} x_j + k_0 \; . \tag{4.1}$$

As with BOD, this holds only if there is no grazing, and algae death is caused by mortality alone. Any algae that are eaten by larger creatures will not contribute to the extinction coefficient. Thus, if there is grazing, D_j in Eq. (4.1) should be replaced by the death rate caused by mortality alone.

4.2. DATA FOR CALCULATING EXTINCTION COEFFICIENTS

The vertical total extinction coefficient is defined by

$$k = \frac{1}{Z} \ln \frac{I_s}{I(Z)} , \tag{4.1a}$$

where Z is the depth, I_s is the surface daylight radiant flux, and I(Z) is the radiant flux at depth Z. Unfortunately, there are no direct measurements of this quantity in the Delta region for the time periods of interest. Instead, the Environmental Division makes routine determinations of the Secchi disc visibility depth. To do this, a white disc (Secchi disc) is lowered in the water until it just disappears from sight. The depth at which this occurs is an indication of the light transmission properties of the water. This method is obviously rough and subjective, but there have been several discussions in the literature of the relationship between the Secchi depth and vertical extinction coefficient [32,33,34]. The general formula is postulated to be

$$k = \frac{C}{S} , \tag{4.1b}$$

where S is the Secchi visibility depth and C is a constant. However, it is clear that the value of the constant is a function of the area and general aquatic conditions. For this reason, we decided not to select a literature value, but rather to determine one from available data. A set of simultaneous measurements of the Secchi depth and extinction coefficient existed for the general Delta region. These were used to derive a value for the constant of 0.824 (with standard deviation of 0.329) when S is in units of decimeters. With this relationship and the Secchi depth data, it was possible to calculate approximate extinction coefficients for the model.

As with the nutrient data, the visibility measurements are made at the fixed stations with varying frequency. The irregularity of these measurements is not very important, because data are sparse in winter when there are no algae blooms. Again, the measured values were used to generate a weighted mean for the entire area, based on the volume of water considered to be represented by each measuring point. This is necessarily only an approximate value, but there was little important variation between the different regions of the Oosterschelde. The weighted mean values of the Secchi depth were then converted into extinction coefficients using the empirical relationship. It must be remembered that these results represent the total extinction coefficient, including the effect of the phytoplankton that were present when the measurements were made. Thus, some correction must be applied to remove their effect and convert the results to true background extinction measurements. To do this, it was necessary to determine the value of the specific extinction coefficient K_j (defined in Sec. 4.1) for a mixed population of algae.

There has been some experimental work to measure the extinction caused by phytoplankton populations. This is often difficult to accomplish in a realistic situation for single species populations. Thus, we must make certain assumptions about the characteristics of algae orders to obtain usable information. Parsons and Takahashi [11, p. 87] have collected the results of previous work. They give the specific extinction coefficients for several individual species and a mixed population of marine phytoplankton, all in units of m^2/mg chl. From these data, mean values have been selected for each of the three orders (diatoms, green algae, and dinoflagellates). These parameters must be regarded with considerable uncertainty, however, because of the restricted number of species measured and the variation between species in any order. The values used in the model are given in Table 4.1.

It can be seen that green algae are considerably more important to the extinction coefficient than are diatoms or dinoflagellates, which have similar properties. The value for a mixed population is an average taken from the literature. With this value, it was possible to make the extinction coefficient corrections described in the previous paragraph. Unfortunately, there are no observations of the phytoplankton concentrations in the Oosterschelde during the periods of interest. The only available information consists of measurements of chlorophyll concentration for an area directly outside the mouth of the estuary. These data generally cover the years 1973 to 1974. To make the correction, the specific extinction for a mixed population was multiplied by the measured chlorophyll concentration for the period. This product was subtracted from the extinction calculated earlier (from the Secchi visibility depth). The result was then assumed to be the background extinction coefficient for the model during that period. In general, these correction factors tended to be small compared with the measured background extinction coefficients.

The last important problem under this heading is that of determining v, the rate constant for eliminating the effect of dead algae on the extinction coefficient. Our literature search could not find any direct investigation of this process, and it is clear that the value of the constant will depend on the phytoplankton type and environmental conditions. Because of lack of data, it was necessary to use one average value for all species in the model. We assumed that the extinction coefficient would disappear at approximately the same rate as organic material in dead

Table 4.1

SPECIFIC EXTINCTION COEFFICIENTS
FOR PHYTOPLANKTON ORDERS

Order	K_j
Diatoms	5.00×10^{-5} m^2/mg dry wt
Green algae	1.64×10^{-4} m^2/mg dry wt
Dinoflagellates	5.00×10^{-5} m^2/mg dry wt
Mixed population	7.00×10^{-3} m^2/mg chl

algae is mineralized. The rate constant determined by Eq. (3.5) was chosen on this basis.

This procedure will give the same value for each order of phytoplankton, but the rate is temperature-dependent and does measure the speed of decomposition. The parameters of this Eq. (3.5) were tested for sensitivity. If 10°C is taken as a reference point, as the equation parameters are changed to rotate the function, there is only a slight effect on the values of the decomposition rate. This must be primarily caused by the limited temperature range in the Oosterschelde, and the distance of this range from absolute zero (the base point for the equation). Such a result is somewhat suspect, and the temperature range over which the equation is valid should be investigated in the future.

4.3. CHLOROPHYLL CONCENTRATION

In algae, chlorophyll is the molecule that absorbs light energy and transforms the energy into a form available for chemical synthesis. (Other molecules, such as carotene, can absorb light energy, but they must transfer it to chlorophyll before it can be used for synthesis.) For this reason, chlorophyll concentration is thought by some to be a useful indicator of the potential productivity of an algae population. Because it is easy to determine by spectrographic techniques, it is also one of the most frequently measured quantities in algae studies. We will find it useful to calculate the chlorophyll concentration associated with each predicted bloom, so that when we "predict" blooms that have occurred in the past, we can compare our calculated chlorophyll concentration with the actual measurements.

Define the symbol

q_j = the chlorophyll content of a unit biomass of species j.

Then the chlorophyll concentration, chl, due to live algae is

$$\mathrm{chl} = \sum_j q_j x_j \quad . \tag{4.2}$$

We recognize that the chlorophyll content of algae depends on the size, age, nutrient status, light intensity, etc. Again, however, data limitations force us to use an average value for each species. It is generally agreed that chlorophyll is degraded very rapidly once an algae cell dies. Thus, there is no contribution by dead algae to the chlorophyll concentration.

4.4. DATA FOR CALCULATING CHLOROPHYLL CONCENTRATIONS AND OTHER BIOMASS RELATIONS

Strickland has compiled a number of average relations between the various parameters used to measure phytoplankton standing crop [31]. From these relations, estimates can be derived for the chlorophyll content of a unit biomass for each of the orders of algae of our model. These average relations are as follows:[1]

$$\text{mg C} = f_1 \times \text{mg chl} \ ,$$

where $f_1 = 30$ for normal, natural populations;

$$\text{mg ash-free organic matter} = f_2 \times \text{dry weight} \ ,$$

where $f_2 = 0.85$ for green algae,
$f_2 = 0.8$ for dinoflagellates,
$f_2 = 0.5$ for diatoms;

$$\text{mg C} = f_3 \times \text{mg ash-free organic matter} \ ,$$

where $f_3 = 0.5$ for most marine organisms.

From the above, we may derive the following relations:

$$\text{mg dry weight} = F \times \text{mg chl} \ ,$$

where $F = 70.6$ for green algae,
$F = 75$ for dinoflagellates,
$F = 120$ for diatoms.

This last measure (mg dry weight) is the unit for algae biomass of our model.

Another useful conversion factor relates caloric content to mg dry weight of phytoplankton. Platt and Irwin [35] have found the following excellent relationships:

$$\text{cal (mg dry weight)}^{-1} = 0.632 + 0.086\ (\%\ \text{C}) \ ,$$

$$\text{cal (mg dry weight)}^{-1} = -0.555 + 0.113\ (\%\ \text{C}) + 0.054\ (\text{C:N}) \ .$$

In the latter case, if the nitrogen content is also known, the prediction is extremely good.

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[1] The original reference should be consulted to determine the errors and limitations inherent in these estimates.

Chapter 5

DETERMINATION OF CONDITIONS FOR A SPECIES TO BE SELF-SUSTAINING

5.1. BALANCE BETWEEN PRODUCTION AND LOSSES

In this section, we will deal with only a single species of algae. This enables us to drop the subscript j from all our quantities, thereby simplifying the formulas. However, it should be kept in mind that our model does deal with multiple species, and hence for each formula found in this section, there is implied an additional similar formula for each additional species.

Define the following symbols:

P = production rate constant of the algae species,
R = respiration rate constant,
D = death rate constant (mortality plus grazing).

Clearly we have for each species

$$\frac{dx}{dt} = (P - R - D)x \ .$$

According to our stationarity assumption, the peak size of a bloom will occur when $dx/dt = 0$. But this requires that either

$$P - R - D = 0 \tag{5.1a}$$

or

$$x = 0 \ . \tag{5.1b}$$

In our model, we permit the respiration and death rates to depend only on temperature, which we denote by R(T) and D(T), respectively, where T stands for temperature. The production rate, however, depends not only on temperature but also on the solar intensity and on the availability of nutrients.

However, we do not have data describing all these dependencies. Rather, we have some data that illuminate the dependence of production rate on temperature and solar intensity, under conditions of nutrient excess. Under these conditions, we express P as

$$P = P_{max}(T)E(I) \ ,$$

where I is the solar intensity, $P_{max}(T)$ is the largest production rate that can be measured at temperature T, and E(I) is the efficiency of production at a particular intensity relative to the maximum possible production. (The largest production rate $P_{max}(T)$ will occur at the intensities I for which the efficiency E(I) equals one.) Nutrient limitations could only reduce the production rate. Thus, we can say that under any conditions, regardless of how scarce or abundant the nutrients are,

$$P \le P_{max}(T)E(I) \ . \tag{5.2}$$

Combining Eqs. (5.1a), (5.1b), and (5.2), we find that a species of algae can only be present in a bloom if its efficiency E(I) satisfies

$$E(I) \ge \frac{R(T) + D(T)}{P_{max}(T)} \ . \tag{5.3}$$

When condition (5.3) is not satisfied for a particular species of algae, that species is excluded from the bloom.

Of course, condition (5.3) is not a complete substitute for condition (5.1a). That is, satisfying (5.3) does not guarantee that (5.1a) will also be satisfied. But if (5.3) is violated, then (5.1a) must be violated as well. Therefore, if condition (5.3) does not hold at the peak of a bloom for a particular species, then (5.1b) must hold, thus excluding that species from the bloom.

5.2. SOURCES OF PRODUCTION DATA

Parsons and Takahashi [11] have an excellent summary of the current understanding of primary photosynthetic production. Our model treatment of this subject generally follows the exposition of this reference. The basic information on relative photosynthesis (E(I) or P/P_{max}) is derived from earlier work of Ryther [36] who carefully measured this parameter as a function of light intensity at constant temperature in the laboratory and found the results compatible with several different sets of ocean measurements. Ryther measured these relations for fifteen different species of algae of the three orders of green algae, diatoms, and dinoflagellates. As described earlier, the results for all species of an order were quite homogeneous, and the data were combined by order. These results of Ryther have been converted to tabular form for incorporation into our model and are shown in Table 5.1.

One can argue that it is not appropriate to characterize phytoplankton orders by specific photosynthetic response curves because of the importance of other factors. Recent literature [37,38] has indicated that other influences, such as sun-shade acclimation, can be significant in determining the response curves of phytoplankton. We feel, however, that our characterization is a valid simplification for the following reason. The species in the Ryther experiments were grown and measured under identical conditions; thus, they should have been acclimated to their surroundings to the same extent. Even if the absolute radiation levels used in the work were not the same as those encountered in the Netherlands, one would expect the relative shapes of the curves to remain reasonably constant. The primary change would be a shifting of the saturation level of radiation toward a lower value,

Table 5.1

THE RELATION BETWEEN RELATIVE PHOTOSYNTHESIS E(I) AND LIGHT INTENSITY AT T = 20°C

Light Intensity, Joules/m^2/hr	Order of Phytoplankton		
	Diatoms	Green Algae	Dinoflagellates
0.00D 00	0.00	0.00	0.00
2.03D 04	0.15	0.35	0.07
4.05D 04	0.29	0.85	0.13
8.11D 04	0.54	0.99	0.22
1.22D 05	0.76	0.99	0.31
1.62D 05	0.93	0.97	0.40
2.03D 05	0.98	0.95	0.51
2.43D 05	1.00	0.93	0.62
2.84D 05	1.00	0.89	0.74
3.24D 05	1.00	0.87	0.85
3.65D 05	0.99	0.83	0.94
4.05D 05	0.98	0.80	0.98
4.46D 05	0.94	0.77	1.00
4.87D 05	0.89	0.73	1.00
5.27D 05	0.83	0.69	1.00
5.68D 05	0.77	0.64	0.98
6.08D 05	0.72	0.60	0.97
6.49D 05	0.66	0.56	0.95
6.89D 05	0.60	0.52	0.92
7.30D 05	0.56	0.48	0.89
7.70D 05	0.51	0.44	0.86
8.11D 05	0.45	0.40	0.82
8.92D 05	0.36	0.32	0.74
9.73D 05	0.31	0.26	0.67
1.05D 06	0.26	0.20	0.60
1.14D 06	0.21	0.14	0.53
1.22D 06	0.18	0.11	0.46
1.30D 06	0.13	0.08	0.39
1.38D 06	0.11	0.05	0.33
1.46D 06	0.08	0.04	0.25
1.54D 06	0.06	0.03	0.20
1.62D 06	0.04	0.02	0.15
1.70D 06	0.02	0.01	0.10
1.75D 06	0.00	0.00	0.00

but this should occur for all orders and species, not just selectively. Thus, the measured curves would still represent a valid difference in the response characteristics of the different orders. We investigated the effect of variations in these response curves and discuss these results in App. B.

To determine P_{max} (T) (the maximum gross production), we turn to Eppley [21], who surveyed the available information on specific growth rate for a wide variety of algal batch cultures growing under conditions in which nutrients were not limiting. Specific growth rate is defined as the rate of increase of cell substance per unit cell substance per day. This survey showed that there is a gradual and exponential increase in growth rate with temperature up to about 40°C. Values for specific growth rates below 40°C fall within an envelope curve of maximum expected value for all algae. An approximate equation for this curve from Eppley is

$$P_{max}(T) = \exp\ (.0633T - 0.16)\ , \tag{5.4a}$$

where T is degrees C. Within the envelope bounded by this curve, each division of algae appears to have a different temperature optimum and temperature range in which it can produce. Above and below this range, it may survive in small numbers and respire but not grow. These feasible temperature ranges for growth are determined as follows for the algae divisions of our model [21]:

Diatoms	0 to 30°C
Green algae..........	12 to 40°C
Dinoflagellates	8 to 35°C

Goldman and Carpenter [22] have conducted a similar survey of maximum growth rate versus temperature from continuous culture experiments on algae. Their curve, which is analogous to Eppley's, is given by the following equation:

$$P_{max}(T) = (5.35 \times 10^{9})e^{-6472/T}\ , \tag{5.4b}$$

where T is degrees Kelvin. For some unknown reason, these continuous cultures give a growth rate about one unit below the batch-culture growth data.

The curves of Eppley and of Goldman and Carpenter define the maximum net productivity; that is, they neither account for the respiratory component of total, gross production nor its alteration with temperature. One alternative for obtaining an estimate of this respiratory component is from Riley [39] who derives the following specific respiration coefficient based on experimental data:

$$R(T) = (1.1326 \times 10^{-7})e^{0.069T}\ . \tag{5.5a}$$

Again, T is degrees Kelvin.

Another alternative is to follow evidence presented by Ryther [36] that respiration is about 10 percent of gross photosynthesis at all temperatures. Respiration on this assumption then becomes (using Eppley's equation for net production)

$$R(T) = \frac{.1\ P_{max}(T)}{.9} = \frac{.1\ \exp\ (.0633T - 0.16)}{.9}\ . \tag{5.5b}$$

A similar relation may be derived from the Goldman and Carpenter equation. In our model, we have chosen Eppley's curve (5.4a) as our estimate of maximum net productivity, and we have taken the respiration component of the maximum gross production according to Eq. (5.5b). The maximum gross production, of course, is the sum of these two components.

Values of specific growth rates are greatly influenced by the technique of measurement used and the environment in which the algae exist. Many of these influences are discussed by Strickland [31] and will not be repeated here. Rates of production measured by the conventional radioactive carbon uptake method are believed to reflect most nearly the net photosynthesis; that is, respiration is not counted [31]. The algae are filtered out and washed before counting, so any radioactive carbon that had been photosynthetically fixed as organic substance and excreted would not be counted. However, algae that die after exposure to the radioactive carbon would have absorbed some active material before death (and some afterward) and be at least partially counted as living biomass. (Experimental incubation periods are usually kept to less than 5 to 6 hours to minimize these errors.) Growth measured as increase of cell carbon per unit of photosynthetic pigment is not subject to these errors, but because this technique does present other difficulties it has not been as widely used.

There is no apparent reason to believe that the $P = P_{max}E(I)$ relations reported by Ryther [36] for temperatures held near 293°K (20°C) should apply for other temperatures—in other words, that production efficiency should be invariant with temperature for each order of algae. In our model, the light intensity I_{max} at which the efficiency is maximum does in fact change with temperature as we move from a temperature range favored by one division of algae to a range in which another order dominates. However, Strickland [31] states that even within the temperature range in which a single order dominates, the shape of the E versus I curve changes with temperature, generally resulting in a marked increase of I_{max} with temperature. He also states that an empirical relation used by Smith [40] fits some data well if 1/K in this equation increases logarithmically with temperature. We may rewrite the Smith equation as

$$E = \frac{I}{(K^{-2} + I^{2})^{\frac{1}{2}}} ,$$

where $1/K = a \exp(bT)$. 1/K has the units of light intensity and is the value of I when $E = 0.7071$. Our observation is that this Smith equation does not fit the data from Ryther shown in Table 5.1. This is especially true at high light intensities, where photosynthesis is observed to be inhibited but where the Smith equation does not show a decline in efficiency. We may, however, still make some use of this equation by observing it states that as the temperature changes, the light intensity I required to maintain a constant efficiency E changes like $\exp(-bT)$. We can use this observation to scale I(T) for temperatures other than 293°K (20°C, which is Ryther's measurement temperature) as follows:

$$I(293) = I(T) \exp [b(T - 293)] , \tag{5.6}$$

where T is the new temperature, different from 293°K. To calculate an efficiency E at a temperature T and a light intensity I(T), we first calculate an equivalent 20° intensity I(20) from Eq. (5.6). Then we find the efficiency corresponding to I(20) from

Table 5.1. This efficiency also corresponds to the intensity I(T) when the temperature is T.

To actually use this idea, we must first evaluate the parameter b. Data found in Ref. 11, Fig. 29B, suggest that b may lie between 0.1 and 0.3. Since this range translates to a ten-fold difference in I(T) when T = 283°K (10°C, a temperature typical of Dutch waters at the time of the spring bloom), this estimate is too uncertain to be usable. In addition, Parsons and Takahashi [11] state that to some extent, populations of algae will adapt to a new temperature regime within a few days. This suggests that b may not be constant. Because of these difficulties, we chose not to include in our model any shift with temperature in the light intensities at which each order achieves its maximum production.

5.3. NATURAL VERSUS MEASURED EFFICIENCY

It is not appropriate, however, to use the efficiency curves from Parsons and Takahashi [11] in condition (5.3). These curves were measured among algae being exposed to a constant solar intensity. In real life, turbulence causes each cell to spend some time near the surface, where the intensity is relatively high, and some time at greater depths, where the light is less intense. In addition, the intensity of sunlight varies with the time of day.

To adjust the measured efficiency curves to the real world of varying intensity, we must average the measured curves both over the 24 hours of the day, and over all depths of water from the surface to the mixing depth. The mechanics of this averaging procedure are given in the next section.

Averaging over the 24 hours of the day is straightforward. However, averaging over a column of water from the surface down to a mixing depth presents an interesting feature. Because the algae influence the extinction coefficient, the light intensities observed at the different depths will vary as the abundance of algae varies. But if this is so, the average production efficiency of each species of algae will also depend on the total algae abundance.

If the algae are too abundant, there may be so little light in most of the water column that the algae cannot sustain themselves. Their average efficiency will not satisfy condition (5.3), and the species in question will not occur in the bloom. This is called self-shading. Similarly, if the intensity is too high, the average efficiency will decrease. Therefore, a too-low as well as a too-high extinction coefficient can exclude a species from the bloom.

Thus, condition (5.3) implies that for each species there is a range in the extinction coefficient within which that species is permitted in the bloom, and outside of which the species is excluded. In other words, there is a minimum value of the extinction coefficient, k_{min}, and a maximum value, k_{max}, such that if

$$k_{min} \leq k \leq k_{max} , \qquad (5.7)$$

then the species can sustain itself as a part of the bloom. (k is the extinction coefficient.) When condition (5.7) is not satisfied, the species is excluded from the bloom. Condition (5.7) thus replaces condition (5.3).

5.4. CALCULATING THE AVERAGE EFFICIENCY

Our calculation of average efficiency assumes that the water is well mixed in the vertical dimension, from the surface down to the mixing depth. Under this assumption, the light intensity, I(z), at a depth z (which is less than the mixing depth z_{max}) is related to the light intensity at the surface, I_s, by

$$I(z) = I_s \exp(-kz) ,$$

where k is the extinction coefficient. The efficiency of an algae cell at depth z is, of course, E[I(z)].

By virtue of our assumption of good vertical mixing, each cell spends an equal amount of time at every depth from 0 (the surface) to z_{max} (the mixing depth). Thus, if the surface light intensity were constant, the average efficiency, EDEP, would be:

$$\mathrm{EDEP} = \frac{1}{z_{max}} \int_0^{z_{max}} E[I_s \exp(-kz)]\, dz . \tag{5.8}$$

For purposes of computational efficiency, we transform Eq. (5.8) as follows. First, we define F(v) as

$$F(v) = \int_0^{v} E[\exp(-s)]\, ds .$$

We then find that (5.8) is equivalent to

$$\mathrm{EDEP} = \frac{F(kz_{max} - \log I_s) - F(-\log I_s)}{kz_{max}} . \tag{5.9}$$

The reader will note from Eq. (5.9) that the efficiency EDEP depends on the surface light intensity I_s. Of course, this light intensity will vary during each 24-hour period, being greatest at midday, and essentially zero during nighttime hours. Thus, to calculate the true average efficiency, we must further average EDEP over all surface light intensities encountered during a 24-hour period. But this is straightforward. Let the surface intensity at time t be $I_s(t)$. For purposes of computational efficiency, we define the function G(v) as

$$G(v) = \frac{1}{24} \int_0^{24} F[v - \log I_s(t)]\, dt . \tag{5.10}$$

Then the final average efficiency, EAVG, averaged over both the depth and the day, is

$$\text{EAVG} = \frac{G(kz_{\max}) - G(0)}{kz_{\max}} \; . \tag{5.11}$$

In the model, Eq. (5.11) would be used to find the values of k, the extinction coefficient, at which the average efficiency EAVG just equals the minimum necessary efficiency calculated in condition (5.3). It would seem from the definition of G(v), however, that we could only do this for a day whose surface light intensity was described by the function $I_s(t)$. That is, it would appear that we must calculate a new function G(v) for each new day.

Fortunately, this is not true. Certain changes in $I_s(t)$ can be accommodated without recalculating G(v). These changes are (1) a change in the number of daylight hours in the 24-hour period, the pattern of intensity remaining similar but occurring at a different rate; and (2) a change in the intensity at each instant of the 24-hour period, but by a constant fraction. Any combination of these two changes can also be accommodated.

To see how to deal with a change in the number of daylight hours (which we denote by the symbol DL for day length), note that when $I_s(t)$ is very small, the argument of F in Eq. (5.10) is very large (the argument of F in this equation is v $-$ log $I_s(t)$). Looking back at the definition of F(v), we note that as its argument v becomes very large, F(v) must approach a constant value, F_{lim}. Now define a new function H(v) to be:

$$H(v) = \frac{1}{\text{DL}} \int_0^{\text{DL}} F[v - \log I_s(t)] \, dt \; , \tag{5.12}$$

where the times t over which we integrate are those for which $I_s(t)$ is not effectively zero. These, of course, are the daylight hours. Clearly, we can express G(v) as

$$G(v) = \frac{\text{DL}}{24} H(v) + \frac{24 - \text{DL}}{24} F_{\text{lim}} \; .$$

Substituting this new expression for G(v) into Eq. (5.11), we find that the terms containing F_{lim} cancel, and we are left with

$$\text{EAVG} = \frac{\text{DL}}{24} \, \frac{H(kz_{\max}) - H(0)}{kz_{\max}} \; . \tag{5.13}$$

According to Eq. (5.13), if two 24-hour periods differ in their day lengths, but their surface light intensity patterns are similar (differ only in the rate at which they are completed), the average efficiencies on the two days should be in the same ratio as the day lengths.

Suppose that we have calculated G(v) for a 24-hour period with a surface intensity pattern $I_s(t)$; we now wish to find the average efficiency for a 24-hour period with pattern $wI_s(t)$, where w is an arbitrary positive constant. Our second 24-hour period has a surface intensity that at every instant is w times as great as the intensity during the first 24-hour period. To calculate this new efficiency, we could recompute G(v) according to Eq. (5.10). That is, we could define a new function G(v) according to

$$\bar{G}(v) = \frac{1}{24}\int_0^{24} F[v - \log wI_s(t)]\ dt \ .$$

However, the old G(v) and the new G(v) are related according to the equation

$$G(v - \log w) = \bar{G}(v) \ .$$

Thus, we can use the old function G(v) to calculate EAVG according to

$$\mathrm{EAVG} = \frac{G(kz_{\max} - \log w) - G(-\log w)}{kz_{\max}} \ . \tag{5.14}$$

Finally, we can combine the methods for dealing with these two changes in the surface light intensity pattern. Consider a 24-hour period with a day length DL and surface intensity pattern during the daylight hours of $wI_s(t)$. Then the average efficiency EAVG is

$$\mathrm{EAVG} = \frac{DL}{24}\,\frac{H(kz_{\max} - \log w) - H(-\log w)}{kz_{\max}} \ . \tag{5.15}$$

In the model, we take advantage of these computational possibilities. Before we actually exercise the model, we precalculate the function H(v) according to a transformation of Eq. (5.12), using a standard surface light intensity distribution (usually corresponding to the pattern at 45° north latitude at the time of the vernal equinox). To calculate EAVG, we specify as inputs a day length DL, a relative intensity w, a mixing depth z_{max}, and an extinction coefficient k. These are then substituted into Eq. (5.15) to yield EAVG.

The transformation of Eq. (5.12) involves expressing the surface light intensity pattern $I_s(t)$ as a probability distribution, which ignores the times of day at which a particular light intensity is observed, instead of expressing it as a function of time. When this is done, and when the variable I_s is transformed into its logarithmic counterpart log I_s, Eq. (5.12) becomes a convolution. It is in this form that we use (5.12) to compute H(v).

To find k_{min} and k_{max}, we set EAVG to its minimum permissible value (from condition (5.3)) and DL, w, and z_{max} to their desired values. Then we treat (5.15) as an equation whose roots k_{min} and k_{max} we wish to solve. It can be shown that when treated this way, Eq. (5.15) has zero, one, or two roots. If it has zero roots, there is no value of the extinction coefficient for which the average efficiency exceeds its minimum permissible value. If there is one root, the efficiency equals or exceeds its minimum permissible value only when the extinction coefficient equals that root. Finally, when there are two roots, the efficiency equals or exceeds its minimum permissible value for all values of the extinction coefficient between the two roots, and is smaller than permitted when the extinction coefficient is not between the roots.

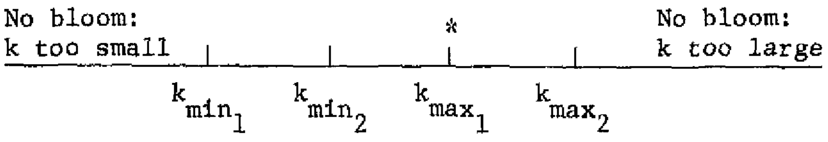
Chapter 6

CALCULATION OF THE BLOOM PEAK

We are now prepared to calculate the maximum size that the algae bloom can achieve. As outlined in the Introduction, this involves defining a sequence of linear programs, each of which corresponds to a different assumption about the extinction coefficient. In the next few sections, we identify the different assumptions that can be made regarding the extinction coefficient, and present the individual linear programs in the sequence. We then show how to extract from this sequence an estimate of the maximum size of the bloom.

6.1. FEASIBILITY INTERVALS FOR THE EXTINCTION COEFFICIENT

Using the methods outlined in the previous section, we determine which species j have minimum and maximum feasible extinction coefficients, $k_{\min_j}$ and $k_{\max j}$. (Note that we have returned to using the subscript j. Hereafter we will be dealing with several species simultaneously.) Those species without a $k_{\min j}$ and $k_{\max j}$, or whose $k_{\min j}$ and $k_{\max j}$ are equal, are excluded from the bloom for all values of the extinction coefficient. Then we take all of the remaining numbers $k_{\min_j}$ and $k_{\max j}$ and put them in ascending order. This is illustrated below for a hypothetical situation with two species. The asterisk (*) marks the value of the extinction coefficient that our model would predict at the peak of this bloom.



Clearly, this procedure partitions the possible range of values that the extinction coefficient can take on into a number of intervals. First, there are the regions where k is either too large or too small for any species to sustain itself. More interesting, however, are the intermediate intervals, where one or more species can exist.

We number these intervals s = 1, 2, . . . from left to right. Denote the lower limit of interval s by L_s. The upper limit, of course, is the lower limit of the next interval, L_{s+1}. In each interval, only some subset of the species can occur. For the others, the extinction coefficient does not satisfy the appropriate Eq. (5.4). Denote the set of species permitted in interval s by S_s. We call these intervals "feasibility intervals," and their associated sets "feasibility sets."

6.2. FINDING THE MAXIMUM POTENTIAL BIOMASS

To find the maximum potential biomass, we first find the maximum biomass that could exist, provided that the extinction coefficient is in each feasibility interval in turn. Then, we estimate the maximum potential biomass to be the largest of these maxima. More explicitly, assume for the moment that at the peak of the bloom, the extinction coefficient was observed to be in feasibility interval s. Then we know that the biomass of algae in the bloom cannot exceed the maximum biomass B_s found by solving the following problem:

PROBLEM s: Find $x_j \geq 0$ (only for those j in S_s),
$w_i \geq 0$, slack$_1 \geq 0$, and slack$_2 \geq 0$, that
maximize $B_s = \sum_j x_j$, subject to the conditions

$$\sum_j \frac{a_{i,j}(D_j + u_i)}{u_i} x_j + w_i = b_i \,, \tag{6.1}$$

$$\sum_j \frac{K_j(D_j + v)}{v} x_j - \text{slack}_1 = L_s - k_0 \,, \tag{6.2}$$

$$\sum_j \frac{K_j(D_j + v)}{v} x_j + \text{slack}_2 = L_{s+1} - k_0 \,. \tag{6.3}$$

Conditions (6.1) through (6.3) have all been derived in earlier sections. Condition (6.1) is identical with Eq. (3.2). The sums on the left-hand sides of conditions (6.2) and (6.3) *are the expressions for the extinction coefficient, as developed in Eq. (4.1).* In (6.2) we subtract from this sum the new variable slack$_1$, which we have demanded be positive. Thus, condition (6.2) requires that the extinction coefficient exceed L_s, the lower limit of feasibility interval s. The symbol k_0 on the right-hand side of this condition is the background extinction coefficient, the value that the extinction coefficient would have if no algae were present. Similarly, in (6.3) we add a new variable slack$_2$ to the expression for the extinction coefficient. Since we demand that this variable also be positive, condition (6.3) *requires that the extinction coefficient* not exceed L_{s+1}, the upper limit on feasibility interval s. Thus, conditions (6.2) and (6.3) merely express the fact that the extinction coefficient must be in feasibility interval s.

We also make the common-sense requirement that no species of algae can exist in negative amounts. Another condition says the same for the dissolved amount of each nutrient. Finally, we prohibit those species from occurring whose $k_{\min_j}$ and $k_{\max_j}$ do not contain feasibility interval s, and hence do not satisfy condition (5.3). These, of course, are the species not contained in S_s.

To repeat, if at the peak of the bloom we observe that the extinction coefficient lies in feasibility interval s, we can be certain that the biomasses x_j of the various algae species, as well as the variables w_i, satisfy conditions (6.1) through (6.3). But this implies that the peak biomass cannot exceed the largest biomass that satisfies these conditions.

The total biomass of algae can be calculated as

$$B = \sum_j x_j \ . \tag{6.4}$$

Our strategy is to calculate the maximum feasible biomass that satisfies conditions (6.1) through (6.3) for each feasibility interval s, using standard linear programming techniques. We denote the maximum biomass within interval s by B_s. Of course, we do not actually know before the fact which feasibility interval will contain the extinction coefficient. However, we can be certain that the observed peak biomass will not exceed the largest of the biomasses B_s. That is, if

$$BMAX = \max_s B_s \ , \tag{6.5}$$

then BMAX provides an upper bound on the peak of the bloom.

6.3. IMPLICATIONS OF LINEAR PROGRAMMING THEORY FOR ALGAE BLOOM COMPOSITIONS

In this section, we introduce some of the more important facts about linear programming as they apply to our model. Our purpose is not simply to describe the features of linear programming, which the reader can find in Refs. 41 or 42. Rather, we wish to point out some of the implications that the mathematical results of linear programming have for algae blooms.

6.3.1. Infeasibility

Problem s need not always have a solution. For example, the extinction coefficient is always required to be larger than L_s. This could imply that the algae biomass contains more of some nutrient than is available. When this happens, problem s is said to be "infeasible."

Generally when this happens, the linear program for a different feasibility interval will be feasible. Thus, our model will find a feasible algae bloom somewhere among its sequence of linear programs. However, it may happen that the program for every interval is infeasible. In this event, our model will predict that no algae biomass can be present. (See Sec. 5.1, especially Eqs. (5.1a) and (5.1b), for justification.)

When a linear program is infeasible, it may happen that a small perturbation of the appropriate parameters will render it feasible. Conversely, if it is feasible, it may be that some small parameter changes will render it infeasible. (It is not always true that only small perturbations of parameters will effect this change; sometimes large perturbations are required.) In nature, parameters could change in response to small alterations in temperature, or to adaptations by algae to slightly different nutrient contents.

Suppose that in certain circumstances, the problem associated with feasibility interval s yielded the maximum biomass B_s. Further, suppose that a small natural change occurred that rendered problem s infeasible. One of the other feasibility intervals must provide a new maximum biomass that might be considerably smaller than the old B_s. Such a change could account for the sudden dying off of a large bloom.

Of course, the converse could also occur. Problem s might originally be infeasible, and a small change in one or more parameters could render it feasible. Then a sudden population explosion could occur among the algae. Thus, through the phenomenon of infeasibility, our model offers an explanation of the sometimes explosive character of algae blooms.

6.3.2. Basic Solutions

Problem s has m + 2 constraints, one each for the m nutrients and two more that provide an upper and a lower bound on the extinction coefficient. The problem also has m + n + 2 variables. Each of the n species has a variable x_j, each of the m nutrients has a variable w_i, and the bounds on the extinction coefficient have the slack variables $slack_1$ and $slack_2$. Any set of nonnegative values for the variables that satisfies the constraints (6.1) through (6.3) is called a "feasible solution" to problem s. If, in addition, no more than m + 2 of these variables are positive, the rest being zero (m + 2 is the number of constraints), the solution is called a "basic feasible solution."

If problem s is feasible, it has at least one basic feasible solution. There is also a basic solution that achieves the maximum possible biomass satisfying the conditions of problem s. This is called a basic optimal solution. (Optimal solutions that are nonbasic are not ruled out. We are only stating that at least one optimal solution is basic.) For a proof of these assertions, see Chaps. 5 and 6 of Ref. 42.

The standard technique for solving a linear program is called the simplex method. This method looks systematically among basic feasible solutions (of which there are a finite number) for one that is optimal. Thus, if problem s is feasible, we will always discover a basic optimal solution. Although it is possible to determine whether nonbasic optimal solutions exist, the standard solution technique does not automatically seek them out.

6.3.3. Limiting Constraints

Assume problem s is feasible. If we solve it, we will find that one or more of the constraints (6.1) through (6.3) limit the size of the bloom. These are called the limiting constraints.

A constraint is limiting if an infinitesimal variation in its right-hand side can cause a change in the maximum biomass of algae. For example, the nutrient silicon would be limiting if a small reduction in silicon caused a reduction in the bloom. One condition this implies is that the "slack variable" of a limiting constraint must be zero ($w_i = 0$ in the case of nutrient i, constraint (6.1), and $slack_1 = 0$ or $slack_2 = 0$ in the cases of constraints (6.2) and (6.3)). Clearly, if nutrient i is present in excess (i.e., $w_i > 0$), it will not increase the bloom to add more nutrient, and not decrease the bloom to remove (within limits) some of that nutrient.

Because a constraint is limiting does not mean that all changes in its right-hand side will cause changes in the maximum biomass. For example, if a nutrient is limiting, reducing it will reduce the bloom. But increasing that nutrient can only increase the bloom up to a point. If too much of this nutrient is added, some other constraint will become more limiting, and further increases in the nutrient will have no effect. It is even possible that this point will come after only an infinitesimal increase in the nutrient. In this case, increases in the nutrient have no effect at all on the bloom, while decreases do have an effect. When the problem is balanced on a knife-edge such as this, it is said to be "degenerate."

6.3.4. Degeneracy

Three kinds of degeneracy are possible in linear programming. We mentioned one of them in the previous section, namely, that a limiting constraint may be on the verge of being nonlimiting. Changing a single parameter (in this case the right-hand side of the constraint) by the smallest amount can eliminate this degeneracy.

A second form of degeneracy occurs when some of the basic variables are zero. (Recall that the standard solution technique seeks out a basic optimal solution.) As in the first kind of degeneracy, an infinitesimal change in the right-hand sides of various constraints can eliminate this. For example, if the variable w_i were in the basis, but had value zero, we could increase b_i slightly. It can be shown that after this change, a basic solution consisting of the same variables, but with w_i increased in value, will be optimal.

The third form of degeneracy occurs when there is more than one optimal solution. In this case, optimal solutions will exist that are not basic, and hence may have more positive variables than there are equations. As in the other kinds of degeneracy, however, infinitesimal perturbations in the appropriate parameters can eliminate this degeneracy.

Suppose nutrient i is limiting (at least one constraint must be limiting) and also that species j is in the bloom. Further, suppose there are different amounts of species j in different solutions. (Such a species must exist. If all species were as abundant in each solution as in every other, all solutions would be identical.) Then an infinitesimal increase in $a_{i,j}$, the amount of nutrient i in a unit of species j, will reduce the degeneracy. If there remain multiple solutions, this process can be repeated.

We argue that in nature these degeneracies will not occur. How likely is it that two nutrients would be exhausted at precisely the same point in the growth of a uni-species population of algae? It is highly probable that at least some minute amount of one nutrient will remain when the last molecule of the other has been used. In addition, the requirements of the various species for nutrients and solar energy are uncertain. Thus, whenever problem s exhibits a degeneracy, it would be valid to restate the problem with slightly perturbed parameters. The new problem would not be degenerate.

6.3.5. The Number of Species in the Bloom

Assuming that the linear programs of our model are not degenerate, we can show that the limiting constraints are exactly those whose slack variables are zero. For example, if slack_2 were zero, the constraint (6.3), which places an upper limit on the extinction coefficient, would be a limiting constraint. Thus, a small increase in this upper limit would cause a change in the maximum biomass B_s. Similarly, if the amount w_i of dissolved nutrient i were zero, a small increase in the total available nutrient b_i would cause a change in the maximum biomass B_s.

Nondegeneracy also implies that exactly $m + 2$ variables will be positive in the optimal solution to problem s. Some of these positive variables may be slacks, and others may be amounts x_j of the various species of algae. To have either more or fewer variables positive would imply that problem s is degenerate.

From these facts it is simple to deduce that if problem s is not degenerate, there must be exactly as many species of algae in the bloom as there are limiting constraints. Note that if k species are in the bloom (k of the variables x_j are positive), then $m + 2 - k$ slack variables must also be positive. But there are a total of exactly $m + 2$ slack variables. Thus, the remaining k slack variables must be zero. It follows that their corresponding constraints are limiting.

Suppose only one species is present. Exactly one constraint will be limiting, either a nutrient constraint or a solar energy constraint (i.e., one of the constraints on the extinction coefficient). Similarly, if there are two species present in a bloom, two constraints must be limiting. We can even say that at least one limiting constraint must be a nutrient constraint. Suppose one of the limiting constraints is a solar constraint, corresponding to constraint (6.3). The other could not possibly be (6.2), because this would simultaneously require the extinction coefficient to equal L_s and L_{s+1}. Thus, one of the constraints (6.1)—a nutrient constraint—must be limiting.

6.4. THE RELATION OF THIS MODEL TO OTHER PHYTOPLANKTON BLOOM MODELS

Because the model we are describing is so different from the more usual kinds of phytoplankton models, its relation to those models is not obvious and will be explored here. In Chap. 5, we wrote the differential equation describing the growth of an algae species:

$$\frac{dx_j}{dt} = (P_j - R_j - D_j)x_j \quad . \tag{6.6}$$

Equation (6.6) is typical of most phytoplankton bloom models (see Refs. 1 and 29 for examples). These models describe phytoplankton in terms of the dependence of their instantaneous growth, respiration, and death rates on external conditions, and then integrate the resulting differential equations to find the abundance of each species of algae at each moment. In many of these models, as in our model, the respiration rate R and the death rate D depend on temperature T. (In most models, the death rate also depends on other factors that we have considered in previous chapters.)

In the usual kind of phytoplankton model, the production rate P must depend on (at least) the temperature T, the light intensity I, and the concentrations w_i of the dissolved nutrients. Thus, it is not enough to have an Eq. (6.6) for each species of algae. We must also have equations that determine the light intensity I and the dissolved nutrient levels w_i. (The temperature T is generally specified exogenously to the model, since it does not depend on the variables x_j. But the light intensity does depend on the x_js through the extinction coefficient—see Eq. (4.1)—and w_i depends on the x_js as well—see Eq. (3.2).)

In a traditional model such as the one we have been describing, a species of algae will continue to increase in abundance until either self-shading or the depletion of a dissolved nutrient reduces its production rate to the sum of its respiration and death rates. (This assumes that at the ambient temperature the production rate exceeds the respiration plus death rate when none of these factors are limiting.)

In our model, these same factors may limit the abundance of algae, but through a different mathematical mechanism, namely, the mechanism of constraints. Thus, we calculate the minimum and maximum values of the extinction coefficient at which each species can maintain itself, and whenever that species is not excluded from the model we constrain the extinction coefficient (and hence the abundances x_j) to lie within these limits. Unlike the traditional model, we need not calculate the actual production rate when the extinction coefficient lies within this interval.

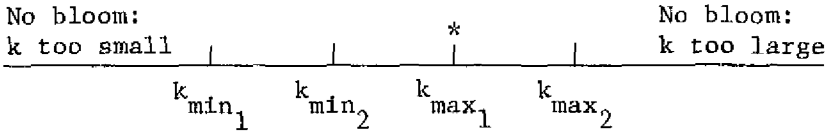
Similarly, we place constraints on the abundances that ensure that no more of any nutrient will be incorporated in algae than is available in the system. Thus, even if there is ample solar energy available to support further growth, the absence of more dissolved nutrients prohibits it. Again, unlike the traditional model, we need not calculate the actual production rate under such conditions. We simply assume that the dissolved nutrient levels have been sufficiently reduced that the production rate of each species in the bloom is equal to the respiration plus death rates.

Of course, in the traditional models, this decrease in production rates would occur at nutrient levels that, although low, are not zero. That is, the peak of a bloom would occur when some small amount of dissolved nutrient still remained. In our model, however, production is only reduced by a nutrient limitation when that nutrient is entirely depleted. Thus, our model would predict that none of a limiting nutrient would remain in the solution at the peak of the bloom. In effect, our model assumes that the production rate of a species of algae is only affected by nutrient limitations when the concentration of a dissolved nutrient is infinitesimal. The traditional model says this effect occurs at small but measurably positive nutrient concentrations. Thus, our model can be viewed as an approximation of the actual situation.

This approximation is probably reasonable. At the peak of a bloom limited by a nutrient, the total amount of that nutrient incorporated in algae cells is many hundreds of times larger than the dissolved nutrient [43]. Thus, our model would predict the bloom to be less than 1 percent larger than the observed bloom might be. This error is insignificant when compared with the uncertainties in the total amount of nutrient available.

If the competitive advantage of phytoplankton species is determined by nutrient concentrations, it may change as nutrients become exhausted. This could result in shifts between dominant species in a bloom, if the peak is sustained over time. Such adjustments should not increase the total biomass above our predicted maximum, if our model has been properly specified. Whether they cause our predictions to be more or less accurate is a function of whether nutrient-poor or nutrient-rich species enjoy more success as the advantage shifts.

There is, in addition, the possibility of a more serious error arising from this approximation. It is conceivable that the different dependencies of the production rates of the various species of algae on dissolved nutrient levels could render unstable a bloom that our model would predict as a maximum. Consider, for example, a bloom that our model predicts will contain two species. Species 1 is limited by self-shading, meaning that the extinction coefficient at the predicted bloom maximum is equal to the maximum feasible extinction coefficient for species 1. However, the second species could maintain itself at either much higher or much lower extinction coefficients. Species 2, therefore, may be said to be nutrient-limited. This situation is illustrated in the figure below. The asterisk (*) marks the value of the extinction coefficient that our model would predict at the peak of this bloom.



But species 1 is also affected by the absence of dissolved nutrient. Unless it can grow far more efficiently than species 2 at very small nutrient concentrations, species 1 is farther from a steady-state condition than species 2. Thus, the immediate response of an algae bloom with the composition predicted by our model would be for a small amount of both species to die, but with a proportionately greater reduction in species 1.

This reduction in species 1 will increase the dissolved nutrient level, and may permit an increase in species 2, perhaps beyond the abundance predicted by our model. This is especially likely if species 2 contains little of the limiting nutrient per unit biomass compared with species 1. The growth of species 2 will cause an increase in the extinction coefficient that may be large enough (depending on the relative values of the parameters K_1 and K_2) to cause k to exceed k_{max1}. Then species 1 will simply disappear from the bloom.

This phenomenon is a special case of a more general event: The differential equations used in the traditional models need not have any steady-state solution close to a solution of the approximate equations we are using—equations in which the production rate of algae is independent of nutrient concentrations as long as these concentrations are larger than infinitesimal. This phenomenon has not been explored further because few phytoplankton models include more than one species of phytoplankton. (With only one phytoplankton species, this phenomenon will not occur if there is any reasonable dependence of production rate on dissolved nutrient levels.) Also, no data are available that would permit the dependence of production rates on dissolved nutrient levels precisely enough to determine when this phenomenon might occur in practice. Consequently, our model may predict a peak for a bloom that is unstable, whereas the actual bloom may seek a lower, stable maximum or may cycle. This is an additional reason our model may overpredict the peak biomass that may occur in a bloom.

Chapter 7

RESULTS AND CONCLUSIONS OF THE STUDY

7.1. DESCRIPTION AND OBJECTIVES

The algae bloom model predicts many aspects of phytoplankton blooms, using information about the abiotic conditions in the environment and the characteristics of the phytoplankton species present. It is able to predict the potential algae bloom under any specified set of abiotic conditions, if the phytoplankton characteristics are known. The predicted magnitude is the *maximum* steady-state amount of biomass that *could* occur, given the constraints included in the model: the availability of several nutrients, the amount of effective solar radiation, and the individual species tolerance for water temperature. Other constraints could have been included, but were not because of the lack of necessary data.

The italicized words emphasize an important feature of the linear programming approach, namely, that the model's predictions of algae biomass are *upper bounds* on the algae biomass that might actually occur under the specified constraints. Significantly, the introduction of additional constraints can only reduce (or, in some instances, leave unchanged) the degree by which the model's biomass predictions are an upper bound. If, under specified constraints, the biomass predicted by the model is not objectionably large, the actual biomass cannot be objectionable. In such instances, the model's predictions would be directly useful for policy evaluation; moreover, they would obviate the need to introduce additional constraints into the model.

The specific outputs of the model include the orders present, species biomass, total biomass and chlorophyll concentrations, limiting constraints on growth, and concentrations of dissolved forms of nutrients. In addition to their policy applications, all of these outputs can be used for either calibration or verification of the model, if sufficient observational information exists for the region of interest. Although direct comparison should give a good indication of the value of the model, it should not be expected to show specific agreement in all factors. The predictions are based on the constraints incorporated in the model, but, as we have said, it is not possible (or necessarily desirable) to make these constraints exhaustive. Thus, the predicted algae blooms may exceed those found in nature, if the actual blooms are constrained by other factors not included in the calculations, for example, vitamin constraints and micronutrient limitations.[1]

In studying algae blooms in the Oosterschelde area, our purpose has been to develop an algae bloom model capable of meeting certain objectives and then to use the model for investigating several important questions. There were four primary objectives the algae bloom model was supposed to meet:

1. To indicate the conditions that can result in the development of objectionable algae blooms.

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[1] Conversely, the observed blooms should not exceed the predictions consistently unless there has been a significant error in the model or its input data. Such an error could take the form of a misspecified parameter or a number of other factors discussed in App. B.

2. To relate physical conditions to biological production.
3. To provide primary production information for the general ecomodel that predicts changes in long-run ecological balances.
4. To provide a management tool for warning about bloom conditions, investigating control measures, and guiding nutrient and thermal discharge plans.

After developing and testing the model, we used it to investigate two general questions:

1. What is the sensitivity of blooms to changes in nutrient levels, incident solar radiation, temperature, and mixing depth?
2. What are the critical times for algae blooms to occur?

Our investigation included studying the sensitivity of algae bloom timing and other characteristics to both external conditions and internal model parameters. There was no attempt to study extensively the effects of the different Oosterschelde design cases (i.e., the risk of future objectionable algae blooms under the alternative barrier and compartment combinations[2]). This was because of the lack of sufficient data about the nutrient, temperature, and visibility conditions to be expected in the future basins. However, some preliminary work was attempted, and the answers to the first two questions also give insight into what conditions, if they occurred in a particular Oosterschelde case, could lead to excessive algae blooms. Because of its general nature, the model can easily be applied to any basin where the abiotic conditions are either known or can be estimated. Thus, it meets the management tool objective 4 listed above.

In general the model proved to be simple and inexpensive to set up and use in practice. A typical run for one year required only 100,000 bytes of core, used less than 7 cpu seconds on an IBM 370/158 computer, and cost less than $2. Besides being easy to operate, the model requires far less data than the normal differential equation models and provides output information that is useful for many types of policy problems. A wide variety of conditions can be examined by changing only a few input parameters and data values; this setup process may require less than an hour of the researcher's time.

7.2. GENERAL RESULTS

The algae bloom model predicts the types and amounts of phytoplankton that maximize the total primary biomass and meet the solar, nutrient, and temperature constraints of the environment. It has been designed to operate with the decade (see the note in Sec. 3.4.1 for a definition of this term) as the basic time period for analysis. The model outputs include

1. Concentrations (dry weight/cubic meter) of phytoplankton species and orders.
2. Concentrations of total biomass and chlorophyll.
3. Concentrations (milligrams/cubic meter) of dissolved nutrients.
4. Limiting nutrients or conditions.

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[2] See R-2121/3 for a discussion of barrier and compartment alternatives.

Before presenting the results of the model, we will discuss the nature and interpretation of the constraints and the assumptions that operate within the model.

7.2.1. Constraints and Their Operation

The nutrient constraints in the model limit algae production and growth in the manner described earlier. All of the available nutrient is used for either living or dead algae, or is left in the dissolved state. When this remainder is zero, the nutrient is said to be limiting. None of it is available to the phytoplankton for further primary production or growth.

For solar radiation, however, the situation is more complex. There are two ways in which solar radiation can be said to limit algae blooms. As described in Chaps. 5 and 6, there is a feasibility interval in the extinction coefficient for each order of phytoplankton. During winter months, when solar radiation is reduced, these intervals either may not exist or may be at a level below the natural background extinction at that time; hence, an order or species is effectively excluded from the bloom. This situation frequently occurs in the model, resulting in a prediction of no phytoplankton whatsoever. This is equivalent to a statement that conditions are such that the species cannot grow and may be existing only in a dormant state.

The other manner in which solar radiation can be a limiting constraint is through the feasibility interval equations as described in Secs. 6.1 and 6.2. This occurs when no more phytoplankton are permitted because they would result in an increase in the extinction coefficient that is sufficient to reduce the efficiency of the species below the level at which it can survive. Both of these mechanisms are valid means by which solar radiation can constrain a species in the model.

In addition, there are temperature restrictions on species (see Sec. 5.1), which may exclude otherwise permissible species at this time. These restrictions may exclude certain species from early spring algae growths because of their inability to reproduce at low temperatures. (Water temperatures in the Delta region are never high enough to limit the growth of any algae species because of its sensitivity to high temperatures. However, maximum temperatures for algae growth are presented in Sec. 5.2.) Thus, green algae, which are most efficient at low solar intensity levels, are not found either in nature or in the model when the water temperature is below 12°C.

7.2.2. Data and Parameter Assumptions

To use the model, it is necessary to specify the values of all of the essential parameters described earlier. Empirical determination of these values has been limited and generally involves considerable uncertainty. For the purposes of this study, however, nominal values have been specified and are given with the other input data sets in App. A. They have been taken from the literature, when available, with mean values used when there was a large range with little certainty.

To determine the effect of changes in these parameters, sensitivity analysis was used extensively. The results of this analysis are described in Sec. 7.3. In general, we have assumed that the estuary is well mixed at all times. This would then give a mixing depth for the area equal to the average depth of the Oosterschelde—8 meters. Under these conditions, the model may not predict a bloom for many decades in the winter months, when such growth might occur in local areas with shallow water. This matter will be considered in more detail later, when the effect of varying mixing depth is discussed.

7.2.3. Model Predictions

Table 7.1 compares the model predictions of chlorophyll concentration with the observed data. These predictions are derived from the nominal set of parameters discussed above and a mixing depth of 8 meters. The table includes predictions for the winter and spring months only. This is because of the lack of adequate productivity data and death rates from grazing for other months. If such data become available, the predictions could easily be expanded to encompass the entire year. This problem will be considered in a later section. Note also that the comparison in the table is made in terms of chlorophyll concentrations. There are several potential difficulties associated with this measure. These are discussed in the error analysis in App. B.[3]

In addition to chlorophyll content, the model also determines the orders of phytoplankton present in each decade. These results are compared in Table 7.2 with the limited data available for the region. These observations are discussed in Sec. 2.2.1 and presented in more detail in Table 2.1.

Unfortunately, there are no direct measurements of the limiting nutrients in the Oosterschelde region. The Environmental Division water quality measurements may give some indication of which dissolved nutrients are in short supply at one time. This, however, is not a sufficient basis for meaningful comparison. There is no indication from measurements of when solar radiation might be a limiting constraint on phytoplankton growth. Also, a nutrient may in fact be limiting even when there is still a measurable amount in some dissolved form in the water. For these reasons, Table 7.3 lists only the constraints that limit growth in the model for the years 1973 and 1974.

It is clear that there can be, and frequently is, more than one limiting constraint on the algae bloom. This is a characteristic of the linear programming nature of the model, which results in one limiting constraint for each species of phytoplankton found in the bloom. There is little observational information to support or deny this conclusion, but there is some theoretical justification for this type of behavior in nature [44]. When measurements of limiting nutrients become more widespread and sophisticated, this should be carefully investigated. It would prove to be strong support for the validity of this type of phytoplankton model if it can be empirically substantiated in nature. It may also prove to be of some value to research if the

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[3] In comparing the model outputs with observed data, it is important to keep several points in mind. In addition to the problems with respect to chlorophyll measurements, there is a more fundamental difficulty in regard to the observational information. At the present time, there are no systematic direct measurements of phytoplankton or chlorophyll concentrations in the body of the Oosterschelde. The only available data pertain to an area of the North Sea outside the mouth of the estuary. As a result, it is not possible to make a direct comparison with any certainty. It must be assumed that the data are representative of the interior area, an assumption that may not be valid. The nutrient concentrations have not been measured simultaneously in both areas, the depth and current structures are different, visibility conditions may differ, and other unknown factors may also not be similar. The primary strength behind this assumption is that the water exchange between the two areas during tidal cycles will act to reduce any differences in the abiotic conditions that might exist between them.

Table 7.1

COMPARISON OF MODEL OUTPUT FOR NOMINAL PARAMETERS WITH OBSERVED DATA FOR THE OOSTERSCHELDE REGION

(mg chl/m^3)

Year	Decade		Observed	Model
1973	January	I	0.2	0.0
		II	0.4	0.0
		III	0.5	0.0
	February	I	0.6	0.0
		II	0.7	0.0
		III	0.8	0.0
	March	I	2.0	0.8
		II	4.3	3.9
		III	5.5	14.6
	April	I	7.8	14.4
		II	9.5	12.8
		III	14.8	9.2
	May	I	10.5	10.7
	October	III	1.7	0.0
	November	I	1.6	0.0
		II	1.5	0.0
		III	1.4	0.0
	December	I	1.2	0.0
		II	1.0	0.0
		III	0.5	0.0
1974	January	I	0.3	0.0
		II	0.5	0.0
		III	0.6	0.0
	February	I	1.1	0.0
		II	1.6	0.0
		III	1.5	4.6
	March	I	1.6	6.6
		II	1.8	5.9
		III	1.6	13.9
	April	I	3.0	19.5
		II	3.5	19.8
		III	8.0	18.8
	May	I	10.2	16.7
	October	II	4.8	1.3
		III	4.2	0.0
	November	I	3.5	0.0
		II	2.8	0.0
		III	2.2	0.0
	December	I	1.6	0.0
		II	1.0	0.0
		III	0.4	0.0

Table 7.2

COMPARISON OF MODEL ORDERS WITH OBSERVATIONS FOR 1974

Time Period	Observed Families	Model
February-March	Diatoms	Diatoms
April I	Diatoms Green algae	Diatoms
May	Diatoms Dinoflagellates	Diatoms Dinoflagellates

Table 7.3

LIMITING CONSTRAINTS FOR MODEL OUTPUT FOR YEARS 1973 AND 1974

Month	Limiting Constraints	
	1973	1974
January	Solar radiation	Solar radiation
February	Solar radiation	Solar radiation
March	Solar radiation Nitrogen	Solar radiation Nitrogen
April	Solar radiation Nitrogen	Nitrogen
May	Solar radiation Nitrogen Silicon	Nitrogen Silicon
June	Nitrogen Silicon	Nitrogen Silicon
July	Nitrogen Silicon	Nitrogen Silicon
August	Nitrogen Silicon	Nitrogen Silicon
September	Solar radiation Nitrogen Silicon	Solar radiation
October	Solar radiation	Solar radiation
November	Solar radiation	Solar radiation
December	Solar radiation	Solar radiation

number of limiting constraints is accurately measured by the number of different species present.

When we examine Tables 7.1, 7.2, and 7.3, we can draw some general conclusions about the model predictions with the nominal set of input parameters. In general, the model seems to give reasonable predictions for the types, times, and magnitudes of recent blooms in the Oosterschelde. There is no means of evaluating its predictions of limiting constraints, because of a lack of observational data, but for the most part, they would appear to be acceptable, considering the restrictions imposed by the available information.

There are, however, periods when the model does not accurately predict the observed algae abundances. During the winter months, the model tends to underpredict, when it excludes all species on the basis of its minimum efficiency and water temperature criteria. This is not unreasonable, because in nature algae growth is constrained by solar radiation and temperature during the winter. It is important that this is a time of low algae abundances, and hence is not significant in determining policy. The apparent underprediction may result from problems with the reliability and accuracy of the measurements. Alternatively, the measurements may be accurate but the algae may be in a dormant or nonblooming state. Under these conditions, the model would not be expected to predict the observed abundances, because it is not currently designed to reproduce this situation.

During the summer and fall months, after the peak of the spring bloom, the model overpredicts the amount of phytoplankton present, by a factor of from two to ten. There are three possible reasons why this occurs. First, the model does not represent all of the nutrient requirements of the algae, only those for nitrogen, phosphorus, and silicon, and thus will tend to overpredict bloom size if vitamins or other micronutrients are actually limiting constraints. Second, as discussed in Sec. 2.2.3, there is some uncertainty in the values of the available nutrients and the ability of the algae to use all of the material present at any time. Because it is important that the model avoid underpredicting at critical times, however, conservative assumptions have been used. Third, the death rates used in the model (see Sec. 3.4.1) do not include grazing—the rate that algae are eaten by other creatures, primarily zooplankton. Grazing was omitted for lack of satisfactory data in the literature. Because it is known to be important during the period from late spring through fall, the failure to include grazing will naturally produce overprediction.

7.3. SENSITIVITY TO ABIOTIC CONDITIONS

A primary question of the study has been the investigation of the sensitivity of algae blooms to variations in the external conditions in the environment. The phytoplankton model provides the means to determine this sensitivity for many of the important parameters of interest, for example, the effect of changing nutrient concentrations, solar radiation levels, temperature, background extinction, and mixing depth in the Oosterschelde. This can be done for each change singly or in combination with others.

7.3.1. Total Available Nutrients

Increases in nutrient concentrations alone have a direct and expected effect on the results. They do not influence the time of appearance of algae blooms, as this is controlled by the solar radiation and water temperature constraints. They do, however, increase the magnitudes of the blooms. In general, this increase is directly proportional to the size of the nutrient increase, with some qualifications. This can best be discussed with reference to Fig. 7.1, which shows the effect of varying available nutrient levels on the total biomass predictions of the model for four representative decades in the year.

The figure demonstrates that the predicted biomass grows at a constant rate with nutrient increases, until it reaches an apparent ceiling level. This ceiling is imposed by the other constraints (temperature and solar radiation) that have then become limiting. Raising the amounts of available nitrogen, phosphorus, or silicon

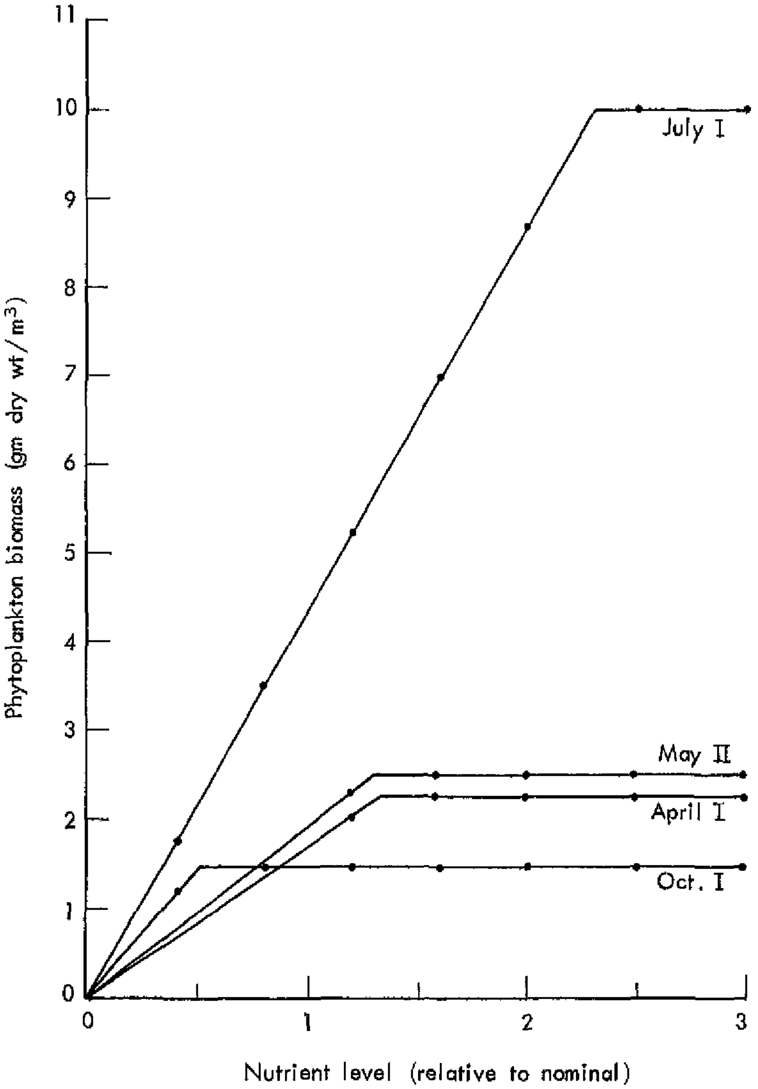

Fig. 7.1 — Effect of nutrient levels on model total biomass predictions

beyond this level clearly will not affect the size of the bloom. This should be obvious, because if a nutrient is not limiting the growth of the phytoplankton, then making more of it available should have no effect. The model thus verifies this conclusion. The variation between maximum biomass concentrations for the different decades is determined by the water temperatures and amounts of solar radiation available. Thus, in October, when solar energy is limited, even the nominal (measured) level of nutrients is more than can be used by the algae. In July, however, solar radiation is so abundant that the nutrient levels could be more than doubled before they would cease to be constraining.

Figure 7.1 describes the situation if all nutrients are increased simultaneously. If one nutrient is limiting and it is increased alone, it is possible that another nutrient could become a limiting constraint before solar radiation intrudes. The result would be the same; the biomass (or chlorophyll concentration) growth would be proportional to the increase in nutrient, up to the point where the other constraint became limiting. If more than one nutrient is limiting, and these are changed simultaneously (when solar radiation is not a limiting constraint), the situation is again similar, but more complex. Such circumstances demonstrate the model's great potential for dealing with multiple changes in abiotic conditions.[4]

7.3.2. Solar Radiation Levels

The consequences of an increase in the amount of available solar radiation are similar to those of increasing total nutrients. When other factors are limiting, additional solar radiation will have no effect on the bloom. But when the bloom is constrained by solar radiation, as this limit is increased the bloom will increase also. This growth in the bloom may be less than proportional to the change in solar radiation, if another constraint enters the solution of the problem.

With solar radiation, it is also possible that the timing of blooms will be altered. Because radiation is the primary constraint prohibiting blooms during the winter months, increases should be expected to cause them to appear sooner and last longer in the year. At higher radiation levels, the algae species should become more efficient during the winter (under the conditions normally found in the Oosterschelde region) and thus may be able to bloom. These results are supported in the literature. Recent work has indicated that light may indeed control the onset of feasible bloom periods, but that during most of the year it is not an important factor under most circumstances [19,45]. Our model analysis of this phenomenon, however, indicates that an increase of 10 percent in solar radiation levels is not in itself *sufficient to change the length of the bloom period significantly in either 1973 or* 1974. To do this, it was necessary to also increase the water temperature at the same time.

7.3.3. Mixing Depth

In general, the mixing characteristics of the water are very important in nature and to the model. When the water is shallow and mixing poor (as in a small closed basin with little wind), solar radiation is effectively much more abundant than in

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[4] In this and the subsequent discussion, we should keep in mind the *potential* problem of degeneracy, as explained in Sec. 6.3.4. For now, it will be assumed that none is present.

other circumstances. It may no longer be a limiting constraint on algae growth, and nutrient concentrations may become important. When the mixing depth is reduced (either in nature or in the model), the phytoplankton are not forced to spend as much time in the relatively dark, deep areas of the water where their photosynthesis is not sufficient to overcome losses caused by normal respiration. Because they are exposed to a higher average level of radiation (again at the below-saturation levels found in higher latitudes during the winter), their average efficiency increases, and they are able to survive over a wider range of the extinction coefficient. Thus, even though blooms are not evident in deep water, they may occur in isolated shallow areas. This can be represented in the model by a decrease in the mixing depth for all species.

As discussed in Sec. 7.2.2, the nominal case results have been produced using an average mixing depth of 8 meters in the Oosterschelde. This depth was appropriate for diatoms and green algae only. Dinoflagellates, because of their ability to swim toward regions of higher solar intensity, were given an effective mixing depth of half that of the other orders. This arbitrary competitive advantage produced reasonable results, causing dinoflagellate species to appear at the proper times in the predictions, where otherwise they could not. These results, however, were not particularly sensitive to the magnitude of the advantage; an effective depth of three-quarters that of the other orders had essentially the same effect.

With the above assumption, the model predicts that blooms will begin in the first decade of March and continue until the second decade of October. We would expect these limits to shift as the mixing depth is varied, and this indeed occurs. The results of mixing depth variation in the model for 1973 and 1974 are presented in Table 7.4.

Table 7.4

EFFECT OF MIXING DEPTH ON ALGAE BLOOM APPEARANCE

Mixing Depth (meters)	Duration of Algae Bloom Period	
	1973	1974
8	March I-October II	February III-October II
6	February III-October III	February II-October II
4	February II-November II	February II-November I
2	January III-November III	January II-November II

From the table, we see that reducing the mixing depth can move the beginning and end of the algae bloom periods considerably into the winter months. The size of existing blooms is not significantly affected, except in those cases near the beginning and end of the year when solar radiation is the limiting constraint. This can be observed in Fig. 7.2, which shows the effect of mixing depth variation on the total biomass predicted by the model for several decades in the year. For most of the months from late spring through early fall, the blooms are nutrient-limited, and the total biomass is independent of the mixing depth (see the July I curve). When solar radiation is a limiting constraint (the other decades shown), the predicted biomass

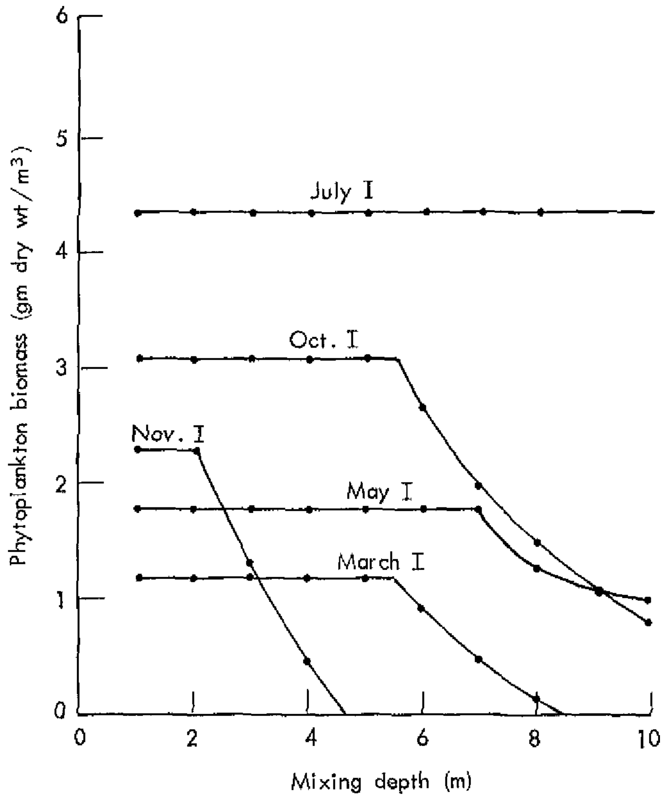

Fig. 7.2 — Effect of mixing depth on model biomass predictions

will increase as the mixing depth is reduced, until nutrients again become limiting. The rate of biomass increase is not linear, because the process is complex. It depends on the relative amounts of nutrients and solar radiation, water temperatures, and the specific algae orders present in the bloom.

7.3.4. Water Temperature

Table 7.4 also shows that the effect of mixing depth variation on the appearance of blooms is independent of the year, and that it is far more important than the variations between years caused by the changing abiotic conditions. This should be expected, because 1973 and 1974 were similar in their abiotic characteristics. One respect in which they did vary is that of water temperature. The winter months were somewhat warmer in 1974, while the summer was cooler. These differences would be reflected more in the winter predictions of the model than in the summer, because of the manner in which water temperature enters the model.

Water temperature is important for several reasons. It directly affects nutrient remineralization rates, the BOD decay coefficient, and algae photosynthesis and respiration rates. Because death rates are not considered to be directly affected, temperature increases will make them less important compared with respiration losses (which increase with temperature). Equation 5.3 indicates that this will result in lower efficiency requirements for the phytoplankton orders. The combination of these circumstances causes the potential temperature sensitivity of algae blooms.

Analysis using the model revealed that small temperature increases can produce definite changes in the characteristics of algae blooms during the year. The results given in Table 7.5 show the magnitude of these effects. The table gives the results of a 2.0°C water temperature increase on the predicted blooms for 1973 and 1974. Only the winter, spring, and fall months are shown, for the reasons discussed earlier (Sec. 7.2.3).

It is clear from Table 7.5 that a temperature increase of as little as 2.0° is sufficient both to lengthen the season in which algae blooms can occur and to increase the magnitude of these blooms. It is also important that the combination of warmer water and mixing depth is able to extend the bloom season almost through the winter, particularly in 1974. This finding makes it necessary to consider carefully the possible effects of future thermal pollution sources in the Oosterschelde region, especially for smaller isolated areas with shallow water.

Table 7.5

EFFECT OF TEMPERATURE INCREASE ON CHLOROPHYLL CONCENTRATION IN ALGAE BLOOMS OF 1973 AND 1974

		1973				1974			
		Nominal		+2.0°C		Nominal		+2.0°C	
		Mixing Depth (meters)							
Decade		2	8	2	8	2	8	2	8
January	I	0.0	0.0	0.0	0.0	1.3	0.0	4.7	0.0
	II	0.0	0.0	0.0	0.0	6.4	0.0	9.8	0.0
	III	14.9	0.0	21.1	0.0	26.6	0.0	29.0	0.0
February	I	13.1	0.0	18.8	0.0	20.7	0.0	27.4	0.0
	II	10.5	0.0	15.7	0.0	19.4	0.0	26.3	0.0
	III	8.6	0.0	13.3	1.1	17.3	4.6	24.1	6.4
March	I	9.7	0.8	14.9	2.6	13.6	6.6	20.0	8.7
	II	11.8	3.9	16.5	6.1	14.7	5.9	20.5	7.9
	III	14.6	14.6	18.8	18.8	16.5	13.9	21.7	16.9
April	I	14.4	14.4	18.2	18.2	19.4	19.4	24.1	24.1
	II	13.3	12.8	16.7	15.7	19.8	19.8	23.9	23.9
	III	13.3	9.2	16.4	15.9	18.7	18.7	22.5	22.5
May	I	14.7	10.7	17.4	12.7	16.7	16.7	20.0	20.0
October	II	20.8	7.7	23.8	8.8	23.2	1.3	27.0	8.0
	III	15.1	0.0	17.9	4.8	17.0	0.0	20.3	2.0
November	I	19.1	0.0	21.1	0.0	22.3	0.0	23.2	0.0
	II	21.7	0.0	23.1	0.0	4.9	0.0	4.7	0.0
	III	9.3	0.0	9.8	0.0	0.0	0.0	0.0	0.0
December	I	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	II	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	III	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

It should be noted that the increase in bloom magnitudes with temperature is greater in the winter than in the summer months. This follows from the dominance of the nutrient constraints during most of the year and the generally weak temperature dependence of these constraints. These factors mean that increases in water temperature will have their greatest effect during the months from late fall through spring, when many phytoplankton species are excluded by low temperatures. They also suggest that there will be a shift in the model away from solar radiation constraints toward nutrient constraints as temperatures are increased, and this shift can be observed in the results of the analysis.

When a temperature increase is combined in the model with either an increase in solar radiation or nutrient levels, the effects are enhanced. For a 2 meter mixing depth and a 10 percent increase in solar radiation, blooms can occur between the second decade in January and the second decade in December in 1973. This is a significant extension of the previous permissible time period. For the 8 meter mixing depth, the effect is somewhat smaller—a two-decade increase to encompass the period of February III to October III. Similarly, simultaneous increases in nutrient concentrations and water temperatures (in certain ranges) can lead to shifts in species present and large changes in the magnitude of blooms early or late in the year. This occurs because a species with relatively low nutrient needs is able to compete more successfully in warmer water and replaces the species that would otherwise have been present.

7.3.5. Background Extinction

A final factor to consider is the sensitivity of the model predictions to variations in the background extinction coefficient. This should have a direct bearing on the amount of solar radiation received by the algae and their ability to survive and grow. Should the water become much clearer, algae blooms would be expected to increase in magnitude and frequency. The analysis indicates that this does occur to some extent in the model, as shown in Table 7.6.

Using 1973 abiotic data, when the Secchi visibility depth is arbitrarily doubled, algae blooms appear two decades earlier in the year and three decades later. In addition, the magnitude of the blooms is increased in those decades where solar radiation has been the limiting constraint. For the months between late spring and early fall, when nutrient limitations are constraining algae growth, there will be no effect on the predicted blooms. These results imply that increasing the clarity of the Oosterschelde water could have a noticeable effect on algae production in the early spring and late fall months. This effect would not be significant, however, if other abiotic conditions remain unchanged during that time.

7.4. POLICY QUESTIONS AND CONCLUSIONS

The analysis using the model centered on: (1) investigating the possibility of objectionable blooms in the present Oosterschelde and (2) determining the sensitivity of algae blooms to possible future changes in abiotic conditions in the area. In the second task, we chose to look at the timing and magnitude of blooms as a function of variations in one or more of the environmental conditions (e.g., solar

Table 7.6

EFFECT OF SECCHI VISIBILITY DEPTH ON CHLOROPHYLL CONCENTRATION IN ALGAE BLOOMS OF 1973

(mg chl/m^3)

Decade		Nominal	2 × Secchi
January	I	0.0	0.0
	II	0.0	0.0
	III	0.0	0.0
February	I	0.0	0.0
	II	0.0	0.4
	III	0.0	8.6
March	I	0.8	9.7
	II	3.9	11.8
	III	14.6	14.6
April	I	14.4	14.4
	II	12.8	13.3
	III	9.2	13.3
May	I	10.7	14.7
	II	16.1	16.1
October	II	7.7	9.8
	III	0.0	2.0
November	I	0.0	2.1
	II	0.0	4.4
	III	0.0	0.0
December	I	0.0	0.0
	II	0.0	0.0
	III	0.0	0.0

radiation, nutrient levels, or water temperature). Such variations could arise from construction activities, increased waste discharges, or other developments in the Oosterschelde area.

7.4.1. Likelihood of Objectionable Blooms

As discussed in Sec. 1.2, algae blooms have many undesirable properties that make them objectionable. The main problem, however, may be the threat of deoxygenation of the water. The normal fish and shellfish populations of the Oosterschelde (those considered desirable by the Dutch) require a minimum oxygen saturation level of 50 percent (dissolved oxygen) for their well-being—and their survival in some cases.[5] Algae blooms can be a threat in two ways. Excessive blooms may reduce dissolved oxygen levels at night through respiration, or may lead to ana-

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[5] This criterion is based on a personal communication from J. C. H. Peeters of the Delta Service, but it is not unlike that recommended by other scientists. The Committee on Water Quality Criteria [46] stated that 4 milligrams per liter should be a minimum acceptable level of dissolved oxygen in marine waters. For the temperature range of most interest to our problem (10° to 20°C), the corresponding 50 percent saturation levels are from 5.4 to 4.0 milligrams per liter in the Oosterschelde.

erobic conditions during the remineralization process after a rapid die-off of the bloom. In either case there is danger to the other species in the area. The algae bloom model provides a means of determining what conditions could lead to excessive growth of phytoplankton and when these conditions may occur.

The general problem of biomass remineralization and deoxygenation of the Oostmeer basin has been investigated by Bigelow and De Haven using a reaeration model developed for that purpose. This model and the analysis are discussed in Vol. V of this series.[6] The authors assumed limited resaturation by atmospheric oxygen, rapid mineralization, good vertical mixing, limited local stratification, involvement of the entire basin in the deoxygenation process, and no flushing exchanges outside the system.

Using similar conservative assumptions, but for a salt water basin, we calculated the maximum allowable algae blooms under varying conditions. These are the blooms that could exist and still maintain at least a 50 percent oxygen saturation level, even under the worst circumstances (simultaneous die-off of all species and no time for significant reaeration from the atmosphere). Thus, an April bloom of diatoms and dinoflagellates in 10° water would have to be of at least 68 mg chl/m^3 to reach this point, while a July bloom of the same order in 20° water would need a magnitude of 49.9 mg chl/m^3. In both cases, these numbers are far above both the measured values and the predictions of the model for the corresponding time periods. Based on this type of analysis, we reached two policy conclusions:[7]

Policy Conclusion One: In general, no basin-wide fish-killing algae blooms are likely to occur in an unchanged Oosterschelde.

Policy Conclusion Two: For an Oosterschelde that has been divided into separate Western (salt) and Eastern (fresh) basins by one of the Oosterschelde alternatives (closed, open, or storm-surge barrier), no basin-wide fish-killing algae blooms are apt to occur in the Western (salt) Basin during the spring months. The present insufficient knowledge of algae death rates restricts this conclusion to the early part of the year; it may be true in general, but this will have to await further research.

The second conclusion is based on a preliminary analysis of the expected future nutrient concentrations in the various basins under the different Oosterschelde alternatives. Although there is some uncertainty in these results and in the future water temperature and visibility conditions, it is not sufficient to invalidate this conclusion at the present time.

It should be emphasized that our inability to draw more general conclusions in this section does not derive from a failure of our model, but rather from a lack of sufficient input data. When better information on algae death rates becomes available, and estimates of future nutrient concentrations and visibility conditions in the various basins are improved, the model can be used to expand the conclusions. In this sense, the model can make a valuable contribution by indicating more precisely what information is necessary and what data need to be collected in the future.

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[6] *Anaerobic Conditions and Related Ecological Disturbances.*

[7] Essentially the same results were produced by the original version of the algae bloom model. The revised model discussed in this report does not differ in any important aspect from the original, as far as results relevant to policy questions are concerned. The original model was somewhat less sophisticated in its treatment of solar radiation constraints. From the results discussed above, it can be seen that this would have its primary effect when solar radiation is limiting, namely, at those times when the deoxygenation problem is least critical.

One can also argue that the prediction of spring blooms (or any blooms not significantly affected by grazing) is at least as important as the prediction of summer blooms. Both periods may witness blooms that are limited by nutrients, rather than by solar radiation, and spring blooms are likely to be greater in magnitude because of the absence of grazing. If in summer, even without grazing, the biomass of the predicted blooms were not objectionable, it would be possible to expand our conclusions to encompass the entire year. As it is, however, the predictions during this time are marginal, and we could not justify using them with any reasonable level of confidence.

7.4.2. Sensitivity of Algae Blooms to External Conditions

In Sec. 7.3 we discussed the analysis of the sensitivity of algae blooms to changes in environmental conditions. The results of this analysis, using the algae bloom model, emphasized the importance of simultaneous changes in more than one factor that may limit algae growth. Although increases in a single nutrient or other constraint may not be important (particularly if it is not limiting), combinations of such increases may produce unexpectedly large effects on subsequent algae blooms. These results lead to several interesting conclusions with implications for water basin management policies.

Policy Conclusion Three: Although there is little likelihood of basin-wide fish-killing algae blooms in the unchanged Oosterschelde or in the Western (salt) basins for any of the Oosterschelde alternatives, there may be some local problem spots under certain conditions of changing solar radiation, mixing depth, and nutrient discharges. If areas of the basins are effectively isolated by poor horizontal mixing, they could at times develop objectionable blooms.

Policy Conclusion Four: Although controlling nutrient discharges may not always be important for limiting objectionable blooms, it is very necessary in areas and at times when solar radiation is effectively abundant. These include the shallow basins and regions with poor mixing, especially during extended periods of sunny windless weather.

Policy Conclusion Five: Future sources of thermal pollution should be carefully investigated to determine their probable effect on algae blooms in the Oosterschelde, particularly in present and future closed basins. This is especially important if there will also be a significant increase in nutrient discharges at the same time.

Comments on Eastern Basin Blooms: Although we were not able to analyze the Eastern Basin of the future Oosterschelde with the available data and the present model, we can nevertheless make some comments about its risk of objectionable algae blooms. First, although the Eastern Basin is still salt, in the period shortly after it has been closed off, the risk of algae blooms would probably be larger than before closure; this is because nutrient concentrations are expected to increase. The size of the risk depends on the increase in nutrients, which remains uncertain. This risk, which should receive future analysis, could be further exacerbated by the factors mentioned above in Policy Conclusions Three through Five.

During the transitional period when the Eastern Basin is becoming brackish, there should be little danger of objectionable blooms. This is because the duration and extent of brackish water should be limited, and the few algae species that can survive under these conditions will not have enough time to become adapted and bloom.

When the basin eventually becomes fresh, it will again face the threat of algae blooms. Conditions would appear to be favorable for the formation of objectionable blooms, as the basin is shallow (meaning small mixing depth and high solar radiation), and present nutrient discharges into it are relatively high. However, as we have said before, our model is not currently constructed to deal with blooms in fresh water, and the necessary data are lacking to estimate accurately the nutrient concentrations that may be present. For these reasons, we cannot at this time draw any conclusions about the possibility of objectionable blooms in a fresh Eastern Basin.

7.5. RECOMMENDATIONS FOR FURTHER RESEARCH

Additional research could improve the model and its predictions in several ways. We need a more complete phytoplankton census for the region, including the types of species present (both abundant and rare) during all periods of the year. Having all potential species represented within the model is necessary if the model is to predict maximum blooms with reasonable accuracy. This census should include measurements of phytoplankton concentrations (either as biomass or chlorophyll) at regular time intervals during the year inside the Oosterschelde itself.

In addition to the census, and even more important, we need a better description of the chemical compositions and physiological characteristics of the algae species. This description should include the biological productivity, dietary and nutrient requirements (particularly those that may be limiting in the region), and self-inhibiting mechanisms. Such a study is especially important for those species that have exhibited the potential to be involved in objectionable algae blooms. Equally important are data about the regional environmental conditions, such as present and future (expected) nutrient discharges, water temperatures, water quality, and turbidity.

To analyze the effect of alternative barrier and compartment designs on the risk of future algae blooms, we need to obtain better estimates of how the alternatives will affect environmental conditions in the various basins. This estimation is a difficult process, and additional information about the nature of the abiotic processes and interactions in the area would considerably reduce the large estimation uncertainty. This is true for all three nutrients currently in the model, but it is particularly true for phosphorus and silicon.

The results from our model also suggest an ecological hypothesis of possible interest, namely, that the number of species of algae in a bloom will be equal to the number of limiting constraints in operation at that time. Although this behavior is always observed in our results because of a property of linear programming, it nevertheless represents a logically plausible hypothesis. Moreover, the hypothesis is supported by the ability of the model to reproduce the measured data reasonably. We have found no observations of this phenomenon mentioned in the literature, but we feel that it is a subject that should be investigated in the future.

Appendix A

INPUT DATA AND MODEL PARAMETERS

A.1. ABIOTIC ENVIRONMENT

The model input data describing the abiotic environment in the Oosterschelde during 1973 and 1974 are presented in Tables A.1 through A.4.

Table A.1

NUTRIENT CONCENTRATIONS FOR 1973 OOSTERSCHELDE

Decade		Nitrogen (mg/l)	Phosphorus (mg/l)	Silicon (mg/l)
January	I	0.92	0.07	0.75
	II	0.92	0.07	0.75
	III	0.92	0.07	0.75
February	I	0.93	0.08	0.83
	II	0.93	0.08	0.83
	III	0.93	0.08	0.83
March	I	1.09	0.08	0.83
	II	1.09	0.08	0.83
	III	1.09	0.08	0.83
April	I	1.09	0.05	0.83
	II	1.09	0.05	0.83
	III	1.09	0.05	0.83
May	I	1.09	0.07	0.83
	II	1.09	0.07	0.83
	III	1.09	0.07	0.83
June	I	1.09	0.08	0.83
	II	1.09	0.08	0.83
	III	1.09	0.08	0.83
July	I	1.09	0.10	0.83
	II	1.09	0.10	0.83
	III	1.09	0.10	0.83
August	I	1.09	0.09	0.83
	II	1.09	0.09	0.83
	III	1.09	0.09	0.83
September	I	1.09	0.11	0.83
	II	1.09	0.11	0.83
	III	1.09	0.11	0.83
October	I	1.09	0.11	0.83
	II	1.09	0.11	0.83
	III	1.09	0.11	0.83
November	I	1.09	0.11	0.83
	II	1.09	0.11	0.83
	III	1.09	0.11	0.83
December	I	1.09	0.09	0.83
	II	1.09	0.09	0.83
	III	1.09	0.09	0.83

Table A.2

GENERAL INPUT DATA FOR 1973 OOSTERSCHELDE

Decade		Water Temperature (deg C)	Solar Radiation (Joules/cm^2 decade)	Chlorophyll Concentration (mg/m^3)	Secchi Depth (decimeter)
January	I	3.2	1,189	0.2	11.7
	II	4.4	2,068	0.4	10.3
	III	4.4	2,972	0.5	15.1
February	I	4.3	2,748	0.6	13.3
	II	3.8	3,992	0.7	11.5
	III	3.4	5,107	0.8	15.4
March	I	3,6	7,738	2.0	14.2
	II	4.8	9,992	4.3	13.0
	III	6.6	14,856	5.5	34.8
April	I	7.1	12,214	7.8	24.1
	II	7.4	11,079	9.5	17.3
	III	8.1	15,042	14.8	10.5
May	I	10.3	14,088	10.5	12.3
	II	12.5	19,895	8.0	18.9
	III	14.1	18,673	6.0	25.5
June	I	14.4	19,848	3.0	20.3
	II	16.7	23,298	3.0	20.2
	III	19.1	22,676	3.4	21.1
July	I	20.8	22,739	3.7	22.0
	II	19.7	14,720	4.0	26.7
	III	18.0	16,264	4.9	19.4
August	I	17.8	17,320	5.5	24.1
	II	18.8	17,433	5.7	28.8
	III	18.9	17,484	5.8	28.6
September	I	18.6	13,772	5.9	31.1
	II	17.4	11,813	4.0	26.8
	III	15.5	9,637	2.2	19.7
October	I	14.6	8,203	1.9	18.8
	II	12.6	6,028	1.8	16.7
	III	10.1	7,029	1.7	14.5
November	I	9.6	3,335	1.6	16.2
	II	9.1	4,572	1.5	13.2
	III	8.2	2,824	1.4	9.5
December	I	7.3	2,249	1.3	8.2
	II	6.4	2,097	1.3	9.2
	III	5.4	1,650	1.2	10.3

Table A.3

NUTRIENT CONCENTRATIONS FOR 1974 OOSTERSCHELDE

Decade		Nitrogen (mg/l)	Phosphorus (mg/l)	Silicon (mg/l)
January	I	1.27	0.09	0.87
	II	1.27	0.09	0.87
	III	1.27	0.09	0.87
February	I	1.35	0.10	0.88
	II	1.35	0.10	0.88
	III	1.35	0.10	0.88
March	I	1.35	0.10	0.88
	II	1.35	0.10	0.88
	III	1.35	0.10	0.88
April	I	1.35	0.09	0.88
	II	1.35	0.09	0.88
	III	1.35	0.09	0.88
May	I	1.35	0.05	0.88
	II	1.35	0.05	0.88
	III	1.35	0.05	0.88
June	I	1.35	0.07	0.88
	II	1.35	0.07	0.88
	III	1.35	0.07	0.88
July	I	1.35	0.07	0.88
	II	1.35	0.07	0.88
	III	1.35	0.07	0.88
August	I	1.35	0.08	0.88
	II	1.35	0.08	0.88
	III	1.35	0.08	0.88
September	I	1.35	0.09	0.88
	II	1.35	0.09	0.88
	III	1.35	0.09	0.88
October	I	1.35	0.12	0.88
	II	1.35	0.12	0.88
	III	1.35	0.12	0.88
November	I	1.35	0.13	0.88
	II	1.35	0.13	0.88
	III	1.35	0.13	0.88
December	I	1.35	0.09	0.88
	II	1.35	0.09	0.88
	III	1.35	0.09	0.88

Table A.4

GENERAL INPUT DATA FOR 1974 OOSTERSCHELDE

Decade		Water Temperature (deg C)	Solar Radiation (Joules/cm^2 decade)	Chlorophyll Concentration (mg/m^3)	Secchi Depth (deci-meter)
January	I	4.4	2,243	0.4	11.4
	II	5.9	2,245	0.4	12.5
	III	5.8	3,930	0.6	11.3
February	I	4.7	3,783	1.1	10.1
	II	4.9	4,842	1.6	15.0
	III	4.8	4,817	1.5	19.9
March	I	4.1	7,326	1.6	20.5
	II	4.8	6,479	1.8	21.5
	III	6.0	11,644	1.6	23.3
April	I	7.8	17,102	3.0	25.1
	II	9.0	17,817	3.5	19.7
	III	9.3	14,691	8.0	21.9
May	I	9.4	13,991	10.2	24.0
	II	11.3	19,978	8.0	26.7
	III	14.0	21,992	5.5	29.4
June	I	16.1	19,588	3.2	36.5
	II	16.4	22,610	4.5	21.8
	III	17.2	18,775	5.1	21.8
July	I	17.8	17,882	6.2	21.8
	II	17.0	16,155	6.8	30.1
	III	17.2	20,015	5.5	37.3
August	I	17.2	15,941	4.3	33.8
	II	17.8	16,559	3.2	30.2
	III	18.8	17,609	2.4	22.4
September	I	16.5	10,180	2.4	17.8
	II	14.8	11,520	3.0	13.1
	III	14.2	6,795	3.8	12.9
October	I	12.7	6,942	4.2	13.5
	II	11.3	7,520	4.8	13.8
	III	10.4	3,894	4.2	14.1
November	I	9.6	4,221	3.5	12.7
	II	8.8	2,229	2.8	13.7
	III	8.4	1,642	2.2	11.1
December	I	8.1	1,551	1.5	8.5
	II	7.5	1,523	1.2	8.6
	III	6.9	2,311	1.0	8.8

A.2. GENERAL MODEL PARAMETERS

The following values constitute the nominal set of model parameters as described in Sec. 7.3: The nutrient remineralization rates are

Nitrogen	0.003 $\text{day}^{-1}\text{C}^{-1}$
Phosphorus	0.690 day^{-1}
Silicon	0.620 day^{-1}

The rate constant for eliminating the dead algae effect on extinction is

$$v = (2.35 \times 10^{-7}) \exp (0.0464T) .$$

Table A.5 contains the day lengths used in the analysis.

Table A.5

DAY LENGTHS FOR THE OOSTERSCHELDE REGION

Decade		Day Length (hours)	Decade		Day Length (hours)
January	I	7.92	July	I	16.55
	II	8.25		II	16.27
	III	8.72		III	15.90
February	I	9.27	August	I	15.25
	II	9.88		II	14.67
	III	10.50		III	14.03
March	I	11.17	September	I	13.30
	II	11.85		II	12.67
	III	12.52		III	12.00
April	I	13.25	October	I	11.33
	II	13.90		II	10.70
	III	14.55		III	9.98
May	I	15.13	November	I	9.38
	II	15.67		II	8.82
	III	16.12		III	8.33
June	I	16.53	December	I	7.98
	II	16.70		II	7.78
	III	16.72		III	7.77

Appendix B

POTENTIAL ERRORS IN THE MODEL AND ITS PREDICTIONS

In the algae bloom model there are several possible sources of error of varying magnitude and importance. Those that could be classified as small can appear in three general areas: (1) data on external conditions, (2) characteristics of specific phytoplankton orders, and (3) general model parameter values. Larger and more uncertain errors could arise from the problem of nonuniformity of conditions or from a variety of model misspecifications. Each of these potential sources will be discussed in turn in this appendix.

B.1. EXTERNAL CONDITIONS

The required input data of most importance to the model consist of (1) nutrient concentrations, (2) water temperatures, (3) day lengths, (4) chlorophyll concentrations, (5) extinction coefficients, (6) solar radiation distribution, and (7) solar radiation levels. In general, these describe the abiotic environment, except that chlorophyll concentrations are not strictly abiotic data. They are included in this category because they are observed values used in computing the algae biomass compensation in the background extinction coefficient calculations (discussed in Sec. 4.2).

B.1.1. Nutrient Concentrations

The measurement errors associated with nutrient concentrations have been discussed in Sec. 2.2.3. It was concluded that the magnitude of the errors was primarily determined by sampling problems, rather than measurement or analysis uncertainties. For this reason, it is difficult to put a limit on the size of the errors.

The b_i values (i.e., the limiting values of the nutrient constraints—see Eq. (2.1)) represent weighted averages of measurements at selected sample points. Even large errors in the weights (considered unlikely) would not affect the values by more than a few percent, because of the dominance of one large uniform region in the basin. Thus, errors of this sort would not be expected to be of more than 20 to 25 percent. From the earlier discussion of the sensitivity of the model to nutrient inputs, it is clear that uncertainties of this size could be directly transferred to the biomass predictions of the model, depending on the limiting constraint and time of year. It would be expected that the errors would be more important in the phosphorous measurements, which would reduce their significance (because phosphorus is not often limiting in the model). The primary limiting nutrients, nitrogen and silicon, would have somewhat smaller uncertainties in their reported values (as discussed earlier), but these would have more frequent effects on the model outputs.

B.1.2. Water Temperature and Day Length

Measurements of water temperature and day length are probably highly reliable and not subject to important errors. Day lengths are very accurately known and do not vary significantly from year to year. Water temperature measurements in the Oosterschelde indicate that the region is quite uniform. This reduces the sampling and averaging errors to negligibly small problems. The only important differences would occur where there are large local sources of thermal pollution, or extreme vertical temperature gradients characteristic of thermal stratification. Such conditions are not now important, but if they develop in the future, they will have to be considered independently in the model.

B.1.3. Background Extinction Coefficients

The determination of background extinction coefficients for the model is dependent on the measurements of Secchi visibility depth and of chlorophyll concentrations. As in the case of the nutrient constraints, the visibility depths are weighted averages of measurements made throughout the basin during selected times. There is reasonable uniformity in these observations for most of the region, making the averaging errors small, compared with the conversion factor uncertainty.

These Secchi visibility depths are then converted to extinction coefficients by means of an empirical formula (Eq. (4.1b)). The uncertainty in this formula is significant, as the standard deviation of the constant is about 40 percent of its value. This may not be a major error, however, in view of the discussion in Sec. 7.3.5, where it was determined that an arbitrary doubling of the background visibility had a limited effect on the model predictions. It caused blooms to occur both earlier and later in the year, but did not affect bloom magnitudes during most of the year, because solar radiation is not usually a limiting constraint. If more effort can be made to determine the relationship between Secchi depth and extinction coefficient, even this potential source of error might be reduced.

The chlorophyll concentration data are needed for conversion of calculated extinction coefficients to net background levels. These data are probably measured with reasonable accuracy, but again they are taken outside the mouth of the Oosterschelde, and therefore may not represent the true nature of conditions inside the estuary. One can argue that this error, even if large, will probably not have a major effect on the conclusions drawn from the model predictions. The correction factors developed using the chlorophyll data are small during the months from fall to early spring, because chlorophyll concentrations are small then. Thus, even large errors in these measurements will have a minor effect on the extinction coefficients at that time and therefore on the model predictions. When the corrections (and the importance of potential errors) may be large (during late spring and summer), solar radiation is not a limiting constraint and thus is of no importance to the results.

B.1.4. Solar Radiation

The final abiotic conditions required as inputs to the model are the solar radiation distribution and level. The distribution function is used in the convolution procedure (discussed in Sec. 5.4) for calculating the extinction coefficient limits on the algae orders. The distribution function that was selected is that of an average

March day at a latitude of 45° north. This should give a reasonable approximation of the solar radiation distributions found in the Netherlands during the time of spring blooms in an average year.

To test the importance of this function in the model, two other functions were chosen. These were at the same latitude, but for June and December. Thus, they should be, respectively, more and less peaked than that for March, and should represent the extremes that would normally be experienced during the year. Although the extinction coefficient ranges varied significantly, the effect on the resulting model predictions was small. There were no changes in the frequency or characteristics of the blooms or limiting constraints, and only a maximum of 4 percent change in the bloom magnitudes. This is far below the errors that could be expected from other sources, so the March distribution was retained for all calculations.

The determination of solar radiation levels is a more difficult problem. Measurements are made typically with a wide spectrum radiometer that covers a wavelength band far greater than the photosynthetic range. In addition, its response curve in the proper range is not the same as that of the algae species, whose curves are also not necessarily the same. For these reasons, it is difficult to determine a conversion factor for reducing measured values to effective radiation levels for the algae photosynthesis. The characteristics of the radiometer indicate that a factor of 0.5 would be appropriate, and this value has been verified by the Environmental Division of the Delta Service. Nevertheless, it must still be regarded as highly approximate.

In addition, the extinction coefficients calculated from Secchi visibility data are based on a particular instrument and its characteristic response band. This adds a probably small, but unknown, factor to the overall uncertainty. It is difficult to place limits on the total uncertainty resulting from all of these factors, but their significance is limited in the model by the relation of solar radiation as a limiting constraint. A 10 percent error is exactly equivalent to an equal change in the solar radiation levels, and this was found to have a small effect on the resulting algae biomass predictions.

B.2. CHARACTERISTICS OF SPECIFIC PHYTOPLANKTON ORDERS

Errors in the characteristics of specific phytoplankton orders can be found in four distinct areas: (1) compositions in terms of nutrients, (2) specific extinction coefficients, (3) chlorophyll contents, and (4) photosynthetic efficiency curves. Each of these will be considered in more detail below.

B.2.1. Compositions in Terms of Nutrients

The chemical compositions of phytoplankton in terms of nutrients have been discussed in Sec. 2.2.2. It was noted that the values in the model were selected to represent the variability found in natural populations. There will still be uncertainties because of the very limited data (particularly for Oosterschelde species) and the normal range of compositions encountered under different nutrient conditions.

In a linear program (and in nature), changes in nutrient composition of species will affect not only the amount of a species present in a bloom, but also whether or not it is even present. Thus, a measure of model acceptability is the comparison of the predictions and their sensitivity with natural observations. As noted earlier, there are only limited data now to do this. The results presented in Tables 7.1 and 7.2 indicate that the model outputs do correspond reasonably well with observations of the species and chlorophyll content of the spring blooms in the basin region. Although encouraging, this cannot by itself be considered adequate confirmation of the species and nutrient compositions used in the model. This will require more research and comparison of model predictions with observations of bloom magnitudes and species compositions.

It has been found that although predictions are not very sensitive to small changes in these values, they do react strongly to large variations. Because specific compositions of phytoplankton are variable and not generally known, it is essential to have reliable measurements for those species present in the Delta area. Until these data are available, the present policy of using extreme variations to represent different phytoplankton orders will have to be continued.

B.2.2. Specific Extinction Coefficients

The influence of various algae species on the extinction coefficient (this being a measure of their self-shading characteristics) is described in terms of their specific extinction coefficients. These have been discussed in Sec. 4.2, where it was concluded that the values are highly variable for each order or species, and that much additional work is necessary in the future.

The inherent uncertainties in the resulting average values for each order of phytoplankton have a variable effect on the output of the model. When these coefficients are increased, solar radiation rapidly becomes much more important as a limiting constraint. When they are reduced, the effect is slight, because the nutrient constraints will still limit bloom composition and size. Relative changes between orders (such as making all values a function of chlorophyll content alone) have the effect of favoring some species and penalizing others in the model, particularly dinoflagellates and green algae compared with diatoms. Thus, it is clear that these values are especially important and probably uncertain at the present time. The only measure of their adequacy (outside of agreement in the literature) is the correspondence of the model predictions with nature.

The problem is somewhat less important for the average value of this coefficient for a mixed population of phytoplankton. This is used to convert the chlorophyll data into correction factors for background measurements. Again, the literature is of little assistance in determining this parameter. A species average was used, but this has obvious problems. The species represented in the bloom will change with time, while the average assumes a fixed composition. Fortunately, the magnitude of the correction is small during much of the year, so the expected error will be small. Also, as nutrients are limiting constraints generally, the correction will not be important in these circumstances, unless the species average is too large, and then only if the error itself is large. Then it would shift the extinction coefficient intervals toward zero and might bring solar radiation into a position where it becomes limiting. This is unlikely, however, as the range of specific extinction coefficients found in the literature is not great, and the value chosen for the model is at the low end of the range. When a larger constant was used, the effect on the results was negligible in almost every case, and was never great.

B.2.3. Chlorophyll Content and Concentrations

The determination of the abundance of marine phytoplankton in nature is a difficult process, especially if it is desired to separate the total algae bloom into individual species. Measurement of the biomass in units of dry weight (an easily used form) is not done normally. Instead, biomass determinations are made by means of chlorophyll measurements. For this reason, the model calculates algae bloom magnitude in terms of dry weight (the quantity maximized by the model) and converts this to chlorophyll values.

This procedure has its drawbacks and uncertainties. It is well known that chlorophyll concentrations vary greatly between orders of algae, between species within orders, and even between individuals of the same species, but of different age. Phytoplankton in mature blooms have a lower chlorophyll content than those in young blooms. Thus, the use of fixed factors for converting from biomass to chlorophyll concentrations must necessarily be approximate. The values derived in Sec. 4.4 are only averages, and as such will lead to varying errors as the year progresses. In early spring as the algae blooms develop, the phytoplankton will have a higher chlorophyll content than the model would compute, while the reverse might occur in late fall as winter approaches and the blooms die out. Because any bloom will be composed of a mixed group of algae, the magnitude of the error from this problem is difficult to assess. It must be remembered that these errors in chlorophyll content do not affect the biomass predictions of the model or the policy conclusions that can be drawn from them. As long as the conversion factors are consistent in all calculations, there will be no error in such work as the reaeration analysis or investigations of objectionable blooms.

There is an additional difficulty associated with the use of chlorophyll concentration calculations in this model. The linear program maximizes the total amount of biomass, rather than the total amount of chlorophyll. As there is a considerable difference in the chlorophyll content of different orders of phytoplankton, this can lead to an interesting result. If conditions are such that there is a shift from a high to a low chlorophyll content species in the bloom, the model will predict an increase in total biomass with a simultaneous decrease in chlorophyll. We do not know if this situation has been reported in the literature, but there would seem to be no reason why it could not occur in nature. It may not happen often, however, because orders tend to be dominant under most conditions, and there is not often a radical shift between them. As this situation does occasionally occur in the model, it must be remembered to avoid misleading conclusions. This discussion of potential problems shows that chlorophyll concentrations can be deceptive when used to compare the size of algae blooms. They must be used, however, until better techniques for measuring plankton biomass come into widespread use.

B.2.4. Light Efficiency Curves

We discussed in Sec. 5.2 the problems of characterizing phytoplankton orders by specific photosynthetic efficiency curves. There is always the possibility of measurement errors and uncertainty in determining the values, and there may be changes in the shapes of the curves or the saturation intensities due to acclimation and other factors. To investigate the effect of these uncertainties, alternative efficiency curves were developed and tested in the model. These curves were selected to represent the following variations: (1) the nominal curves, (2) a uniform 20 percent increase, (3) a uniform 20 percent decrease, (4) a leftward shift in maximum efficiency toward lower intensity, and (5) a rightward shift in maximum efficiency toward higher intensity. The effect of the alternative cases on the L_s values was calculated for each order of phytoplankton; then the results were used in the model. The greatest change in the L_s limits came from alternatives 2 and 3, which shifted the limits by about 20 percent in the expected directions. This is equivalent to saying that an increase or decrease in efficiency will extend or contract the acceptable extinction coefficient interval for an order by about the same percentage as the magnitude of the efficiency change.

When these intervals were applied to the model, the results varied, depending on the time of year and the direction of the change. In general, when solar radiation was not limiting, increasing the efficiency had no effect. Thus, the changes were restricted to extending the time in which blooms can occur during the year. The reduction in efficiency had the effect of increasing the importance of solar radiation as a limiting constraint during the year, but it did not reduce the number of decades in which blooms take place. It was found that solar radiation replaced a nutrient limitation in a few decades, with a corresponding reduction in the predicted bloom. It was also possible to adjust the efficiencies of the three orders to favor one or more of them. This usually had the desired effect, to a limited extent, but such manipulations do not seem warranted by either the efficiency measurements themselves or the model results.

B.3. GENERAL MODEL PARAMETERS

The general parameters of the algae bloom model are those that are considered either to be characteristic of all phytoplankton orders or of the dissolved nutrient components of the system. They include (1) phytoplankton death rates, (2) nutrient remineralization rates, and (3) the extinction coefficient elimination rate.

B.3.1. Phytoplankton Death Rates

Phytoplankton death rates are particularly important to the model, because they are not inherently constant with time, place, abiotic conditions, or species of phytoplankton. Measured data are scarce and uncertain because of the difficulty of defining and making proper observations. Many phenomena such as grazing, self-inhibition, diffusion, sinking, natural death, and environmental stress enter the determination of death rates in nature, and these factors vary significantly with time. Section 3.4.1 discusses the data used in the model. It is clear that these values are valid only for the particular conditions under which they were measured, and it was necessary to argue that they are at least reasonable for use in the Oosterschelde region.

Although they are in general agreement with the other literature, the data apparently do not represent significant amounts of grazing activity by zooplankton. This is clearly reflected in the large measure of overprediction that characterizes the model results for summer months. During this period, grazing activity should be high. To investigate this situation, we ran the model with the nominal parameters and arbitrary multiples of the death rates. The results are given in Fig. B.1, which shows the effect of this variation on model biomass predictions for 1973. It can be seen that as the death rates are increased, the biomass is rapidly reduced in all time periods. There is also a slight shift in the occurrence of blooms away from the winter months, but this is limited in extent.

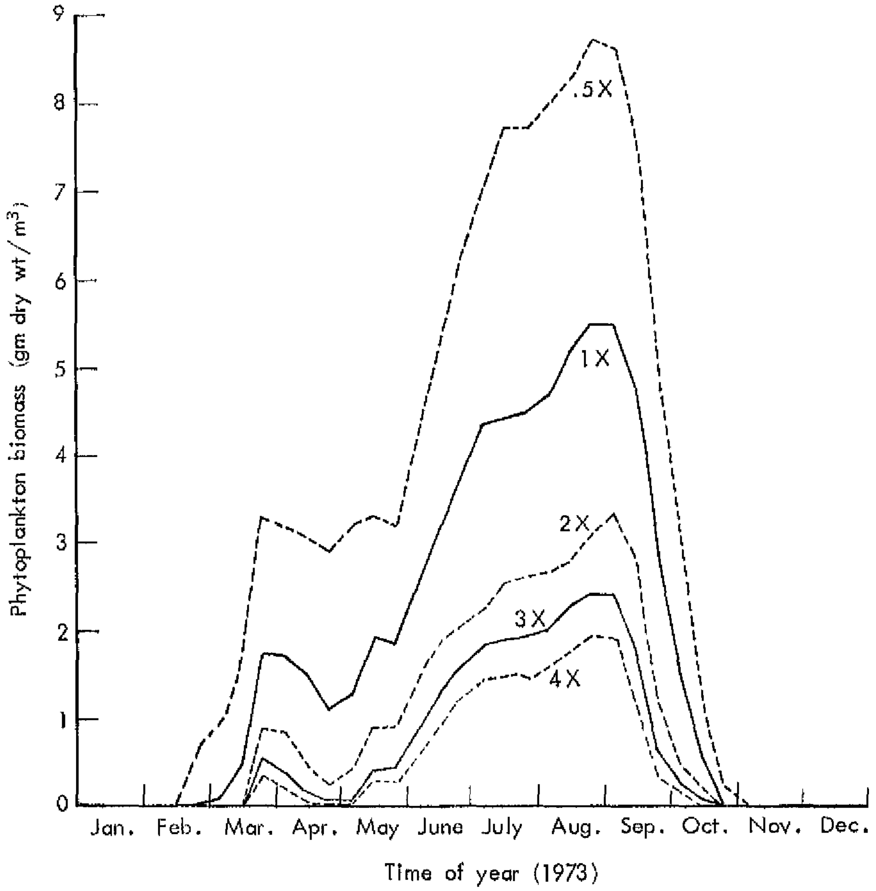

Fig. B.1 — Effect of death rate on model biomass predictions

It is not difficult to see why death rates are of such importance in the model; they affect every constraint equation. For that reason, any uncertainty in these quantities will directly influence the predictions. The summary of the constraint equations in Sec. 6.2 shows that the general formula for the coefficients is

$$\text{Coefficient} = Q \frac{D + x}{x} ,$$

where Q and x are general terms for other variables, and D is the death rate. This relationship means that the uncertainty in the death rates will depend on the size of D compared with x. When x is quite small relative to D (nitrogen constraint), errors in D will be far more important than when x is larger (other constraints). But, in all cases, x is never large with respect to D, so the value of D is always important.

The results of the sensitivity analysis shown in Fig. B.1 indicate that the actual grazing in the Oosterschelde may be of comparable size to (or greater than) death from other factors. Without other confirmation or justification, though, one should not try to draw such conclusions from the model. There is still uncertainty in other parameters and input data that confuses the situation and makes it difficult to isolate causal relationships so specifically. Grazing might be of more or less importance, with other unknown factors creating the compensating differences. Until death rates are actually measured or derived for the Oosterschelde region, there can be no direct confirmation of any assumed values that include a factor for grazing.

B.3.2. Nutrient Remineralization Rates

Nutrient remineralization rates are also important, but less so than the death rates. As indicated in Sec. 3.4.2, these rates have been measured, but with limited success. Table 3.2 shows the range of values and the lack of data for many important parameters, particularly with respect to silicon and phosphorus. The complex nature of the reactions, the multiple avenues of nutrient release, and the difficulty of measurement account for this deficiency. The rates used in the model represent measured values or averages, where there is some disagreement. In some cases, no literature data could be located, so parameters were set by comparison with known processes and reasonable assumptions.

Variations in remineralization rates for the three nutrients have different effects. In the nominal case, nitrogen is the primary limiting nutrient, so changes in the rates for phosphorus and silicon must be substantial before significant changes are observed. Because nitrogen has the most extensive study, this is, in one sense, fortunate. When the rate constants for the other nutrients are changed sufficiently, nitrogen is not generally removed as a limiting constraint, but phosphorus and silicon are brought into the set of limiting constraints, and more phytoplankton species are predicted. The remineralization rate for nitrogen must be increased beyond the range found in the literature before it is excluded from the model. Thus, the biomass predictions of the model are very dependent on the specific rate chosen for nitrogen. If the value used has a large uncertainty, this translates into a similar uncertainty in the biomass predictions. The uncertainty will have a ceiling, however, because other constraints will become limiting at some point. A much more extensive analysis of this problem will be required before final conclusions can be drawn.

B.3.3. Extinction Coefficient Elimination Rate

The rate constant for eliminating the effect of dead algae on the extinction coefficient in the model has been discussed in Sec. 4.2. Because there has been no measurement of this parameter, its value must be estimated from an understanding of the physical processes. There are conflicting arguments about the appropriateness of the use of the BOD removal rate. For diatoms with inert shells, this may be an overestimation. Much of the light absorption, though, is accomplished by the chlorophyll in the algae, and this disappears at a higher rate than BOD. The more refractory materials may be less important because they tend to scatter rather than absorb light. Only part of this scattered light will be lost to the system, as much of it will be absorbed by other phytoplankton in the vicinity.

When variations in this rate were introduced into the model, the effect was slight. Changing the constants in Eq. 3.5 to alter the function had only a small effect on biomass and none on the species or limiting constraints. An arbitrary multiplication of the rate had a similar small effect on the predictions, primarily because solar radiation is not frequently a limiting constraint when any bloom is present. Because the chosen rate is probably lower than that found in nature, most of the uncertainty should be of little importance.

B.4. ERRORS CAUSED BY NONUNIFORMITY OF CONDITIONS

A primary cause for overpredicting or underpredicting a bloom would be the problem of nonuniformity of conditions. The values used in the model are determined to be representative averages of the conditions found in the Oosterschelde. For that reason, they will be more constraining than some locations and less constraining than others. This will be particularly true if horizontal mixing is weak in any areas, especially those that are shallow or heavily nutrient loaded.

Variations of this type can be dealt with through alterations of input conditions in the model. The results of this analysis were discussed in Chap. 7, where it was found that the mixing depth and temperature were the most important factors. This is not to say, however, that large anomalies in the other constraining factors, such as the nutrients, could not be important. Errors of this type can only be avoided by a thorough understanding of the local microconditions at the present time or in the future. The predictions of the model should not be taken to represent the entire basin, but only that part which is similar to the input data.

B.5. POTENTIAL SOURCES OF LARGE ERRORS

In some situations one would expect our model to overpredict or underpredict the peak of a bloom by a very large amount, perhaps by an order of magnitude. When this occurs, it will most likely be for one of the following reasons, all of which have been considered in greater detail in earlier chapters.

We would overestimate a bloom for two primary reasons. It would happen if we overestimated the amount of nutrients available (b_i). For example, some of a nutrient that we counted as available might be in a form that algae cannot use, such as residual organic material resistant to further mineralization. We would also overestimate the bloom if the algae death rates are badly underestimated. It has been noted that this is most likely to occur when grazing is an important factor. Overestimation could also be a problem if some constraint were operating that we have ignored. For example, some species of algae require an external source of certain vitamins. If these vitamins are not limiting, we can safely ignore this factor. But if vitamins are limiting, ignoring this requirement will cause us to overpredict the bloom.

We would underestimate the bloom if we underestimated the available nutrients. This only applies if the nutrient in question is limiting. Such an underestimate might arise from failing to consider a pool of nutrients that is in fact available for algae growth, for example, nutrients in the bottom sediments.

We would also underestimate the bloom if we had too many constraints. For example, some algae use nitrogen only in the form NH_3, while others require it in the form NO_3. Thus, we might be tempted to treat each form of nitrogen as a separate nutrient, and include a separate constraint for each. This would neglect the fact that organisms exist that can convert nitrogen from either form to the other, and therefore nitrogen in either form is effectively available to all species of algae.

The most likely reason that we might underestimate a bloom is that there are species present in the bloom that are not represented in the model. If they are more adaptable to the abiotic conditions, or require fewer nutrients, the underestimation could be large. We have tried to minimize this possibility in two ways. Nutrient compositions for the different species were chosen to represent a reasonable range of variation. We would expect that any unknown species should not deviate too much from the ones we have included. Also, variations in the photosynthetic efficiency curves were investigated (as discussed earlier) to determine their effect on the biomass predictions. In general, the results indicated that the probability of drastically underestimating a bloom should be small. This probability does exist, however, and it serves to emphasize the need for further study of the Oosterschelde region.

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