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

VOL. III, ASSESSMENT OF LONG-RUN ECOLOGICAL BALANCES

PREPARED FOR THE NETHERLANDS RIJKSWATERSTAAT

J. H. BIGELOW, J. C. De HAVEN, C. DZITZER,
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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 in 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 would 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 would be 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 must provide protection against a storm so severe that it might be expected to occur only once in 4000 years.[1] Second, it must 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 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 in place of the existing dikes around its perimeter to protect the land.

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

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

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 methodology 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 selected three alternative cases to analyze in the POLANO project: a closed case, an open case, and a reduced-tide (storm-surge barrier) case. These three cases are not fully described by what is done to the mouth of the Oosterschelde. It is necessary to describe several other features of each case, the most important for ecology 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 design "4,"* the dam is located near Wemeldinge, where it produces a larger Eastern Basin than that in compartment design "3." In *compartment design "3,"* the dam is located considerably closer to the rear of the Oosterschelde, where it produces a smaller Eastern

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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.

Basin.[5] In both compartment designs, the Western Basin remains saltwater whereas the Eastern Basin becomes freshwater.

In the *closed case*, the mouth of the Oosterschelde is completely closed with a dam, while the existing dikes are left basically unchanged. Compartment design "4" produces the larger Eastern Basin, which, in contrast with the original plan, is the only part of the Oosterschelde that becomes a freshwater 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 design "3" produces the smaller Eastern Basin.

In the *storm-surge barrier case*, a storm-surge barrier[6] with an aperture of 11500 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 design "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 kind and populations of species that comprise 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 in interrelated industries; the quantity and quality of the *water supply* available in various locations; and the many *social* impacts, including the displacement of households and the disproportionate effects on the Zeeland economy.

POLANO also made a number of sensitivity analyses to see how the impacts would change with variations in the designs of the alternative 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 methodology that had been developed and summarized the results of the POLANO analysis. After this, Rand helped the Dutch members of the POLANO team to 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

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

[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 bottom of the Oosterschelde. This barrier concept has been called "pillars on pits."

June 1976. (The Parliament also requested additional analysis by the Rijkswaterstaat to establish the best aperture size for the barrier.)

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 presents a detailed analysis of the security offered by the three cases, both in the long-run and during the construction period, and shows 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 included different apertures for the storm-surge barrier, different sizes for the Western (saltwater) 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, using data from the Grevelingen, an estuary adjacent to 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 saltwater 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 conditions are favorable, algae may grow explosively. The resulting bloom may be objectionable in its own right, because it discolors the water or poisons fish. Or, when conditions become unfavorable, the bloom may suddenly die off and the bacterial mineralization of the dead algae may then deplete the water of oxygen. This, in turn, can cause the death of desirable fish and produce bad odors. 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 created in the Eastern Basin during its construction can, by interfering with the normal action of certain bacteria, cause bad odors and murky water while it is being converted into a freshwater lake. Using the model, this report shows that the large and small Eastern Basins associated

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

with compartment designs "3" and "4," respectively, 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 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. III of the POLANO series, describes a mathematical model, called the general ecomodel, that we developed to predict the effect of the different cases—open, closed, and storm-surge barrier—on the long-term average abundances of species (more accurately, groups of species) found in the Oosterschelde. The report details how we calibrated and attempted to validate the model. It also presents a detailed analysis of how the many relevant factors that differ among the cases—tidal amplitude, size of the saltwater basin, fishing rates, etc.—would influence the ecology of the Oosterschelde, and draws conclusions about the different impacts of the alternative cases. Finally, it makes recommendations for further research.

While we wish this report could have been shorter, the following factors made its great length inevitable. First, the ecosystem we have considered is complex; no other model, to our knowledge, has been successfully applied to the analysis of so complex an ecosystem. Second, the analysis is quite comprehensive; it considers many ways in which the ecology of a large estuary will respond to changes in many different factors. Third, the presentation style is tutorial; the report presents a step-by-step description of the development of both the methodology and the analysis, instead of merely summarizing the end product. Because it is tutorial, we hope that the report will serve as a primer for government officials, engineers, regional planners, and others in fields outside ecology who wish to learn how a policy analysis of complex environmental questions can be carried out in practice.

However, we expect that the report's largest audience will be those who study ecology or construct models of ecosystems. Because it contains quite detailed descriptions of the model and how it was implemented and applied, the report will be of limited interest to the casual reader. (It is precisely this detail, however, that should make the report useful to the nonecologist as a primer for environmental policy analysis.) We have tried to avoid the use of technical language throughout the report, so that the reader unconversant with ecology can master it. Moreover, although we do use some mathematics, and an acquaintance with mathematical notation will be helpful, the report has been written so that a knowledge of mathematics is not necessary to its understanding.

The general ecomodel is unlike traditional mathematical models of ecological systems. The traditional model attempts to predict the day-to-day changes in the abundances of species (or groups of species); consequently, it must consider the day-to-day dynamic relations among them. By contrast, our general ecomodel attempts to predict only the long-term average abundances, and thus need only consider the average—and therefore static—relations among groups of species. Because it attempts less, our model requires less data, and is easier to calibrate, validate, and apply than a traditional model of the same ecosystem.[8]

Of course, to predict some ecological impacts, it would be necessary to determine the daily and seasonal fluctuations in abundances. But, surprisingly many impacts of prominent concern in the Oosterschelde depend primarily on how the long-term average abundances change, and only secondarily on daily or seasonal fluctuations. Among these impacts are how well the Oosterschelde can serve as a feeding and nesting area for birds, as a location for the commercial culturing of oysters and mussels, and as a nursery for the young individuals of various fish and shrimp populations from the North Sea.

In this report, we have tried to demonstrate the value of the general ecomodel's nontraditional approach, both through arguments and attempts at validation. Although the results of validation were less than ideal, because of limitations in the available data, they nevertheless tended to support our approach. The Rand Corporation and the Rijkswaterstaat are continuing their joint work in ecology, this time concentrating on freshwater systems, and we expect that this work, including as it does an extensive data-gathering program, will afford opportunities to further develop and validate the concepts of this nontraditional approach to ecological modeling.

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[8] In addition, our model is economical. The time needed to prepare the input for a single case is only a few minutes, and the money cost of examining a case is never more than a few dollars.

SUMMARY

S.1. THE OOSTERSCHELDE PROBLEM

This volume describes a major component of a study of how to protect the lands bordering the Oosterschelde (an estuary in the southwestern part of the Netherlands) from flooding. The major factors considered in the study were safety from floods, the cost of the protective measures, and the ecological consequences of the protective measures. In this volume, we describe our methods for estimating some of the ecological consequences (called impacts in the study) and the results and conclusions we obtained by the use of those methods.

S.1.1. Particular Environmental Concerns

The original Delta plan, which called for the closure of the Oosterschelde, was stalled by the opposition of various action groups. Their objections centered on the possible adverse effects that closure might have on the ecology of the region.

Before the execution of the Delta Project, the Delta region, with its estuaries, sea arms, shoals, and salt marshes, formed an ecologically rich, natural reserve of international significance. Of this ecologically significant area, only the Oosterschelde remains in its original state as a tidewater area. The water quality of the Oosterschelde, in ecological terms, has in fact improved in recent years. This improvement is due to the completion of various elements of the Delta Project and the resulting greater isolation of the Oosterschelde from contaminated river water.

Because of its special characteristics, the Oosterschelde provides the northernmost living area for a number of species that enrich the diversity of the region. The tidal shoals and mud flats provide food and habitats for a wide range of flora and fauna. The Oosterschelde, in its present tidal form, is a highly important area for birds: it is an important north-south migratory route and serves as a breeding and overwintering area. If these tidal flats and surrounding areas are eliminated by closure, sufficient areas may not remain in Europe to serve these purposes. The rarer species of birds may be affected most adversely.

Besides sheltering birds, the Oosterschelde functions as a breeding ground and nursery for commercially important sea fish and shrimps. It is also an attractive area for Dutch and Belgian sportfishermen. Shellfish, especially oysters and mussels, have been harvested in important commercial quantities in the Oosterschelde. The influence of tide in preserving shellfish culture is complex and not completely understood. Thus, changes in tidal levels, within certain ranges, may have a severe adverse effect on the abundance of shellfish as well as on other species important for both sport and commercial fishing.

S.1.2. Alternative Solutions

Opposition to the original Delta plan led Parliament to reexamine it. Three alternative approaches to protecting the Oosterschelde were identified:

- Closing the Oosterschelde, a solution denoted here by the letter "D."
- Leaving the Oosterschelde open, denoted by the letter "A."
- Building a storm-surge barrier across the mouth of the Oosterschelde, denoted by the letter "C." A storm-surge barrier would reduce the area through which a tide could flow (called the aperture), and thereby reduce the tidal amplitude.

Two compartment designs for separating the Oosterschelde into saltwater and freshwater basins were recommended for use with the above approaches. Compartment design "3" (Fig. S.1a) has a small freshwater eastern basin (the Zoommeer), separated from the large saltwater western basin by the Oesterdam. Design "4" (Fig. S.1b) has a large freshwater eastern basin, separated from a small saltwater basin by the Wemeldingedam. In both designs, there is a second dam, called the Philipsdam, that separates the northern Volkerak region from the saltwater basin. The dashed lines at the mouth of the Oosterschelde in Figs. S.1a and S.1b show the position of the proposed dam (for a closed case) or barrier (for a reduced-tide case).

An alternative solution (termed a *case*) combines an approach to protection with a compartment design. *A case will be identified by a letter denoting what is done to the mouth of the Oosterschelde, followed by a number denoting how the Oosterschelde is partitioned into saltwater and freshwater basins.* For example, A3 means that the mouth is open and compartment design "3" is chosen; and D4 means that the mouth is closed and compartment design "4" is chosen. In a reduced-tide case, an additional identifier is needed, namely the area of the aperture (called the "μA"). For example, alternative reduced-tide cases are C3, $\mu A = 20000$ sq m, and C4, $\mu A = 6500$ sq m.

S.2. SCOPE AND LIMITATIONS OF THE GENERAL ECOMODEL

Our task was to assess the various impacts that different cases would have on the ecology of the Oosterschelde. Among the assessment tools we developed was the general ecomodel described in this volume. This model addresses many of the concerns expressed by the opponents of the original closure plan.

Their concerns are subsumed in general by the question: What will happen to the abundances of the different species in the Oosterschelde in response to each case that might be chosen? It was necessary, therefore, to include in the general ecomodel a large number of species living in a variety of habitats. Furthermore, to distinguish among the impacts of the alternative cases, we had to design an ecomodel to predict the influence on these species of such changes as reductions in the tidal amplitude, changes in the sizes of the habitats (caused by the creation of the freshwater lakes in the different compartment designs), and changes in sport and commercial fishing rates. But given the present state of ecological knowledge, the ecomodel had to be limited, in several dimensions, as follows:

Geographical Limitation. Our general ecomodel includes only the ecology of the saltwater basin to the west of the Oesterdam (in compartment design "3") or the Wemeldingedam (in compartment design "4"; see Fig. S.1). The general ecomodel does not encompass the ultimate fate of the freshwater lakes created by each compartment design.

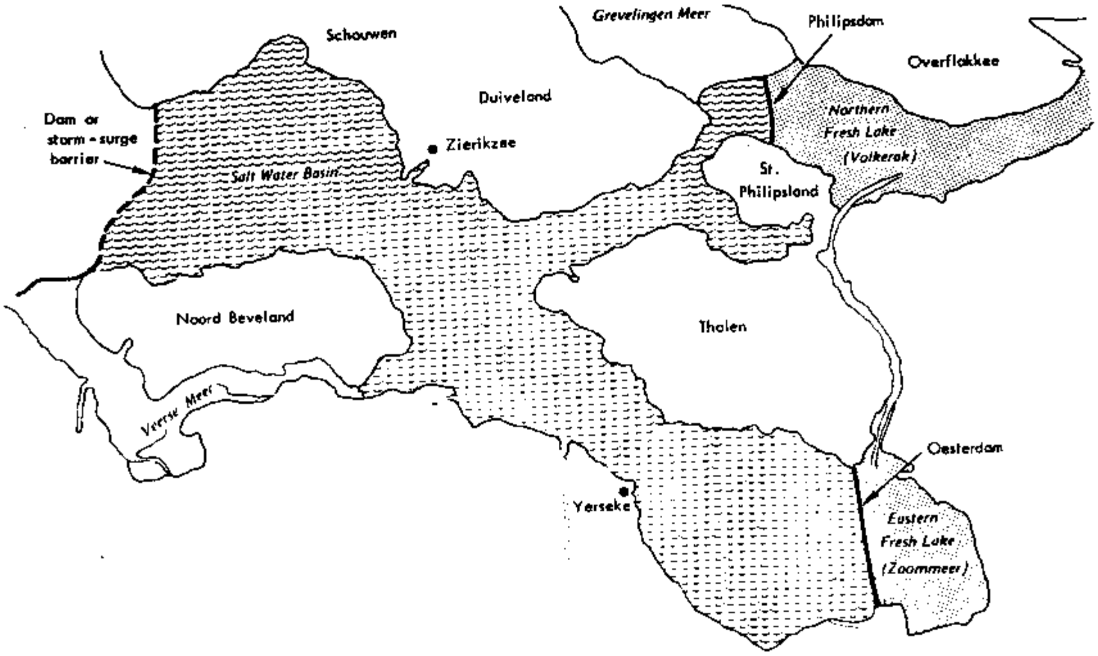

Fig. S. 1a — Compartment design "3"

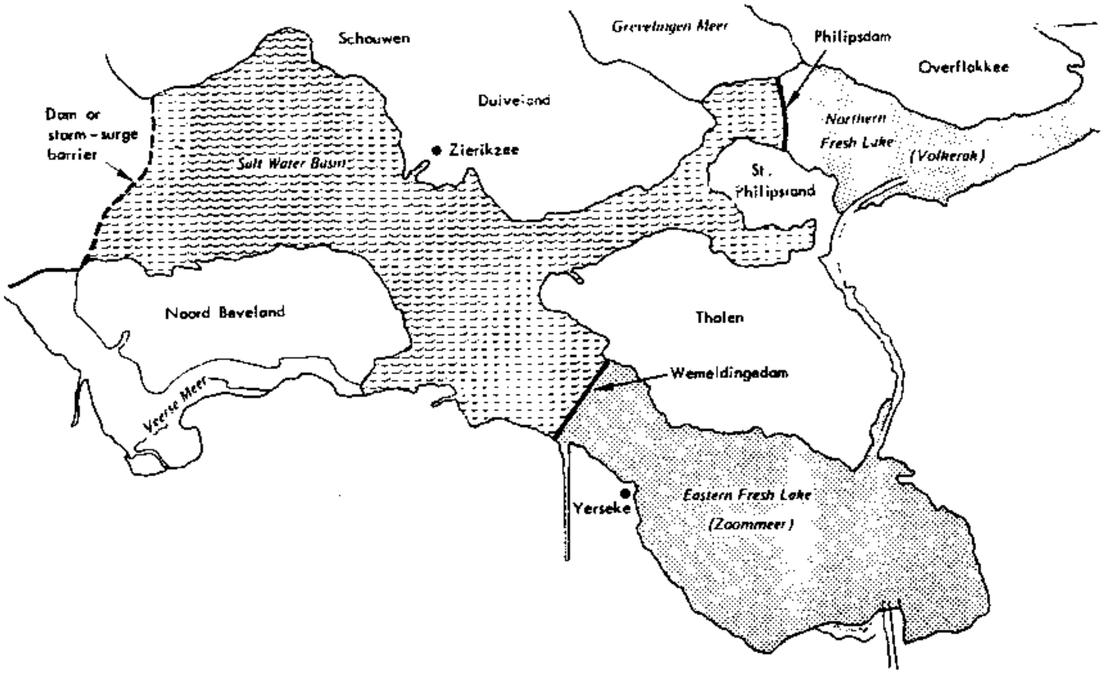

Fig. S. 1b — Compartment design "4"

Biological Limitation. Our general ecomodel does not predict, individually, the abundance of every one of the more than 2000 species found in the Oosterschelde. In the model, similar species are combined into aggregates called ecological groups, or *ecogroups* for short. Species in the same ecogroup eat similar things, have similar predators, and live (and feed) in similar places. Our ecomodel of the Oosterschelde has 18 ecogroups. Among them, the ecogroups contain all organic matter in the Oosterschelde, including dead organic matter (detritus), as well as photosynthetic organisms and heterotrophs (organisms that live by eating organic material, rather than by synthesizing it from inorganic nutrients and solar energy as do plants). Heterotrophs are further divided into three kinds of birds, four kinds of fish, zooplankton, and eight kinds of bottom dwellers.

The places where the ecogroups live are called *segments* in the model. Our model of the Oosterschelde has the following four segments: the *pelagic segment*, which consists of the bulk of the water; *oyster and mussel beds*, where shellfish are cultivated; *tidal flats and shallow bottoms*, from the mean high water down to 3 m below mean low water but excluding the oyster and mussel beds, all of which also lie in this depth range; and the *deep bottoms*, more than 3 m below mean low water.

Temporal Limitation. Our general ecomodel predicts only the long-term average abundances of the ecogroups in each segment, not the daily or seasonal variations in abundances. Nor does it predict the random fluctuations in abundances that one would expect to observe from year to year. We refer to the state of the ecology that is characterized by long-term average abundances as the *stable ecostate*.

To illustrate the latter concept, imagine the present Oosterschelde as being entirely blocked off from the North Sea by the construction of a closure dam. Our studies have suggested that starting from the moment of closure, the abundances of most organisms in the Oosterschelde would decline, because closure would prevent the substantial import of detritus, a major food source, from the North Sea.

This decline in abundances would be rapid at first, then slower, and after many years would be so slow that the natural seasonal and annual fluctuations would mask it completely. At this point, perhaps 10 or more years after closure, the downward trend in abundances could be said to have disappeared. The ecosystem would have adjusted to a new stable ecostate characterized by new long-term average abundances. This new stable ecostate is what the general ecomodel would predict.

S.3. HOW THE GENERAL ECOMODEL WORKS

The structure of the general ecomodel is based on the food web. In the following discussion, we define a food web and relate its components to the independent and dependent variables of the model. Then we outline how these variables are functionally interrelated.

S.3.1. The Food Web

Most transfers of mass among ecogroups take place when one ecogroup eats another. This process can be conveniently described by a network called a *food web*. Figure S.2 shows an exemplary food web for a system with five ecogroups in one segment. Here, each node (shown as a circle) corresponds to an ecogroup. (The actual food web used in our model of the Oosterschelde may have as many as four nodes for each ecogroup, one for each segment in which the ecogroup is found.)

The arcs connecting one node to another (or to itself) describe the transfer of mass among nodes as a result of feeding. For example, the arc from node "herbivores" to node "carnivores" indicates that carnivores eat herbivores. Note that there is no arc from any node to the "detritus" node, even though there is a transfer of mass to detritus from every other ecogroup. For example, plants die and become detritus, and heterotrophs produce feces. The reason that such arcs are not shown is that these transfers of mass do not occur as a result of eating.

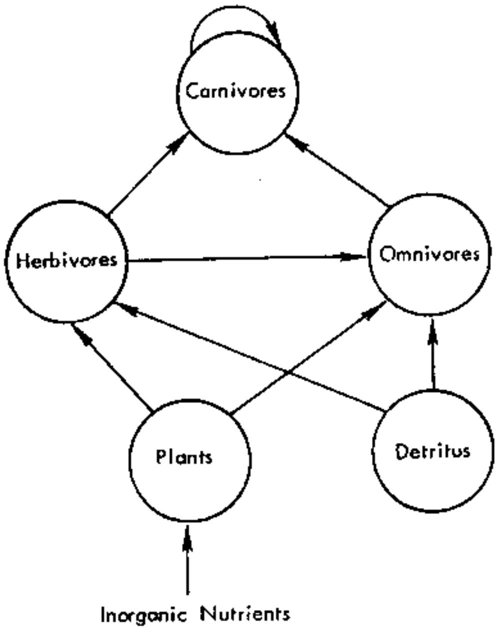

Fig. S.2—An exemplary food web

Arcs starting at a node but leading out of the web indicate biomass leaving the ecosystem. Conversely, arcs leading into a node but originating from outside the food web indicate organic matter entering the ecosystem. In Fig. S.2, the single arc of this kind denotes the incorporation of inorganic material in living organisms (photosynthesis). In our multisegment model of the Oosterschelde, we included arcs denoting detritus entering the Oosterschelde from the North Sea, and living organisms entering and leaving because of fishing and migration. The rates of mass transfer into and out of the ecosystem are important independent variables (see below).

S.3.2. Independent Variables

The independent variables of our model are factors that influence the ecosystem in a relatively direct way. They are the size of each segment; the average fishing and migration rates of each heterotroph; the average rate of photosynthesis;

and the average import rate of detritus. Fishing and migration rates, the rate of photosynthesis, and the rate of detritus import are all rates of mass transfer into and out of the ecosystem. They can be dealt with in a straightforward way, since the model is based on the idea of a food web, which is, in turn, based on rates of mass transfer.

But segment sizes must be dealt with differently. In addition to biomass, a great deal of biologically inert *filler* material will be found in each segment. In bottom segments, this material is sand or mud; in the pelagic segment, water. We have included the mass of filler in a segment as an additional variable in that segment. The size of a segment is directly proportional to the amount of filler in the segment. Thus, to change the size of a segment, we simply change the amount of filler.

Many factors whose effect on the ecology is less direct are not among the independent variables. Their influence is exerted in the model through their effects on the independent variables. For example, construction of a compartment dam would reduce the segment sizes by the amounts that would lie behind the dam. This reduction in the area of the saltwater basin would also reduce the rate of photosynthesis, because the total incidence of solar energy is proportional to area, and photosynthesis needs solar energy. Further, the detritus import rate would decline because the volume of water (and hence organic matter) brought in by the tide is also related to area.

S.3.3. Dependent Variables

Each arc of the food web corresponds to a dependent variable in the model. (A few dependent variables that correspond to the respiratory activity of photosynthetic organisms and the mineralization of detritus are not represented by arcs.) The dependent variables can be interpreted as abundances. For example, the dependent variable corresponding to the arc from "herbivores" to "carnivores" in Fig. S.2 is interpreted as the long-term average abundance of carnivores that support themselves by consuming herbivores. Alternatively, it is the total long-term average abundance of carnivores, multiplied by the fraction of the carnivores' nutritional energy that is contributed (albeit unwillingly) by herbivores. This abundance is related to the rate of mass transfer from herbivores to carnivores (which is what the arc depicts) by a factor called the *daily ration* (or daily food requirement) of carnivores.

In addition, each dependent variable is specific to a segment. This is irrelevant to the one-segment example shown in Fig. S.2, but in our multisegment model of the Oosterschelde, a dependent variable is interpreted as the abundance of one ecogroup that lives in a given segment and supports itself by consuming some other ecogroup. Alternatively, the variable is the abundance of the one ecogroup in the specified segment, multiplied by the fraction of nutritional energy contributed by the other ecogroup. Thus, the dependent variables contain information about the abundances of the ecogroups and the mixture of items in their diets (their *diet mixes*).

S.3.4. The Mass Balance Equations

In a stable ecostate, the long-term average abundance of each ecogroup must (by definition) be constant. This means that additions of mass to each such abundance, because of growth and reproduction, must equal subtractions due to predation, fishing, and net outward migration. Also, each ecogroup must consume enough to support its normal rates of metabolism, growth, and reproduction. When these conditions are satisfied, we say that the ecogroup is *in balance*.

The mass balance requirements are expressed as linear equations involving the dependent variables. The coefficients in these equations are determined from such quantities as the daily ration, the metabolic rates, growth rates, and "fecal fractions" of each ecogroup. (The fecal fraction of an ecogroup is the fraction of a meal consisting of that ecogroup that will be excreted as feces.)

There is one mass balance equation for each ecogroup and at least one node per ecogroup.[1] There is one variable for each arc in the food web. But as the arcs always outnumber the nodes, the dependent variables outnumber the balance equations. By themselves, therefore, the mass balance equations cannot uniquely determine values for all the dependent variables. That is, there are many ecostates that satisfy the balance requirements.

S.3.5. The Gibbs Function

To enable the model to arrive at a unique stable ecostate, we assumed that the ecosystem obeys a minimum principle—i.e., as it evolves, some measurable characteristic of the ecosystem tends continuously to diminish. Various characteristics of ecosystems have been proposed to obey a minimum principle (or equivalently, a maximum principle), including diversity, biomass, and power output. The characteristic we selected is the Gibbs function. Thus, the general ecomodel operates by finding the ecostate that minimizes the Gibbs function, while simultaneously satisfying all the balance equations. While we have no proof that the Gibbs function is the proper function to use for this purpose, it is attractive for several reasons.

One reason is thermodynamical: In numerous papers, ecologists have proposed using the Gibbs function as a measure of the energy in ecological systems.

Second, the Gibbs function is intimately related to the mass-action law of chemical kinetics. As frequently applied in ecology, this law states that the rate at which one species preys on another is proportional to the product of their abundances.

The third reason for using the Gibbs function is statistical. Certain parameters of the Gibbs function can be interpreted as initial estimates of the probabilities that the different ecogroups will be found in a sample taken from a given segment.[2] Minimizing the Gibbs function subject to the balance constraints can then be viewed as developing a revised set of probabilities that incorporate the information that the abundances must be in balance.

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[1] We could write a separate balance equation for each node in the food web. This might mean writing several equations for each ecogroup, one for each segment that the ecogroup inhabits. However, we have chosen to write only one equation for each ecogroup and to include terms for every segment that the ecogroup inhabits. This approach permits a net average gain of an ecogroup in one segment to compensate for a net average loss in another segment, e.g., by organisms migrating from the one segment to the other. Writing separate balance equations for each segment would prohibit this compensatory migration.

[2] Accordingly, values for these parameters can be estimated from whatever ecogroups are found in samples taken from the Oosterschelde, or (as was necessary in many instances) by inferring what a sample taken from the Oosterschelde ought to contain from what was found in a sample taken from a similar ecosystem.

Finally, there is the reason of practicality. Combining the Gibbs function with the balance equations yields a model that is easy to calibrate and use, and that behaves in reasonable ways. As just one example of its reasonable behavior, the model obeys an ecological version of Le Chatelier's principle: If a stress is applied to a system in a stable state, then the system will adjust, if possible, to reduce the stress. To illustrate this principle ecologically, when the size of a segment is reduced, the biomass in that segment diminishes as well, and the organisms that need the greatest amount of space per unit biomass suffer the greatest relative reduction.

S.4. PREPARING THE MODEL FOR USE

S.4.1. Calibrating the Model

To calibrate the general ecomodel, we adjusted the parameters in the Gibbs function so that when the independent variables were given values that characterize the present Oosterschelde, the values of the dependent variables obtained from the model were characteristic of the present Oosterschelde. Calibration thus required knowledge of the values of the independent and dependent variables that characterize the present Oosterschelde. In this discussion, we describe how we estimated values for the independent variables. We also describe our iterative procedure for estimating the abundance and diet mix of each ecogroup—i.e., the dependent variables—such that each ecogroup is in balance, and no ecogroup has a preference for any diet item that is out of proportion to that item's abundance.

Selecting Values for Independent Variables. For the most part, determining values for the independent variables that characterize the present Oosterschelde was straightforward. Segment sizes could be measured on a map. The average rate of photosynthesis had been measured in neighboring areas, from which we estimated that approximately 455 tons ash-free dry weight was photosynthesized in an average day in the Oosterschelde. Fishing and migration rates, although difficult to quantify, proved to be not very important.

The rate of detritus import into the Oosterschelde was both crucial and difficult to estimate. The biota in the Oosterschelde are ultimately sustained by a combination of photosynthesis within the Oosterschelde and the import of detritus from outside. Energy from these two sources must balance the energy dissipated by the combined metabolism of the biota of the Oosterschelde, plus smaller losses due to bacterial decomposition of detritus (mineralization), and losses from fishing and net outmigration.

However, no data exist from which we could directly estimate the rate of detritus import. Therefore, we inferred the rate from the requirement that the total energy input to the entire ecosystem must balance the total energy lost by all pathways. We estimated the total metabolic rate of the entire biota of the Oosterschelde from the abundances and metabolic rates of each individual ecogroup. To this we added a reasonable allowance for mineralization, fishing, and migration, and subtracted our estimate of the rate of photosynthesis.

In contrast to most estuaries in the United States, which are believed to be net exporters of detritus, we found that the Oosterschelde appeared to be a net importer of detritus. This was not a surprising result, since the same had been found for several other Dutch estuaries (the Waddensea, and the Grevelingen when it was open to the North Sea). However, we were surprised to find that a very large rate (700 tons/day) of detritus import is required to support the biomass in the present Oosterschelde. Because this rate greatly exceeds estimates by others, it should be viewed with reserve. We therefore recommended that direct measurements be made of the detritus import rate. Plans are now being made, and tests carried out, pursuant to this recommendation.

Adjusting Initial Abundance Estimates. Next, we estimated the dependent variables—the abundance and diet mix of each ecogroup in each segment—directly from sampled data, combined, as was often necessary, with tentative assumptions (for example, lacking data on the density of benthic grazers in the Oosterschelde, we assumed the same density as in a similar estuary nearby, as discussed below). We used these estimates to calculate values for the parameters in the Gibbs function. Then, using the values of the independent variables for the present Oosterschelde as inputs, we applied the model to obtain its predictions of the dependent variables—abundances and diet mixes—in the present Oosterschelde. If the direct estimates of dependent variables had satisfied the mass balance requirements, then the model's predictions would have been identical with the direct estimates.

However, the direct estimates were not in balance, and so the predictions did not match the estimates. We took this mismatch to signify that the original, unbalanced estimates were wrong, as was expected because they involved numerous tentative assumptions. We then modified or replaced some of the least tenable of the assumptions, and reestimated the dependent variables and the parameters in the Gibbs function. To calibrate the model of the Oosterschelde to our satisfaction, we reestimated the parameters and dependent variables more than twenty times.

As an illustration of the tentative assumptions we were forced to make, and later to modify when the estimates of abundances based on them proved not to be in balance, consider the case of benthic grazers. These very abundant organisms have never been sampled in the Oosterschelde. Our only direct data concerning their abundance were obtained from samples taken in the Grevelingen, a sea arm just to the north of the Oosterschelde that was dammed off in May 1971 and transformed into a saltwater lake.

We based our initial estimate of the abundance of benthic grazers in the tidal flat and shallow bottom segment of the Oosterschelde on the assumption that their density was the same as that found on the tidal flats in the Grevelingen. But we found that such a large abundance of benthic grazers could not be in balance; their food supply was too small to support them, and their growth and reproduction was too great for their predators to consume. Thus, we changed our assumption and reduced our estimate of their abundance, as follows:

Benthic grazers are not found much in permanently submerged areas. Since the tidal flats make up only 58 percent of the shallow bottom and tidal flat segment, we felt justified in reducing our estimate to 58 percent of its original value. Furthermore, benthic grazers are not abundant where wave action is prevalent. But the tidal flats in the western part of the Oosterschelde are subjected to considerable wave action. We therefore further reduced our estimate of benthic grazers on shallow bottoms and tidal flats to 40 percent of our initial estimate.

S.4.2. Validation

The model validation process is a determination of how well the model reflects the realities it is intended to represent. One test of a model's validity is how reasonably its predictions vary as the inputs are changed. Another, more definitive, test involves determining how well the model predicts a known circumstance other than the one to which it was calibrated (the present Oosterschelde).

Reasonable Behavior for a Simple Ecosystem. We tested the model by applying it to the simple example ecosystem whose food web appears in Fig. S.2. We found that the responses of this ecosystem to a variety of stresses imposed from outside were reasonable: Each stress caused the abundances of the different ecogroups to change in the appropriate directions and by what seemed to be appropriate relative (to one another) amounts. Because we had no actual data, we could not determine whether the magnitudes of the responses were appropriate to the stresses.

Comparison of Predictions to Grevelingen Data. We also attempted to validate the model by comparing its predictions to data collected in the Grevelingen. A considerable number of samples of biota were taken in the Grevelingen, mostly before closure, but to some extent after closure as well. We calibrated the model to reflect the observed situation in the open Grevelingen, and then compared the model's predictions for the closed Grevelingen with the data sampled there.

The most striking prediction by the model was that the total biomass in the closed Grevelingen, as well as the abundances of most ecogroups, would be considerably smaller than in the open Grevelingen. This agrees with the decline in abundances that was observed after the Grevelingen was closed. (The model also correctly predicted that phytoplankton in the pelagic segment would increase.)

However, the model typically overpredicts abundances of ecogroups in the closed Grevelingen by a factor of 2. If our estimates of long-term average abundances were perfect, we would conclude that the model was a poor representation of reality; but since these estimates are extremely uncertain—because of weaknesses in the underlying data—it is hard to know what to conclude.

In some instances, in fact, the model's predictions would appear to be better than the estimates made directly from the sampled data. For example, the model predicted that there should be 750 tons (ash-free dry weight) of cocklelike creatures (cockles, mussels, limpets, and oysters) in the closed Grevelingen. The data indicated that about 325 tons of cockles should be found there—but mentioned no mussels, oysters, or limpets. However, when the Institute for Fisheries Research conducted their recent mussel-fishing experiment in the closed Grevelingen, they recovered about 400 tons (ash-free dry weight) of mussels, which is the difference between our prediction and the original estimate of the abundance of cocklelike creatures. If anything, then, we appear to have underpredicted, and not overpredicted, the abundance of cocklelike organisms in the closed Grevelingen. We believe, therefore, that our model has been validated as well as the available data permit.

Implications for the Model's Predictions. These validation results have two important implications for predictions and conclusions regarding the Oosterschelde (which is our primary concern in this study): (1) Predictions by the model have large uncertainties, which reflect the uncertainties and deficiencies of the available data. (2) Nevertheless, the model can usefully distinguish between two alternatives if its predictions are very different.

The same arguments support both of these implications. First, the large uncertainties in our abundance estimates preclude the model from making precise predictions. Second, it should be remembered that our model predicts long-term average abundances and diets; individual measurements, in contrast, give information about instantaneous abundances only, which show large seasonal and annual variations.

However, our model has correctly predicted the directions in which abundances have changed since the Grevelingen was closed, and, in addition, it has been in rough agreement with the magnitudes of those changes. We conclude, therefore, that because of data limitations, and natural yearly variations in abundances, predictions by the model are much more significant in a relative sense rather than in an absolute one. In other words, large changes from case to case are significant, whereas small changes are probably not significant. And, of course, the direction of a large change is significant.

S.5. ESTIMATING INDEPENDENT VARIABLES FOR CASES ANALYZED

The cases we have analyzed, in addition to the present Oosterschelde (for the purpose of calibrating the model), are the open case, with both compartment designs "3" and "4" (see Fig. S.1); the closed case, again with both compartment designs; and numerous reduced-tide cases, with both compartment designs. These reduced-tide cases differed in the apertures of their barriers, and consequently in their tidal amplitudes. In the cases analyzed, the major independent variables are the rate of photosynthesis, the rate of detritus import, the mussel and oyster harvest rate, and the sizes of the segments. Other independent variables—the fishing rates and the migration rates—turned out to be of minor importance, since the model's predictions proved insensitive to realistic changes in the values assumed for these quantities.

S.5.1. Detritus Import Variable

To estimate the detritus import rate for the cases to be analyzed, we had to devise methods other than the one we used for the present Oosterschelde. That method requires that the abundances of all the ecogroups be known, whereas these are the unknowns we want to predict with our model for each case.

Closed Cases. The North Sea is the source of almost all imported detritus. If the Oosterschelde were completely dammed off from the North Sea, the detritus import rate would essentially drop to zero, although a minor amount of detritus could be imported through sluices in the dam.

Open Cases. The open cases differ from the present Oosterschelde primarily in the size of the saltwater basin, which is reduced by the compartment design. Detritus import would change only if the amount of detritus carried in or out with the tide were to change. Since there seems to be no reason for the concentration of detritus in tidal water to change due to compartmentation, any change in detritus import must result from a change in the tidal volume. Therefore, for the open cases, we assume that detritus import changes from the present situation in proportion to the change in tidal volume, becoming 546 tons/day with compartment "3" and 341 tons/day with compartment "4."

Reduced-Tide Cases. Based on the previously mentioned observation that the Oosterschelde is a net importer of detritus, we inferred that imported detritus must all be particulate matter, rather than dissolved matter.[3] When the tidal volume is reduced by the barrier, interior currents (except at the mouth of the Oosterschelde) will be reduced as well. Thus, the particulate matter brought in by the tide will have more time to settle, the concentration of particulate detritus in the outgoing water will diminish, and a larger fraction of the organic matter brought in with the tide will remain trapped in the Oosterschelde. We developed a relation for these processes that estimates detritus import from the area of the tidal basin and the aperture of the storm-surge barrier. Using this relation, we calculated that with compartment design "3," detritus import would reach a maximum of 990 tons/day when the aperture is 11500 sq m. With compartment design "4," the detritus import rate would generally be smaller, reaching a maximum of 619 tons/day when the aperture is 6500 sq m.

S.5.2. Sedimentation Variable

If more particulate organic matter settles to the bottom in the reduced-tide cases, it is natural to expect that deposit feeders (such as worms and snails) would receive a larger share of total detritus. To simulate this process, we introduced a new parameter called the *sedimentation factor* that apportioned an extra share of detritus to the deposit feeders. We then ran the model for a range of values for the sedimentation factor to see how much the abundances of other detritus eaters—suspension feeders and pelagic filter feeders—would change. Among other things, we found that the abundance of pelagic filter feeders (such as herring and anchovy) decreased as the sedimentation factor increased; this is natural, since more detritus deposited on the bottom means less remaining in the pelagic (bulk water) segment.

How did we decide which nominal (best estimate) values to use for the sedimentation factor in analyzing the different cases? For cases in which apertures equaled or exceeded the aperture giving the maximum detritus import, we picked the value of the sedimentation factor so that the suspension feeders (such as cockles, mussels, and oysters), who feed on suspended detritus and phytoplankton just above the bottom, would neither suffer nor benefit from the increase in detritus import; this value fell in the middle of the range of reasonable values for the sedimentation factor. For cases in which the apertures were less than the aperture giving the maximum detritus import, we assumed that each of the three types of detritus eaters received essentially the same fraction of the total available detritus as it had in the case with maximum detritus import. We say "essentially" the same fraction because of the influence of the remaining balance constraints. (This assumption is tantamount to believing that the amount of deposition of detritus from the pelagic

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[3] In simplified form, the inference proceeds as follows: Dissolved detritus would tend to move from the Oosterschelde toward the North Sea, because it moves in the direction of decreasing concentration and its concentration is higher in the Oosterschelde. Therefore, since there is a net import of detritus into the Oosterschelde, the imported detritus must be particulate.

segment onto the bottom and the concentration of suspended detritus near the bottom are proportional to detritus import.) Although we used these nominal values in our analysis of each case, we also tested the sensitivity of the model's predictions for the range of reasonable sedimentation factor values.

S.5.3. Other Independent Variables

The other independent variables are the segment sizes, the rate of photosynthesis, and the oyster and mussel harvest rate. In Sec. S.3.2, we discussed how the segment sizes depend on the compartment design. A reduction in tidal amplitude caused by a storm-surge barrier will reduce the areas of the tidal flat and shallow bottom segment, and the deep bottom segment, by lowering the mean high water level and raising the mean low water level. Changes in segment sizes will, in turn, affect the rate of photosynthesis, since the rate of photosynthesis is proportional to the area of the saltwater basin.

Although the model requires the harvest rate of mussels and oysters as an input, we can nevertheless use the model to investigate what harvest rates would be feasible in the different cases. In particular, we can determine which cases can sustain the present harvest rate of 30000 tons live weight/year (3.34 tons ash-free dry weight/day). The method we used to answer this question was to examine the sensitivity of the model's predictions of abundances to changes in the harvest rate. From these sensitivities, we inferred the maximum potential harvest, using arguments described in Sec. S.6.3.

S.6. IMPACTS CONSIDERED AND HOW THEY WERE CALCULATED

In our analysis of the different cases, we considered several *ecological impact categories:*

- Biomass of ecogroups.
- Potential abundances of birds.
- Potential shellfish culture.
- Nursery function.
- Transients.

Impacts in the biomass and nursery function categories were calculated directly by the general ecomodel described above. But the impacts in the other categories required additional calculations outside the general ecomodel. For example, the actual abundances of birds are not predicted by the model, because their abundance is strongly influenced by factors remote from the Oosterschelde. But the model can be used to determine what abundances of birds the Oosterschelde could *potentially* support. In this discussion, we will define the impacts in the different categories and describe how they were calculated.

S.6.1. Biomass of Ecogroups

Since they come directly from the model, the most straightforward impacts to predict are the abundances of the 18 ecogroups, expressed in units of biomass.

These impacts constitute the basic inventory of the ecosystem. We found the total biomass to be a useful ecological index because it correlates well with other impacts. But it is also useful to separate the total biomass into four components: fish; noncommercial bottom species such as worms and snails; cockles, mussels, and oysters (commercial bottom species); and all other ecological groups. The last category includes the birds and all the planktonic organisms. We separated the fish and the commercial bottom species because of the great social and/or commercial interest in them, and the noncommercial bottom species because most of them are the deposit feeders who benefit from increased detritus sedimentation in the reduced-tide cases.

S.6.2. Potential Abundance of Birds

Because the environmental groups who opposed closing the Oosterschelde expressed great interest in birds, we included three bird ecogroups in the model: plant-eating birds, fish-eating birds, and benthos-eating birds. In our model, no ecogroup preys upon birds. This causes the mass balance equation for each bird ecogroup to take a special form that uniquely specifies the abundance of that ecogroup. Consequently, the bird abundances are inputs to our model rather than outputs, and the model cannot directly estimate them.

Nevertheless, the model could be used to help determine whether bird abundance estimates obtained by other techniques are consistent with what the Oosterschelde ecology could support. The primary technique we used was a so-called competition model; such a model assumes that the abundance of a bird ecogroup was limited by its competition with other ecogroups for a fixed food supply. Note that both the abundances of the competing ecogroups and the fixed food supply are predicted by the general ecomodel. If the competition model was appropriate for a particular bird ecogroup, then the abundances predicted by the general ecomodel should respond when we increased the abundance of that bird ecogroup.

Plant-Eating Birds. When we applied the general ecomodel for a wide range of different abundances of plant-eating birds, the results disclosed no substantial impact on the other ecogroups. The competition model thus provided no insight into the differential responses of plant-eating birds to the alternative cases. To estimate the impacts on plant-eating birds, we therefore resorted to a comparison with the experience in the Grevelingen. In the Grevelingen, plant-eating birds increased fifteenfold after closure, probably because the sea-grass beds increased, providing a greater nesting area. We expect that the sea grass would also increase in the closed Oosterschelde but not in the open or reduced-tide cases. On this basis, we predict no substantial impact on plant-eating birds in the open and reduced-tide alternatives, but a large increase in the closed cases (comparable to the closed Grevelingen).

Fish-Eating Birds. We also applied the general ecomodel for a wide range of abundances of fish-eating birds. The model predicted that in each case, a constant total amount of food would be available to fish-eating birds and fish-eating fish. Thus, as the abundance of fish-eating birds was increased, the predicted abundance of fish-eating fish was observed to decrease. Of course, the total combined food consumption was different for each case.

In our analysis, we assumed that in every open or reduced-tide case the fish and the birds would have the same relative success in competing for food, but that their actual numbers would rise and fall in proportion to their combined consumption. In the closed cases, in contrast, we expected that all the fish-eating fish presently found in the Oosterschelde would disappear (because they are migratory), and that fish-eating birds would increase enormously to take advantage of the increased food supply. In fact, this phenomenon has been observed in the Grevelingen, where fish-eating birds have increased twentyfold since closure.

Benthos-Eating Birds. Finally, we applied the general ecomodel for a wide range of abundances of benthos-eating birds. Again, the model predicted that, in any case, the total combined consumption of benthos-eating birds and benthos-eating fish would be the same regardless of the assumed abundance of benthos-eating birds. However, the total combined food consumption would be different for each case. As with fish-eating birds, we estimated the abundance of benthos-eating birds, in any case, to be proportional to the total combined consumption.

It is conceivable that benthos-eating birds are limited, not by the competition for food, as assumed in the competition model, but by the size of their feeding area. Most benthos-eating birds are waders, and cannot feed in water deeper than about 30 cm. Consequently, we made another estimate of the abundance of benthos-eating birds in each case; the technique we used was to assume that the abundance of benthos-eating birds in each case would be proportional to the area of the bottom within 30 cm of the water surface at mean low water. In general, this technique predicts lower abundances than the competition model.

S.6.3. Potential Shellfish Culture

We sought to shed light on two questions concerning shellfish (mussel and oyster) culture: (1) Which of the cases will preserve the shellfish culture? (2) Which of the cases will permit mussels from the Waddensea to be rewatered in the Oosterschelde? (There are special areas in the Oosterschelde, characterized by a very firm bottom, that are used for cleaning and storing mussels grown in both the Waddensea and the Oosterschelde before sale. These are called rewatering plots.)

To investigate whether shellfish culture is possible in a case, we varied the assumed shellfish harvest (an independent variable) and observed the effect on the ecosystem. Figure S.3 shows the results of such an experiment for the cases with compartment design "3." Also included are the results for the present Oosterschelde. In each case, we found that the greater the harvest, the larger the standing stock of mussels needed to sustain that harvest. Also, the larger the harvest of mussels and oysters, the more it was necessary to control their predators. We also found that increasing the harvest by as much as a factor of 3 had no significant effect on any ecogroup except mussels and oysters and their predators.

Note that in Fig. S.3 the amounts of standing stock and predator control required in the present Oosterschelde are relatively insensitive to modest changes in the harvest rate. However, large changes, such as tripling the harvest, would require significant increases in the abundance of cultured shellfish, and significant control of their predators. We argue that changes such as these would require substantial changes in the techniques now being used for shellfish culture in the Oosterschelde. These changes would probably be expensive and difficult. Thus, if shellfish culture is to continue under economic conditions similar to those of today, the sensitivity of shellfish abundance and of their predators to variations in the harvest cannot be much greater than observed at present.

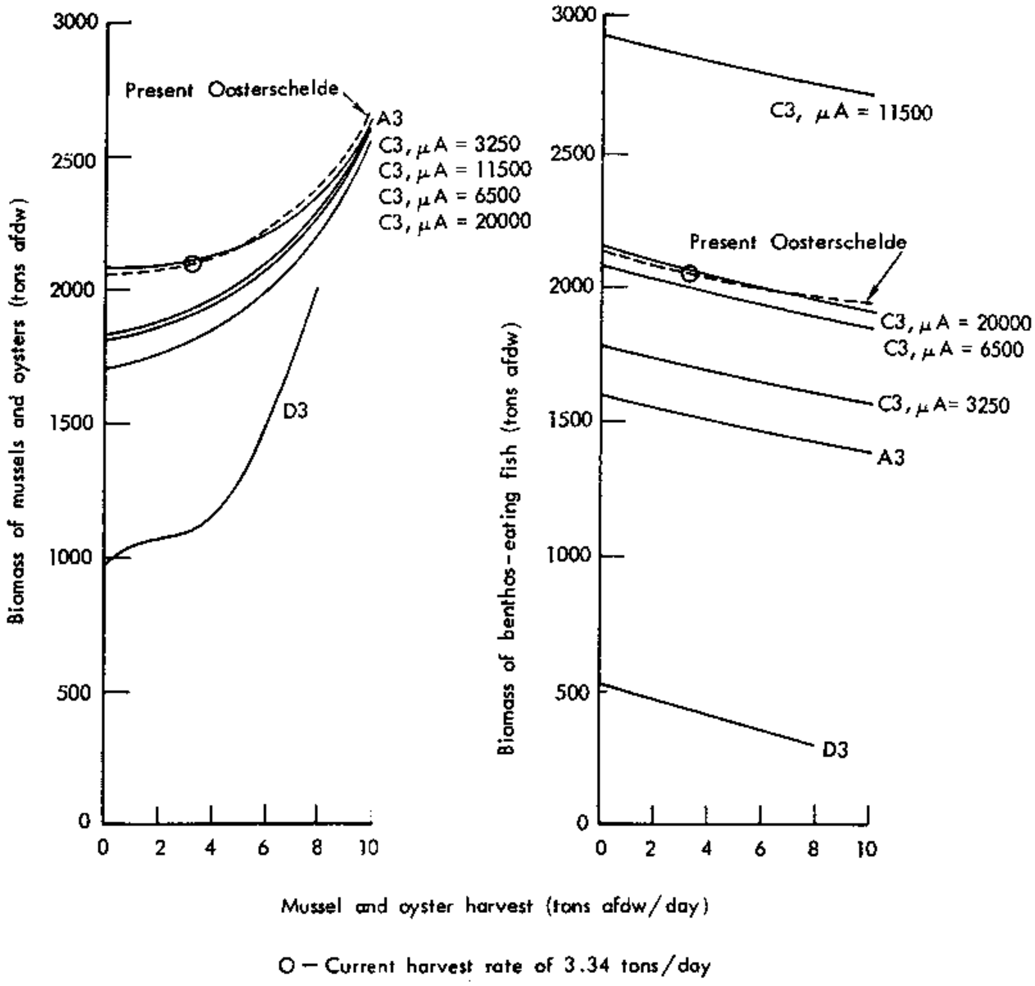

Fig. S.3—The effect of variations in the mussel and oyster harvest in cases with compartment design "3"

To illustrate, in Fig. S.3, the dependence of mussel and oyster abundance on the harvest rate of mussels and oysters appears to be much the same in all cases with a tide, but much greater in the closed case than it is in the present Oosterschelde. We can expect, then, that mussel and oyster culture, on the same scale as it is carried on at present, will remain commercially feasible in the open case A3, and in all reduced-tide cases in which the apertures are greater than 3250 sq m, but not in the closed case.

Our model could not help us to determine if any case will adversely affect the rewatering (storage and cleaning) of mussels in the Oosterschelde. However, a separate analysis led us to conclude that the cleaning and storage functions of the rewatering plots in the Oosterschelde could be satisfactorily replaced, if these functions are not maintained in their present state, in every case we considered.

S.6.4. Nursery Function

Juvenile individuals of a number of commercially important species (e.g., plaice, sole, brown shrimp) use the shallow areas near the open coast of the Netherlands, the Waddensea (both Dutch and Danish), and Zeeland (including the Oosterschelde), as nurseries. Although the Oosterschelde has only minor importance as a nursery, compared with the total nursery area serving the North Sea, its local importance to fish and shrimp populations in the southernmost part of the North Sea might be considerable. We asked in each case: Would the Oosterschelde nursery function be reduced or eliminated?

Whether the Oosterschelde can act as a nursery depends on two factors. First, it is necessary that juvenile organisms be able to migrate into and out of the Oosterschelde, and that adults be able to spawn there. This should be true so long as migration is unrestricted, which we expect in all but the closed cases. In the closed cases, we nominally assume that no migration can occur and so the nursery function would be eliminated. The second factor that determines nursery capacity is the suitability of the area for juveniles of the migratory species. In particular, there must be areas where the water is shallow, and food must be plentiful. These factors are considered by our model. In those cases in which migration can occur, therefore, we have used the model's predictions of the abundances of migratory ecogroups (shrimp and fish) as indices of the change in nursery capacity.

S.6.5. Transients

In each case, the abundances of each ecogroup must adjust, during some time period, from the present abundances to the long-term average abundances characteristic of that case. These adjustments will probably take place in two steps. First, any biomass trapped behind the compartment dams (Oesterdam or Wemeldingedam) will die rapidly when the eastern basin is turned fresh. If, in addition, the tidal range is reduced, some of the area to the west of the compartment dam that is presently submerged at high tide will be left dry. Any biomass that cannot move a few feet to the new high-water mark will also die. We define the "rapid kill" associated with a case to be the amount of biomass that dies from these two causes.

Next, the density of biomass in the remaining saltwater basin will adjust. This may take years, if the required adjustment is large. Further, ecological disasters may occur during this adjustment period. For example, small, rapidly reproducing organisms might undergo population explosions in the early years before their larger predators can respond to the larger food supply. (People living near the IJsselmeer suffered from gnat plagues during an adjustment period of this kind immediately after that lake was made fresh.) As indices of the severity of this threat, we used both the change in the density (grams per square meter) of the benthic biomass and the time it would take for the density to adjust to within 1 g/sq m of its final value. We calculated the adjustment time by assuming that the adjustment from the present density, which we knew, to within 1 g/sq m of its predicted long-term average, occurred exponentially with a half-time of 2 years. (We chose a half-time of 2 years because it approximates the doubling time for some of the most abundant benthic organisms in the Oosterschelde, such as cockles, mussels, and benthic grazers. Choice of a different half-time would change all of our estimates of adjustment times by the same factor.)

In calculating the rapid kill and the slow adjustment, we considered only the ecogroups included among the commercial and noncommercial bottom species. We excluded fish and birds because we think they can quickly escape from the eastern basin before it is separated from the western saltwater basin and turned fresh, and hence avoid the rapid kill. These ecogroups will participate in the slow adjustment, of course, but differently than less mobile creatures. Immobile organisms must adjust their numbers by changing their reproduction and growth rates—e.g., by starving slowly—whereas birds can fly to the Westerschelde or the Grevelingen, and fish can escape to the North Sea. We also excluded primary producers and zooplankton from these indices. Our reasoning is that these organisms have such rapid growth rates, and such short generation times, that they are continually transient. (Transient ecological disturbances from algae blooms and anaerobic conditions are discussed in POLANO series Volumes IV and V, respectively.)

S.7. DISCUSSION OF RESULTS

S.7.1. Comparison of Nominal Cases

From among the many cases that we analyzed, we selected five *nominal* ones:

- An open case, A3.
- A reduced-tide case (96 percent of present tide), C3, $\mu A = 20000$ sq m.
- A reduced-tide case (67 percent of present tide), C3, $\mu A = 11500$ sq m.
- A reduced-tide case (43 percent of present tide), C3, $\mu A = 6500$ sq m.
- A closed case, D4.

These cases served as baseline cases from which excursions were made to test the sensitivity of our results to changes in the assumptions.

Table S.1 shows the most important of the ecological impacts examined in the previous discussions for these cases. Here, for each impact, we compare the cases and rank them based on how well they preserve the present ecology or increase its biomass. The rankings for each impact are shown by shading: white for the best ranking; black for the worst; and grey for intermediate. (Such a table is called a *scorecard*; see Vol. I for discussion.) In discussing and ranking the impacts, we have taken the view that it is better for an ecogroup to be more, rather than less, abundant—at least up to its biomass density in the present Oosterschelde. For brevity, we label this viewpoint *ecological preservation*; we believe it to be the predominant viewpoint in the Netherlands.

We note that the closed case stands out in almost every impact category. Its total biomass is very low compared with that of the present Oosterschelde and any of the other nominal cases. Its potential for both shellfish culture and nursery function is virtually nonexistent. It causes by far the largest rapid kill, and it is the only case that causes a significant decrease (during the slow adjustment) in the density of benthic biomass. Only fish-eating and plant-eating birds appear to benefit from this case. For the most part, the biota of the Oosterschelde would suffer greatly from its closure.

Table S.1

ECOLOGICAL IMPACTS OF THE FIVE NOMINAL CASES

		Reduced-tide Cases C3			
Item	Open Case A3	µA = 20000 sq m	µA = 11500 sq m	µA = 6500 sq m	Closed Case D4
Key inputs					
Salt basin area (sq km)	369.5	369.3	364.5	352.4	202.0
Tidal range at Zierikzee (m)	3.0	2.9	2.0	1.3	0.0
Primary production (tons/day)	352.9	352.7	348.1	346.1	193.8
Detritus import (tons/day)	546.0	640.0	990.0	916.0	0.0
Primary food availability (% of present)[a]	78	86	116	85	17
Total biomass					
Amount (tons afdw)	21300	24200	29700	27550	5160
Percent of present amount	75	85	104	96	18
Potential abundance of birds					
Benthos-eaters (tons afdw)	6.6-7.3	6.3-9.7	4.9-13.0	3.5-11.7	0.4-1.4
Fish-eaters (tons afdw)	0.0345	0.0445	0.063	0.0566	3.94
Plant-eaters (tons afdw)	Unch.	Unch.	Unch.	Unch.	Incr.
Potential shellfish culture					
Mussels (% of present)	100	90	90	90	13
Oysters (% of present)	100	90	90	90	0
Nursery function					
Shrimp (% of present)	50	150	400	350	0
Fish (% of present)	73	98	133	125	0
Transients					
Rapid kill of benthic biomass (tons afdw)	4220	4231	4491	5148	11492
Rapid kill (% of present benthic biomass)	25	25	27	31	68
Change in average density of benthic biomass from present (g/sq m)	-0.8	7.3	21.9	19.8	-25.0
Time for slow adjustment (yr)	0	4	6	6	6.5

[a]Primary food availability = primary production rate + detritus import rate.

Rankings: ☐ Best ☐ Intermediate ■ Worst

In the remaining cases, it is not clear whether these impacts would appear significantly different to most people. True, the reduced-tide cases C3 with µA = 11500 sq m and C3 with µA = 6500 sq m have total amounts of biomass almost 40 percent larger than the biomass in the open case. But considering the great seasonal and yearly variation in biomass in the Oosterschelde, such a change in the long-term average total biomass might be noticed only by scientists after several years of careful measurements.

Only the nursery function impacts, and possibly the increases in the density of benthic biomass from the present, might distinguish the two reduced-tide cases, C3 with µA = 11500 sq m and C3 with µA = 6500 sq m. However, given the uncertainties in both the inputs and the assumptions concerning detritus import and sedimentation, the results in Table S.1 are far from conclusive in showing that these two reduced-tide cases are significantly different from either the open case or the other reduced-tide cases with compartment design "3." To delve further, we examined the sensitivities of these impacts to changes in the two most crucial assumptions. Because the reduced-tide case C3 with $\mu A = 11500$ sq m is so similar to the reduced-tide case C3 with $\mu A = 6500$ sq m, we examined the sensitivity to these assumptions by using only case C3 with $\mu A = 11500$ sq m.

S.7.2. Are the Nominal Reduced-Tide Cases Significantly Better Than the Open Case?

We have already discussed the importance of detritus import in determining how much biomass an alternative will have. Since we feel that the detritus import rate of 990 tons/day (see Sec. S.5.1) assumed in case C3 with $\mu A = 11500$ sq m is more probably an overestimate than an underestimate, the apparent advantage of this case as compared with the open case may be illusory.

Another crucial assumption concerned how much of the detritus that is imported can be used by organisms that feed on suspended particles of organic matter, and how much detritus sediments so fast that it benefits only deposit feeders. Our nominal assumption was that deposit feeders benefit from the increases in detritus import, but that suspension feeders (particularly cockles) neither benefit nor suffer.

In Fig. S.4, we show the results of an exercise in which this assumption was varied by changing the sedimentation factor (see Sec. S.5.2) that measured the relative benefit derived by deposit feeders from the increased sedimentation of detritus.

It can be seen from Fig. S.4 that the biomass reaches its maximum when the sedimentation factor is equal to its nominal value. For sedimentation factors smaller than nominal, most ecogroups are less well off. Only mussels, oysters, and cockles benefit from a reduction in this factor. However, since the commercial shellfish culture can be carried on at current levels, even in this case with the nominal sedimentation factor, it is not clear that the ecostates predicted using smaller values of this factor would be more attractive to those concerned with preserving the ecology. Similarly, factors larger than nominal favor noncommercial bottom species, such as snails and worms, at the expense of all other organisms. We think that most people would prefer the ecostate calculated with the nominal sedimentation factor to one using a higher value. Any change from the nominal sedimentation factor must therefore diminish the attractiveness of the reduced-tide cases.

S.7.3. Is the Closed Case Really So Bad?

The nominal results, shown in Table S.1, portray the closed case as being by far the worst nominal case from the point of view of preserving the present ecology. To some degree, however, this impression is misleading. This case has compartment design "4," whereas all other nominal cases have compartment design "3." That is, this closed case has a smaller saltwater basin than the other cases, which causes it to have a lower total biomass and lower abundances of every ecogroup individually (since our model deals only with the ecology of the saltwater basin). It also means that a larger freshwater basin is created in the eastern end of the

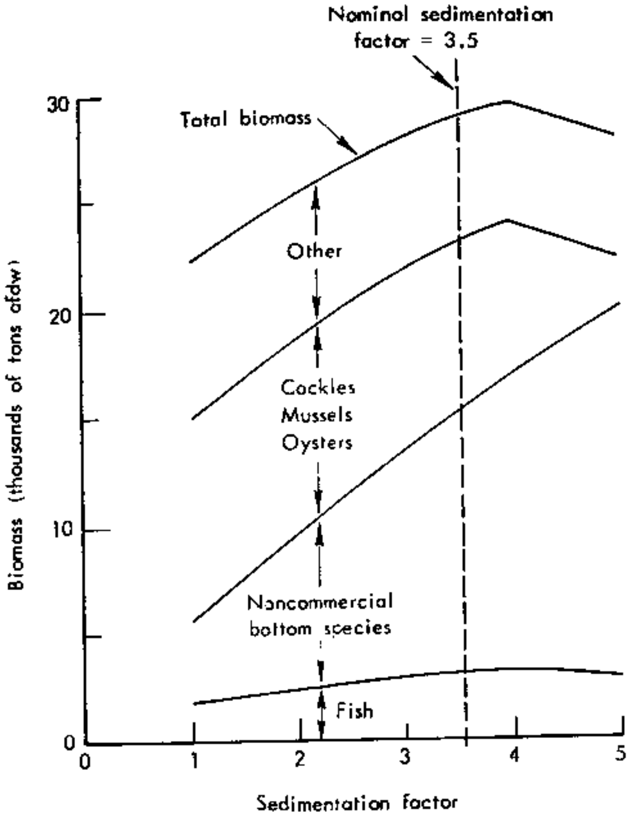

Fig. S.4—Biomass by component for a range of detritus sedimentation factors in case C3, μA = 11500 sq m

present Oosterschelde, which accounts for the great difference in rapid kill between this case and the others. A fairer comparison of the quality of the ecology in a closed case with that in the open and reduced-tide cases would be based on a common compartment design.

In Table S.2, we present the ecological impacts for the open and closed cases, each with compartment designs "3" and "4," to illustrate both the relative importance of closing the Oosterschelde and the choice of compartment design. Clearly, both factors are important. Changing from compartment design "3" to "4" causes a reduction of approximately 45 percent in total biomass, and similar changes in other impacts, whether the comparison is between the two open cases or the two closed cases. Similarly, closing the basin results in a 55 percent reduction in total biomass, whichever compartment design is considered. Thus, the nominal closed case D4 compares poorly with the other cases, both because of its compartment design, and because it is closed and therefore has no detritus import.

We can do nothing about the effect of the size of the saltwater basin. To some degree, however, the biomass that does not appear in the saltwater basin will be compensated for by other organisms that will live in the freshwater basin to the east of the Wemeldingedam. By contrast, the effect of closure might be countered

Table S.2

ECOLOGICAL IMPACTS OF CASES A3, D3, A4, AND D4

	Compartment Design 3		Compartment Design 4	
Item	Open Case A3	Closed Case D3	Open Case A4	Closed Case D4
Key inputs				
Salt basin area (sq km)	369.5	332.7	230.9	202.0
Tidal range at Zierikzee (m)	3.0	0.0	3.0	0.0
Primary production (tons/day)	352.9	317.8	220.5	193.8
Detritus import (tons/day)	546.0	0.0	341.2	0.0
Primary food availability (% of present)[a]	78	27	48	17
Total biomass				
Amount (tons afdw)	21300	9300	12400	5160
Percent of present amount	75	33	43	18
Potential abundance of birds				
Benthos-eaters (tons afdw)	6.6-7.3	0.7-2.5	3.8-4.1	0.4-1.4
Fish-eaters (tons afdw)	0.0345	6.85	0.0179	3.94
Plant-eaters (tons afdw)	Unch.	Incr.	Unch.	Incr.
Potential shellfish culture				
Mussels (% of present)	100	50	50	13
Oysters (% of present)	100	50	0	0
Nursery function				
Shrimp (% of present)	50	0	10	0
Fish (% of present)	73	0	37	0
Transients				
Rapid kill of benthic biomass (tons afdw)	4220	6218	9972	11492
Rapid kill (% of present benthic biomass)	25	37	59	68
Change in average density of benthic biomass from present (gm/sq m)	-0.8	-22.2	-3.1	-25.0
Time for slow adjustment (yr)	0	6	2	6.5

[a] Primary food availability = primary production rate + detritus import rate.

by building sluices and using them to "pump" detritus into the closed Oosterschelde. Thus, we ask how much detritus would have to be imported to make the nominal closed case appear as ecologically favorable as the open case with compartment design "4."

Figure S.5 suggests an answer: The total biomass in the nominal closed case would achieve the value in the corresponding open case (12400 tons) at a detritus import rate of approximately 400 tons/day. Since the concentration of organic matter in the coastal waters of the North Sea is approximately 1.5 g/cu m, this rate could be achieved if all the organic matter in about 3000 cu m/sec of North Sea water were trapped in the Oosterschelde. Because water can flow into the Oosterschelde only when the tide outside is above mean water level, and because entrapment will not be complete, this rate of detritus import would actually require sluices

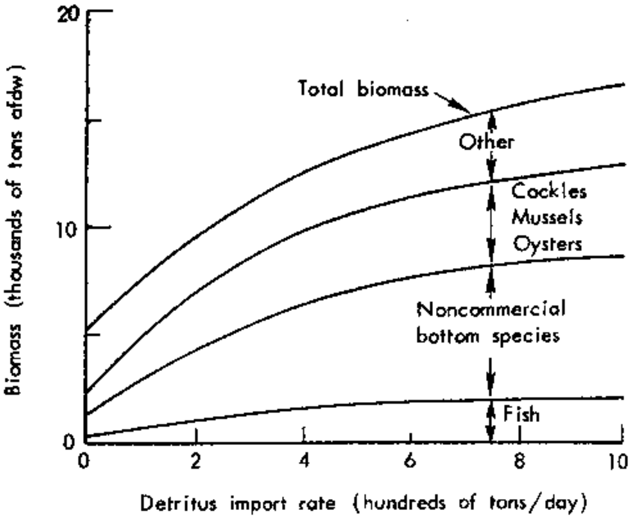

Fig. S.5—Biomass by component for a range of detritus import rates in case D4

with a greater than 10000 cu m/sec capacity. Such sluices are at least possible, but they are equivalent to a storm-surge barrier with an aperture of about 3000 sq m; they are not just ordinary sluices.

Furthermore, even this rate of detritus import would not permit the mussel industry to operate in the nominal closed case as it does in the present Oosterschelde. In fact, no rate of detritus import in the nominal closed case will permit mussels to be cultured at today's level. The reason is that the Wemeldingedam, which separates the freshwater and saltwater basins in compartment design "4," lies to the west of all the oyster beds and 30 percent of the mussel plots. These areas, then, become part of the freshwater basin, and unsuitable for shellfish culture operations.

S.7.4. Conclusions about Cases Analyzed

From the standpoint of ecological preservation, we conclude that the closed case with compartment design "4" is the least desirable of all the nominal cases. Furthermore, its shortcomings cannot be fully remedied either by increasing the size of the saltwater basin (changing to compartment design "3") or by building sluices that will allow detritus to be imported from the North Sea. While a combination of the two measures would make the closed case as attractive as the other nominal cases, the sluices needed to import sufficient detritus would be so large as to constitute a storm-surge barrier. We conclude, therefore, that no closed case could compete favorably with the open or reduced-tide cases.

This is not meant to imply that the closed case would be ecologically disastrous. Organisms would continue to inhabit the basin, just as they have continued to live in Grevelingen since its closure in May 1971. In fact, we believe that a closed Oosterschelde would be very similar to the present Grevelingen. But closing the

Oosterschelde would result in a major reduction in the density and the amount of biomass of all kinds, and in the elimination of commercial shellfish cultivation in the Oosterschelde.

The open case most closely preserves the ecology of the present Oosterschelde. In the part of the Oosterschelde that remains salt, we predict that the *density* of each ecogroup will remain as it is at present. Thus, the relative abundances of the ecogroups would be unchanged. However, the total biomass in the saltwater basin would be reduced from that in the present Oosterschelde. The reduction would be proportional to the reduction in the area of the saltwater basin caused by the compartmentation.

For the cases with a storm-surge barrier (the reduced-tide cases), the size of the aperture will largely determine the character of the ecology that results. Apertures of at least 20000 sq m would produce an ecology virtually indistinguishable from the open case (A3), both in terms of total biomass and relative species abundance.

Apertures between 6500 and 11500 sq m would tend to maximize the total biomass. However, there would be a shift in relative abundances of the present species in favor of noncommercial bottom species, such as snails and worms. Also, the transition period would be longer and would perhaps include some objectionable ecological transients.[4]

Apertures smaller than 6500 sq m would result in smaller total amounts of biomass, and larger shifts in relative abundances, than the larger apertures.

We find, therefore, that one's preference among the alternatives depends on his ecological goal. If the goal is to minimize change from the present ecology, then the preference will be the open case or a reduced-tide case with a large aperture (20000 sq m). But if the goal is to maximize total biomass, one will probably prefer to build a storm-surge barrier with an aperture between 6500 and 11500 sq m.[5] However, the preference should not be firm, because of the uncertainties concerning detritus import and sedimentation in the reduced-tide cases. Thus, although ecological considerations may help one to reject case D4, they do not distinguish strongly enough between the open case A3 and the reduced-tide cases in which the storm-surge barrier aperture exceeds 6500 sq m to much affect a choice between them. The choice among these alternatives will therefore depend strongly on other factors, such as cost and security.

S.8. RECOMMENDATIONS FOR RESEARCH

One of the reasons that our conclusions do not distinguish more strongly between the open and the reduced-tide cases is our uncertainty about detritus. We have already recommended that detritus import (a crucially important quantity) be measured directly. These measurements should be made during storms as well as during calm periods, because of the disturbing possibility that a substantial

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[4] Our best estimate is that biomass would be maximum for compartment design "3" with an 11500 sq m aperture. In addition, the shift in relative abundances ought to be less for this aperture than for smaller apertures, such as 6500 sq m.

[5] Neither ecological goal should influence one to choose the closed case or a reduced-tide case with a small storm-surge barrier aperture (under 6500 sq m).

fraction of the average annual detritus import occurs during storms.[6] In addition, we think that detritus mineralization rates should be measured, both in the pelagic zone and in the bottom sediments. Finally, we recommend that investigations of sedimentation and resuspension of detritus should be made, with particular emphasis on how these processes interact with living organisms.

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[6] This possibility is disturbing because, if true, it could seriously restrict the choice of an operating policy for the storm-surge barrier. Any operating policy that caused the barrier to be closed often enough during storms to substantially reduce the detritus import would seriously degrade the long-term ecology of the Oosterschelde.

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Without the support of H. Engel, presently Chief Engineer-Director of the Delta Service, and his predecessor, H. A. Ferguson, now retired, the work reported here could not have been completed. Their faith in and encouragement of our untraditional—and hence controversial—approach to this important problem were essential to its success.

CONTENTS

PART I: MODEL FORMULATION

PART II: MODEL IMPLEMENTATION AND PARAMETER EVALUATION

PART III: RESULTS AND CONCLUSIONS

FIGURES

TABLES

Chapter 1

INTRODUCTION

1.1. BACKGROUND

The Oosterschelde area, part of the Delta region in southwestern Holland (see Fig. 1.1), felt the greatest impact of the tragic and costly storm that unexpectedly struck the Netherlands in February 1953. This catastrophic event provided the stimulus for studies of ways to increase the security of the entire Delta region against future storm disasters. These studies culminated in the passage of the Delta Act of May 1958, which laid out the general procedures to be followed by the government to ensure that such devastating floods did not occur again in this region.

The Delta Act, which provided both general guidelines and detailed implementation plans, emphasized safety and security features of project designs. Secondary consideration was given to project effects on communications, recreation, transportation, agriculture, commercial fishing, and water management. After much detailed study and discussion of alternatives, a Delta Project was formulated. Its purpose was to separate several estuaries (Veerse Gat, Haringvliet, Grevelingen, and Oosterschelde) from the sea by means of dams. The Westerschelde and the Rotterdam waterways were to remain open to the sea because they are important ship entrances to Antwerp and Rotterdam, respectively. It was decided that the major components of the overall project would be built in the order of smaller to larger so as to gain the necessary engineering know-how for executing the final large closure in the Oosterschelde, initially scheduled to occur in 1978. The Royal Decree of 22 January 1969 gave the exact position of this dam and implied the method of closure to be used.

As initial contruction activities began on the Oosterschelde closure, a groundswell of opposition arose to this final step of the Delta Project. It was initiated by various action groups and centered on possible bad effects of the closure, as planned, on the ecology of the region.

1.2. ENVIRONMENTAL CONCERNS

Before the execution of the Delta Project, the Delta region with its estuaries, sea arms, shoals, and salt marshes formed an ecologically rich, natural reserve of international significance. Today, only the Oosterschelde remains in its original state as a tidal water area. The water quality of the Oosterschelde has, in ecological terms, actually improved in recent years as various components of the Delta Project have been completed and have isolated the Oosterschelde from contaminated river water.

Because of its special characteristics, the Oosterschelde provides the northernmost living area for a number of species that enrich the ecological diversity of the region. The tidal shoals and mud flats provide food and habitats for a wide variety

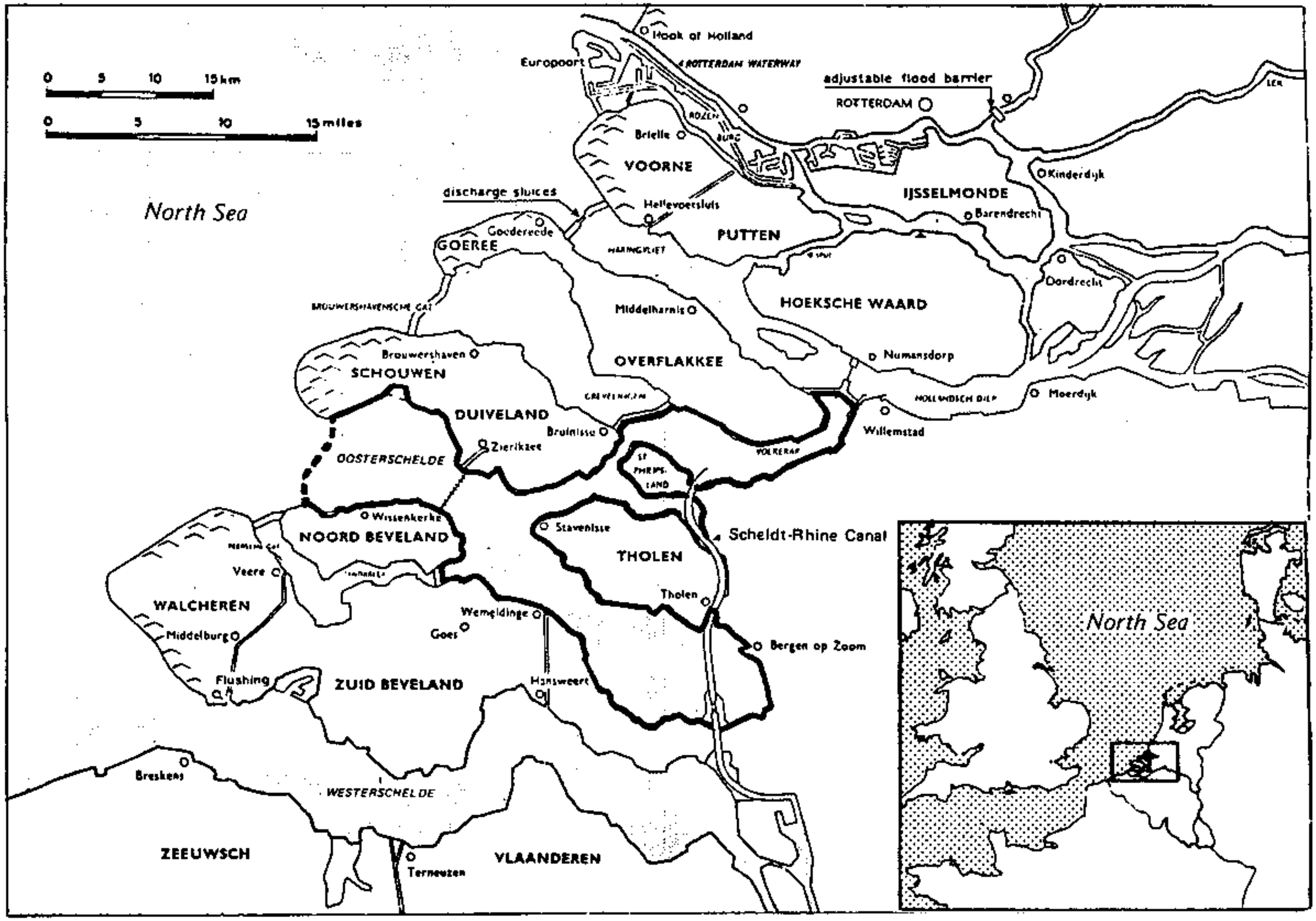

Fig. 1.1 — The Delta region in the southwest part of the Netherlands
(The heavy black line outlines the study area)

of flora and fauna. The Oosterschelde, in its present tidal form, is a highly important area for birds: it is an important north-south migratory route and serves as a breeding and overwintering area. If these tidal flats and surrounding areas are eliminated by closure, there may not be a sufficient number of such areas remaining in Europe to serve these functions. The rarer species may be most adversely affected.

Besides sheltering birds, the Oosterschelde is a breeding ground and nursery for commercially important sea fish and shrimps. It is also an attractive area for Dutch and Belgian sport fishermen. Shellfish, especially oysters and mussels, have been harvested in commercial quantities in the Oosterschelde. Unfortunately, the influence of tide in preserving shellfish culture is complex and not completely understood; thus, changes in tidal levels, within certain ranges, may severely affect the abundance of these species as well as other species important to both sport and commercial fishing.

These ecological factors, coupled with increased public awareness of the importance of the environment, and with improvements in the science and art of hydrology and heavy construction since the project was originally designed, caused the government to request that the plan for complete closure of the Oosterschelde be reexamined. They wanted to determine if alternatives to complete closure could be devised that would preserve the ecology and other environmental elements, yet meet stipulated security and financial goals. It was in connection with this reexamination that Rand was requested to assist the Rijkswaterstaat[1] in evaluating ecological and other effects of various project design alterations. This report is one of a series describing the results of Rand's evaluation of these effects and the ecological models that were constructed to implement this evaluation.

1.3. THE ALTERNATIVE OOSTERSCHELDE PLANS CONSIDERED

Many different types of projects and designs are technically conceivable. From an ecological point of view, however, it was not necessary to examine all or even a large fraction of them. Rather, we considered three alternative plans for dealing with the mouth of the Oosterschelde that would bracket the range of possible effects on the ecology:

1. The closed alternative. It involved building a dam across the mouth of the Oosterschelde, thereby converting the basin into a stagnant lake. Although the lake could be either freshwater or saltwater, we consider only the saltwater alternative.
2. The open alternative. This plan involves reinforcement of the peripheral dikes, but leaves the mouth of the Oosterschelde open.
3. Reduced-tide alternative (storm-surge barriers). In this alternative, a barrier with gates would be constructed across the mouth of the Oosterschelde. During calm weather, the gates would be open, allowing the tide to flow through an area of as much as 20000 sq m (the present, unobstruct-

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[1] The Rijkswaterstaat is the Dutch Government agency responsible for water control and public works.

ed flow area is about 80000 sq m). During storms, the gates could be closed, and the barrier would act like a dam. Specific cases can differ according to the degree of tidal reduction, which depends on the size of the aperture in the barrier.

These three alternatives are denoted by the letters "A" for the open alternative, "C" for the reduced-tide alternative, and "D" for the closed alternative.

Two internal compartmentations of the Oosterschelde were considered in combination with each of these alternatives. One was designated as design "3" (two others were considered previously and rejected) and the other as design "4." The compartmentations are shown in Fig. 1.2. The difference between the designs is in the placement of the compartmentation dam in the eastern part of the Oosterschelde, which affects the size of the saltwater basin to the west of the dams, and the freshwater lake to the east.

A complete alternative for the Oosterschelde therefore consists of two components: a plan for the mouth (denoted "A," "C," or "D") and an internal compartmentation (design "3" or "4") (see Fig. 1.2). These complete alternatives are named by combining the letter designation for what is done to the mouth of the Oosterschelde with the number designation for the interior compartment design. Thus, "A3" is the open alternative with compartment design "3"; "D4" is the closed alternative with compartment design "4"; and "C3" is a reduced-tide alternative with compartment design "3." In addition, we used the present Oosterschelde (denoted "A0," with the "0" implying no compartmentation) as the calibration point for our model and the basis for comparison of the other alternatives.

1.4. OUR APPROACH TO EVALUATING ECOLOGICAL IMPACTS

Upon examination of the kinds of ecological problems and environmental changes that are likely to occur with the different project designs being considered, we concluded that a model should primarily *be able to predict changes in abundances of the various species concerned.* Also important was that it *be able to include a large number of species living in a variety of habitats.* But any model with such abilities will be, given the present state of ecological knowledge, *unable to follow short-term, transient phenomena.* The general ecomodel we developed, therefore, is capable of estimating the abundances of a large and varied combination of species, but represents only changes in abundances that occur over long times, measured at the minimum in periods of several years. That is, our general ecomodel estimates long-term *average* abundances, and not how the instantaneous abundances of the various species will fluctuate from season to season and year to year.

To be able to evaluate the influences of shorter-term changes that may result in unwanted ecological disturbances, we constructed two "disaster" models capable of following such short-term phenomena. The first model reflects a problem that may occur when the lake to the east of the compartment dam in either compartment design (see Fig. 1.2) is turned from salt to fresh. The conversion will kill any marine organisms trapped behind the dam, and the decomposition of the resulting dead organisms might deplete the lake of oxygen. This model, and the results

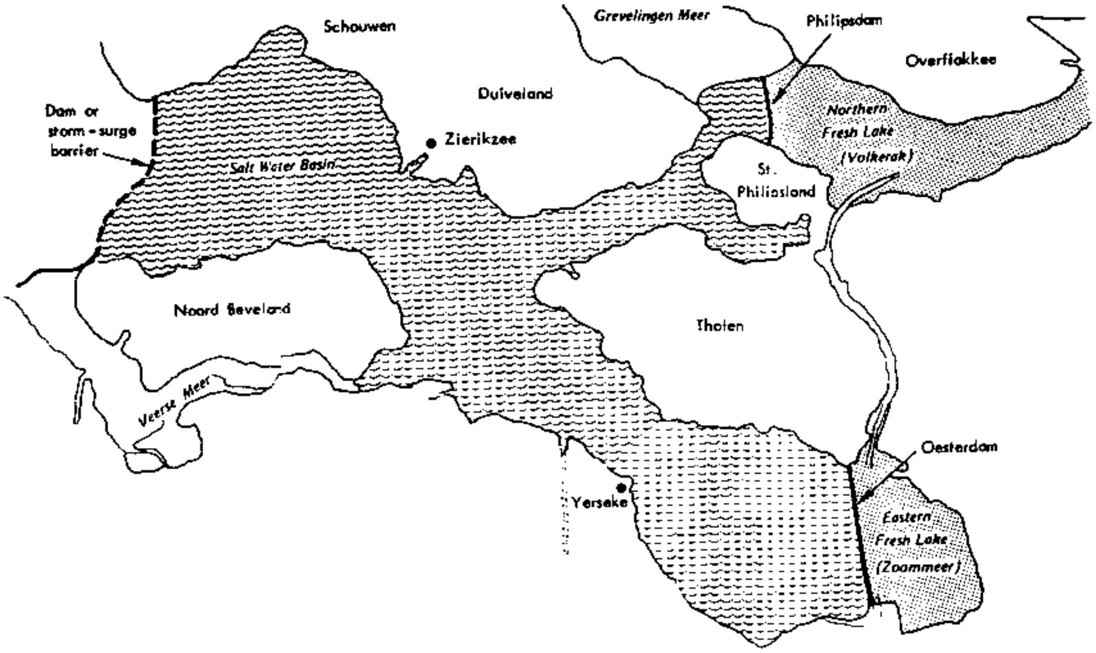

Fig. 1.2a — Compartment design "3"

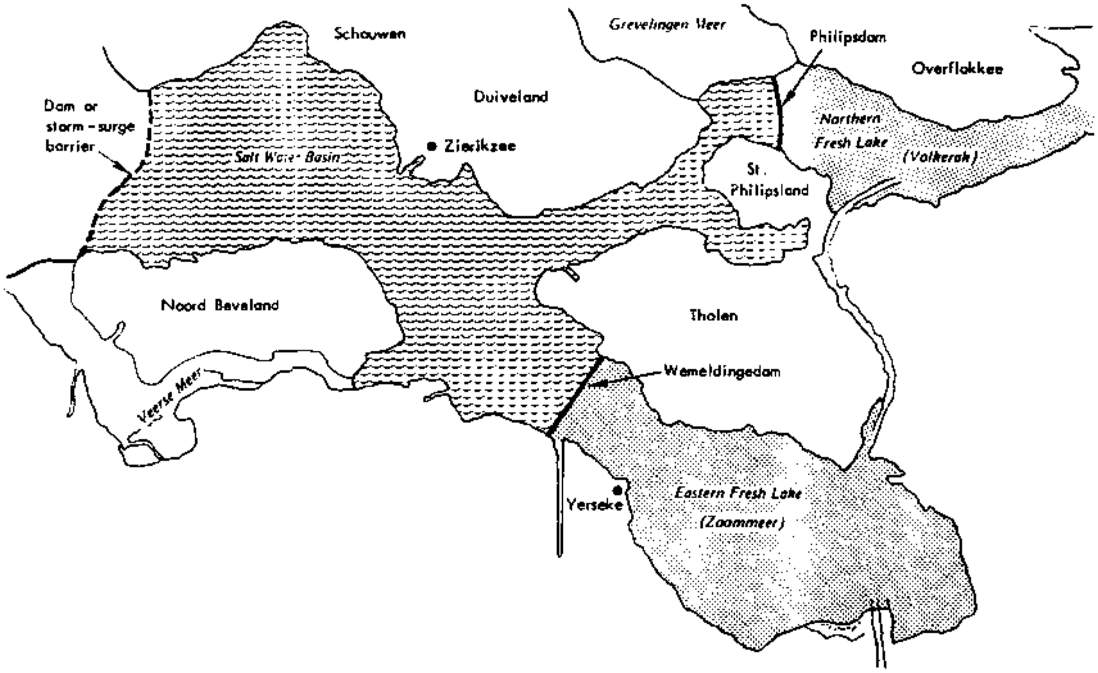

Fig. 1.2b — Compartment design "4"

obtained from it, are described in Volume V of this series, *Anaerobic Conditions and Related Ecological Disturbances.*

The second model deals with the possibility that an objectionably large algae bloom might occur in the Oosterschelde under one or another of the proposed alternatives. We concluded that this was unlikely, although objectionable local blooms, for example in shallow parts of the Oosterschelde, would be more apt to occur. This model, and the conclusions it led us to, are reported in Volume IV of this series, *Assessment of Algae Blooms, A Potential Ecological Disturbance.*

Returning to the general ecomodel, we chose (for reasons that are given later) to describe an ecological system in terms of a mathematical model that minimizes a convex function subject to linear constraints. These constraints require that each species must be "in balance." This means two things: first, that on the average each species must have enough of the right things to eat for normal life and growth; and second, that enough of each species must be eaten, or otherwise removed from the ecosystem, so that its long-term average growth rate is zero.

These constraints do not limit the long-term average abundance of each species to one value. However, although many *different* abundances are "in balance," logically only *one set of abundances*—only one ecostate—actually occurs. We designed our model to select the ecostate that minimizes the Gibbs function as the one that will occur in response to a given alternative. That is, our general ecomodel operates by minimizing the Gibbs function, subject to the constraints that all species must be "in balance."

There are many possible justifications for our using the Gibbs function in this way. The most straightforward justification considers ecological systems in thermodynamic terms, and takes the Gibbs function to be an appropriate expression of the energy relations that exist among different species in the ecosystem. A related justification relies on the fact that the Gibbs function is closely related to the mass-action laws of chemical kinetics (i.e., that the rate of interaction between two species will be proportional to the product of their abundances), and that the mathematical equations that describe chemical kinetics are similar to those most often used to describe ecological systems. Statistical theory provides yet another justification. Minimizing the Gibbs function can be regarded as incorporating into our estimates of the abundances of the various species the information that they must be "in balance" in the long term. However, our main justification is practical. Use of the Gibbs function in the way we have described yields a model that is easy to calibrate and use, and which behaves reasonably.

1.5. CONTRAST WITH OTHER POSSIBLE APPROACHES

Various approaches to making predictions about long- and intermediate-term ecological effects might have been taken. First, we could have relied upon expert judgment alone. The objection is that the reasoning behind the judgment is hidden. What simplifications were made? How was it decided that some factors were dominant, while others were of little importance? Or, of course, the expert may simply refuse to make a judgment, or may unduly hedge his predictions.

Second, we could have adopted a traditional modeling approach. But traditional models typically attempt too much, e.g., they try to predict the entire future course of an ecosystem rather than its end-state or some other critical state. This is impractical for any but the simplest of ecosystems. Also, these models seek to replace, rather than to supplement, expert judgment.

Third, we could have undertaken a new, hybrid modeling approach. Although such a model would combine the explicitness and formality that characterizes modeling in general, it would leave considerable room for expert judgment where appropriate.

We chose the third approach. Our model abundantly marshals information, more than any single person can apply effectively without explicitly defined formal procedures, and uses it to estimate a single ecostate, the long-term average state that would eventually result from a proposed alternative. We also investigate how sensitive this state might be to variations in a number of parameters, such as fishing rates. detritus import, etc. Armed with this information, human experts can judge whether the predicted stable state is reasonable or likely; how the ecology may move from its present state to the new stable state (for example, can we expect "disasters"—i.e., large, relatively sudden changes in the abundance of one or more species); and how large the fluctuations around this state may be (i.e., seasonal changes, or random fluctuations from year to year).

Our approach is challengeable on many grounds. But, given the state of knowledge, so is any other approach to estimating effects on the ecology. If these effects must be estimated—and we believe they must—then the basic choice is between using a model and estimating them directly, based solely on expert judgment. We believe that the use of a formal model has several advantages over a reliance on expert judgment: assumptions are more explicit; they are concerned with the components of the problem rather than its entirety; their effects on estimates of the impacts may be tested by means of the model itself; and computer automation of the model permits examination of a greater number of factors and interactions. some of them counterintuitive.

1.6. FEATURES OF THE GENERAL ECOMODEL

There are three features that make a model useful for policy analysis: economy, breadth, and transparency. A model lacking one or more of these features is not necessarily useless for policy analysis, but it will be more useful if it is economical, broad in scope, and transparent, even though accuracy or amount of detail must be compromised.

The first feature is *economy*. By economy we mean it should be inexpensive to examine each policy alternative, not only in money but also in skilled manpower and elapsed time. Economy is desirable because, in policy analysis, one usually wishes to examine many different alternatives under a variety of assumptions. In our study, for example, we wish to examine the open and closed alternatives, as well as several cases with different tidal reductions, in combination with two internal compartmentations. In addition, because of uncertainties, we want to examine many of these alternatives under a variety of assumptions about fishing and migration rates, the sedimentation rate, etc. Thus, we used the general ecomodel to examine hundreds of different cases. This is typical of policy analysis.

Our general ecomodel is economical. The money cost of examining an alternative is variable, but never more than a few dollars. The chief requirement is for skilled manpower to prepare the inputs and interpret the results. Although collecting the data to initially formulate and calibrate the model was a lengthy, tedious process, it had to be done only once. The additional time needed to prepare the input for a single alternative is only a few minutes, and if a logical sequence of cases is to be run (e.g., ten cases differing only by one or two fishing rates), the input for the entire sequence can be prepared in half an hour or less. The model presents its output in the form that we have found most convenient for interpretation (giving both a detailed output and a useful summary). Finally, the computer installation we have used for running this model affords such fast turnaround, that dozens of runs, each consisting of five to ten cases, could be completed in a single working day.

The second feature is *breadth*. By breadth we mean that a policy analysis model should estimate a broad range of impacts, an important feature because a policy study typically considers a broad range of alternatives. It cannot be clear early in the study (while a policy model is being formulated) whether a single impact can distinguish adequately among all the alternatives. Usually it is found that no single impact is adequate. If nothing else, the consumers of a policy study will disagree concerning the relative importance of the different impacts. Thus, the model must consider as broad a menu of impacts as possible.

Our general ecomodel appears to have this feature. Not only does it predict the total biomass in the Oosterschelde, it also separates the total into the individual abundances of eighteen different groups of species, including three different classes of birds, four different classes of fish, and eight different classes of benthic organisms. These groups of species are further separated among four different kinds of habitats. Also, by considering the sensitivities of various abundances to changes in fishing rates, etc., one can estimate practical limits on those rates. Finally, by comparing the densities of various kinds of organisms under a policy alternative with the corresponding densities in the present Oosterschelde, one can gain an appreciation for how long it might take for the ecological state to "stabilize" if that alternative were implemented.

The third feature is *transparency*. Transparency is the ability of a model to produce *explicable* results. In policy analysis, it is vital to be able to explain how the output of the model resulted. This is important for all models, but especially important for policy models, because the latter are typically formulated, implemented, and used to produce results before adequate data are available for a completely satisfactory validation.

Our general ecomodel seems to be transparent. The model is based on simple, reasonable, universally accepted predator-prey relationships. The influence of any parameter change can be traced through the model, step by logical step. And the arguments leading from a cause to an effect need never be long or convoluted.

1.7. ORGANIZATION OF THIS REPORT

This report consists of three parts, each of which is divided into several chapters. Part I, which comprises Chaps. 2, 3, and 4, discusses the formulation of our general ecomodel. In Chap. 2, we present the several elements from which the model is constructed, and in Chap. 3, we discuss how these elements are combined into the mass balance equations—the equations that ensure that an ecostate is "in balance." Our use of the Gibbs function to select the stable ecostate from among the many ecostates that are "in balance" is described in Chap. 4.

Part II comprises Chaps. 5 through 11, dealing with the problems of implementing the model. After outlining our approach in Chap. 5, we discuss, in Chaps. 6 and 7, how we obtain values for the parameters that play a role in the mass balance equations. Then, in Chaps. 8, 9, and 10, we describe how we calibrate the model to the present-day Oosterschelde. This calibration involves making preliminary estimates of each group of species in the model (Chap. 8), estimating the composition of the diets of each group (Chap. 9), and then adjusting these preliminary estimates until a final estimate of abundances is achieved that is "in balance" (Chap. 10). In the last chapter in this part (Chap. 11), we discuss how we have validated our model.

Part III comprises Chaps. 12 through 15, in which we present our results and conclusions. In Chap. 12, we describe in detail the various alternatives that we have considered, including leaving the Oosterschelde open, or closing it altogether, or constructing a storm-surge barrier. We also discuss the nominal assumptions that we have made regarding fishing rates, sedimentation rates, etc., for each of the alternatives. In Chap. 13, we present the predictions of our model for each of the alternatives under the nominal assumptions. We discuss these results at length in Chap. 14, including our investigations of the effects of changing some of the more important assumptions. Finally, in Chap. 15, we point out areas of further research that would improve both the model and the results.

The subject of the importation of organic matter into the Oosterschelde is addressed in the appendix. Every organism in the Oosterschelde is ultimately supported by a combination of primary production (photosynthesis), which takes place inside the Oosterschelde, and imported organic matter. Perhaps our most important conclusion is that imported organic matter accounts for more than half of this ultimate food supply. However, this conclusion has been criticized on several grounds, and so we discuss, in the appendix, the arguments for and against such a large rate of organic matter import.

An Addendum to this report will be issued as a separate volume. This Addendum will contain a detailed discussion of how we chose the ecological groups of species that appear in our model, and how we determined the predator-prey relationships among them. We will also describe the basic data we have used and our methods for using it.

PART I

MODEL FORMULATION

Chapter

Chapter 2

ELEMENTS OF THE MODEL

2.1. SCOPE AND LIMITATIONS OF THE MODEL

Our model is bounded in scope in three ways. First, it is limited geographically. In its present version, it is concerned with only the Oosterschelde, but it could, of course, be recalibrated to handle a different region. Second, its predictions concern only organic matter, including dead organic matter, plants, and marine animals. Other ecologically important quantities, such as inorganic nutrients for plants, appear in the model only through their influence on its inputs. Third, it is limited in temporal aspects. Specifically, it cannot cope with day-to-day transients (changes in abundances of different organisms), or indeed with transients generally (although we inferred certain things about transients, such as their durations, from model outputs). Rather, it deals with long-term average quantities.

The subject matter of the model is the total organic material, living and dead, inside the Oosterschelde. Thus, the quantities that our model predicts—i.e., its outputs, or dependent variables—correspond to the abundances of various forms of organic matter found in the Oosterschelde. These include marine animals (fish, mussels, worms, etc.), photosynthetic organisms (sea grass, seaweeds, benthic diatoms, phytoplankton), and detritus (shed exoskeletons, feces, dead plant matter, carcasses, etc.).

These dependent variables are influenced by a number of factors, which occur as independent variables, or inputs, in the model. The latter include the net rates of exchange of organic matter between the Oosterschelde and the rest of the universe (mostly the North Sea). Such exchanges may be due to fishing, migration of living organisms (e.g., shrimp), or import and export of detritus and unicellular organisms by tidal action.

Note that we are concerned with net rates. If a particular kilogram of detritus is brought into the Oosterschelde from, say, land runoff, and is then taken out by the tide, it will not contribute to the net detritus import. Also, detritus that is brought in and either consumed by animals or mineralized by bacteria counterbalances detritus that is produced in the Oosterschelde and then exported. Similar comments apply to the in- versus out-migration of animals, and to the addition and removal of fish or shellfish during commercial fishing or culturing operations.

One important independent variable represents primary (photosynthetic) production in the Oosterschelde. By this process, inorganic nutrients and solar energy are transformed into organic matter. To represent this process in the model, we chose as an input the rate at which organic matter is produced by photosynthesis. We are aware, of course, that this rate depends on the availability of inorganic nutrients and the intensity of solar radiation, as well as on various other factors (e.g., temperature). Indeed, we have taken these factors into account in choosing the photosynthetic rate to input to the model. However, these factors are not explicitly represented in our model.

Other independent variables involve the sizes of the various categories of living space (called segments) in our model. These sizes influence the organisms that occupy the segments through their effect on the density of the biomass present. (An aversion of the various organisms in the Oosterschelde to very high densities is a characteristic of the model.) The sizes of the segments are, in turn, determined from the tidal range in the Oosterschelde—which is itself determined from the aperture in the mouth of the Oosterschelde—and by the positioning of the various compartmentation dams. As with inorganic nutrients and solar radiation, however, these factors are not among the independent variables. Their effect is only implicitly felt through their influence on segment sizes.

Parametric inputs to our model describe the biological and behavioral characteristics of the organisms present; they remain constant, whereas the independent variables mentioned earlier may be changed to represent an altered Oosterschelde (e.g., with a storm-surge barrier). Among these parameters are the food requirements, metabolic rates, growth rates, and prey preferences of each organism in the model.

The model predicts the abundances of a variety of forms of organic matter in the Oosterschelde, but it does not, as stated earlier, predict changes in the abundances that occur from day to day, or even from year to year. Rather, it predicts abundances that characterize a stable ecological state as a function of the independent variables—abundances which, although not constant from day to day, season to season, or even year to year, show no long-term trends so long as the independent variables do not change.

To illustrate this point, imagine that the present Oosterschelde is entirely blocked off from the North Sea by the construction of a closure dam. Our studies suggest that, starting from the moment of closure, the abundances of most organisms in the Oosterschelde will decline because closure will eliminate the substantial import of detritus, a major food source, from the North Sea.[1]

This decline in abundances would be rapid at first, then slower, and after many years would be so slow that the natural seasonal and annual fluctuations would mask it completely. At this point, perhaps 10 or more years after closure, the downward trend in abundances could be said to have disappeared. The ecosystem would have adjusted to a new stable state characterized by new long-term average abundances.

In predicting long-term average abundances as a function of the changes in the independent variables that characterize the closure of the Oosterschelde, our model does not tell us how long this transition may take, or what abundances may be observed at various times during the transition. (This is in marked contrast to the dynamic models usually encountered in ecology. Such a model would undoubtedly focus on the transition itself, especially its rapid early stages, rather than on its end result.) Nevertheless, one can make an educated guess at the speed of the transition, knowing the relative change in abundances that will occur and the "rates of living" (e.g., metabolic rates or generation times) of the important organisms present.

Our model is also silent on how large or rapid the fluctuations around these long-term averages may be, once the new stable state has been achieved. We

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[1] Our results indicate that imported detritus, most of it probably originating in the North Sea, constitutes as much as one-half of the primary food supply that supports the ecology in the present Oosterschelde. This finding contradicts the commonly accepted view that estuaries are net exporters of organic material. However, other Dutch estuaries (the Waddensea, and the Grevelingen when it was open to the North Sea) have also been found to be net importers of detritus. See the appendix for further discussion.

recognize that large and rapid fluctuations in abundances may be undesirable, and that it is a shortcoming of the model that it ignores this question. However, we found that to construct a single model that could deal with ecological phenomena on both very short time scales (e.g., algae blooms) and very long time scales (e.g., the response to closure described above) was not feasible. We have therefore separated the two problems by dealing with short-term phenomena in individual "disaster models," and with the prediction of long-term average abundances in the general ecomodel.

2.2. ECOLOGICAL GROUPS

About 2400 species have been found in the Oosterschelde. So many species would be extremely clumsy to model, even if enough data were available on each; instead, we group them into aggregates of similar species called *ecological groups*. Species placed into the same ecological group eat similar things, have similar predators, and live in similar places. Consequently, our Oosterschelde model has 18 ecological groups:

1. Photosynthetic organisms (phytoplankton, benthic diatoms, sea grasses, and seaweeds).
2. Detritus (dead organic material), bacteria, micro- and meiofauna.
3. Zooplankton and planktonic larvae of various creatures (oysters, mussels, cockles, lugworms, all have planktonic larvae).
4. Oysters and mussels.
5. Cockles and limpets.
6. Selective deposit feeders having planktonic larvae.
7. Shrimp, shore crab.
8. Sea stars.
9. Deposit feeders having nonplanktonic larvae, and filter-feeding worms.
10. Omnivores and infaunal predators.
11. Benthic grazers (e.g., periwinkles).
12. Planktivorous fish (e.g., anchovy, herring, sprat).
13. Benthos-eating fish (e.g., eel, plaice, sole, dab, flounder).
14. Fish-eating fish (e.g., mackerel, cod, whiting).
15. Plant-eating fish (e.g., mullet).
16. Fish-eating birds (e.g., grebe).
17. Plant-eating birds (e.g., mallard, teal).
18. Benthos-eating birds (e.g., oystercatcher, plover).

Of course, this grouping has flaws. Species that appear to differ significantly from one another—e.g., shrimp and shore crab—are in the same ecological group. Although we tried to avoid it, individuals of the same ecological group are occasionally of radically different sizes, a disparity that usually implies that they will eat and be eaten by different individuals in other ecological groups. We did try to ensure that whenever any individual in one ecological group is a prey of some individual in another group, so are all other individuals in the one ecological group prey to at least one individual in the second group.

The shortcomings and approximations in such a brief list of ecological groups were apparent to us. Indeed, we initially considered using 46 different groups of species, and further subdividing them by size into a total of 180 ecological groups. However, our model requires an estimate of the abundance of each group in the present Oosterschelde for calibration purposes. Unfortunately, data that would permit us to make abundance estimates for so many groups were simply not available, even though our model could easily contain a greater number of groups. (See the Addendum to this report for a further discussion of our choice of ecogroups and our estimates of their abundances.)

2.3. UNITS OF ABUNDANCES

We sought to "keep accounts" on each ecological group in order to estimate its abundance. To this end, units in which to express the abundances must be selected.

The accounts for an ecological group are changed by additions to and subtractions from its abundance that occur because of processes both internal and external to the model. Internal processes include predation (one creature eating another), mortality (an organism dying and becoming detritus), and production of feces (a form of detritus), among others. External processes include migration, fishing, and photosynthesis (creation of organic matter from solar energy and inorganic molecules).

Predation is the single most important internal process that occurs in the model. Thus, the units chosen to express abundances must conveniently measure the changes due to predation. Since predation affects the abundances of both predator and prey, the units should be readily comparable among different species. For example, the number of individual organisms is a poor choice of abundance units. Who can say how many shrimp are equivalent to one red-necked grebe?

A measure of biomass might be a good choice. A predator whose diet includes both fish and shrimp should be willing, considering only nutritional energy, to trade a given mass of fish for an equal mass of shrimp. Superficially, then, it seems reasonable to value equal weights of organisms equally. This would imply that total live weight is a good unit of abundance to select.

But total live weight is not a good estimator of nutritional energy. It includes the weight of both the water contained in an organism and any shell or skeleton, components that have no nutritional value. Thus, to better approximate nutritional energy, total live weight should be modified to eliminate nonnutritional weight.

Ecologists have devised such a modification: "ash-free dry weight" (abbreviated afdw). The ash-free dry weight of an organism is measured as follows (Winberg, 1971). First, the killed organism is homogenized, and then heated for several hours in an oven at approximately 100° C. Almost all the water is driven off, without igniting any of the carbonaceous material. What remains is the "dry weight" of the organism.

Next, the sample is heated in air or oxygen to about 500° C, so that all the carbonaceous material burns—i.e., combines with oxygen and produces water vapor and CO_2. These combustion products are allowed to escape, leaving a residuum called "ash." The ash-free dry weight of the organism is then calculated as the difference between the dry weight and the weight of the ash.

The ash-free dry weight of an organism appears to be a good measure of the nutritional energy to be gained from eating that organism. After all, the process of measuring ash-free dry weight parallels the body's process for using food—metabolism is nothing more than the controlled combustion of food molecules. However, it is true that not all food molecules provide equal amounts of nutritional energy from equal ash-free dry weights. Thus, the accuracy of ash-free dry weight as an estimator of nutritious energy depends on different organisms' containing similar proportions of the three different broad groups of food molecules—fats, carbohydrates, and proteins.

The need to assume similar proportions of different food molecules would be avoided by using the results of calorimetric measurements of the food energy contained in different organisms. However, calorimetric measurements have not been made for many of the organisms that are of interest to us. But relatively complete determinations of ash-free dry weight as a fraction of total live weight have been made (see the Addendum). We are therefore led to express abundances in units of ash-free dry weight.

A final, very interesting, way of looking at abundances is in terms of entropy. (Unfortunately, this way of looking at abundances is not very practical because of measurement problems and lack of data. See Scott (1965) for a discussion of measurement problems.) Thermodynamics tells us that the entropy of a thermodynamic system can be calculated from the state of that system. (The state of the system concerns what that system contains and how those contents are arranged.) Entropy is important because, in any thermodynamic system that is isolated from outside influences, the entropy can never decrease. Furthermore, if any process at all is occurring in an isolated system, that system's entropy must continually increase.

To see why this is important (and relevant to ecology), consider a living organism as a thermodynamic system. If this organism were isolated in a thermodynamic sense, its entropy would necessarily increase. (Many processes—one example is the metabolism of glucose, another the synthesis of protein—are continually occurring in living organisms. Thus, their entropy must increase continually.) Consequently, the state (content and arrangement of parts) alters, i.e., deterioration occurs. To prevent this deterioration (or even to retard it), outside influences must continually act upon the organism. Hence the organism must eat, excrete, and radiate heat. It can thus be regarded as a low-entropy region of space that continually transfers its natural increase in internal entropy to its environment.

It follows that the abundance of a species could be expressed as an entropy level, which would be smaller (more negative) the greater the abundance. The organism could be further characterized by the rate at which its entropy would increase if the creature were isolated. The additions and subtractions involved in keeping accounts for this creature would include a term for its natural internal increase in entropy, and other terms for the change in entropy due to its consumption of food and its excretion of waste.

2.4. SEGMENTS

Segments are defined here as the places where ecological groups live and feed. They are more or less homogeneous with regard to the activities of each ecological group: If shrimp feed heavily in one part of a segment, they will feed heavily in all parts of that segment. Our Oosterschelde model has four segments:

1. The bulk of the water (pelagic segment).
2. Oyster banks and mussel beds, where shellfish are cultivated.
3. Tidal flats and shallow bottoms, from the mean high water level down to 3 m below mean low water (shallow benthic segment), but excluding the shellfish culture areas, all of which also lie in this depth range.
4. Deep bottoms, more than 3 m below mean low water (deep benthic segment).

As with the ecological groups, our classification of segments has flaws. For example, Wolff (1973) has found that the bottom type (e.g., sand vs. mud) is an important factor in determining where each benthic creature lives. Wolff also found that the amount of wave action in shallows and on tidal flats is a significant factor. However, our model requires as inputs the size of each segment, and data were so scanty that it proved impossible to estimate the sizes of segments if they were defined using these additional factors. This is true, incidentally, for the present form of the Oosterschelde, not to mention its modified form under various possible future alternatives (e.g., with a storm-surge barrier).

Data on ecological groups were also too scanty to justify more refined segments. As mentioned in Sec. 2.2, our data on species abundances were limited to a short list of very aggregately defined ecological groups. This limitation prevented us from estimating abundances of ecological groups in more finely defined segments (see the Addendum).

2.5. BALANCE EQUATIONS

We wish "to keep accounts" on each ecological group to assess its abundance. Sometimes we may wish to keep more than one account for an ecological group because it occurs in more than one segment. For example, detritus occurs suspended in the pelagic segment, but it can also be found mixed with the bottom sediments. Or mussels are most prevalent in the mussel beds, where they are cultured, but they also grow wild intertidally and on shallow bottoms. Alternatively, we may sometimes want to keep only a single account for an ecological group, even though it can be found in several segments. For example, if members of the ecological group are mobile, or have a very mobile life stage (e.g., larval stage), they may quickly adjust their abundance in one segment by drawing on their numbers in another. It would be inappropriate to keep separate accounts for this ecological group in the different segments. On the other hand, if, because of predation or fishing, adjustment is slow compared with abundance changes, then a separate account will be appropriate for each segment in which the ecological group occurs.

For each ecological group, therefore, we will define one or more *accounting quantities* (abbreviated AQ), each one corresponding to one or more segments in which we wish to keep account of the abundance of that group. Our model keeps an account for an AQ by means of an equation that balances all the changes in its abundance. Additions to its abundance (as measured by its ash-free dry weight) that result from growth and reproduction, as well as from migration, are represented. Subtractions of biomass because of fishing and predation are also present. Each equation requires, over the long term, that additions to the biomass of its AQ equal the subtractions. We have called these equations "balance equations."

We must stress that balance is required only over the long term. As pointed out in Sec. 2.1, the model attempts to predict only the long-term average abundances of organisms. From one day to the next, an individual animal may alternately fast or glut itself, thus being out of balance at every moment. At the same time, however, it must—and logically can—be in balance on the average, and this is what our equations require.

It is necessary to define three kinds of AQs. One kind corresponds to photosynthetic organisms, the first of our ecological groups. The second corresponds to detritus, the second ecological group. The third, encompassing all other groups, corresponds to heterotrophs—creatures that obtain their nourishment exclusively by absorbing and digesting organic material. The organic material that heterotrophs eat, of course, belongs to one or another of the ecological groups.

As mentioned above, the accounts for an AQ consist of the additions and subtractions to its abundance, measured as ash-free dry weight, that occur because of various processes both internal and external to the model. The pattern of additions and subtractions is different for the three kinds of AQs. This, of course, is the reason for distinguishing among them. For example, additions and subtractions due to internal processes that involve heterotrophs are the result of predation.[2] Thus, these additions to heterotroph abundances are always accompanied by subtractions from other AQs, since as an animal feeds it must feed on something. By contrast, photosynthetic organisms grow only by incorporating inorganic nutrients into complex organic molecules. Finally, detritus is formed as a by-product of every addition and subtraction involving other AQs. For example, feces (one form of detritus) are produced whenever a heterotroph feeds.

The pattern of additions and subtractions can be described by a network called a "food web," a common concept in ecology (e.g., see Petipa et al., 1970). In a food web, there is one node corresponding to each AQ. Figure 2.1 illustrates a food web for an ecosystem with five AQs. The food web in our model of the Oosterschelde, of course, contains many more nodes.

In Fig. 2.1, the arcs connecting one node to another (or to itself) describe eating habits. The arc from node "herbivores" to node "carnivores," for example, indicates that carnivores eat herbivores. Note that there is no arc from any node to the "detritus" node, even though every other ecogroup contributes to the abundance of detritus. Plants die and become detritus, and heterotrophs produce feces. The reason that no such arcs exist is because these transfers of organic material do not occur as a result of the activity of eating: *the arcs connecting the nodes describe eating habits only.*

Arcs starting at a node but leading out of the web indicate biomass leaving the ecosystem. There are no such arcs in our simple example, but if carnivores migrated into and out of the ecosystem, or if man harvested herbivores, then there would be an arc leading out of the node "carnivores" or "herbivores," as there is in our model of the Oosterschelde.

Arcs leading into a node but originating from outside the food web indicate biomass entering the ecosystem. In Fig. 2.1, the single arc of this kind denotes the

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[2] In our model, we have assumed that the carcasses of heterotrophs that die naturally are eaten rapidly in lieu of live organisms by their normal predators. Natural death thus becomes indistinguishable from predation. A failure of this assumption to hold would imply that numerous carcasses, in all stages of decomposition, should be found in the Oosterschelde. We take the absence of reports of such carcasses as support for this assumption.

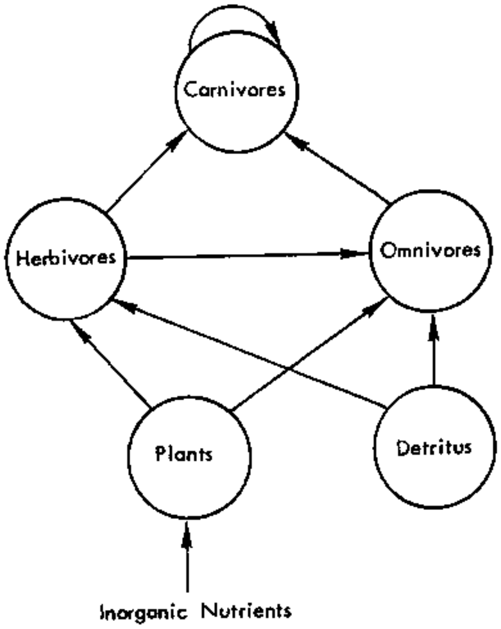

Fig. 2.1 — An exemplary food web

incorporation of inorganic material in living organisms (photosynthesis). In our model of the Oosterschelde (as opposed to the primitive example given above), there are also arcs denoting living creatures or detritus entering the Oosterschelde from the North Sea (migration, or storage of Waddensea mussels).

2.6. INDEPENDENT VARIABLES AND OUTPUTS

The independent variables of our model are factors that influence the ecosystem but that do not themselves correspond to organic matter in the Oosterschelde (and hence cannot be dependent variables). Four factors whose effect on the ecology is relatively direct have been selected:

1. Sizes of segments.
2. Average rates of fishing and migration.
3. Average rates of photosynthesis (there are as many of these as there are photosynthetic AQs).
4. Average rates of detritus import (there are as many of these as there are detritus AQs).

Many factors with an indirect effect on the ecology are not explicitly among the independent variables. Examples are the available amounts of inorganic nutrients that are important determinants of the biomass of phytoplankton present. The influence of nutrients is felt through their effect on the rate of photosynthesis. Hence, we can reflect the nutrient situation when we specify the rate of photosynthesis.

Similarly, constructions in the Oosterschelde—the storm-surge barrier, the compartmentation dams, etc.—are not explicitly represented among the independent variables. However, their influences are felt in the model through their effects upon the sizes of the segments. Thus, the construction of a compartmentation dam would reduce the segments by the amounts of the present segments that would then lie behind the dam. Or, if the aperture in the storm-surge barrier were small enough to reduce the tidal range, then the tidal flats and shallow bottoms would be reduced because of the lowering of mean high water and the raising of mean low water. The influence of every important factor can therefore be introduced into the model, either directly as one of the independent variables or indirectly through its effect on one or more of the independent variables.

Some input quantities are treated as parameters rather than as independent variables, e.g., the biological and behavioral characteristics of the ecogroups, such as metabolic rates, growth rates, prey preferences, etc. These characteristics will generally remain constant from one alternative to another, even though the independent variables are changed.

The outputs of our model are the dependent variables, and are denoted as $x_{i,j,s}$. The quantity $x_{i,j,s}$ can be interpreted as the long-term average abundance of AQ j that supports itself by consuming AQ i in segment s. Alternatively, it can be interpreted as the abundance of AQ j in segment s, multiplied by the fraction of its nutrition derived from AQ i. We can express the total biomass W_j of an AQ j as a partial sum of the variables, namely,

$$W_j = \sum_s \sum_i x_{i,j,s} \ .$$

According to the second interpretation of the variables $x_{i,j,s}$ given above, we can express the amount of the diet of a heterotrophic AQ j that is made up of biomass from AQ i by transforming these variables as follows: Define $y_{i,j,s}$ to be the daily amount of AQ i that is consumed by AQ j in segment s. This is related to the variable $x_{i,j,s}$ by the equation

$$x_{i,j,s} = \frac{(1 - f_i)y_{i,j,s}}{r_j} ,$$

where f_i is the average proportion of the ash-free dry weight of AQ i that will be excreted as feces and urine, and r_j is the average amount of food that AQ j must assimilate daily to live and grow normally.

2.7. THE GIBBS FUNCTION: A MEANS FOR CHOOSING A UNIQUE ECOLOGICAL STATE

In our model, there are many more variables $x_{i,j,s}$ than there are AQs, and hence balance equations. Consequently, the balance equations cannot by themselves determine unique values for all the variables, i.e., there are many ecostates in which every AQ is in balance.

To be useful in this study, however, our model must select a single, unique ecostate as its prediction, or at least reduce the possible ecostates to a small range. We have designed our model to do this by selecting the one ecostate that yields the smallest possible value of the Gibbs function, the mathematical form and properties of which are presented in Chap. 4. The model operates by minimizing the Gibbs function, while simultaneously requiring that all the balance constraints be satisfied.

2.7.1. Possible Additional Constraints

Of course, this was not our only option. Instead, we could have formulated constraints, in addition to the balance constraints, that would exclude most (preferably all but one) of the balanced ecostates from consideration. We see nothing theoretically objectionable about this possibility; in fact, we investigated the use of a simple rule of diet selection as the basis for these additional constraints.

Various people have observed that most organisms select a prey for their diet in rough proportion to that prey's abundance relative to other possible prey (Thijssen et al., 1974; Edwards and Steele, 1968; Braber and DeGroot, 1973; McIntyre and Eleftherion, 1968; Daan, 1973; Ursin, 1973; Ellis et al., 1976; Ivlev, 1961). These authors agree, however, that this rule is only approximate, with many species showing definite preferences. We could use this rule, modified to account for the segments in which the different ecological groups in our model feed and live, to develop enough additional constraints so that they, together with the balance constraints, would determine a unique ecostate. Section 9.1 suggests how this might be done.

We chose not to build our model on this basis for several reasons. First, the rule is at best only approximate, many species showing definite preferences for one prey even when another is more abundant. Second, the rule applies only at each instant in time, for it is an empirical rule derived from moment-to-moment observations. It does not apply when averaged over long periods. For example, a migratory predator and its migratory prey may be present in the Oosterschelde only during the winter, while a second, resident prey species is present during that time in below-average numbers. (Typically, the abundance of a resident species reaches its annual minimum in winter.) Even if each meal consumed by the predator includes the two prey species in proportion to their current abundances, the predator will overconsume the migratory prey and underconsume the resident prey, when judged on the basis of long-term average abundances.

The final reason we chose not to do so was that the resulting model would have been insensitive to the sizes of the various segments. For example, one could dredge the bottom of the Oosterschelde to a uniform depth throughout of 10 m, thereby increasing the size of the deep bottom segment at the expense of the shallow and intertidal bottoms. But the model would have predicted no change in the abundances of the various species. To avoid this erroneous result, one would require constraints that, unlike the diet-selection constraints we considered, would contain factors dependent on segment sizes.

No doubt there are other, more satisfactory, possibilities for generating additional constraints. But none suggested itself to us. Therefore, we chose a different method for selecting a unique balanced ecostate: We assumed that the ecological system obeyed a minimum principle.

2.7.2. An Ecological Minimum Principle

A minimum principle for an ecosystem is simply a statement that, as the system evolves, some measurable characteristic of the system continuously tends to diminish. This is the same as a maximum principle, in which the characteristic continuously tends to increase, since the measurable characteristic in the one case can be taken as the negative of the characteristic in the other.

The idea that an ecosystem may obey a minimum (or maximum) principle is not new to ecologists, at least as a philosophical idea. We frequently read in textbooks and in the general literature that ecosystems evolve toward a climax community, in which diversity, or biomass, or power output is maximized (Kormondy, 1969, p. 158; Odum and Pinkerton, 1955).

In addition, modelers who describe the behavior of ecosystems with systems of differential equations, as is traditionally done, have found ecostates (or sets of ecostates) in their models that seemingly "attract" the ecosystem—states that the evolving ecosystem tends to approach and remain near. One can consider each ecostate as having a sort of "altitude," some states being "high" whereas others are "low." The collection of all possible ecostates thus forms a pseudoterrain. In such a terrain, the evolution of the ecosystem is toward ever "lower" ecostates. Like water, the ecosystem flows "downhill." A function describing this terrain is a characteristic that obeys a minimum principle.

One important consequence of assuming a minimum principle is that it implies that an ecosystem must approach a stable ecological state.[3] This does not mean that the ecosystem must occupy a single state forever, with no variation from season to season or year to year. Rather it means that the system must eventually reach a condition in which it exhibits no long-term trends, i.e., the long-term average abundances will eventually cease to evolve and will assume constant values.[4] It is these constant values that our model seeks to predict.

2.7.3. The Gibbs Function

The characteristic that we believe will obey the minimum principle is the Gibbs function. Precisely how we define the Gibbs function in terms of the variables in our model is described in Chap. 4. In this section we discuss why we chose the Gibbs function as our characteristic rather than some other function.

Our first justification is thermodynamical. The Gibbs function as a measure of energy has been proposed for use in ecology on numerous occasions, by numerous

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[3] This is not a mathematical necessity. If the characteristic obeying the minimum principle is poorly chosen—e.g., if it is independent of an important state variable of the system—or if the system is unbounded, so that its state variables can evolve toward infinite values, then the system need not evolve toward a stable state. In addition, a recent mathematical development, called "catastrophe theory," suggests that an ecosystem obeying a minimum principle may have several stable states, and may suddenly "jump" from one to another as a result of large perturbations in environmental conditions.

[4] The question arises, Over what period of time do we mean the "long-term average" of abundances to be taken? Our practical answer is 5 to 10 years. We thus rule out adaption of species by evolution, which requires hundreds or thousands of generations.

Abundances averaged over periods no longer than 10 years, however, will not converge precisely to constants. The random fluctuations that occur from year to year will be damped, but not eliminated, by averaging over such a short period. Our model cannot therefore actually predict long-term averages. Rather, we consider that our model predicts the expected value—a concept from probability and statistics—of these averages, and that these averages will be good estimates of their expected values when the time comes to check the model's predictions against observations.

people, beginning with the famous theoretical physicist, Erwin Schroedinger (1944). The discussion of this proposal in the literature has included attempts to measure the appropriate thermodynamic quantities in ecosystems (Battley, 1960a and 1960b), and careful consideration of the advantages and limitations of the thermodynamic approach to ecology (Scott, 1965). Our use of the Gibbs function in an ecological model thus has considerable precedent.

Scott discusses two main limitations of the thermodynamic approach to ecology. One is that, in addition to the requirement that there must be a net energy gain by a predator from his predation, other necessary conditions must be satisfied. For example, suitable feeding mechanisms and appropriate enzymes must be present to utilize the particular foods at a useful rate. A side of beef should contain sufficient negentropy or free energy to support Slobodkin's (1960) zooplanktonic *Daphnia* and their cousins, uncles, and aunts almost indefinitely if they could only chew and digest it. They would, however, probably starve to death if the beef were the only food available, instead of algae. The energy required for the mechanical disintegration of food to suitable particle size for ingestion is probably far larger than generally realized. For example, the mechanical creation of fiber from cordwood for papermaking requires so much energy that the papermaking industry is one of the most energy-intense of all industries.

We think we have overcome this limitation by means of our balance equations. Embodied in these equations is a food web that prevents organisms from eating many of the ecological groups. Sides of beef, for example, would not be among the permissible diet items of zooplankton, even if sides of beef were an ecological group in our model.

The second limitation Scott mentions is the great difficulty of properly measuring free energy values—which are parameters in the Gibbs function—of organisms in the laboratory. (He denies the possibility of measuring free energy values in the field.) Consequently, says Scott, there are insufficient data for defining free energy parameters for natural systems. We believe we have overcome this objection by using field measurements of abundances to make inferences about free energy parameters. We describe how this is done in Chap. 10.

A related justification for using the Gibbs function as our characteristic involves its relation to the mass-action law of chemical kinetics. This law, in the form in which it usually appears in ecology, states that the rate of interaction (usually predation) between two species will be proportional to the product of their abundances. Among the people who have proposed or used this law in studying ecosystems are Volterra (1931), Lotka (1956), and Garfinkel and Sack (1964). For a discussion of the relation between the Gibbs function and the mass-action laws of chemical kinetics, see Bigelow (1970) and references therein.[5]

Still another justification is statistical. Transformations of certain parameters of the Gibbs function (the same parameters we earlier called free energy parameters) can be interpreted as the prior probabilities that the different species will be

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[5] The question arises about what units should be used to express abundances. There appear to be two reasonable choices: biomass and numbers of individuals. On the basis of the mass-action justification for using the Gibbs function, one might argue that the numbers of individuals unit is the appropriate one, since encounters leading to predation are encounters between individuals. On the other hand, a predator will continue to seek encounters until he is sated, a phenomenon that occurs when he has eaten a sufficient biomass, and not when he has encountered some particular number of prey. We have thus chosen to use units of biomass.

found in a sample taken from a given habitat in the Oosterschelde. Minimizing the Gibbs function subject to the balance constraints can then be viewed as incorporating the information that the abundances of the various species must be "in balance" into a revised set of probabilities, called the posterior probabilities. Theoretical discussions of the use of the Gibbs function in this way and related ways can be found in Jaynes (1962, 1967, and 1968), and in Kullback (1959). A related discussion from the point of view of information theory may be found in Brillouin (1962, pp. 289-291).

Finally, there are practical justifications. First, use of the Gibbs function makes it possible to calibrate the model easily to any set of observations that satisfies the balance constraints. No balanced ecostate is ruled out unless it violates some constraint. This feature is discussed more fully in Sec. 4.2.

Second, when we use the Gibbs function, our model has several desirable properties. For example, it obeys an ecological version of LeChatelier's principle: If a stress is applied to a system in a stable state, then the system readjusts, if possible, to reduce the stress. To illustrate: When the size of a segment is reduced, the biomass in that segment diminishes as well, and creatures who need the greatest amount of space per unit biomass suffer the greatest relative reduction. A more complete discussion of the properties of our model can be found in Secs. 4.3 and 4.4.

Thus, there are many arguments in favor of minimizing the Gibbs function as a means for choosing a stable ecological state. Our own reasons are the practical ones: The model thus formulated is relatively easy to calibrate, and shows reasonable behavior. We do not subscribe to any particular interpretation of the Gibbs function in ecology. However, we have advanced several: thermodynamical, statistical, and kinetic.

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Chapter 3

MASS TRANSFER EQUATIONS

3.1. THE REQUIREMENT FOR BALANCE

The model seeks a stable ecological state consistent with the input values specified. This state is described by the values of the output variables $x_{i,j,s}$, which represent abundances. The fact that an ecological state is stable does not mean that the abundance of each AQ must be constant. We recognize that the abundances will vary systematically with the season, and will vary randomly from year to year. These variations, systematic or otherwise, are compatible with an ecostate being stable. The only requirement for stability is that the time series of abundances must constitute a stationary stochastic process. Among other things, this implies that the long-term average abundance of each AQ follows no trend.

The long-term average abundances will depend on the input values specified. As explained in Sec. 2.1, the closed Oosterschelde would have different input values than the present, open Oosterschelde (notably a detritus import rate of zero), and in consequence it would have different (generally smaller) long-term average abundances. Although our model will predict the long-term average abundances in the closed Oosterschelde, or will reproduce the observed abundances in the present Oosterschelde (which perforce we have assumed to be long-term average abundances), as presently formulated it will not predict anything about the transition from the one state to the other. The model cannot make such a prediction because it relies on the assumption that the abundances of the AQs follow no long-term trends, and during the transition the ecostate would certainly exhibit a trend.

For the long-term average abundances not to follow trends, they must be in balance. Mass is continually being added to, and subtracted from, the abundance of each AQ. To be in balance, the additions and subtractions must be equal. (In the model, of course, the reverse is not true, i.e., a balanced ecostate need not be stable.)

We are naturally aware that the rates of additions and subtractions depend on the abundances of the various AQs. The more abundant a species becomes, the more food will the total population of that species consume, and the more that population will become prey to other species. We can account for this by considering a rate of mass transfer to be the product of an abundance and the relative rate at which a single individual of the appropriate AQ would accomplish this transfer of mass.

The individual (or specific) rates of mass transfer are not constant. As with the abundances themselves, these specific rates—e.g., the rates for growth and reproduction—will change from one season to another. The food requirements of an individual animal depend on the temperature, and on the animal's activity rate and body weight. However, these rates must, of course, have average values, and because of the static nature of the model, we must necessarily use these averages (or some other representative single value) rather than complete time histories.

In the model, we distinguish two different kinds of mass transfers. Some mass transfers occur entirely within the Oosterschelde, between ecological groups represented in the model. These are called "internal mass transfers." Other mass transfers occur between an AQ and the outside world. Examples are photosynthesis (incorporation of inorganic nutrients into organic molecules), fishing, and migration. These are called "external mass transfers."

The model treats the two kinds of mass transfers differently. External mass transfers are inputs. Their rates must be specified by the user of the model. Internal mass transfers, however, are calculated by the model and, if desired, can be presented as output.

3.2. MASS TRANSFERS INVOLVING HETEROTROPHS

For most AQs—all but photosynthetic organisms and detritus—many of the additions and subtractions are due to predation. These AQs correspond to the heterotrophic creatures, the ones that live by eating organic material. For convenience, we refer to these AQs as "heterotrophic accounting quantities," or HAQs. Other mass transfers involving HAQs are those to and from outside the ecosystem. These include migration, fishing, etc.

Mathematically, we express the mass transfers involving heterotrophs as follows. Suppose that the index "j" denotes an HAQ that preys upon the AQ denoted by the index "i." (The AQ "i" need not be a heterotroph. It could be detritus, or a photosynthetic organism.) Finally, suppose that this mass transfer takes place in the segment denoted by s. We define

$y_{i,j,s}$ = the expected average rate (metric tons afdw/day) of mass transfer from AQ i to HAQ j in segment s.

The quantities $y_{i,j,s}$ are not actually the variables we use in our model, but they are closely related. The major difference is that we wish to interpret our variables as abundances, whereas the $y_{i,j,s}$'s are defined as rates. Earlier, in Sec. 2.6, we showed the relationship between these rates and the model variables.

Many of the mass transfers $y_{i,j,s}$ are zero, because no heterotroph's diet includes all AQs. For example, some creatures cannot digest plant matter, whereas others cannot digest meat. Also, creatures cannot regularly catch prey that are quicker than themselves, or hold prey that are stronger. Finally, no creature can be found in all segments. If a particular creature is not found in a segment, mass transfers involving that creature cannot occur there. In our model we omit zero mass transfers. However, for notational simplicity, we write our formulae as if all mass transfers can occur.

When HAQ j eats some of AQ i—i.e., when a mass transfer $y_{i,j,s}$ occurs—several things happen. First, some of the food is excreted as feces. In our model, we assume that the fraction that is excreted depends only on the type of food eaten, and not on the organism that eats it (see Sec. 6.5 for discussion on this point). Generally about 20 percent of animal flesh becomes feces, and 50 percent of plant material and detritus. We define the fecal fraction f_i to be

f_i = the average proportion of AQ i that cannot be assimilated. This fraction will appear as excreta (either feces or urine) regardless of what HAQ eats AQ i. (For further details, see Sec. 6.5.)

Food that is not excreted is assimilated. The fraction assimilated is used either for production (including growth by individual creatures and reproduction) or for metabolism. The fractions used for these purposes depend on the creature assimilating the food, and not on the kind of food being assimilated. Important factors for determining these fractions are the weight of the creature, the maximum weight it may eventually achieve, and whether it is homeothermic or heterothermic (Fenchel, 1974). Further discussion of assimilation, metabolism, and production appears in Sec. 6.3. We define

g_j = the proportion of the assimilated food that contributes to the production (growth plus reproduction) of HAQ j,

m_j = the average proportion of the assimilated food that is used for metabolism by HAQ j.

Since these are the only uses for assimilated food, we have

$$g_j + m_j = 1 .$$

Finally, a certain amount of HAQ j may enter or leave the ecosystem per day. This may be due to migration, fishing by man, or any other cause. We define

L_j = the expected net average rate (tons afdw/day) at which biomass of HAQ j is lost from the ecosystem. Note that this is a net rate, and will therefore contain both loss terms and gain terms. Note also that this is a loss rate, so that if there is a net gain of HAQ j, L_j will be negative.

Many losses, for example losses due to outward migration, may reasonably be regarded as proportional to the abundance of the accounting quantity in question, HAQ j. Other losses are best specified independently of the abundance of HAQ j. We have dealt with fishing rates in this fashion.[1] We therefore express the loss rate L_j as a linear function of the abundance of HAQ j, i.e., as

$$L_j = b_j + MIG_j W_j ,$$

where b_j = the constant part of the net loss rate, nominally due to fishing (a negative value signifies a net gain),

W_j = the abundance (metric tons afdw) of HAQ j,

MIG_j = the average net proportion of HAQ j lost from the ecosystem daily, nominally due to migration. (A negative value signifies a net inward migration.)

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[1] We are aware, of course, that fisheries biologists generally consider fishing rates to depend strongly on the abundance of the species fished. However, fishing rates also depend on a host of other factors. Among these are the fishing effort, the design of the fishing gear, and the fishermen's knowledge of their quarry's behavior. These factors are, in turn, influenced by the market for the catch, whether other fisheries are competing for shares of that market, whether subsidies are offered the fishermen, etc. It seems preferable to us simply to specify fishing rates outside the model, and observe the consequences, instead of trying to subsume these complex relationships within the model.

3.3. BALANCING MASS TRANSFERS FOR HETEROTROPHS

We can think of each HAQ as a "pool" of biomass to which there are continual inputs and from which there are continual withdrawals. Using the quantities defined in the previous section, we can describe all of these inputs and withdrawals, as shown in Fig. 3.1.

Mathematically, the effect of these transfers of mass on the abundance of HAQ j can be expressed as follows. As before, we define

W_j = long-term average abundance (tons afdw) of HAQ j.

Then

$$\frac{dW_j}{dt} = - L_j + g_j \sum_s \sum_i (1 - f_i) y_{i,j,s} - \sum_s \sum_k y_{j,k,s} \ .$$

In a balanced ecostate, the long-term average abundance of each HAQ must be constant; i.e., $dW_j/dt = 0$ for every HAQ j. From this observation and the above differential equation, we obtain the following balance requirements:

$$L_j = g_j \sum_s \sum_i (1 - f_i) y_{i,j,s} - \sum_s \sum_k y_{j,k,s} \ . \tag{3.1}$$

There is one such balance requirement for each of the HAQs. Recall that there remain the additional, nonheterotrophic ecological groups: "photosynthetic organisms" and "detritus." For these groups, we shall derive balance equations later.

3.4. RELATING BIOMASS TO MASS TRANSFERS

For heterotrophs, we intend that the final balance conditions should require that

- Each HAQ that is present in the model have enough of the appropriate things to eat.
- The amount of each HAQ that is eaten, plus the net loss of mass from the ecosystem, be enough to counterbalance the growth of that HAQ; i.e., we want to ensure that the long-term growth rate is zero (no population explosions allowed).

Conditions (3.1) require the growth rate of each HAQ to be zero. For these conditions to deal with dietary requirements, however, we must first relate the mass transfers $y_{i,j,s}$ to the biomasses of the various HAQs. Thus we define

r_j = the average daily ration of HAQ j (tons afdw assimilated per day per ton afdw biomass of HAQ j). This ration is the average amount that each unit of HAQ j needs to assimilate each day to support both metabolism and normal production. A unit of HAQ j will actually consume more than it assimilates, and will excrete the balance as feces.

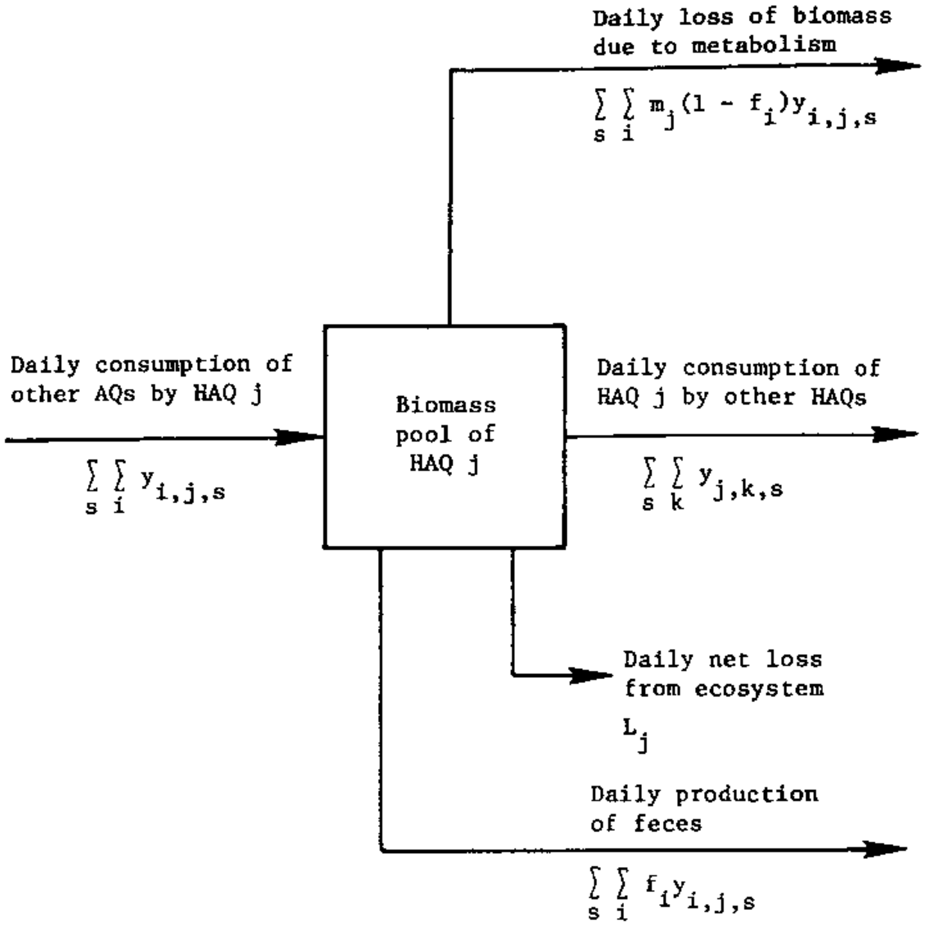

Fig. 3.1 — Mass flows involving a heterotroph

As we shall discuss in Chap. 6, experimental work has shown that r_j will differ for individuals of HAQ j of different weights. For our model, however, we must choose a single value of r_j for each HAQ. The value we choose is intended to be representative of the entire range of daily rations that would be encountered within the population of HAQ j.

The condition for HAQ j to eat sufficiently is

$$\sum_s \sum_i (1 - f_i)y_{i,j,s} = r_j W_j \ . \tag{3.2}$$

If we knew the abundances W_j of the various heterotrophs, then requiring that the mass transfers $y_{i,j,s}$ satisfy conditions (3.2) would ensure that each HAQ had enough of the right things to eat. And by further satisfying conditions (3.1), each heterotroph would maintain a zero average long-term growth rate.

3.5. THE FINAL BALANCE CONDITIONS FOR HETEROTROPHS

Unfortunately, the abundances W_j are not known. Indeed, it is the purpose of the model to predict these quantities. Thus, instead of including Eqs. (3.2) in the model as constraints, we use them as a method for computing the abundances W_j. Before doing so, we transform the variables $y_{i,j,s}$ as follows:

$$x_{i,j,s} = \frac{(1 - f_i)y_{i,j,s}}{r_j} . \tag{3.3}$$

The variables $x_{i,j,s}$ are quantities that our model predicts. We have replaced the quantities $y_{i,j,s}$ by the variables $x_{i,j,s}$ because the latter can be interpreted as abundances, whereas the former can be interpreted only as rates. To clarify, we determine the units of $x_{i,j,s}$ from those of f_i, $y_{i,j,s}$, and r_j. We find that the $x_{i,j,s}$'s have the units "tons afdw of HAQ j." Substituting the new variables $x_{i,j,s}$ into Eqs. (3.2), we express the long-term average abundance of HAQ j as

$$W_j = \sum_s \sum_i x_{i,j,s} . \tag{3.4}$$

Equation (3.4) gives the total abundance W_j of HAQ j as the sum of a number of partial abundances $x_{i,j,s}$, each one associated with the activity of consuming a different AQ i. We can therefore regard the variable $x_{i,j,s}$ as the long-term average abundance of HAQ j that supports itself by consuming AQ i in segment s. (Recall, however, that we have not yet considered variables that represent biomasses of photosynthetic organisms and detritus, i.e., the nonheterotrophic AQs.) As a measure of abundance, each variable $x_{i,j,s}$ must be greater than or equal to zero. A negative abundance makes no sense. That is,

$$x_{i,j,s} \geq 0 . \tag{3.5}$$

We pointed out above that L_j is not a constant but a linear function of the abundance W_j of AQ j. That is,

$$L_j = b_j + MIG_j W_j . \tag{3.6}$$

Substitution of Eqs. (3.3), (3.4), and (3.6) into Eq. (3.1) yields the final balance equation for HAQ j:

$$b_j = (g_j r_j - MIG_j) \cdot \sum_s \sum_i x_{i,j,s} - \frac{\sum_s \sum_k r_k x_{j,k,s}}{1 - f_j} . \tag{3.7}$$

Note that the divisor $(1-f_j)$ has been factored out of each term involving HAQ j as a prey of some other HAQ. This can be done because of our assumption that the fecal fraction f_j depends only on the prey and not on the predator. (See Sec. 6.5.)

The comments that we made earlier regarding the quantities $y_{i,j,s}$ also apply to the $x_{i,j,s}$: No HAQ will eat all AQs in all segments. Thus, many of the variables $x_{i,j,s}$ will necessarily be zero. In our model, we omit zero variables, but for notational simplicity, we write our formulae without concern for zero variables.

3.6. PHOTOSYNTHETIC ORGANISMS

We deal with each photosynthetic AQ by means of a balance equation. A balance equation for photosynthetic organisms differs from that for heterotrophs because photosynthetic organisms do not eat other AQs. Instead, they grow by absorbing inorganic nutrients and using solar energy to convert them into organic molecules.

In our model, the photosynthetic process occurs at a constant rate, and this rate is specified externally rather than being calculated by the model—a treatment that is consistent with our earlier description of what is internal to the model and what is external. Photosynthesis converts inorganic molecules, which are external to the model, into organic substances, which are internal. Thus, photosynthesis is an external mass transfer, and in accordance with our conventions, it is specified as a model input.

We recognize that the rate of photosynthesis by an organism will, in general, depend on a multitude of factors, including the turbidity of the water, the availability of nutrients, the temperature, the intensity of the solar radiation, the amount of cloud cover, etc. While none of these factors is explicitly represented in our model, we have considered all of them when specifying the photosynthetic rates for our model. (See Sec. 7.1.)

Each photosynthetic organism also has a metabolic rate and a mortality rate, which means that some of the photosynthetic production must be used to support the plants themselves. The support requirement is proportional to the abundance of the plants. The material that the photosynthetic organism metabolizes is lost to the ecosystem, but the organisms that die (mortality) are not. They become detritus, which may then be eaten by other organisms.

Finally, of course, other creatures eat plants. These mass transfers are among the quantities $y_{i,j,s}$ defined in Sec. 3.2 and are related to the variables $x_{i,j,s}$ through Eq. (3.3).

Now, suppose that index "i" denotes a photosynthetic organism and, as before, index "s" denotes a segment. We can then define

$x_{i,i,s}$ = the long-term average abundance of the photosynthetic organism i in segment s.

This definition is consistent with our interpretation of the variables $x_{i,j,s}$ defined previously. Recall that we interpreted the earlier variable $x_{i,j,s}$ as the biomass of HAQ j that supports itself by consuming AQ i in segment s. But a photosynthetic organism supports itself by metabolizing away its own substance—i.e., $x_{i,i,s}$ is the biomass of photosynthetic organism i that supports itself by consuming photosynthetic organism i in segment s. We define

r_i = the average daily ration (tons afdw consumed per day per ton afdw standing stock) for photosynthetic organisms i. This ration is composed of the amount that a ton of standing stock metabolizes each day, and the amount that dies and becomes detritus.

m_i = the average fraction of the daily ration of photosynthetic organism i that is used for metabolism,

b_i = the average production rate (tons afdw/day) of photosynthetic organisms i.

Like the constant part of the external mass transfers b_j that we defined earlier for heterotrophs, the term b_i defined here is also an external mass transfer, involving as it does the incorporation of inorganic nutrients into organic molecules by means of photosynthesis. However, b_i differs from b_j in that it is a rate of mass input into the ecosystem, whereas the earlier terms b_j were rates of mass output. Also, note that unlike our treatment of heterotrophs, we do not consider any external mass transfer of photosynthetic organisms that depends on their own abundance W_i. The external mass transfer rate is entirely described by the constant term b_i.

We derive a balance equation for photosynthetic organisms i as follows. We define

W_i = the long-term average abundance of the photosynthetic organism i.

Then

$$\frac{dW_i}{dt} = b_i$$

$$- (\text{metabolism and death of photosynthetic organisms } i)$$

$$- (\text{consumption by HAQs of photosynthetic organisms } i).$$

Term by term we have

$$\text{Metabolism and death of photosynthetic organisms } i = \sum_s r_i x_{i,i,s} \ ,$$

$$\text{HAQs eating photosynthetic organisms } i = \frac{\sum_s \sum_j r_j x_{i,j,s}}{1 - f_i} \ .$$

If the ecosystem is to be balanced, then W_i must remain constant. Thus $dW_i/dt = 0$. This requirement yields the following balance equation for photosynthetic organism i:

$$b_i = \sum_s r_i x_{i,i,s} + \frac{\sum_s \sum_j r_j x_{i,j,s}}{1 - f_i} . \tag{3.8}$$

3.7. DETRITUS

In our model, detritus includes all dead organic matter, whether suspended in the pelagic segment or deposited on the bottom. It has many sources—carcasses, feces, shed exoskeletons, fragments of organisms, regurgitations, excretions and secretions, dead plants and phytoplankton, etc. Associated with detritus, and included with it as part of the same ecological group, are the bacteria and fungi that live largely by decomposing detritus. In our model, we have also included microbenthic organisms (microfauna and meiofauna) in the detritus group, because their main interaction with the other ecological groups appears to be competition for detritus as a source of food.

Like other AQs, a detritus AQ has its own balance equation, and like other balance equations, a detritus equation contains both gain terms and loss terms. Gains may be made from any other AQ. Heterotrophs excrete feces and urine, of which the ash-free dry portion is detritus. When plants die, they become detritus. Similarly, loss terms may involve most other AQs. Some creatures, such as worms, eat detritus. This is probably the most important mechanism for eliminating it. But bacteria also deplete it by mineralization.

Detritus can be transported from one segment to another. For example, detritus found on the bottom can be stirred up into the pelagic segment, transported by water movements (currents), and redeposited on the bottom some distance from its place of origin. Transportation both adds and subtracts detritus in each segment.

Finally, there is detritus import.[2] Detritus is carried into the Oosterschelde by tidal action and is trapped by a variety of mechanical and biological processes. Some detritus is carried into the Oosterschelde by water from the Rhine as it flows through the Volkerak locks. Detritus also enters the Oosterschelde as a component of both drainage of agricultural lands and outflows of household and industrial sewage. Some of the runoff from the land may occur invisibly as part of the groundwater flow.

Of course, there is also an export of detritus. Not all the detritus brought in by the tide, or imported from other sources, is trapped in the Oosterschelde. As the tide retreats, it carries some detritus out of the Oosterschelde with it. Some detritus may also be deposited as peat (which may eventually become oil, coal, or natural gas). However, our studies have led us to believe that detritus import exceeds detritus export by a very large margin; that detritus import is crucial to the ecology of the Oosterschelde as we know it now; and that competition by heterotrophs for this food source is so intense that little if any detritus may be deposited as peat.

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[2] The organic matter that is imported into the Oosterschelde includes both dead and live matter. For example, phytoplankton that grow in the North Sea near the mouth of the Oosterschelde are frequently swept inside by the tide. For convenience, we have included imported live organisms as part of the detritus import rate, even though the same live organisms grown inside the Oosterschelde would belong to a different ecological group.

(See the appendix for a detailed discussion of the role of detritus in the Oosterschelde.)

For our model, let us suppose that the index "k" denotes one of the detritus AQs. We then define

$x_{k,k,s}$ = the long-term average abundance (tons afdw) of detritus k in segment s.

This definition is also consistent with our earlier interpretations of variables $x_{i,j,s}$. Recall that we combined detritus with bacteria in one ecological group. (It also includes microfauna and meiofauna.) Hence, when bacteria mineralize detritus, it appears in the model as though this ecological group is consuming itself. We now define

r_k = the average fraction of detritus k mineralized per day,

b_k = the average net export (tons afdw/day) of detritus k either to other detritus AQs or to outside the ecosystem. If this parameter is negative, then there is a net addition to detritus k from other detritus AQs or from outside the system.

Note that, as with photosynthetic organisms, we do not consider the external mass transfer rate of detritus to depend on the abundance of detritus. The external mass transfer rate is thus entirely described by the constant term b_k.

To write the balance equation for detritus k, we must first know which of the sources of detritus contribute to detritus k as contrasted with other detritus AQs. Each variable $x_{i,j,s}$, except for the detritus abundance variables themselves, corresponds to an activity that produces detritus. If the activity is an HAQ consuming an AQ, then the detritus produced is the feces of the HAQ. If the activity is the dying of a photosynthetic organism, then the detritus produced is the dead vegetation. Whether an activity produces detritus k or some other detritus AQ will generally depend on the segment in which the activity takes place. We therefore define

P_k = the set of variables $x_{i,i,s}$ associated with photosynthetic organisms that become detritus k when they die,

H_k = the set of variables $x_{i,j,s}$ associated with the activities of HAQs that contribute feces to detritus k.

We derive a balance equation for detritus k as follows. We define

W_k = the long-term average abundance of detritus k.

Then

$$\begin{aligned}\frac{dW_k}{dt} = &- b_k\\ &+ \text{(photosynthetic organisms becoming detritus k)}\\ &+ \text{(feces of heterotrophs becoming detritus k)}\\ &- \text{(detritus k being eaten by heterotrophs)}\\ &- \text{(detritus k being mineralized).}\end{aligned}$$

Term by term we have

(i) Photosynthetic organisms becoming detritus k $= \sum\sum_{P_k} r_i(1 - m_i)x_{i,i,s}$.

(This double sum includes all variables $x_{i,i,s}$ corresponding to photosynthetic organisms that become detritus k when they die. It is a double sum because there are two indices to consider, i and s. See above for the definition of the set P_k.)

(ii) Feces of HAQs becoming detritus k $= \sum\sum\sum_{H_k} \frac{f_i r_j x_{i,j,s}}{1 - f_i}$.

(This term includes all variables $x_{i,j,s}$ corresponding to activities of heterotrophs that contribute feces to detritus k. It is a triple sum involving the three indices i, j, and s. See above for the definition of the set H_k.)

(iii) Detritus k eaten by HAQs $= \frac{\sum_s \sum_j r_j x_{k,j,s}}{1 - f_k}$,

(iv) Mineralization of detritus k $= \sum_s r_k x_{k,k,s}$.

If the ecosystem is to be balanced, then W_k must remain constant. Thus $dW_k/dt = 0$. This yields the following balance equation for detritus k:

$$b_k = - \sum_s r_k x_{k,k,s} - \frac{\sum_s \sum_j r_j x_{k,j,s}}{1 - f_k} + \sum\sum_{P_k} r_i(1 - m_i)x_{i,i,s} + \sum\sum\sum_{H_k} \frac{f_i r_j x_{i,j,s}}{1 - f_i} . \tag{3.9}$$

3.8. CONSTRUCTING THE MASS-BALANCE COEFFICIENT MATRIX

So far we have considered each AQ individually, looking at transfers of biomass involving only that AQ; this approach led to the balance conditions (3.7), (3.8), and (3.9), which must be satisfied by the variables $x_{i,j,s}$ if the ecosystem is to be in balance. In the model, however, we construct the balance constraints by examining each mass transfer individually, and its simultaneous influence upon all AQs.

Let us consider a variable $x_{i,j,s}$. In each of the balance equations, this variable will have a coefficient. (Recall that there is one balance equation corresponding to each AQ.) Most of the coefficients will be zero, but as many as three may be nonzero. The values of these coefficients depend on only a modest amount of information describing the various AQs. This information is as follows:

For each AQ we require:

(i) A name or other identifier.

(ii) A type (photosynthetic organism, detritus, or heterotroph).

(iii) r_j, its average daily ration.

(iv) f_j, its average fecal fraction.

(v) m_j, its average metabolic fraction.

(vi) b_j, the constant part of its average net export rate (for photosynthetic organisms this is the production rate). This is the entire net mass transfer rate for all AQs except heterotrophs.

(vii) MIG_j, the coefficient of abundance in the variable part of the net export rate of heterotrophs. This does not apply to photosynthetic organisms or to detritus.

(See earlier sections of the text for more complete descriptions of these quantities.) It may appear that this list is incomplete because it lacks the growth fraction g_j. (Recall that g_j appears as a factor in the balance equations for heterotrophs.) Instead, we have included the metabolic rate m_j. Since food, once assimilated, is used either for growth or for metabolism, we can calculate the growth fraction as $g_j = 1 - m_j$.

How we calculate the coefficients of $x_{i,j,s}$ will depend on the type of variable we are dealing with. We specify the variable as follows:

For each variable $x_{i,j,s}$ we require:

(i) The segment s in which its corresponding activity occurs.

(ii) AQ i, the name of the consumee.

(iii) AQ j, the name of the consumer.

(iv) AQ k, the name of the detritus AQ produced when this activity is carried out.

We then compute its coefficients according to the following rules:

Case I: *AQ i, AQ j, and AQ k do not differ.* Then we have detritus variable $x_{k,k,s}$. In this case, there is a nonzero coefficient only in the balance equation for AQ k, which corresponds to the rate at which detritus k is mineralized. The Case I coefficient is

In the equation for AQ k: $-\ r_k$.

Case II: *AQ i and AQ j are the same, and apply to a photosynthetic organism.* Then the variable $x_{i,i,s}$ denotes the biomass of that photosynthetic organism. In this case, there are two nonzero coefficients. One is in the equation for AQ i and corresponds to the death plus mineralization rates of AQ i. The other is in the equation for detritus k, the kind of detritus the photosynthetic organism becomes upon death. The Case II coefficients are

In the equation for AQ i: r_i,

In the equation for AQ k: $r_i(1 - m_i)$.

Case III: *AQ j is a heterotroph.* This case has several variants, but in general three AQs are involved. First, AQ i is consumed. HAQ j then uses this food to grow. Finally, some of the food is excreted as feces, becoming detritus k. The Case III coefficients, by variant, are

Variant (a) AQ i is a photosynthetic organism:

In the equation for AQ i: $r_j/(1 - f_i)$,

In the equation for AQ j: $g_j r_j - MIG_j$,

In the equation for AQ k: $f_i r_j/(1 - f_i)$.

Variant (b) AQ i is a heterotroph different from j, or AQ i is a detritus AQ different from k:

In the equation for AQ i: $- r_j/(1 - f_i)$,

In the equation for AQ j: $g_j r_j - MIG_j$,

In the equation for AQ k: $f_i r_j/(1 - f_i)$.

Note that variant (b) differs from variant (a), where AQ i is a photosynthetic organism, only in the sign of the coefficient in the equation for AQ i.

Variant (c) AQ i is the same as j, i.e., this heterotroph is a cannibal:

In the equation for AQ j: $g_j r_j - MIG_j - r_j/(1 - f_j)$,

In the equation for AQ k: $f_j r_j/(1 - f_j)$.

Note that variant (c) is the same as variant (b) except that the coefficients in the equations for AQs i and j have been added together.

Variant (d) AQ i is the same as k, i.e., this heterotroph eats detritus of the same kind as his feces:

In the equation for AQ j: $g_j r_j - MIG_j$,

In the equation for AQ k: $- r_j$.

Note that variant (d) is the same as variant (b) except that the coefficients in the equations for AQs i and k have been added.

3.9. AN EXAMPLE MASS-BALANCE COEFFICIENT MATRIX

An example in which the mass-balance coefficient matrix is constructed may make the preceding rules clearer. Consider a simple exemplary ecosystem whose food web is depicted in Fig. 2.1. In this example, we have five AQs, as shown in Table 3.1, and ten variables, as shown in Table 3.2. Because there is a balance equation for every AQ, our example gives rise to five equations, one each for plants, detritus, herbivores, omnivores, and carnivores.

Table 3.1

DESCRIPTIVE PARAMETERS FOR AQs IN EXAMPLE

AQ Name	Type	Daily Ration	Fecal Fraction	Metabolic Rate	Net Export Rate
1. Plant	Photosynthetic organism	0.1	0.5	0.1	100[a]
2. Detritus	Detritus	0.1	0.5	--	0.0
3. Herbivore	Heterotroph	1.0	0.2	0.8	0.0[b]
4. Omnivore	Heterotroph	0.5	0.2	0.9	0.0[b]
5. Carnivore	Heterotroph	0.2	0.2	0.9	0.0[b]

[a] Recall that for plants, this is the production rate, and not an export rate.

[b] We are assuming that there is no migration. Thus $MIG_j = 0.0$ for all three heterotrophs.

The mass-balance coefficient matrix is best constructed one column at a time. The first column corresponds to variable $x_{1,1}$, which represents a photosynthetic organism. Thus, we apply the instructions under Case II, in which we have only two nonzero entries. In equation 1 (plants), we enter r_1, which according to Table 3.1 is 0.1. In equation 2 (detritus), we enter $r_1(1 - m_1)$, which is 0.1×0.9, or 0.09. All other entries are zero.

The second column corresponds to variable $x_{2,2}$, which is a detritus variable. The rule for constructing its column is found under Case I. Consequently, there is only one nonzero entry, namely $-r_2$ in equation 2 (detritus). Table 3.1 shows that $r_2 = 0.1$. All other entries are zero.

The third column corresponds to $x_{1,3}$. As Table 3.2 shows, this variable represents a herbivore (heterotroph) eating a photosynthetic organism (plants). Variant (a) of Case III applies, and this column has the following three nonzero entries:

Table 3.2

VARIABLES AND ASSOCIATED MASS TRANSFERS

Variable Name	AQ Consumed		Consumer AQ	
	Number	Name	Number	Name
$x_{1,1}$	1	Plant	1	Plant
$x_{2,2}$	2	Detritus	2	Detritus
$x_{1,3}$	1	Plant	3	Herbivore
$x_{2,3}$	2	Detritus	3	Herbivore
$x_{1,4}$	1	Plant	4	Omnivore
$x_{2,4}$	2	Detritus	4	Omnivore
$x_{3,4}$	3	Herbivore	4	Omnivore
$x_{3,5}$	3	Herbivore	5	Carnivore
$x_{4,5}$	4	Omnivore	5	Carnivore
$x_{5,5}$	5	Carnivore	5	Carnivore

	Formula	*Value*
1. In equation 1 (plants)	$r_3/(1 - f_1)$	2.0
2. In equation 2 (detritus)	$f_1r_3/(1 - f_1)$	1.0
3. In equation 3 (herbivores)	g_3r_3	0.2

The fourth column corresponds to the variable $x_{2,3}$, which according to Table 3.2 represents a heterotroph (herbivores) eating detritus. Variant (c) of Case III applies, and there are only two nonzero entries in this column. Equation 2 (detritus) contains $-r_3 = -1.0$, and equation 3 (herbivores) contains $g_3r_3 = 0.2$. All other entries are zero.

The fifth and sixth columns correspond to $x_{1,4}$, omnivores eating plants, and $x_{2,4}$, omnivores eating detritus. They are constructed by the same rules as were the third and fourth columns, respectively.

The next three columns correspond to heterotrophs eating other heterotrophs. Variant (b) of Case III applies to all of them. Taking the seventh column as an example (corresponding to $x_{3,4}$, omnivores eating herbivores), we identify the following three nonzero entries:

	Formula	*Value*
1. In equation 2 (detritus)	$f_3r_4/(1 - f_3)$	0.125
2. In equation 3 (herbivores)	$-r_4/(1 - f_3)$	-0.625
3. In equation 4 (omnivores)	g_4r_4	0.05

The tenth and final column (Table 3.3 has an 11th column containing the b_j) corresponds to the variable $x_{5,5}$, which Table 3.2 shows is a heterotroph (carnivores) eating itself. Variant (c) of Case III applies, and the column has only two nonzero entries. These entries are shown in the last column of Table 3.3, which also contains the other columns of the mass-balance coefficient matrix. The entries in any column not discussed can be derived from the parameter values in Table 3.1 by applying the rules given earlier.

Table 3.3

THE EXEMPLARY MASS-BALANCE COEFFICIENT MATRIX

	Variable										
AQ Name	$x_{1,1}$	$x_{2,2}$	$x_{1,3}$	$x_{2,3}$	$x_{1,4}$	$x_{2,4}$	$x_{3,4}$	$x_{3,5}$	$x_{4,5}$	$x_{5,5}$	b_j's
Plant	0.1		2.0		1.0						100
Detritus	0.09	-0.1	1.0	-1.0	0.5	-0.5	0.125	0.05	0.05	0.05	0.0
Herbivore			0.2	0.2			-0.625	-0.25			0.0
Omnivore					0.05	0.05	0.05		-0.25		0.0
Carnivore								0.02	0.02	-0.23	0.0

3.10. THE OVERALL SYSTEM BALANCE

Until now, our development has stressed internal mass transfers. External transfers have been treated as given. Nevertheless, external mass transfers are no less important than internal ones. Indeed, without them the ecosystem could support no biomass whatsoever.

To show this property of the ecosystem, we combine the balance equations for all the AQs into a single equation that describes the overall system balance. First, we sum the balance equations corresponding to photosynthetic organisms. From this sum we subtract all the other equations, i.e., those corresponding to detritus AQs and heterotrophic AQs. The result is a linear equation in which each variable $x_{i,j,s}$ has a coefficient, and which possesses a constant term.

The coefficient of the variable $x_{i,j,s}$ is the sum of the coefficients of this variable in the equations for photosynthetic organisms less its coefficients in all other equations subtracted. Table 3.4 shows the results. Note that except for the term MIG_j in the coefficient for heterotrophs, these coefficients denote the rate at which each unit of biomass of the appropriate AQ transforms organic material into inorganic material. This is done to detritus by mineralization. Other AQs transform by metabolism. When each coefficient is multiplied by its corresponding variable, the product is the loss per day of organic material from the ecosystem as a result of that activity. By adding all of these terms together, we can determine the total loss per day of organic material as a result of internal mass transfers. To these metabolism and mineralization losses are added the heterotroph losses, usually minor, due to migration.

Table 3.4

COEFFICIENTS IN THE OVERALL SYSTEM BALANCE EQUATION

If the Variable $x_{i,j,s}$ Is—	Its Coefficient in the Overall Balance Is—
Detritus	r_j
Photosynthetic organism	$m_j r_j$
Heterotroph	$m_j r_j + MIG_j$

The constant term of the overall balance equation is obtained from the constant terms (i.e., the external mass transfers b_j) of the individual balance equations in the same way as the coefficients above were obtained. That is, the constant term is the rate of photosynthesis, minus the net rate of detritus export, minus the net loss rate of heterotrophs due to fishing. The constant term of the overall balance equation is thus the total net rate of import of organic material resulting from external mass transfers.

The above discussion explains why the equations for photosynthetic organisms were added, and all other equations subtracted, to form the overall balance equation. Constant terms for photosynthetic organisms were originally defined as inputs of organic material by photosynthesis. All other constant terms were defined as net rates of loss of organic material to the outside; and in the development of the overall balance equation, their directions (i.e., their algebraic signs) were reversed.

The overall ecosystem balance equation therefore requires that the total daily loss of organic material from internal mass transfers be replaced, on the average, by the net input of organic material from outside our system boundaries (including photosynthesis; see Sec. 2.1). Furthermore, except, possibly, for a net inward migration, the coefficient of every variable is positive. Metabolism or mineralization causes every particle of biomass in the ecosystem to expend some of the organic material present. Consequently, there cannot be any mass in the ecosystem at all unless it is supported by photosynthesis, detritus import, or the migration of living creatures from outside.

As mentioned in Sec. 2.3, instead of describing all abundances in terms of ash-free dry weights, we could have used units of food energy. Discussed in these terms, the transformation of organic material into inorganic material is nothing more than a loss of food energy, as that energy is converted into heat and dissipated. In the same terms, photosynthesis is a reverse transformation, namely the trapping of light energy and its incorporation into high-energy food molecules. Thus, the overall balance equation, as well as the mass-balance equations for individual AQs, can be interpreted as specifying requirements that there be a sufficient input of food energy to replace that lost by metabolism, migration, and (for individual AQs) predation.

Yet another way of looking at these balances involves entropy. As we discussed earlier (Sec. 2.3), the abundance of each AQ can be described in terms of "entropy units." Because of long-standing thermodynamic convention, these units act contrary to intuition—i.e., an increase in the biomass of an AQ is denoted by a decrease in the number of entropy units of that AQ. (The reader may find it more comfortable to think in terms of the negative of entropy. Enough people have felt this way so that this alternative to entropy has been given the name "negentropy.")

Each internal mass transfer involves an increase in the entropy of the entire system. Hence, when one creature eats another, the predator accomplishes a decrease in his own entropy at the expense of a larger increase in the entropy of his prey. Each AQ needs to decrease its entropy continually in order to counter its natural and continuous increase in entropy because of metabolism. The continual entropy decrease is accomplished either by preying upon other AQs, or by receiving "negentropy" directly from outside the system.

Metabolism and mineralization are the ultimate entropy-increasing processes in ecology. Both of them reduce organic material, which can be used to decrease the entropy of an AQ, into inorganic material, which cannot. According to the overall system balance, the net result of all internal mass transfers is always a combination of metabolism and mineralization. The system cannot maintain itself without a continuous influx of low-entropy material—i.e, of "negentropy." The latter material consists of organic molecules that are either brought into the Oosterschelde from outside (e.g., from the North Sea), or are newly photosynthesized inside the basin.

Viewed in any of these ways, the ecosystem may be compared to an engine. Fuel must be provided to keep the engine running. In one interpretation—the one we have selected to use in our model—the fuel is organic matter, measured in terms of ash-free dry weight. In another, the fuel is the food energy contained in organic molecules. And in the third interpretation, the fuel is the "negentropy"—i.e., the capacity to absorb entropy—that characterizes highly structured organic molecules.

3.11. THE USE OF AVERAGES

As we pointed out earlier, average quantities have been used throughout our model development. Our measures of abundance are long-term average abundances. The coefficients in the balance equations are calculated by using average rates: average daily rations; average metabolic and production rates for heterotrophs; average production rates for photosynthetic organisms; average migration rates for heterotrophs; and average import rates for detritus. These measures ignore fluctuations in rates and abundances that occur from one season or one year to the next.

In this section, we ask (and suggest an answer) whether our use of averages limits the validity of the balance equations, whose coefficients are computed from average quantities. When we perturb the segment sizes, or the net export rates of the various AQs, we continue to use the same coefficients in the balance equations. If, in the natural situation, the average quantities on which these coefficients are based would change, then the balance equations will be invalid for all but the initial ecostate.

Many fluctuations in abundances and rates are consequences of adaptive changes in the behavior of animals. For example, when less food is available, most creatures respond by eating less and growing less. Some, like sea stars, can go without food for long periods, losing as much as half of their original weight. The reverse adaptive change occurs when food becomes more abundant. Then creatures eat more and grow faster. In addition, they become more fertile, so that the number of individuals in the population grows as well as the total biomass.

The latter adaptation reflects a time delay in the ecosystem. It is well known that when such delays in response are present in an ecosystem, fluctuations generally occur in the abundances of the different species. Thus, the fact that a particular species is very fertile at one point in time may cause its population to increase beyond its food supply. As a result, individuals then eat less and become less fertile, which permits the food supply once again to become abundant relative to the size of the population it must feed.

In addition to fluctuations due to adaptive changes, there are fluctuations due to environmental factors. For example, if the temperature changes, so will the metabolic rates of the cold-blooded creatures in a marine ecosystem (Kinne, 1970, p. 2; Ikeda, 1970; Paloheimo and Dickie, 1966). Or, changes in fishing rates may cause fluctuations of abundances.

Fluctuations of these quantities about their averages do not by themselves vitiate the balance equations. The averages themselves must change. For example, suppose that the average amount of food eaten by an individual sea star declines because the shellfish culture in the Oosterschelde is eliminated. In the short run, of course, this change will render the balance equation(s) for sea stars incorrect. These creatures will be eating less per unit biomass, so that their abundance could be greater than the balance equations would appear to allow.

However, over the longer run, one would expect the numbers of sea stars to adjust downward in response to the reduction in their food supply. (This downward adjustment might take the form of fluctuations around a downward-sloping trend line.) Each sea star that survived would find its daily ration rising once again toward its previous level. In general, then, we expect that changes in the average rates would be largely self-correcting.

Long-term changes in average rates would probably occur because of changes in the size distribution of the population of a species. (Such a change in size distribution could be due to a change in predation pressure upon the species. Heavy predation would reduce the average lifespan, and hence the average age and size of the prey.) Generally, food consumption by a large individual of any species is smaller per unit body weight than consumption by a small individual, although, of course, the larger individual will have greater total food consumption than the smaller one. Thus, if one population is composed of individuals smaller, on the average, than those of a second population, then the first population will require more food per unit biomass than the second. But the effect would be relatively small—e.g., an eightfold increase in the average size of the individual is needed to produce a twofold reduction in food consumption per unit biomass (see Sec. 6.3). The validity of the balance equations would, therefore, not be seriously affected.

It is not entirely true that small changes in the average rates are without important effect. Suppose, as a hypothetical example, that we observe an ecosystem containing "n" creatures whose eating habits could be described by a chain. That is, creature 2 eats only creature 1, creature 3 eats only creature 2, and so on. We will suppose that the total production of creature 1 is constant, and we ask how the biomasses of the other creatures depend on the proportion of their daily ration that they use for growth—i.e., on the value of the parameter g_j. Let us then suppose that suddenly all the growth fractions g_j are reduced to 90 percent of their former values.

The abundance of creature 2 will not be affected at all. Its daily ration is unchanged (as are all the other daily rations), and its food supply is also unchanged. But its growth rate, and therefore the amount of food available to creature 3 is reduced by 10 percent—i.e., to 90 percent of its former value. Consequently, the abundance of creature 3 must also be reduced to 90 percent of its former level. But the production rate of creature 3 is also reduced to 90 percent of its earlier value. If its abundance is reduced as well, the food available to creature 4 must be 90 percent of 90 percent of its former value—a reduction of 19 percent.

The reduction in growth fractions thus propagates along the food chain. The abundance of creature 4 is reduced to 81 percent of its earlier level. Creature 5 is reduced to 72.9 percent, creature 6, to 65.6 percent, and creature 7, to 59 percent. The higher the trophic level a creature occupies, the greater will be the impact of this change in average production.

In the problems we are dealing with, we do not expect this multiplier effect to trouble us. First, our model contains only six trophic levels through which a multiplier can act. Furthermore, although there are chains in the model containing as many as six ecological groups, each ecological group also occurs in a chain containing no more than three different ecological groups. Second, none of the changes in the Oosterschelde are the kind that would change the average growth or metabolic rates of all creatures simultaneously. This kind of change might be produced by some kinds of pollution, but not by the changes in tidal range or basin size with which we are dealing.

We expect, therefore, that the parameters in the balance equations will not change substantially from one ecological stable state to another. The instantaneous rates can and regularly do change over the short term. But in the alternatives considered in the present study, their averages are unlikely to change substantially from one ecological stable state to another.

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Chapter 4

PREDICTING THE ECOSTATE

4.1. LIMITS OF THE BALANCE CONSTRAINTS

The mass balance constraints given in Eqs. (3.7), (3.8), and (3.9) of Chap. 3 form a set of simultaneous linear equations equal in number to the AQs. However, since each AQ is likely to be involved in two, three, or even more internal mass transfers, there will be more variables $x_{i,j,s}$ than there are equations. The balance equations are therefore insufficient to determine unique values for all the variables.

To illustrate, we consider the simple exemplary ecosystem used in Chap. 3 to construct the mass-balance coefficient matrix. There were five AQs (plants, detritus, herbivores, omnivores, and carnivores), all in the same segment, that were related by the food web depicted in Fig. 2.1 and again in Fig. 4.1. We also constructed a mass-balance coefficient matrix in Chap. 3 (see Sec. 3.9), and the result, shown earlier as Table 3.3, is repeated for convenience as Table 4.1. We describe this matrix as follows: Each row corresponds to one of the five balance equations, and hence to one of the AQs. The name of the AQ to which a row corresponds appears

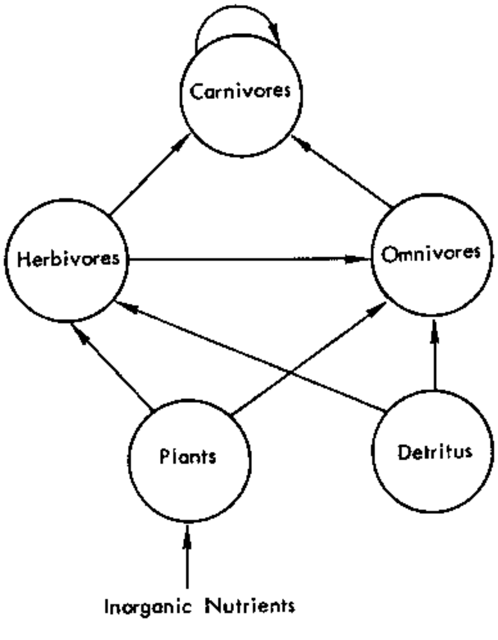

Fig. 4.1 — An exemplary food web

Table 4.1

THE EXEMPLARY MASS-BALANCE COEFFICIENT MATRIX

	Variable										
AQ Name	$x_{1,1}$	$x_{2,2}$	$x_{1,3}$	$x_{2,3}$	$x_{1,4}$	$x_{2,4}$	$x_{3,4}$	$x_{3,5}$	$x_{4,5}$	$x_{5,5}$	b_j's
Plant	0.1		2.0		1.0						100
Detritus	0.09	-0.1	1.0	-1.0	0.5	-0.5	0.125	0.05	0.05	0.05	0.0
Herbivore			0.2	0.2			-0.625	-0.25			0.0
Omnivore					0.05	0.05	0.05		-0.25		0.0
Carnivore								0.02	0.02	-0.23	0.0

in the left-hand border. Each of the ten columns of the matrix corresponds to the variable whose name appears at the head of that column. (Note that the variables do not have a subscript denoting the segment to which they belong. In our example, there is only one segment, so a subscript denoting segment is not necessary.) A bordering column contains the net export rates (for plants, the production rate) for the various AQs.

The balance equation for any AQ follows easily. For example, the balance equation for plants is

$$0.1x_{1,1} + 2.0x_{1,3} + 1.0x_{1,4} = 100 \ .$$

We constructed this equation by taking the coefficients in the "plant" row, multiplying each by its corresponding variable, and equating the sum of these products to the production rate (or, in general, the net export rate).

Similarly, the balance equation for herbivores is

$$0.2x_{1,3} + 0.2x_{2,3} - 0.625x_{3,4} - 0.25x_{3,5} = 0.0 \ .$$

Here, as we did for plants, we multiplied each variable by its coefficient in the row of Table 4.1 labeled "herbivore" and then equated the sum of these products to the net export rate of herbivores, which in this example is zero. All five balance equations can be constructed in just this fashion.

There are many values for the variables that satisfy all five equations simultaneously. We have singled out five such solutions, as shown in Table 4.2. Among these solutions, one may find the maximum and minimum values for the abundances of each ecogroup separately, and of all the ecogroups combined (i.e., the total biomass). In fact, we obtained these solutions by using standard linear programming techniques (the simplex method; see Dantzig, 1963) to maximize and minimize each of these abundances in turn. The reader can verify that all five solutions satisfy all five balance equations.

Table 4.2

FIVE SELECTED SOLUTIONS TO THE BALANCE EQUATIONS OF TABLE 4.1

Variable	Solution Number				
	1	2	3	4	5
$x_{1,1}$	1000.0	0.0	0.0	1000.0	0.0
$x_{2,2}$	0.0	0.0	0.0	900.0	521.74
$x_{1,3}$	0.0	0.0	50.0	0.0	50.0
$x_{2,3}$	0.0	0.0	54.54	0.0	0.0
$x_{1,4}$	0.0	100.0	0.0	0.0	0.0
$x_{2,4}$	184.0	104.44	0.0	0.0	0.0
$x_{3,4}$	0.0	0.0	0.0	0.0	16.0
$x_{3,5}$	0.0	0.0	83.64	0.0	0.0
$x_{4,5}$	36.8	40.89	0.0	0.0	3.2
$x_{5,5}$	3.2	3.56	7.27	0.0	0.28

The fact that there are multiple solutions to the balance equations does not mean that they do not contain any information. Indeed, among the five solutions shown in Table 4.2 one can find both the maximum and the minimum biomass of each AQ that is consistent with the balance equations, as well as the minimum and maximum total biomass. (We do not include detritus in total biomass.) For example, the biomass of plants must lie between 0 (solution 2) and 1000 (solution 1). The biomass of herbivores (calculated as $x_{1,3} + x_{2,3}$) must lie between 0 (solution 1) and 104.54 (solution 3). Similarly, the biomass of omnivores ($x_{1,4} + x_{2,4} + x_{3,4}$) is constrained to lie between 0 (solution 3) and 204.44 (solution 2). The biomass of carnivores ($x_{3,5} + x_{4,5} + x_{5,5}$) is bounded between 0 (solution 4) and 90.91 (solution 3).

Maximum total biomass is not the same as the sum of the individual maxima. That is, not all the AQs can simultaneously achieve their maxima. The maximum total biomass of 1224.0 units is achieved in solution 1. This is smaller than the sum of the individual maxima, which is 1399.2 units. Similarly, the minimum total biomass of 69.48 units, which is achieved in solution 5, is greater than the sum of the individual minima (0.0).

None of these solutions is a reasonable estimate of the abundances one should find in an ecosystem. In three of the solutions, the plant biomass is zero. In the fourth solution, all other abundances are zero. However, many solutions to these equations appear to be quite reasonable. Consider, for example, the solution shown in Table 4.3, which was chosen arbitrarily as a reasonable-looking solution from among the infinity of possible solutions. In this solution—again, the reader can verify that it satisfies all five balance equations—there are 237.04 units of plants, 78.79 units of herbivores, 41.15 units of omnivores, and 19.77 units of carnivores. These abundances can be calculated as the appropriate partial sum of the variables, in the manner suggested a few paragraphs above. It should not surprise an investigator to discover relative abundances such as these in, say, a planktonic community.

Table 4.3

A REASONABLE SOLUTION TO THE EXAMPLE BALANCE EQUATIONS

Variable	Value
$x_{1,1}$	237.04
$x_{2,2}$	124.16
$x_{1,3}$	35.56
$x_{2,3}$	43.23
$x_{1,4}$	4.98
$x_{2,4}$	14.92
$x_{3,4}$	21.25
$x_{3,5}$	9.92
$x_{4,5}$	8.27
$x_{5,5}$	1.58

4.2. THE FORM OF THE GIBBS FUNCTION

As we explained in Sec. 2.7, our model selects the unique stable ecostate from among the multitude of balanced ecostates by minimizing the Gibbs function. There are a number of justifications for doing so. For example, minimizing the Gibbs function has the statistical interpretation of modifying the probabilities of finding different ecological groups in a sample to take account of information about their mass-balances. Alternatively, the Gibbs function may be accepted in its normal role as a measure of energy; in this interpretation, the ecosystem is deemed essentially similar to a thermodynamic system. In a different but related view, use of the Gibbs function is justified on the basis of its connection with the mass-action law of chemical kinetics, a law that has gained widespread acceptance in ecology. For the authors of this study, however, the main justification is that the Gibbs function works well: The model is easy to calibrate and use, and its behavior is reasonable.

As we use the Gibbs function in our model, the mathematical form of its function is

$$F(x) = \sum_{s} \sum_{j} \sum_{i} x_{i,j,s} \left(c_{i,j,s} + \log \frac{x_{i,j,s}}{\bar{x}_s} \right) + \sum_{s} Z_s \log \frac{Z_s}{\bar{x}_s} , \tag{4.1}$$

where Z_s is a parameter that controls the response of the ecostate to changes in the size of segment s.

$$\bar{x}_s = \sum_{i} \sum_{j} x_{i,j,s} + Z_s . \tag{4.2}$$

Our sole reason for introducing the parameters Z_s is so that the stable ecostate predicted by our model will be sensitive to changes in the sizes (areas or volumes) of segments. We will model a decrease of, say, 25 percent in the area of shallow bottoms and tidal flats by reducing the corresponding Z_s by 25 percent. The sensitivity of the ecostate to such a change will depend, as we will show later, on how large the initial or nominal value of Z_s is chosen to be. The larger we choose the nominal Z_s, the more sensitive will be the ecostate to a given percentage change in Z_s.

However, there is some justification other than this practical one for introducing the parameters Z_s. According to the statistical justification for using the Gibbs function (see Sec. 2.7.3), we can interpret the ratio $x_{i,j,s}/\bar{x}_s$ as the probability of finding species j with an appropriate fraction of species i among its stomach contents in a sample from segment s. This is the same as the fraction of the sample that one expects to consist of species j. modified appropriately for the fraction of species i among its stomach contents.

But most of the sample will not be biomass at all. It will be the "filler" substance of segment s (sand and mud for benthic segments, and water for the pelagic segment), which is biologically inert. We interpret the ratio $Z_s/\bar{x}_s$ to be the fraction of the sample that consists of this filler. *Thus,* Z_s *can be interpreted as the mass of filler in segment s.*[1]

There remains the question of how the mass of the filler and the biomass in a segment are related to the size of that segment. One view is that the segment can hold only a certain maximum mass, and any gain in biomass must be compensated by a loss in the mass of the filler. The other view holds that the mass of the filler in a segment remains constant, regardless of the biomass in that segment, unless the mass of filler is changed by dredging, or by partitioning the basin with compartment dams, etc.

We do not see that either view has any theoretical advantage, and hence we make our choice on practical grounds. The choice we make is that the mass of filler in a segment should remain constant when biomass is added or removed. Our reason for this choice is that it does not place a rigid limit on the biomass that can occupy a segment, whereas the first view does. We see no reason for imposing an essentially arbitrary limit on the biomass that can occupy a segment.

The parameters $c_{i,j,s}$ in the Gibbs function are to be adjusted during calibration so that the model will reproduce, as nearly as permitted by the balance equations, the observed present ecostate. They will depend, to some extent, on the nominal values of the Z_s. However, for any values of the Z_s, we can always find values for the $c_{i,j,s}$ that will cause the model to reproduce any desired "balanced" ecostate. Thus, we can always calibrate our model just as well with one set of Z_s's as with another.

In constructing our model, we have chosen the nominal Z of each segment to be large compared with the initial amount of biomass in that segment. That is, we chose Z_s to be a large fraction of $\bar{x}_s$ (typically in excess of 95 percent). This has the effect of maximizing the sensitivity of the model to changes in segment sizes. (Further increases in Z would have negligible effect on this sensitivity.) We made this choice based on the observation that in the Oosterschelde, each segment is

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[1] This interpretation should be modified for organisms that are territorial in nature. Such organisms may act as though their essential being extends beyond the outline of their bodies, and hence includes some of the filler.

mostly composed of "filler" (water for the pelagic segment, sand or mud for the benthic segments).

We now let A be the matrix of coefficients in the balance equations, x the vector of variables $x_{i,j}$, and b the vector of average net export rates (or production rates, for photosynthetic organisms). The operation of the model can then be compactly described in matrix notation as finding the value of x that solves the following constrained extremum problem:

$$\left.\begin{array}{l}\text{Minimize } F(x) \\[1ex] \text{subject to } Ax = b,\ x \geq 0\ .\end{array}\right\} \qquad (4.3)$$

The literature describing problems such as (4.3), and techniques for their solution, is extensive. For example, in the work of Abadie (1967), Fiacco and McCormick (1968), and Rosen (1960), one finds rather general methods, applicable to a large class of problems containing (4.3). More specialized techniques, applicable only when F(x) is the Gibbs function, appear in studies by Clasen (1965) and Bigelow (1970a).

It can be shown that in our case there is a unique solution "x" to problem (4.3) whenever there is any vector $x \geq 0$ that satisfies the balance constraints (see Bigelow, 1970b). It can also be shown that, given any $x > 0$ (i.e., with all variables strictly positive) that satisfies the balance constraints $Ax = b$, a vector c, with components $c_{i,j}$, can be found such that the given x is the unique solution to (4.3). This means that we can always calibrate our model to any observations that are consistent with the balance equations.

4.3. PROPERTIES OF THE GIBBS FUNCTION

In this section and the next, we would like to derive and describe some of the characteristics that the Gibbs function lends to the model. Our vehicle for doing so will be the simple exemplary ecological system we described earlier, involving only plants, detritus, herbivores, omnivores, and carnivores. In this section, we will concentrate on the consequences of minimizing the Gibbs function. We will ignore the balance equations entirely, so that we can separate the effect of requiring the Gibbs function to be minimized from the effect of requiring that the balance equations be satisfied. Thus, to specify this abbreviated model, we need only assign values to the parameters $c_{i,j}$ of the Gibbs function, and the Z of the single segment of the example. We therefore arbitrarily set $Z = 10000$, and set the parameters $c_{i,j}$ as shown in Table 4.4. How these values were obtained will be explained immediately.

The values for the parameters $c_{i,j}$ were not chosen arbitrarily. The reason for choosing them becomes evident when one minimizes the Gibbs function with these specific values for the $c_{i,j}$'s. Thus, we wish to find values for the $x_{i,j}$'s that minimize

$$F(x) = \sum_j \sum_i x_{i,j} \left(c_{i,j} + \log \frac{x_{i,j}}{\bar{x}} \right) + Z \log \frac{Z}{\bar{x}}\ ,$$

where

$$Z = 10{,}000 ,$$

$$\overline{x} = \sum_j \sum_i x_{i,j} + Z .$$

As stated above, we are ignoring the balance equations. In this case, elementary calculus tells us that when this function has achieved a minimum, all of its partial derivatives will be zero. Further, because F(x) is convex (Shapiro and Shapley, 1965), whenever all of its partial derivatives are zero, it will be at a minimum. But the partial derivative of F(x) with respect to $x_{i,j}$ is just

$$\frac{dF(x)}{dx_{i,j}} = c_{i,j} + \log \frac{x_{i,j}}{\overline{x}} . \tag{4.4}$$

In fact, we obtained the values for the $c_{i,j}$'s in Table 4.4 by substituting the values for the $x_{i,j}$'s from Table 4.3 into Eqs. (4.4) along with Z = 10000, setting the derivatives to zero (so that F(x) would be minimized), and solving the resulting equations for the parameters $c_{i,j}$.

Table 4.4

VALUES FOR THE $c_{i,j}$'s IN THE EXAMPLE PROBLEM

Parameter	Value
$c_{1,1}$	3.7910
$c_{2,2}$	4.4376
$c_{1,3}$	5.6880
$c_{2,3}$	5.4927
$c_{1,4}$	7.6538
$c_{2,4}$	6.5565
$c_{3,4}$	6.2029
$c_{3,5}$	6.9647
$c_{4,5}$	7.1466
$c_{5,5}$	8.8018

The reader may wish to verify that the values of the $x_{i,j}$'s from Table 4.3 not only make the derivatives of F(x) zero, but that no other values of $x_{i,j}$ will do so. To show this, we set the derivatives in Eqs. (4.4) to zero, and solve for $x_{i,j}$. The result is

$$x_{i,j} = \overline{x} \cdot \exp(-c_{i,j}) . \tag{4.5}$$

Since we don't yet know the value of $\bar{x}$, we sum Eqs. (4.5), one for each variable, and add Z = 10000 to the result. Recalling the definition of $\bar{x}$, we obtain

$$\bar{x} = \bar{x} \sum_{j} \sum_{i} \exp\ (-c_{i,j}) + Z \ . \tag{4.6}$$

Substituting the values of $c_{i,j}$ from Table 4.4 into Eq. (4.6), we find that

$$\bar{x} = 0.04762\ \bar{x} + Z\ , \tag{4.7}$$

which, since Z = 10000, implies that $\bar{x}$ = 10500.91. Note that no other value of $\bar{x}$ can satisfy Eq. (4.6) when Z = 10000 and the $c_{i,j}$'s are as in Table 4.4 When the reader substitutes this value of $\bar{x}$ into Eqs. (4.5), he will find that each variable x also has a unique value, and that value is the one appearing in Table 4.3.

Recall that in our example, we chose the value of Z arbitrarily. Now, still ignoring the balance constraints, let us determine the effect of varying the value of Z. In our model, this represents changing the size of the segment. In particular, we will suppose that the parameters $c_{i,j}$ remain the same, but that Z is now changed from 10000 to 6000 units—a reduction by 40 percent. When we now solve Eq. (4.7) for the value of $\bar{x}$, we obtain $\bar{x}$ = 6300.55. It is no accident that this is precisely 60 percent of its former value. Again, when each of the Eqs. (4.5) is solved for a new value of $x_{i,j}$, we find that each $x_{i,j}$ has also been reduced to 60 percent of its former value.

The results we have illustrated in this section are actually quite general. Even without the balance equations, and even with more than one segment, minimizing the Gibbs function will always yield unique values for all the variables. (As it happens, this is also true when the balance equations are considered, so long as they can be satisfied by at least one set of values of the variables.) It is also true that without the balance equations, the model will always respond to a change in Z_s, with a proportionate change in all variables belonging to segment s. However, when we begin to consider the balance equations, this will no longer be the case

4.4. PROPERTIES OF THE COMPLETE MODEL

In this section, we will continue our description of some of the behavioral characteristics of the model. Again, our vehicle will be the simple exemplary ecosystem involving only plants, detritus, herbivores, omnivores, and carnivores. Now, however, we will consider all elements of the model together, including both the Gibbs function and the balance equations. All the necessary parameters have been specified earlier. The coefficients in the balance equations and the external mass transfer rates can be found in Table 4.1. The parameters $c_{i,j}$ are given in Table 4.4. As before, we set Z = 10000.

Now suppose that we repeat the experiment in which we vary Z. The reader can verify that the solution we obtained when we did this before will not satisfy the balance constraints. Hence, in the presence of the balance constraints, the solution must be different. In Fig. 4.2 we see the result. The abundance of plants increases almost proportionately with Z, but only (of course) up to the maximum abundance permitted by the balance equations. In addition, the balance requirements prevent the other species from increasing at all. Plant production is fixed at 100 units per day. As plants increase, they metabolize more of their own production, leaving less for herbivores and omnivores to eat. Hence herbivores and omnivores decline in abundance. But this, in turn, reduces the food supply for carnivores, and therefore the abundance of carnivores must decline as well.

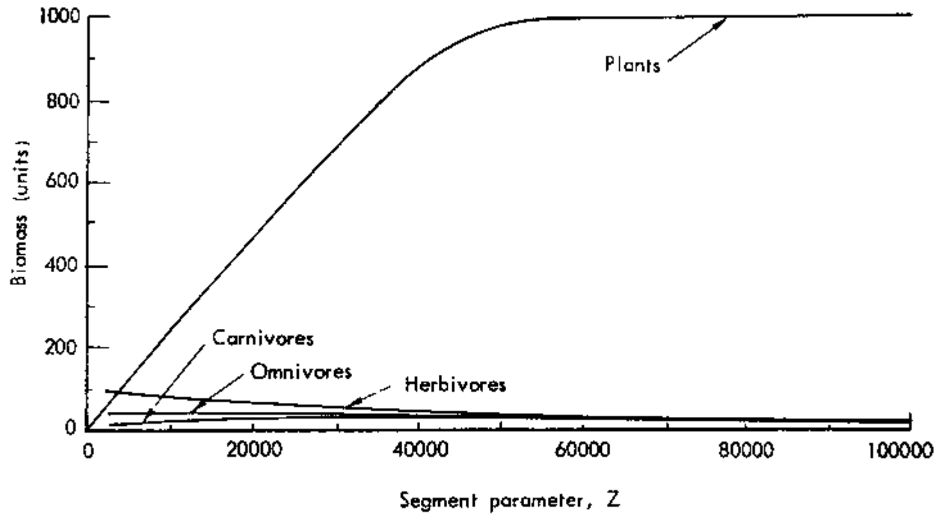

Fig. 4.2 — Abundances vs. segment parameter, Z
(nominal value of Z = 10000)

Recall that we chose Z = 10000 arbitrarily. We could have chosen any other value for Z and used it in Eqs. (4.4) to calculate different values for the parameters $c_{i,j}$. To see the effect of this, let us set Z = 100. The corresponding values for the $c_{i,j}$'s are shown in Table 4.5.

Once again, we repeat the experiment of varying Z. We see the result in Fig. 4.3. This figure has many of the same features as Fig. 4.2, which shows the result of the same experiment when the starting or nominal value of Z is 10000. (In Fig. 4.3, of course, the nominal value of Z is 100.)

As before, the abundance of plants increases almost proportionately with segment size, and, as before, the balance requirements force the abundances of the other three species to decline. However, now the increase in plant abundance is much less marked for the same relative change in Z. In Fig. 4.2, for example, the effect of doubling Z from 10000 to 20000 is to increase plant abundance by nearly a factor of 2. But, in Fig. 4.3, the effect of doubling Z from 100 to 200 is to increase plant abundance by only 33 percent. This confirms a statement we made earlier: that the choice of the nominal value of Z governs the sensitivity of the model to

Table 4.5

ALTERNATIVE VALUES FOR THE $c_{i,j}$'s
CORRESPONDING TO Z = 100

Parameter	Value
$c_{1,1}$	0.9302
$c_{2,2}$	1.5769
$c_{1,3}$	2.8272
$c_{2,3}$	2.6319
$c_{1,4}$	4.7930
$c_{2,4}$	3.6957
$c_{3,4}$	3.3421
$c_{3,5}$	4.1039
$c_{4,5}$	4.2858
$c_{5,5}$	5.9410

changes in the size of its segments, and that the larger one chooses the nominal Z, the more sensitive will be the model.

Now we return the nominal value of Z to 10000, and consider the effect on this simple ecosystem of varying the rate of plant production. This experiment is shown in Fig. 4.4. Immediately one is struck by the fact that, once plant production is higher than approximately 50 units per day, further increases in production have little effect on plant abundance. Rather, almost the entire increase in production

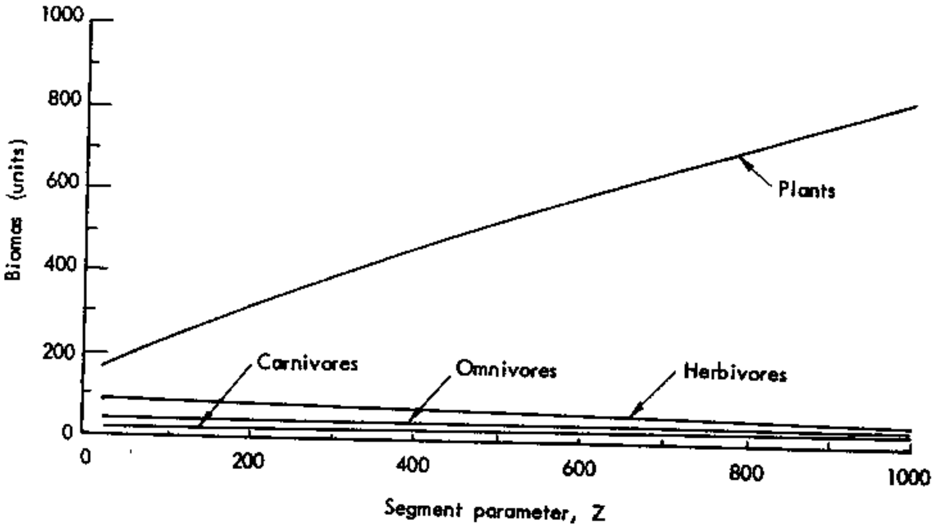

Fig. 4.3 — Abundances vs. segment parameter, Z
(nominal value of Z = 100)

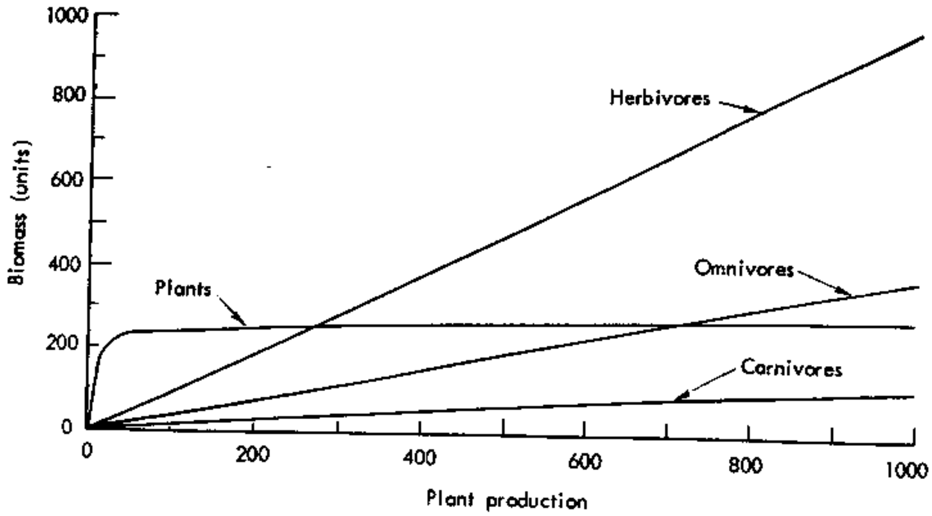

Fig. 4.4 — Abundances vs. plant production (nominal value of Z = 10000)

is absorbed by an increase in animal life. Herbivores and omnivores increase, both of which eat the plants, and carnivores increase because their food supply—herbivores and omnivores—increases.

One way of describing this phenomenon is in terms of the efficiency with which plant production supports the biomass in the ecosystem. Quantitatively, we define this measure of efficiency as the ratio of total biomass to plant production: The higher the ratio of biomass to plant production, the more efficient is the ecosystem in supporting life. This ratio reaches a maximum in solution 1 of Table 4.2. We will choose our units so that the efficiency in this case is 1.0.

Although this is difficult to see from Fig. 4.4, the model does predict that as production increases, the efficiency of the ecosystem will decline. Thus, the efficiency declines from 0.86 when plant production is 20 units per day, to 0.14 when plant production is 1000 units. (In the initial state, in which plant production is 100, the efficiency is 0.31.)

This prediction of declining efficiency may seem unrealistic, until one remembers that the model responds to changes in the density of biomass in each segment. As the plant production increases, the biomass and its density also increases. In a sense, then, as the plant production increases, one may think of the organisms in the ecosystem as shifting from competition for food to competition for space. When food is scarce, organisms that will be favored need relatively little food to support a unit of biomass. More than anything else in the model, this property characterizes plants. Hence, when plant production is low, most of that production is used to support plant biomass. Conversely, when plant production is high, herbivores are favored, because they require the largest amount of food to support each unit of biomass. This illustrates a general property of the model: It predicts that an ecosystem will tend to use the most limiting resources as efficiently as possible, while often appearing quite wasteful of more abundant resources.

A property of the model that we emphasize is that two species can coexist in what our model describes as the same niche. Unlike most ecological models, our model will not predict that one or the other of the species will become extinct. While we do not question the conventional wisdom that two species cannot occupy the same niche, we are gratified that our model permits the user to describe the ecosystem in a much simpler way than is necessary with most models. For two herbivores to coexist, most models require that two different niches be defined, and this may involve the use of more factors—or more values for the factors—than the data will reasonably support. But, a difference in the niches of two different species need not be explicit in a model. For the purposes at hand, that difference may be constant, and therefore an unnecessary addition to an already complex model.

To illustrate, we modify the simple exemplary ecosystem by forbidding omnivores to eat herbivores. Then, what used to be an omnivore is now a second kind of herbivore. We can picture this in a new food web, shown in Fig. 4.5. The only difference between this food web and the previous one is that the arc from "herbivores" to "omnivores" has been deleted. Thus, the only difference between our earlier example and a model that uses the revised food web of Fig. 4.5 is that the variable corresponding to the deleted arc—namely $x_{3,4}$, omnivores eating herbivores—is omitted. The new model, therefore, has a mass-balance coefficient matrix like that of Table 4.1 except that the column labeled "$x_{3,4}$" is removed.

In this revised ecosystem, the two herbivores are indeed different species. The original herbivore must assimilate his own body weight in food each day in order

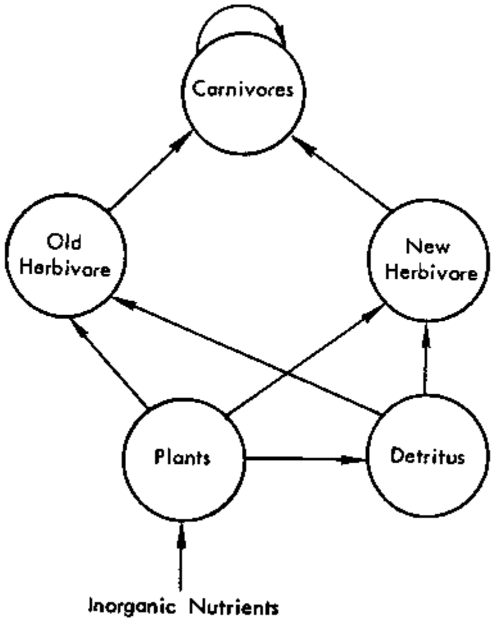

Fig. 4.5 — New exemplary food web with two competing herbivores

to live and grow normally. The other herbivore—the converted omnivore—needs to assimilate only one-half of his body weight each day. In addition, the metabolic fractions m_j are different for the two herbivores.

It is also true that, as far as the model is concerned, both herbivores occupy the same niche. As explained above, we concur with the idea that they must in fact occupy different niches. For example, their microhabitats might differ, although in the example there is only one habitat (a single segment). Or, the carnivore ecogroup, which we have represented as a single kind of organism, might in fact consist of several species with different relative preferences for the two herbivores. Or the herbivores might prefer different plants as their major food sources, although in the model only a single kind of plant is provided. In fact, the model recognizes none of these potential niche differences between the two herbivores. Even their relative preferences for plants instead of detritus are the same.

The experiment we use to illustrate the coexistence of the two herbivores is to determine the dependence of the abundances on plant production. This experiment is depicted in Fig. 4.6. As plant production increases, both herbivores take advantage of the increasing food supply. However, because there is a difference in the assimilation and production rates of the two herbivores, the model does distinguish between them (although it is not obvious from Fig. 4.6).

Recall that the original herbivore must assimilate his own body weight in food each day. The other herbivore—the converted omnivore—only needs to assimilate one-half of his body weight each day. The model predicts that the original herbivore will be relatively favored over the converted omnivore when food is abundant (i.e., when plant production is high), whereas the converted omnivore will be favored when food is scarce (i.e., when plant production is low). Indeed, the model predicts that the ratio of converted omnivores to original herbivores will drop from 1.0,

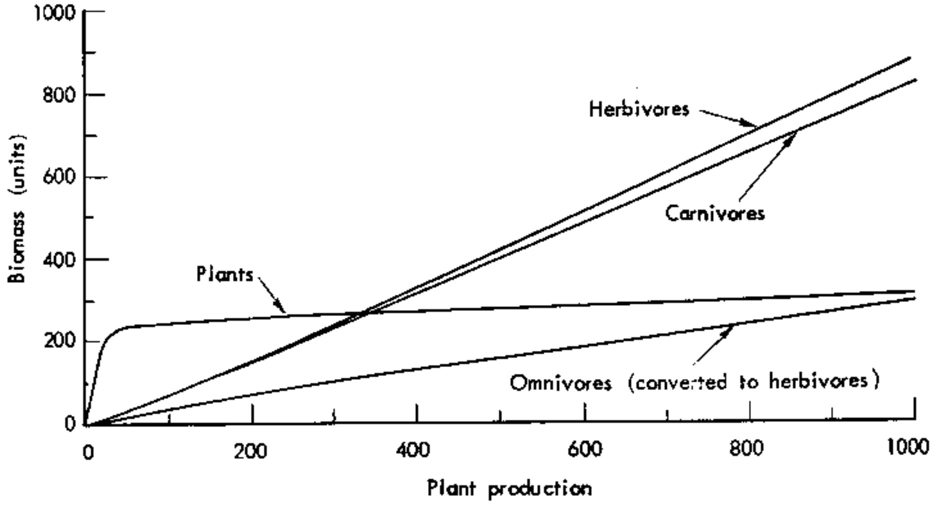

Fig. 4.6 — Abundances vs. plant production with two competing herbivores (nominal value of Z = 10000)

when plant production is 20 units per day, to .33, when plant production is 1000. This is another manifestation of the model's characteristic of seeking an efficient use of scarce resources.

We are particularly interested in the influence of fishing on the ecosystem. Consequently, as our final exemplar we calculate the dependence of the abundances on the rate at which the original herbivores are removed from the ecosystem. The results are shown in Fig. 4.7. Here we have used the revised food web, in which the organism that began as an omnivore has been converted into a herbivore.

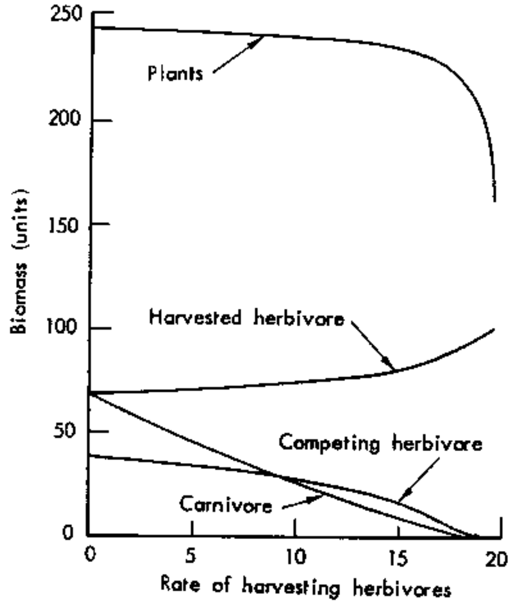

Fig. 4.7 — Abundances vs. herbivore harvest rate with two competing herbivores (nominal value of Z = 10000)

The results tell us that if no harvesting is taking place—i.e., if this ecosystem is free from exploitation—then the abundances are as follows: plants, 240 units; original herbivores, 67 units; converted omnivores (now the new herbivores), 37 units; and carnivores, 67 units. Looking back at Table 3.1, we find that the original herbivores grew at a rate that added 20 percent of their mass daily. Thus, in the unexploited state, these organisms are producing 20 percent of 67, or 13.4 units of biomass daily.

Suppose now that man exploits this ecosystem by harvesting these herbivores. If the harvest rate is modest compared with the natural production rate of 13.4 units per day, then all that happens is that man replaces the carnivore as the exploiter of herbivores. The abundance of the competing herbivore is somewhat less than in the case with no harvesting, but significantly this reduction is smaller, even in relative terms, than the reduction in carnivores.

If the harvest rate is comparable to the natural production rate of 13.4 units per day (say, in the range of 10 to 15 units), the abundance of the original herbivore must be larger than in the no-harvest case. At these levels of exploitation, there is little predation by carnivores and little competition from the other species of herbivore.

Finally, if the harvest rate is above 15 units per day, it is necessary not only that the abundance of herbivores be substantially greater than in the no-harvest case, but that the amount of plant production that is dissipated by plant metabolism be smaller as well. In the model, this reduction is accomplished by decreasing plant abundance. In a real ecosystem, it might be accomplished by replacing one kind of plant with another. Ultimately, of course, the model predicts that too large a harvest rate (20 or more units per day) simply cannot be maintained.

When interpreting these results, it is necessary to keep in mind that the model assumes that the ecosystem is in long-term balance. Thus, when it predicts that at harvest rates of 10 to 15 units per day there will be little predation by carnivores and little competition from the other herbivores, it is saying that if the ecosystem is in balance, these things will be true. It is always possible, in a real ecosystem, to exploit a population so heavily for a short time that its production falls below the harvest rate, and its population collapses. But if this happens, the ecosystem was surely not in balance at that exploitation rate. Similarly, when the model predicts that the population of the exploited herbivores will rise if the harvest rate is increased, it is saying that if the harvest rate is increased and the population is not made to rise (either by protecting it from predation or competition, or by supplementing its food supply), then the increased harvest rate cannot be long sustained.

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PART II

MODEL IMPLEMENTATION AND PARAMETER EVALUATION

Chapter 5

GENERAL APPROACH TO IMPLEMENTATION

To implement the model for use in our study of the Oosterschelde, we must evaluate all the parameters. The guiding principle is that, once the parameters have been chosen, the model should reproduce the current ecological situation. In other words, given, as inputs, the external mass transfer rates and the segment sizes that characterize today's Oosterschelde, the model should produce, as outputs, our estimates of today's abundances of the various AQs.

To remind the reader, the model can be expressed mathematically as

$$\left.\begin{array}{l} \text{Minimize } F(x) \\ \text{subject to } Ax = b,\ x \geq 0\ , \end{array}\right\} \tag{5.1}$$

where A is the matrix of coefficients in the balance equations, b is the vector containing all the external mass transfers, x is the vector of variables, and F(x) is the Gibbs function.

In Sec. 3.8, we discussed at length how to construct the matrix A from such quantities as daily rations, metabolic rates, etc. In Chap. 6 we will discuss how to obtain the values for these necessary quantities, and in Chap. 7, the various external mass transfer rates. Then, there will remain only the question of how to estimate values for the parameters in the Gibbs function.

Again to remind the reader, the form of the Gibbs function is

$$F(x) = \sum_s \sum_j \sum_i x_{i,j,s} \left(c_{i,j,s} + \log \frac{x_{i,j,s}}{\bar{x}_s} \right) + \sum_s Z_s \log \frac{Z_s}{\bar{x}_s}\ , \tag{5.2}$$

where Z_s = the segment parameter (mass of filler) for segment "s" and

$$\bar{x}_s = \sum_i \sum_j x_{i,j,s} + Z_s\ . \tag{5.3}$$

To evaluate each $c_{i,j,s}$ we first estimate initial values for each of the variables $x_{i,j,s}$. Next, we choose nominal values for the segment parameters Z_s (which are, to a large extent, arbitrary, as discussed in Sec. 4.2). Finally, we set

$$c_{i,j,s} = -\log \frac{x_{i,j,s}}{\bar{x}_s}\ . \tag{5.4}$$

(See Sec. 4.4, especially Eq. (4.4).)

The most crucial task in evaluating the parameters $c_{i,j,s}$ is to find initial values for the variables $x_{i,j,s}$. We have determined the values in three steps. First, we estimated the abundance of each ecological group in each segment, a time-consuming task, the difficulties and inherent errors of which we discuss in Chap. 8. The reader should refer to the Addendum to this volume for descriptions of the data and the detailed procedures used to make these estimates.

The second step, which we discuss in Chap. 9, was to partition the abundances of heterotrophs by diet item. Recall that the abundance of a heterotrophic ecological group in a segment can be expressed as a sum of certain of the variables $x_{i,j,s}$. Having estimated the values of these sums in the first step, we must now break the sums down into their components. These components relate to the degree to which the heterotroph depends for its food on each of its diet items. Unfortunately, virtually no data exist from which to estimate these degrees of dependence. Thus, we based our estimates on the assumption that a heterotroph will eat each of its diet items in rough proportion to that item's abundance.

The second step was carried out only for heterotrophs. It is not necessary for either detritus AQs or photosynthetic AQs. Strictly speaking, a photosynthetic AQ has no diet items, although it does metabolize part of its own substance to maintain itself. Hence, the abundance of a photosynthetic AQ is represented by a single variable rather than a sum of variables, and there is no need to partition this abundance into components. Similarly, the abundance of a detritus AQ is also represented as a single variable, and so there is no need to partition this abundance either. (See Secs. 3.6 and 3.7 for a discussion of photosynthetic and detritus AQs.)

The third step in finding initial values for the variables $x_{i,j,s}$ was to ensure that they satisfied the balance equations—i.e., were "balanced." This subject is treated in Chap. 10. In general, the values of the variables estimated in the first two steps will not be balanced because of natural variations in the abundances of the different ecogroups, both from place to place and from season to season or year to year, and because of measurement errors. These values must be adjusted to make them balance. To this end, we used a combination of mathematics and computation on the one hand, and common sense (or "expert judgment") on the other.

First, we computed values for the variables $x_{i,j,s}$ that were, in a mathematical sense, "close to" estimates from the first two steps, but which were balanced. Then, where these balanced estimates did not seem to be close enough to the original estimates, we changed the original estimates by judgment, within what we regarded as their range of uncertainty. The purpose of these changes was to make our original estimates more nearly satisfy the balance equations, so that when we calculated a new balanced estimate, it would be closer to the revised, unbalanced estimate. By repeated application of this technique, we arrived at balanced estimates that we believe to be within the range of estimation and measurement error for the variables $x_{i,j,s}$ in the present Oosterschelde.

One very interesting and useful observation is that the balance equations have two logical interpretations. The first is that each balance equation is another logical constraint on the "true" values of the variables. That is, in all circumstances the variables must satisfy the balance equations. This is the interpretation we have implicitly assumed throughout our development.

The second interpretation evolved as a result of our learning that there were almost no data from which to estimate the average net rate of detritus import. This interpretation is that if the balanced values of the variables are known, then they imply the external mass transfer rates with which they are in balance. Therefore, while we were finding balanced values for the variables, we omitted the detritus balance equation and required only that the variables satisfy the remaining equations. Once we had found an initial solution that satisfied these remaining equations, we used it to calculate a net rate of detritus import. That is, we substituted the balanced values for the variables $x_{i,j}$s into the detritus balance equation, and calculated the detritus import rate. (See Chap. 10 and the appendix for further discussion.)

Chapter 6

DAILY RATIONS, METABOLIC RATES, AND FECAL FRACTIONS

In this chapter, we shall present methods for obtaining estimates of the parameters necessary to construct the matrix A. What these parameters are, and how the matrix A is constructed from them, has been given in Sec. 3.8, but for convenience, we repeat the information here. For each ecogroup j, the parameters include: the daily rations r_j, which is the fraction of body weight assimilated each day; the metabolic fraction m_j, which is the fraction of the daily ration that is metabolized; the production fraction g_j, which is the fraction of the daily ration used for growth or reproduction; and the fecal fraction f_j. (When an organism of ecogroup j is eaten by an individual from either the same or a different ecogroup, f_j is the fraction of that meal that is excreted as feces.) One other parameter—the migration rate MIG_j—is required to construct the matrix A, but we shall defer its discussion until we deal with external mass transfer rates in the next chapter.

Our method uses the classical energy budget of an animal (Winberg, 1956, and others), which equates the daily ration (net assimilation) to the sum of metabolism (also called respiration) and production (growth plus reproduction). Since we have expressed metabolism m_j and production g_j as fractions of the assimilated daily ration r_j, the energy budget is expressed as

$$m_j + g_j = 1 .$$

Thus, it is necessary to estimate only one of the quantities, m_j or g_j, for each ecogroup. In this chapter, we will discuss how we have evaluated r_j, m_j, and f_j for each ecogroup j. We begin with r_j and m_j, for which we have considered the following four cases:

1. *Detritus.* The metabolic fraction m_j is always assumed to be 1.0, and r_j is the fraction of the mass of detritus that is mineralized per day. We shall explain later (in Sec. 10.8) that the value of r_j for detritus was adjusted to prevent the requirement for detritus import from being impossibly large. It was not evaluated on the basis of direct measurements of mineralization rates.
2. *Photosynthetic organisms.* The daily ration r_j is the fraction of the plant biomass that is consumed by the processes of plant metabolism ($r_j m_j$) and plant mortality ($r_j(1 - m_j)$). The latter is the amount that dies and becomes detritus. How we have estimated r_j and m_j for photosynthetic organisms will be discussed in Sec. 6.1.
3. *Birds.* These ecogroups have been extensively treated by Wolff et al. (1975). We have adopted Wolff's estimates of the daily rations of these groups. It is not necessary to estimate their production fractions g_j, since none of them are preyed upon, and therefore all that they assimilate is lost to the ecosystem. The daily rations of birds are discussed in Sec. 6.2.

4. *Heterotrophs other than birds.* To estimate r_j and m_j for the remaining ecogroups, we adopted a simple model that related these quantities to the average and maximum body weights of the organisms in the ecogroup. We discuss the model in Sec. 6.3.

Finally, it is necessary to estimate fecal fractions f_j for each ecogroup. These estimates are described in Sec. 6.5, where we also discuss our assumption that fecal production depends on what is being eaten, and not on what is doing the eating. The data concerning fecal production are so scanty that our estimates of the parameters f_j are highly uncertain. So, we discuss the effects of varying these estimates upon the A matrix and upon our model's estimates of the ecological state of the Oosterschelde.

6.1. DEATH AND METABOLISM OF PHOTOSYNTHETIC ORGANISMS

Two variables in the model represent photosynthetic organisms. One is the pelagic segment, and represents phytoplankton. The other is in the shallow and intertidal segment, and represents sea grasses and benthic diatoms. Because these variables represent such different species, we estimated different death rates for each.

We estimated the death rate of phytoplankton as follows. According to Petipa et al. (1970), more than 50 percent of the phytoplankton produced die and become detritus. Our estimate of total production of photosynthetic organisms (see Sec. 7.1) is 455 tons/day. By comparison with the Grevelingen (Wolff, in preparation), we assume that 72 percent of this production is due to phytoplankton. If 75 percent of that production dies and becomes detritus, then the rate of death must be 246 tons/day. Comparing this with our estimate of 1300 tons for the average abundance of phytoplankton (see Table 8.4), we calculate a value for $r_j(1 - m_j)$ of 0.19. This value compares fairly well with estimates made for freshwater phytoplankton (Jassby and Goldman, 1974).

We used a similar method to estimate the death rate for photosynthetic organisms in the shallow and intertidal segment. For these species, however, we assumed that 90 percent of their production would die and become detritus. Their production is the remaining 28 percent of the total production of 455 tons/day, or 115 tons/day. Comparing this with our estimate of 7770 tons for their average abundance (Table 8.4), we find a value for $r_j(1 - m_j)$ of 0.0149.

According to Ryther (1956), metabolism (also called respiration) by phytoplankton is approximately 10 percent of production. We would expect metabolism by sea grass and benthic diatoms to be less. Thus, a maximum of 45 tons/day of the production is lost from the ecosystem because of metabolism by photosynthetic organisms. This is substantially less than our estimate of the amount that dies and becomes detritus. Furthermore, we do not know either the total production rate or the death rate to an accuracy of 45 tons/day. We have therefore ignored this factor.

Our final estimates of the parameters for photosynthetic organisms are

In the pelagic segment .... $r_j = 0.19$, $m_j = 0.0$

In the shallow/intertidal segment ... $r_j = 0.0149$, $m_j = 0.0$

6.2. DAILY RATIONS OF BIRDS

Our estimates for the daily rations of birds were derived from Wolff et al. (1975) whose Tables I, II, and III contain data on birds in the open and closed Grevelingen. Wolff estimated the standard metabolism (m) in kilocalories per day by means of the equation

$$\log m = \log 78.3 + 0.723 \log W ,$$

W being the body weight in kilograms. Body weights were taken from the literature. To obtain consumption per bird, the standard metabolism was multiplied by 5, which is taken from the literature as being a reasonable estimate of the ratio between food consumption and standard metabolism.

We formed weighted averages of Wolff's (1975) estimates of food consumption by each species of bird for our three bird ecogroups: plant-eaters, benthos-eaters, and fish-eaters. As weights for these weighted averages, we used the average population of each species observed in the Grevelingen, measured in units of ash-free dry weight. Data for calculating these weights can be found in Tables II and III of Wolff (1975). To obtain daily rations, we adjusted these consumption estimates for each bird ecogroup to account for the fraction of consumption that is excreted as feces (20 percent for benthos-eaters and fish-eaters, 50 percent for plant-eaters; see Sec. 6.5). The average daily consumption and ration values for birds in the Oosterschelde as a fraction of body weight are listed in Table 6.1.

Table 6.1

DAILY CONSUMPTION AND DAILY RATIONS FOR BIRD ECOGROUPS

Ecogroup	*Consumption*	*Ration*
Benthos-eating birds	0.26	0.208
Plant-eating birds	0.43	0.215
Fish-eating birds	0.51	0.408

6.3. HETEROTROPHS OTHER THAN BIRDS

We obtained estimates for net assimilation and metabolism for heterotrophs other than birds by means of a small submodel. This submodel applies only to heterothermic (cold-blooded) creatures (i.e., fish, macrobenthic fauna, etc.) and has been well substantiated for a large class of organisms. Examples of some of these studies will be mentioned below. This submodel assumes that net assimilation, r, and metabolism, mr, are both proportional to body weight raised to a power. That is

$$r = aW^{b-1} , \tag{6.1}$$

$$mr = cW^{d-1} , \tag{6.2}$$

where W is the weight of the animal, a and c are proportionality constants, and b and d define the rate of change of assimilation and metabolism with body weight. In Eqs. (6.1) and (6.2), we subtracted 1.0 from each exponent because our assimilation and metabolism quantities are expressed as fractions of body weight per unit time, whereas in the literature they are expressed as amounts per individual per unit time. The difference is a factor of body weight, W, or a change of 1.0 in the exponents.

A number of studies have found the exponent d to be close to 0.8 (Kleiber, 1975). For example, Weymouth et al. (1944) showed such a relationship for poikilothermal animals according to experiments on a kelp crab. Zeuthen (1947), working on marine microfauna, found a similar relationship. The review of Zeuthen (1953, 1970) extended this concept to organisms from bacteria to large mammals. It has been found to hold true for plankton (Ikeda, 1970, and others). Conover (1960), working on copepods, amphipods, and euphasids, and Rajagopal (1962), working on a hydromedusa, etenophores, copepods, decapods, and a tunicate, stated that the log respiration correlates well with the log dry body weight of animals.

Winberg (1956) fitted data from a very large number of sources to Eq. (6.2) and suggested that a value of $d = 0.8$ is a reasonable approximation for most kinds of fish. The value of the scale parameter, c, is influenced by temperature, food concentration, and activity, but characteristic values can be assigned to particular groups of fish performing routine metabolism at a particular temperature.

MacKinnon's (1973) values for American plaice based on observed values for the low routine oxygen consumption level concurred with values predicted from the general equation by Winberg (1956) for the metabolism of all fishes. The pooled data for the rate of oxygen consumption, R, at weight, W, are represented by the equation

$$R = 0.0582W^{0.8} ,$$

once again exhibiting an exponent of 0.8.

Edwards, Finlayson, and Steele (1972) report that $d = 0.82$ for anaesthesized cod at 12°C.

Paloheimo and Dickie (1966), approaching the question by an analysis of data on food and growth, found that respiration, R, calculated from R = assimilation minus production (meaning growth and reproduction), showed the same kind of relationship to body weight as that found in other respiratory studies. Like the others, Paloheimo and Dickie found that fish were remarkably constant in the level of the exponent d, most values being close to 0.8.

Finally, Ryszkowski (1975) found that $d = 0.813$ was representative of a wide variety of species. We used this value in our submodel of heterotroph assimilation and metabolism.

Other studies have suggested that the exponent b in Eq. (6.1) should be close to two-thirds. For example, this value has been suggested for crustacea of various types of feeding, including filter-feeders, "scavengers," and predators (Suschenya, 1970). Daan (1973) described the assimilation of North Sea cod as proportional to the weight raised to the two-thirds power. Hughes (1970), studying the energy budget for a tidal flat population of the bivalve *Scrobicularia plana*, arrived at similar relations.

Concerning the parameter c, Fenchel (1974) suggested that it will be the same for all heterothermic species. From Daan's (1975) model of the growth of North Sea cod, we estimated the value of c to be 0.036. Thus, only parameter a of Eq. (6.1) remained to be estimated for each ecogroup. This we did, not by estimating it directly, but by estimating the maximum weight that an individual organism can achieve, and deriving parameter a from the fact that at this weight, the growth rate of the organism must be zero.

However, the two terms we defined in Eqs. (6.1) and (6.2) are not sufficient to calculate the growth rate of the individual. We calculated production simply by subtracting metabolism from assimilation. But to obtain growth, we also subtracted that portion of production that is not growth—i.e., reproduction. Again from Daan's (1975) North Sea cod model, we assumed that the rate at which reproductive substances are manufactured is proportional to body weight, and that the constant of proportionality is 0.00055 per day. (We were aware, of course, that the individuals of most species do not reproduce until they reach a certain minimum size or age. However, considering all the uncertainties in our model, and in the data necessary to implement it, we felt justified in omitting this complication.) The resulting equation for growth rate is

$$\frac{dW}{dt} = aW^{0.667} - 0.036W^{0.813} - 0.00055W \ . \tag{6.3}$$

Substituting $W = W_{max}$ (the maximum weight that can be achieved by an individual) into Eq. (6.3), and setting the growth rate dW/dt to zero, we evaluated the parameter a.

Given the value of parameter a for an ecogroup, we could not estimate either the daily ration r_j or the metabolic fraction m_j without information on the actual (as opposed to maximum) weight that organisms in the ecogroup can achieve. Ideally, this information would take the form of a distribution of weights of the individual organisms. In practice, of course, such detailed information is not available—in fact, not even the average weight is always available. We were compelled to use a "reasonable" estimate for the weight of an individual organism. The selected weight was one-half the maximum weight, W_{max}. The consequences of this choice are explored in the next section.

Once an actual weight was selected, we substituted it into Eqs. (6.1) and (6.2) to obtain estimates of both r_j and m_j.

6.4. SENSITIVITY OF r_j AND m_j TO INDIVIDUAL WEIGHTS

In this section, we will explore the consequences to the parameters r_j and m_j of perturbing the maximum weight, W_{max}, and/or the actual weight, W, of an individual organism in an ecogroup. First, we consider the effect of perturbing W_{max}, since this perturbation has its direct effect only upon the parameter a (see Eq. (6.3) and the text following it). Table 6.2 shows the dependence of parameter a on W_{max}.

Table 6.2 covers a range for W_{max} extending from 10 μg (the average weight of a zooplankter) to 10 kg (the weight of a large fish such as cod). Note that this

Table 6.2

THE DEPENDENCE OF PARAMETER a, AND HENCE OF r_j, UPON W_{max}

W_{max}	a
0.00001	0.0067
0.0001	0.0094
0.001	0.0132
0.01	0.0185
0.1	0.0260
1.0	0.0366
2.0	0.0405
5.0	0.0465
10.0	0.0516
20.0	0.0572
50.0	0.0658
100.0	0.0731
1000.0	0.1042
10000.0	0.1499

enormous range in maximum weights makes only a twentyfold difference in the value of parameter a. Smaller changes in W_{max} make correspondingly less difference. Thus, a tenfold error in one's estimate of W_{max} causes only a 40 percent error in this parameter, and a twofold error in W_{max} causes an error of only 10 percent. The size of the errors do depend to some extent on the actual value of W_{max}. For large values of W_{max}, a substantial fraction of the daily ration will be devoted to reproduction (8 percent if $W_{max} = 10$ kg), whereas if W_{max} is small, reproduction will be negligible compared with metabolism. In the former case, the error in parameter a caused by any given relative error in W_{max} will be larger than in the latter case. The above-stated errors are based on an assumption that W_{max} is relatively small, which is true of most organisms in the Oosterschelde.

Next, note that the daily ration, r, is proportional to the actual body weight, W, raised to the minus one-third power (see Eq. (6.1)), and hence is not very sensitive to W. For example, an error in W of a factor of 2 results in only a 20 percent error in r. Similarly, dividing Eq. (6.2) by (6.1), we find that m, the metabolic fraction, is proportional to W raised to the power 0.146. Thus, a twofold error in W results in only a 10 percent error in m. These results are for the case where W_{max} is constant.

Our arguments suggest that no very important errors can arise from misestimating either the maximum or the actual (or representative) weights W_{max} and W by even as much as a factor of 2. This suggestion is misleading, however, because many elements of the matrix A are calculated by using the difference between the daily ration, r, and the metabolism, mr. In Sec. 3.8, these terms are given as gr − MIG. As we shall now show, even moderate errors in W and W_{max} can cause significant errors in gr.

As our example, we choose W_{max} to be relatively small, so that reproduction is small compared with metabolism. This enables us to calculate the parameter g (= 1 − m) as a function of W/W_{max}. The result is shown in Table 6.3.

Table 6.3

THE EFFECT OF MISESTIMATING W ON THE GROWTH FRACTION g

W/W_{max}	g
0.1	0.2855
0.2	0.2094
0.3	0.1612
0.4	0.1252
0.5	0.0962
0.6	0.0719
0.7	0.0574
0.8	0.0321
0.9	0.0153

The ratio $W/W_{max} = 0.5$ everywhere in our work, so that according to Table 6.3, about 10 percent of the daily ration is used for production (growth plus reproduction). (The magnitude will be slightly different for ecogroups with very large values of W_{max}, notably fish-eating fish.) But if the population of an ecogroup were better represented by a weight as high as, say, 70 percent of their W_{max}, then less than 6 percent of their daily ration would be devoted to production. This difference in W would be characteristic of the difference between a youthful population of organisms and one composed of old organisms.

Such an error could have grave consequences for the predators of an ecogroup. By reducing the production fraction of this ecogroup by a factor of almost 2, as we have in our example, while changing its daily ration hardly at all (recall that r is insensitive to W), the food supply of any predators that depend heavily on this ecogroup is reduced by half. Hence, the predators must also be reduced by half. This source of error is therefore potentially very important.

If the dependence of an ecogroup's predators on the value of W assumed for that ecogroup could be used to estimate W, then, given the abundance and daily ration of a predator, one could estimate the necessary production of its prey. This production, of course, is just the difference between assimilation, r (Eq. (6.1)), and metabolism, mr (Eq. (6.2)).

More generally, one could let the representative weight, W, for each ecogroup be a constant to be determined during the calibration procedure. However, as we describe later, we found this to be unnecessary for our model and determined that the blanket assumption that $W/W_{max} = 0.5$ for every heterotroph (except birds) yields a satisfactory calibration.

6.5. FECAL FRACTIONS

Values for feces production are widely varying in the literature. Welch (1968) listed energy budgets compiled from the literature. Table 6.4 lists assimilation efficiencies for a variety of organisms consuming a variety of food types.

A study of an algae browser by Trama (1957) concluded that 53 percent of the ingested calories were assimilated. Johannes (1964), working on the phosphorous

Table 6.4

ASSIMILATION EFFICIENCIES OF ORGANISMS

Experimental Animal	Food	Assimilation Efficiency (%)
Carnivorous fish		80
Euphausia pacifica	*Artemia nauplii*	88
Esoxlucius	Minnows	72
Cyprinus carpio	Chironomid larvae	74
Tubifex tubifex	Detritus	50
Navanax enermis	Opisthobranchs	63
Macrocyclops albidus	*Paramecium*	30
Lestes sponsa	Tubificids, *Daphnia*	36.6
Aplysia punctata	*Plocamium*	65
Aplysia punctata	*Enteromorpha*	59
Aplysia punctata	*Ulva*	75
Aplysia punctata	*Heterosiphonia*	71
Aplysia punctata	*Cryptopleura*	71
Aplysia punctata	*Delesseria*	45
Aplysia punctata	*Laminaria*	53
Acanthamoeba	*Saccharomyces*	58
Daphnia pulex	*Chlamydomonas*	31.1
Daphnia pulex	*Chlamydomonas* (highest concentration)	13.7
Calanus hyperboreus	*Thalassiosira*	19.1
	Thalassiosira	20.7
	Thalassiosira	20.3
	Thalassiosira	26.8
Euryoercus lan ellatus	Detritus	20
Abramis brama	*Bosmina*	70
Diaptomus ziciloides	Algae	48.8

budget of a marine amphipod that feeds on diatoms, found that of the phosphorus ingested, only about 16 percent was assimilated, the remainder being ejected. Arakawa's study (1970) on suspension (detritus)-feeding bivalves (mollusks) indicates that the proportion of consumption that is egested is larger for these organisms as compared with animal eaters.

Berezina (1957) worked on a carnivore, *Aeshna grandis*, and Fisher on *Lestes sponsa* (Mann, 1969). The latter study involved rearing the animals in the laboratory on a diet of *Daphnia* and *Tubifex*. Similarly, Sushchenya and Claro (1966) studying the energy balance of the crab *Menippe mercenaria* found that the assimilation efficiency on a fish diet was 96 percent. From the above studies described by Mann (1969), and other studies, it is noticeable that the assimilation efficiencies are generally much higher for the carnivores and therefore the fecal fractions are generally lower. Even for epiplankton, the herbivores appear to have a higher rate of defecation than the carnivores (Petipa et al., 1970; Table 3). N. Daan (personal communication) believes that feces production in cod amounts to no more than 5 to 10 percent of their daily ration.

In our estimates of fecal production, we assumed that when one organism eats something, the amount of feces produced depends on what is eaten, and not on what organism is doing the eating. This is not the only possible assumption. One can argue, for example, that the amount of feces will depend on the length of the consumer's digestive tract, or on whether it possesses the enzymes necessary to digest certain molecules (e.g., cellulose). Nevertheless, we assumed that these factors express their effect more in what the organism will choose to eat than in the amount of feces it will produce from a given meal. Under this assumption, it should make little difference whether the fecal fraction is made to depend on the consumer or the consumee.

Almost inadvertently, we confirmed the latter insensitivity. In an earlier version of the model, one that will be mentioned again in our later discussion of calibration, we assumed that the fecal fraction depended on the consumer, and not on the consumee. That is, an omnivore, which eats both plant and animal matter, would produce the same amount of feces from equally large meals of each. In fact, we calibrated this earlier model, and carried out much of our analysis with it. When we shifted to the newer model, the one described here, we recalibrated under the assumption that the fecal fraction depended on the consumee, and not on the consumer. In the new model, an omnivore produces more than twice as much feces from a meal of plants than from a meal of equal size consisting of animal matter. When we reanalyzed some of the important cases with the new model, we found that the results were essentially the same as we had obtained with the old model.

Our estimations of fecal fractions, given in Table 6.5, are based on examination of the references mentioned above. These percentages are not absolute; i.e., the amount of feces excreted probably varies with temperature, food concentration, etc., as is indicated by Arakawa (1970) for suspension-feeding bivalves. Table 6.5 indicates, however, that a plant feeder or detritus feeder tends to excrete more feces than a carnivore.

Table 6.5

FECAL FRACTIONS FOR DIFFERENT CLASSES OF FOODSTUFFS

Food Type Consumed	*Percentage Excreted* (f_j)
Detritus	50
Plant matter (phytoplankton diatoms, algae, etc.)	50
Animal matter (heterotrophs)	20

6.6. Values of r_j, m_j, and f_j for Each Ecogroup j

In Table 6.6, we recorded the values of r_j, m_j, and f_j for each ecogroup j. For heterotrophs other than birds, we also recorded our estimate of the maximum weight to which an organism in this ecogroup can grow. The reader should be aware that the maximum weights reported are the meat weights (because the models from which we derived the parameter values in Eqs. (6.1), (6.2), and (6.3) expressed weights in these units), and that ash-free dry weight is generally considered to be 20 percent of meat weight. Also, the reader should remember that we

Table 6.6

VALUES USED IN THE MODEL FOR THE PARAMETERS r_j, m_j, AND f_j

Ecological Group	Meat Weight	Daily Ration (r_j)	Metabolic Fraction (m_j)	Fecal Fraction (f_j)
Zooplankton/pelagic larvae	5.5×10^{-6}	3.90×10^{-1}	9.23×10^{-1}	2.0×10^{-1}
Oysters/mussels	1.875	3.70×10^{-2}	8.92×10^{-1}	2.0×10^{-1}
Cockles/limpets	1.375	3.80×10^{-2}	8.95×10^{-1}	2.0×10^{-1}
Selective deposit feeders with pelagic larvae	1.94×10^{-1}	5.60×10^{-2}	8.93×10^{-1}	2.0×10^{-1}
Crabs/shrimp	1.5×10^{-1}	5.60×10^{-2}	9.30×10^{-1}	2.0×10^{-1}
Sea stars	1.04×10^{1}	2.60×10^{-2}	8.85×10^{-1}	2.0×10^{-1}
Deposit feeders with nonpelagic larvae	7.44×10^{-1}	4.30×10^{-2}	8.84×10^{-1}	2.0×10^{-1}
Omnivores and predatory worms	2.5×10^{-2}	8.00×10^{-2}	9.00×10^{-1}	2.0×10^{-1}
Benthic grazers	4.5×10^{-3}	9.50×10^{-2}	9.20×10^{-1}	2.0×10^{-1}
Planktivorous fish	5.0×10^{-1}	4.10×10^{-2}	8.90×10^{-1}	2.0×10^{-1}
Benthos-eating fish	2.81×10^{1}	2.50×10^{-2}	8.64×10^{-1}	2.0×10^{-1}
Fish-eating fish	2.255×10^{2}	1.50×10^{-2}	8.67×10^{-1}	2.0×10^{-1}
Plant and detritus-eating fish	1.62×10^{2}	1.70×10^{-2}	1.00	2.0×10^{-1}
Fish-eating birds		2.08×10^{-1}	1.00	2.0×10^{-1}
Plant-eating birds		2.15×10^{-1}	1.00	2.0×10^{-1}
Benthos-eating birds		4.08×10^{-1}	1.00	2.0×10^{-1}

have assumed that the actual weights of organisms in an ecogroup are well represented by one-half the maximum weight.

The model for estimating r_j and m_j (see Secs. 6.3 and 6.4) is identical with Daan's (1975) model describing the growth of North Sea cod. Thus, our estimates of r_j and m_j should be reasonable for the larger heterotrophs. However, because zooplankton are so light compared with the other heterotrophs, we felt it necessary to check our estimates of r_j and m_j in Table 6.6 against direct measurements reported in the literature. From Petipa et al. (1970), we find that zooplankton consume between 0.5 and 1.5 times their body weight daily. Since they eat largely phytoplankton and suspended detritus particles, about 50 percent should be excreted as feces, leaving a daily ration of between 0.25 and 0.75. Table 6.6 gives 0.39 as our estimate of the daily ration from the weight of an individual zooplankton. Therefore our model suffices even for very small organisms. Note that we have included in Table 6.6 only the parameters for heterotrophs. We will discuss the corresponding parameters for photosynthetic organisms and for detritus in the next chapter.

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Chapter 7

EXTERNAL MASS TRANSFERS IN THE PRESENT OOSTERSCHELDE: FISHING, MIGRATION, AND PRIMARY PRODUCTION

7.1. PRIMARY PRODUCTION

This section will discuss the problem of estimating the rate of primary production for the entire Oosterschelde. Primary production is the rate at which energy is stored by photosynthesis and the chemosynthetic activity of plants in the form of organic substances that can be used as food by heterotrophs. It is important to distinguish between two kinds of primary productivity. Gross productivity refers to the total carbon (or energy) stored by plant matter. Net productivity refers to the amount of fixed carbon (or energy) available to the first link in the food web after the plants have used some of the energy stored in their own organic matter for their own respiration. The amount of respiration is usually added to measurements of net productivity as a correction in order to obtain estimates of gross productivity. We seek to estimate the gross productivity of the Oosterschelde.

Primary producers include pelagic phytoplankton (mostly diatoms, with some dinoflagellates and possibly some green algae), benthic microflora (usually diatoms), and attached macroalgae (seaweeds and sea grasses). These organisms are adapted to different environments. Phytoplankton thrive in the pelagic segment, within the upper layer of water that is penetrated by sunlight (i.e., the euphotic zone). Benthic microflora live on tidal flats. (Some production of phytoplankton occurs here as well, but less than in deeper water because the tidal flats are never submerged to the full depth of the euphotic zone and are frequently free of water altogether.) Finally, sea grasses grow in shallow water in areas sheltered from wave action. Few such areas exist in the Oosterschelde, and sea grasses are rare there.

We concluded that regardless of the type of microenvironment, the total rate of photosynthesis that occurs by all photosynthetic organisms taken together will average approximately 180 grams of carbon per square meter per year (abbreviated gC/sqm/yr). (Variations from the average value by a factor of 2 readily occur from one place or time to another.) This production rate corresponds to 455 tons afdw produced per day in the entire present Oosterschelde.

Our conclusion is supported by a number of independent production studies carried out on different organisms in different environments. It is also suggested by a number of studies that found incident solar energy to be a reasonably good predictor of total production in a wide variety of locations and environments.

7.1.1. Production by Phytoplankton

Yearly production by phytoplankton has been extensively reported in the literature. Cadee and Hegeman (1974b) estimated annual production by phytoplankton to be 100 gC/sqm in the western Waddensea, and 120 gC/sqm in the eastern

Waddensea. This compares well with measurements by Postma and Rommets (1970), who estimated the annual production in the deep tidal gullies of the Waddensea to be approximately 100 gC/sqm (after correction for the same self-absorption factor as was used by Cadee and Hegeman). Vegter (1975a,b) reported phytoplankton production in the open Grevelingen graphically, from which we determined that the annual production in the deep tidal gullies there was about 180 gC/sqm. The phytoplankton productivity in the Grevelingen during 1971, which was the year of closure, appears to be approximately the same (Vegter, 1975b). Farther afield, Platt (1971) measured the annual phytoplankton production in St. Margaret's Bay, Nova Scotia, as 190 gC/sqm, with a standard deviation of 60 gC/sqm. Finally, in summarizing other data, Cadee and Hegeman (1974b) reported that production by phytoplankton in the IJsselmeer is 400 gC/sqm/yr. (This is a fresh-water lake, and hence may lack comparability with marine habitats considered in the other reports.)

These sources obviously cover a wide range of values. Since we must choose a single nominal value, we selected the one measured nearest to the Oosterschelde, namely Vegter's value of 180 gC/sqm/yr, taken from the open Grevelingen. Not only was his value obtained in an estuary geographically close to and otherwise similar to the Oosterschelde, but it also has the advantage of being a rough average of all the reported production rates. But, we could have justifiably chosen any phytoplankton production rate between about 100 and 250 gC/sqm/yr.

The value of 180 gC/sqm/yr applies to phytoplankton production only in deeper water. In shallow water, and even more on the tidal flats, production by phytoplankton will be reduced. In 1970, Zweep (1974) measured phytoplankton production in the water above the tidal flats in the Waddensea and found it to be 20 gC/sqm/yr. This phytoplankton production is only part of the production for open water, because the tidal flats are submerged only part of the day and because the height of the water over the flat is always less than the euphotic depth (about 5 m). Phytoplankton production in the water above shallow bottoms that are nevertheless always submerged will be intermediate between these two rates.

7.1.2. Production by Microphytobenthos

We found a number of studies that discuss production by microphytobenthos (benthic diatoms). One was by Marshall (1970), who estimated production by benthic microflora in an estuarine shoal in southern New England to be 90 gC/sqm/yr. In another study, Grontved (1960) suggested a production of 116 gC/sqm/yr for benthic microflora in the shoals of Danish fjords. A third study was that of Cadee and Hegeman (1974a). They estimated that benthic diatoms produced about 100 gC/sqm/yr on the tidal flats of the western Waddensea. Thus, they concluded that total production on the flats was of the same order of magnitude as the phytoplankton productivity in deeper waters.

7.1.3. Production by Macrophytobenthos

Concerning macrophytobenthos (sea grasses and seaweeds), we have found the following: Mann (1972, 1973) summarizes what is known about *Zostera marina*, the most abundant species of sea grass in the Oosterschelde and Grevelingen, and estimates its productivity to be between 58 and 340 gC/sqm/yr. Neinhuis (1976) calculates production of seaweeds and sea grasses for the closed Grevelingen as 5750 tons afdw/yr, or 2880 tons of carbon (divide ash-free dry weight by 1.9 to get carbon). The area covered by sea grass and seaweed vegetation is 51 million sqm, and the cover is assumed to be 50 percent. Thus, we arrive at a figure of about 113 gC/sqm/yr for the area of sea grass and seaweed. (It would be proportionately greater if we assumed a higher-percentage cover.) We conclude that production by sea grasses and seaweeds per unit area of the sea grass beds is similar to, or perhaps somewhat smaller than, production in other areas by other primary producers.

7.1.4. Total Primary Production

As mentioned in Sec. 7.1, we adopted an overall primary production rate of 180 gC/sqm/yr for all environments and all primary producers that might occupy those environments, an estimate that is in rough agreement with numerous studies. For example, Wolff (in preparation), using many of the same sources cited above, estimated primary productivity in the open Grevelingen to be between 160 and 224 gC/sqm/yr. The same is true for other temperate zone areas. In shallow stations off the continental shelf of New York, productivity was found to be about 165 gC/sqm/yr, and New England shelf waters have a rate of 135 to 160 gC/sqm/yr (Ryther and Yentsch, 1958). A value for Long Island Sound was estimated to be 180 gC/sqm/yr (Ryther, 1966). Oregon coastal waters have a reported 125 gC/sqm/yr rate (Anderson, 1972). Gieskes and Kraay (1975) found that, during the first half of the growing season of 1974 (February to July), primary productivity in the Dutch coastal zone averaged 80 to 90 gC/sqm. Assuming that most production occurs during the growing season, we doubled this value to arrive at an annual productivity of 160 to 180 gC/sqm/yr. Primary productivity in the whole North Sea is very roughly 100 gC/sqm/yr, but the rate for the Southern Bight is higher (Postma, 1973).

There is good reason to expect that productivity per unit area will be roughly equal in two neighboring microenvironments. This is because both environments, being neighbors, will receive the same amount of solar energy in any period. Solar energy, of course, is one of the important "raw materials" used during photosynthesis, so that its rate of reception should limit the rate of production.

Of course, many environmental variables affect estuarine productivity. In addition to solar radiation, there are nutrient availability, turbidity (water transparency), depth of the wind-mixed layer, temperature, and the nature of the bottom. Of these, however, solar radiation seems to be the best predictor of productivity. Pamatmat (1968) found microbenthic primary productivity to be correlated with solar radiation and temperature, the former being the most important. Leach (1970) found primary microbenthic productivity to be correlated with solar radiation, functional chlorophyll a, and temperature, in order of importance.

To identify the key factors influencing productivity, Brylinsky and Mann (1973) made a large-scale statistical analysis of data from 55 lakes and reservoirs distributed from the tropics to the Arctic. They found that variables relating to solar energy input have greater influence over production than variables relating to nutrient concentration or morphology. Latitude, alone, which integrates the effects of day length, sun's altitude, length of growing seasons, air and water temperature, etc., explained about 57 percent of the variability in production.

Nevertheless, other factors do play a significant role, and consequently one must expect considerable variation in primary productivity from one environment to another. Platt (1971), for example, in summarizing primary productivity data from different marine habitats, mentions a range of 45 to 350 gC/sqm/yr. Further, the studies we have cited in previous sections show considerable disparity.

Part of this disparity is due to difficulties in obtaining complete and consistent measurements of production in a natural environment. Data are widely scattered geographically, are usually limited to a single observation for a given location often for too brief a time period, and often may not be comparable because of the use of different methods. Many assumptions are made in measurements, conversions, corrections, and calculations, and these assumptions may differ from one study to another. Thus, 180 gC/sqm/yr in one study may correspond to a different quantity than the same value in another study. In calculating organic carbon from chlorophyll, Finenko and Zaika (1970) assumed that in the Black Sea and Azov Sea, 1 mg of chlorophyll was equivalent to 35 mg of carbon; and in the Arabian Sea and tropical Atlantic Ocean, 1 mg of chlorophyll was equivalent to 75 mg of carbon. However, chlorophyll cannot be used as an index of phytoplankton concentration because the chlorophyll concentration per unit volume of algae varies considerably, depending on the species, their cell size, and their physiological condition (e.g., a large standing crop of large-celled species or cells in poor condition may be found at quite low chlorophyll concentrations). The ratio of chlorophyll a to total carbon may range from 1:20 to 1:100 (Riley and Chester, 1971).

The most widely used technique for measuring primary productivity, especially of phytoplankton and microphytobenthos, involves measuring the uptake of carbon-14 by the photosynthesizing organism. Boney (1975) pointed out a number of possible sources of error in the estimates obtained by this technique. For example, the data may indicate something between the net and the gross production (Steemann Nielsen, 1957; Strickland, 1960, 1965). Estimates as measured by the carbon-14 or oxygen techniques represent production in the absence of sinking, grazing, etc. Various types of corrections for respiration are also appropriate.

Some of the disparity in productivity values, however, is due to natural variations in production. Primary productivity often varies significantly from year to year, season to season, from one station to another, and from one depth to another. Cadee and Hegeman (1974a) found yearly variations in the Waddensea, especially during the summer. For example, in 1968 and 1969, summer values amounted to 500 to 600 mgC/sqm/day; in 1970 and 1971, to 100 to 500 mgC/sqm/day; and in 1972, to 500 to 1100 mgC/sqm/day. In this case the maximum annual productivity is about three times the minimum annual productivity. In the Georgia Bight in southeastern United States, the primary productivity estimated from seasonal data was 285 gC/sqm/yr in waters of 0 to 20 m deep and 132 gC/sqm/yr in waters of 20 to 200 m deep (Haines and Dunstan, 1975).

In view of these facts, we contend that for the purposes of our model there is no better assumption than that the long-term average primary production rate is proportional to the area in which it occurs. We further contend that the factor of proportionality is approximately 180 gC/sqm/yr. Production will take place at this rate on the entire area of the Oosterschelde that is submerged at high tide. For the present Oosterschelde, this area is 476.4 sq km, which implies an average production of 455 tons afdw/day.

7.2. FISHING AND MIGRATION

Fishing and migration rates in the present Oosterschelde are largely unknown, and any estimates are little better than guesses. This is especially true for migration rates, which have never been measured in the Oosterschelde, or indeed, anywhere in the North Sea coastal area, insofar as we are aware. But it is also true of fishing rates, which one would expect could be measured with relative ease.

One difficulty with data on fishing is that only the amounts of fish landed at each harbor are reported; no information is given about where the fish were actually caught. Many of the boats that land their catches in Oosterschelde harbors do most of their fishing in the southern North Sea. Thus, the reported catch is a combination of (a) the fishing rate inside the Oosterschelde, which we wish to estimate, (b) migration from the Oosterschelde to fishing grounds in the southern North Sea, and (c) migration from other places (e.g., the Westerschelde) to fishing grounds in the North Sea. Of course, only a fraction of migrating fish will be caught and landed in Oosterschelde harbors.

A second difficulty with data on fishing rates is that catches are not always reported accurately. This may be deliberate on the part of fishermen, who may feel that honest reporting will put them at a disadvantage compared with other fishermen (e.g., the Danish, the English, etc.) because of, for example, quota regulations. (We do not wish to fault Danish or English fishermen any more than Dutch fishermen. However, the economic and legal aspects of North Sea fishing tend to reward evasion of quota restrictions, and so it would be surprising if evasion did not take place.)

7.2.1. Oysters and Mussels

The fishing rates of oysters and mussels are the best known of any fishing rates. This is because these creatures are immobile, and the fishing areas are well known. Further, oysters and mussels are the object of an intensive aquaculture industry.

For oysters, Drinkwaard (1975) reported that the harvest is about 1 million kg/yr (live weight). The ash-free dry weight of an oyster is 20 percent of its meat weight, which is, in turn, only 15 percent of its total weight. Thus, the oyster harvest is 0.0822 ton afdw/day.

Some question exists, however, concerning whether oyster production actually takes place in the Oosterschelde or oysters are merely stored there. Heuer (1976), for example, reported that although 1.2 million kg/yr of oysters are exported (slightly higher than Drinkwaard's estimate of 1 million kg), a still larger amount are imported (1.6 million kg/yr during the period 1970 through 1974). Heuer therefore concluded that oyster production in the Oosterschelde hardly exists. In view of this information, we have reduced our oyster fishing rate to 0.05 ton afdw/day.

The harvest of mussels in the Oosterschelde has been reported as 30 million kg/yr live weight (Ministry, Annual Report, 1971, Table 11). About 4 percent of this harvest is ash-free dry weight, from which we estimate a harvest of 3.29 tons afdw/day (this is a metric ton, equal to 1000 kg). In addition, about 70 million kg of mussels are brought into the Oosterschelde from the Waddensea for storage and cleaning (rewatering). These mussels arrive fully grown, and gain little weight while in the Oosterschelde. Thus, they contribute little or nothing to the net mussel harvest.

Because oysters and mussels form a single ecogroup in our model, we shall combine their fishing rates. The fishing rate for this ecogroup is therefore 3.34 tons afdw/day.

7.2.2. Sea Stars

Sea stars are not fished commercially, but since they are abundant on the mussel plots, they are caught whenever these more desired creatures are harvested. Originally, we assumed that the shellfish growers caught sea stars accidently as they harvested shellfish, and therefore the ratio of fishing rate to abundance on the shellfish culture plots was the same for both sea stars and shellfish. This led to an estimated fishing rate for sea stars of 0.0529 ton afdw/day. (As we describe in Chap. 8, our initial estimates of the abundances of sea stars and of oysters and mussels were 19 tons and 1200 tons, respectively.)

As we shall explain later, our estimates of the average abundances were modified during the calibration procedure. In particular, our final estimate of the oyster and mussel abundance was 2139 tons, rather than 1200 tons. If we had used our "ratio rule" with the final abundance estimates to compute a fishing rate for sea stars, a fishing rate of 0.023 ton/day, instead of 0.0529 ton/day would have resulted. However, we discovered that the mussel growers actively seek to kill the sea stars to prevent decimation of the mussel population (sea stars are a major predator of mussels). Thus, the mussel growers probably fish for sea stars more intensively than the ratio rule would predict. We have therefore retained the fishing rate for sea stars that we first estimated, namely 0.0529 ton afdw/day.

7.2.3. Cockles

Cockles are a shellfish similar to mussels. However, in the Oosterschelde they grow wild, unlike mussels, which are cultured. Nevertheless, cockle fishing has become important in the last several years. We were informed (A. C. Drinkwaard, J. D. Holstein, and L. C. Abrahamse, personal communication) that in 1974, 2000 tons of cockle meat (of which 16 percent is ash-free dry weight) was removed from the Oosterschelde, while in 1975, the harvest rose to 7000 tons of meat. This translates to a harvest of 0.88 ton afdw/day in 1974, and 3.07 tons afdw/day in 1975.

We selected the value of 3.07 tons afdw/day as the harvest rate to use in our model. We considered whether to use a larger value, since the harvest rate appears to be increasing rapidly, and might be expected to continue increasing. However, we were assured that all commercially exploitable areas of cockle growth were being exploited, and even overexploited.

In our model, cockles and limpets are combined into a single ecogroup. But the rate of limpet fishing is very small compared with that of cockle fishing (A. G. Drinkwaard, J. D. Holstein, and L. C. Abrahamse, personal communication), and hence the fishing rate of 3.07 tons afdw/day applies to the entire ecogroup.

7.2.4. Shrimp

It is difficult to estimate shrimp fishing in the Oosterschelde because the landings in the Zeeland harbors are from several areas (Westerschelde, Oosterschelde, North Sea). Total shrimp landings vary between 3 and 10 million kg/yr in the Netherlands, averaging perhaps 6.5 million kg/yr (Boddeke, 1976).

Becker and Postuma (1974) conclude that only 5.2 percent of the shrimp production takes place in Zeeland estuaries. If we assume that half of it occurs in the Oosterschelde, then between 78 and 260 tons of shrimp per year are removed from the Oosterschelde by fishing and migration. The average is 169 tons, of which 16 percent, or 27 tons, is ash-free dry weight. However, because little shrimp fishing occurs in the Oosterschelde itself, we will attribute the entire export to migration.

In our model, shrimp and shore crabs have been combined into a single ecogroup. Crabs are not fished, however, and do not migrate. We can therefore apply the rates given for shrimp to the entire ecogrop. Since we estimate that there are, on average, 46.8 tons of shrimp and crab in the Oosterschelde, the migration rate is about 0.0016 ton/day/ton afdw of standing stock. We have used this figure, along with a null fishing rate, in our model.

7.2.5. Planktivorous Fish

Included in the planktivorous fish ecogroup are herring, anchovy, and sprat. Catch data for these fish are reported for anchovy and herring, but not for sprat (Ministry, Annual Reports). Sprat catches are probably included with the herring figures. The catch figures shown in Table 7.1 relate to the Oosterschelde, according to the Ministry of Agriculture and Fisheries (Annual Reports).

Table 7.1

LANDINGS OF PLANKTIVOROUS FISH IN THE OOSTERSCHELDE

Year	Anchovy (kg)	Herring (kg)
1969	2738	597120
1970	18920	192075
1971	32306	43100
1972	31075	42500
1973	31879	170495

We take the average catch of anchovy to be the average of the final three quantities (31750 kg), and take the average catch of herring to be the average of the final four quantities (112000 kg), because the others appear to be anomalous. Consequently, the catch of the planktivorous fish in the Oosterschelde is 144 tons/yr, or (multiplying by 0.2 to obtain ash-free dry weight and dividing by 365), 0.79 ton afdw/day.

Most of these fish were probably caught in the Oosterschelde itself, rather than being caught outside and landed at Oosterschelde harbors. For example, the Ministry of Agriculture and Fisheries (Annual Reports) reported that the entire 1971 catch of anchovy was taken from the back (i.e., the eastern end) of the Oosterschelde in the months of May, June, and July. We thus take the entire reported fishing rate to be the fishing rate for the model.

These fish are also migratory. Since we have no data on their rate of migration, we have arbitrarily assumed the migration rate to be about one-half the production rate, or 0.00225 ton/day/ton of standing stock. In the absence of data, of course, we have no grounds on which to defend this estimate. But we did test the sensitivity of our conclusions to changes in this rate, and to changes in the migration rates of other ecogroups as well. Within broad limits, changes in these rates have only a moderate influence on the results, and none at all on our conclusions.[1]

7.2.6. Benthos-Eating Fish

Benthos-eating fish include eel (a resident fish), plaice, sole, flounder, and dab (migratory fish). For eel, we have only catch data. The official data (Ministry, Annual Reports) are that only 40000 kg of eel were caught in 1973. In opposition, A. G. Drinkwaard (personal communication) claimed that 5 million guilders' worth were caught, at a price of f8/kg. His estimate yields 625000 kg, or, multiplying by 0.2 to get dry weight, a catch of 0.342 ton afdw/day.

For the remaining benthos-eating fish, we have data only on abundances. Reputedly, they are not much fished in the Oosterschelde. One of the authors recalled the amount of 30000 kg/yr live weight, which is 0.0164 ton afdw/day. The total fishing rate for benthos-eating fish is thus 0.3584 ton afdw/day.

As with planktivorous fish, the migration rate of benthos-eating fish is unknown. Again, we have assumed the rate to be about one-half of the production rate, or 0.002 ton/day/ton of standing stock. Since eel do not migrate, our assumption implies that migratory benthos-eating fish migrate at a rate greater than one-half of their production rate and that less than one-half of their production is available to be eaten by their predators. However, since they are large fish, and their predators are not abundant, it is not unlikely that most of their production in the Oosterschelde survives to be exported by migration.

Again, as with planktivorous fish, we have no grounds for defending our choice of a migration rate. We investigated the sensitivity of our conclusions to changes in this rate and learned that unless the migration rate of benthos-eating fish (including eel) becomes nearly equal to their production rate, changes in migration have no significant effect.

7.2.7. Fish-Eating Fish

Fish-eating fish include mackerel, cod, whiting, garfish, and sea trout. The catch data for these fish in 1973, as reported by the Ministry of Agriculture and Fisheries (Annual Report, Table 9), are given in Table 7.2.

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[1] Changes in migration rates have only a moderate influence on the results because these rates just apply to shrimp, which are not very abundant, and to fish. Fish occupy nearly the highest trophic level, being eaten only by other fish and by birds. Changes in their migration rates exert their major effect on still higher trophic levels (birds, whose abundances are in any case prescribed by the model; See Sec. 7.2.8), and have little influence on lower levels, which most of the biomass occupy.

Changes in migration rates have no influence on our conclusions because we have been careful not to conclude anything that depends importantly on uncertain parameters, such as migration rates.

Table 7.2

CATCH OF FISH-EATING FISH IN 1973

Mackerel	1336 kg
Cod	1761 kg
Whiting	693 kg
Garfish	3008 kg
Sea-trout	(a)

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[a] None was reported for 1973. Catches were negligible in other years.

As the table shows, the total catch for 1973 was less than 7000 kg. We multiplied by 0.2 to get ash-free dry weights, and divided by 365 to get a daily catch rate. The result was 0.00373 ton afdw/day.

The migration rate of fish-eating fish is no better known than the migration rates of other fish. Again we assumed a migration rate of about one-half the production rate, or 0.0008 ton/day/ton of standing stock. We then tested the sensitivity of our conclusions to this migration rate and found that, within broad limits, their sensitivity is low.

7.2.8. Summary of Fishing and Migration Rates

We collected all the nominal fishing and migration rates used in our model and assembled them as Table 7.3. These rates are highly uncertain, the migration rates in particular being sheer guesswork. Nevertheless, it is desirable to have certain reasonable rates specified as nominal, if only to provide a point for comparison and a point of departure.

Table 7.3

NOMINAL FISHING AND MIGRATION RATES

Fishing or Harvest Rates	*Tons afdw/day*
Mussels or oysters	3.4
Sea stars[a]	0.0529
Cockles	3.07
Planktivorous fish	0.079
Benthos-eating fish	0.3584
Fish-eating fish	0.00373
Migration Rate	*Tons afdw/day/ton biomass*
Planktivorous fish	0.00225
Benthos-eating fish	0.002
Fish-eating fish	0.0008
Shrimp	0.0016

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[a] Sea stars are a major predator of mussels and are controlled by mussel growers to limit damage to the mussel crop.

The reader will note that we have not specified migration rates for birds, or a migration or fishing rate for plant- and detritus-eating fish, despite the fact that birds are migratory organisms and that plant- and detritus-eating fish are certainly being fished in the Oosterschelde. These rates are not specified because of the following interesting feature of our model.

In our model, birds and plant- and detritus-eating fish are not preyed upon by any ecological groups. This is not to say that these organisms never die in the Oosterschelde. For example, from time to time a disease such as botulism may kill significant numbers of some birds. But their numbers are not controlled by predation in the Oosterschelde. (We will discuss shortly how the death of these organisms, and their becoming a potential food source in the Oosterschelde, would affect the model.)

The consequence, in the model, is that the balance equations for these ecogroups contain only terms corresponding to their eating other AQs, and hence (see Sec. 3.8) all the nonzero coefficients in one of these balance equations are the same, and equal to $g_j r_j - MIG_j$. Depending on the value of MIG_j, therefore, we could choose one of two methods for handling these ecogroups. First, we could set

$$MIG_j = g_j r_j \ .$$

If we chose this course, the balance equations for birds and plant- and detritus-eating fish would not act as constraints, since all of the coefficients would be zero. The equations would read "$0 = b_j$." In this case, we would simply omit these balance equations from the model—although we would of course retain the variables corresponding to the abundances of these ecogroups—and let the model determine on the basis of all the other equations what these abundances should be. The model would then predict that these ecogroups would always be just abundant enough to consume all of their available food.

The second possibility was to set MIG_j to any value other than $g_j r_j$. This was the choice we made, and we arbitrarily chose to set MIG_j to -1 and g_j to zero. Note that when this is done, the bird balance equation becomes

$$\sum_i \sum_s x_{i,j,s} = \frac{b_j}{g_j r_j - MIG_j} = b_j \ .$$

This equation says that the abundance of AQ j, which is one of the ecogroups in question, must be equal to b_j. That is, the bird balance equations prescribe the abundances of the bird ecogroups, and the plant- and detritus-eating fish balance equation prescribes the abundance of this ecogroup, according to the choice of the right-hand side parameters b_j.

Our rationale for this choice was our belief that factors outside of the Oosterschelde influence the numbers of birds and plant- and detritus-eating fish found in the Oosterschelde. If we had made the first choice, no parameter in the model could be varied in order to investigate the consequences in the Oosterschelde of changes in those outside factors. The choice we did make yields a model in which such parameters do exist, namely the right-hand side parameters b_j.

As promised, we will now discuss how the death of some of these organisms would affect our model. We would model the death rate of a heterotroph from causes other than predation and fishing by subtracting the rate from the coefficients of the appropriate variables in that heterotroph's balance equation, and adding the death rate to the coefficients of the same variables in the detritus balance equation. The appropriate variables, of course, are those whose sum is the abundance of the heterotroph whose natural death rate is being modeled.

Applied to a heterotroph that is not being preyed upon, such as birds and plant- and detritus-eating fish, this procedure would subtract the death rate from all the otherwise nonzero coefficients in the corresponding balance equation. In particular, all of these coefficients would remain equal to each other, and the corresponding balance equation would still prescribe the abundance of the ecogroup.

But once the abundance and the death rate have both been prescribed, the rate at which the death of these organisms adds to the store of detritus is known. It is just the product of the abundance and the death rate. Instead of modifying the coefficients in the detritus balance equation to take account of the death rate, we can equivalently modify the rate of detritus import by the known rate of addition of these dying organisms to the detritus store.

However, as we have mentioned before, and as we discuss at length in the appendix, the rate of detritus import is highly uncertain, although we believe it to be large. The minor contribution to detritus import from the deaths of birds and plant- and detritus-eating fish is insignificant compared with this uncertainty. Therefore, if, in order to account for the deaths of birds and plant- and detritus-eating fish, we modify the rate of detritus import instead of the coefficients in the detritus balance equations, we will have no practical need to estimate the death rates of these organisms. Accordingly, that is the choice we make.

One consequence of prescribing these abundances is that our model cannot predict the actual abundance of these ecogroups. In essence, the abundance is an input quantity, not an output. But as we shall see in Part III, we can use the model outputs in conjunction with one or another assumption, and arrive at reasonable estimates of the effect of alternative abundances.

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Chapter 8

ESTIMATING ABUNDANCES

8.1. GENERAL PROBLEMS OF MEASURING LONG-TERM AVERAGE ABUNDANCES

Data on abundances in natural ecosystems are generally difficult and costly to collect. This is because the ecosystems in which we are interested are large and varied. The Oosterschelde, for example, covers an area of approximately 400 sq km, and the various species in its ecosystem are far from uniformly distributed. To form a reasonably reliable estimate of abundances, numerous samples must be taken from widely separated locations. Since techniques for ecological sampling have not been automated, many man-days of skilled labor are required, both for sampling and for identifying and quantifying the species found in the samples.

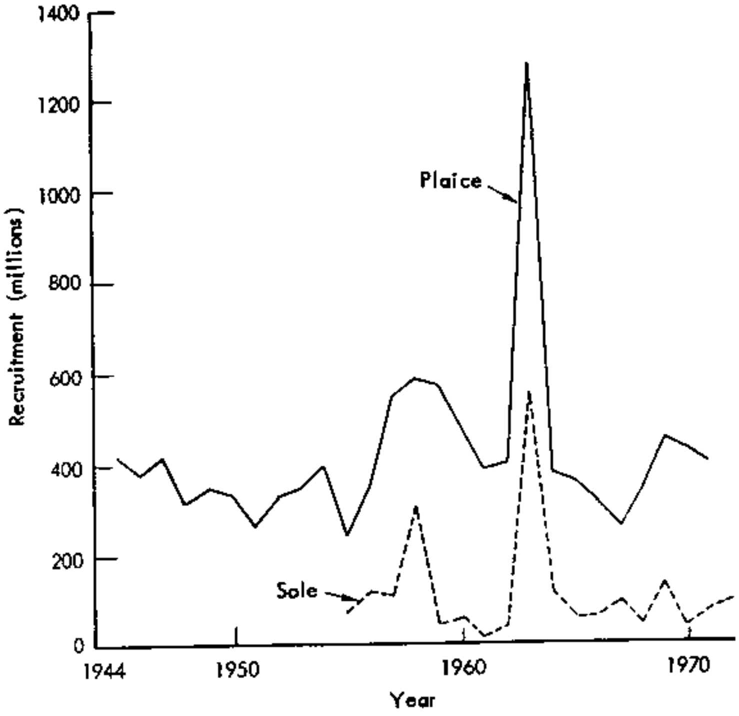
Furthermore, the abundances of many creatures vary rapidly over wide ranges. Some organisms migrate (e.g. plaice), so that at a particular (and often unknown) signal, they all disappear from the Oosterschelde. Others are very mobile (e.g., birds), and may change their distribution within the ecosystem almost from day to day. Still others have very short lifespans (e.g., phytoplankton) or undergo rapid changes in size and weight (e.g., young fish). Consequently, samples should be taken frequently throughout the year, and simultaneously at many locations within the ecosystem.

Not only do the abundances change from one season of the year to another. They also change from year to year. One year may be exceptionally cold, retarding the reproduction of one species while promoting that of another. During the next year, one will observe smaller than average numbers of the first species but larger than average numbers of the second. This will in turn affect the abundances of both their prey and their predators. The potential magnitude of these year-to-year variations is suggested by some estimates of sole and plaice recruitment in the North Sea (see Fig. 8.1). (Recruitment figures for these species are equivalent to the abundances of two-year-old individuals.) One can see that for sole there is an estimated fortyfold difference between the year of maximum recruitment (1963) and that of minimum recruitment (1961). This phenomenon suggests that many years of data should be collected to give a reliable estimate of long-term average abundances, which are what our model estimates.

We obtained abundance data from a variety of sources. These sources, which ecological groups they measured, what methods they used, and what specific problems they encountered, are described below.

8.2. BIRDS

Data about abundances of birds were collected by the Hydrobiological Institute, Yerseke, and by the Environmental Division (H. L. F. Saeijs), 's-Heer Arendskerke (now situated in Middelburg) by means of visual observation, either from boats or from the shore. The most important species observed are shown in Table 8.1.



Source: J.F. DeVeen, Institute for Fisheries Research (personal communication)

Fig. 8.1 —Annual recruitment of North Sea sole and plaice at age two years

Table 8.1

SPECIES OF BIRDS IN THE DELTA REGION

Benthos-eating Birds	Plant-eating Birds	Fish-eating Birds
Goldeneye	Brent goose	Great crested grebe
Eider	Teal	Grey heron
Shelduck	Wigeon	Red-breasted merganser
Oystercatcher	Pintail	Cormorant
Grey plover	Mallard	Sandwich tern
Turnstone	Shoveler	
Curlew	Pochard	
Bar-tailed godwit	Mute swan	
Redshank	Coot	
Knot		
Dunlin		
Avocet		
Black-backed gull		
Herring gull		
Common gull		
Black-headed gull		
Common scooter		

There is only one important problem in estimating abundances of birds in the Oosterschelde. Counts of birds must be made simultaneously over a large area because birds are so mobile that a single observer, counting birds at different locations on two different days, may well count many birds twice—including those birds who are curious about him. A simultaneous count requires the concentrated effort of many persons for a short period of time. Finding enough people who can recognize different species of birds on sight, and who can accurately estimate their numbers, is difficult.

A complication is that the birds may obtain some food in areas other than the Oosterschelde (e.g., Westerschelde or Grevelingen). To the degree that they do this, their abundance in our model should be reduced. Estimates of the degree to which they rely on other food sources can be obtained only by observing birds, not only in the Oosterschelde itself, but in the entire Delta area.

8.3. FISH

Data on the abundances of benthos-eating fish were collected by the State Institute for Fisheries Research (R.I.V.O.), IJmuiden. Many (but not all) of these data have been published in their semiannual surveys (Demersal Surveys). Their basic method for collecting these data is by trawling. A net is lowered from a ship and dragged along the bottom for a specified distance. This distance, multiplied by the width of the net, is the area dragged. The numbers of different organisms caught in the net, divided by the area dragged, is indicative of the density of these organisms in the general area from which the sample was taken.

Sampling by trawling is subject to the general problems of ecological sampling, as well as to unique problems of its own. For example, fish are nonuniformly distributed near the bottom of the Oosterschelde. Most fish are found in the shallower depths, and at high tide one finds large numbers of them (especially the younger and smaller individuals) feeding on the tidal flats. This creates a special problem for the ships used by R.I.V.O., since they have too great a draft to sample in shallow waters. Also, some groups of fish are difficult to catch in the nets used, either because they are too mobile or too small. Corrections to the measured densities for gear efficiencies have been estimated, but they are based on poor data and tenuous assumptions. Finally, most benthos-eating fish found in the Oosterschelde are young and rapidly growing. Typically they leave the Oosterschelde for the North Sea when they reach adult size (some return annually for spawning). Thus, because of their rapid growth and their migratory behavior, their abundance varies significantly during the year.

Other fish (planktivorous fish, fish-eating fish, and plant-eating fish) are not sampled systematically, and so we were compelled to estimate their abundances from reported catches by commercial fishermen. These estimates are highly speculative for the following reasons. First, there is no clear relation between the size of the catch of a species and its abundance. Only if the catch represents a sustained yield can one say that the abundance must be sufficiently large so that natural growth and reproduction will replace the fishing losses. And even then, no upper bound on the abundance can be estimated. Second, what is reported is not the catch taken in the Oosterschelde, but the amount of fish landed there. Some may have been caught elsewhere. Third, the quantities reported are often inaccurate. We suspect misreporting may be deliberate (see Sec. 7.2).

The most important species of fish found in the Oosterschelde are shown in Table 8.2.

Table 8.2

SPECIES OF FISH IN THE OOSTERSCHELDE

Benthos-eating Fish	Plant-eating Fish	Fish-eating Fish	Planktivorous Fish
Eel Plaice Sole Dab Flounder	Grey mullet	Mackerel Cod Whiting Garfish Sea-trout	Anchovy Herring Sprat

8.4. MACROBENTHOS

As the name implies, macrobenthic organisms are relatively large organisms that live on or in the bottom of the Oosterschelde. Our data on abundances of most of these ecological groups came from the Hydrobiological Institute, Yerseke. (Shrimp and shore crabs are exceptions. R.I.V.O. obtained data on these organisms while trawling for benthos-eating fish. Ecologically, however, shrimp and shore crab properly belong among the macrobenthos.) Their program for collecting these data involved taking core samples of the bottom sand and clay, sifting the sample to find any macrobenthos present, and obtaining the ash-free dry weights of each species by age class. The major species they found are listed in Table 8.3.

Barring shrimp and shore crab, these organisms are generally not mobile. The work of sampling them need not be done simultaneously at all sampling locations. However, many of these organisms have very different abundances in different seasons, and hence must be sampled several times during the year. In addition, their distribution is highly irregular. Most greatly prefer shallow bottoms and tidal flats to deeper bottoms. (Large boats that can carry motor-driven sampling grabs cannot float over these areas, so collecting samples requires hard, manual labor.) Some prefer coarse sandy bottoms to bottoms covered with finer silt. Some like areas sheltered from wave action, whereas others prefer more open areas. Thus, a sampling program must be extensive and well planned if its results are not to mislead the investigator.

One of the problems encountered during this effort was the refusal of the mussel growers to permit sampling on their culture plots. It is known that these plots are very rich in biomass, but because of the growers' refusal, direct measurements of that biomass are not available. Instead, indirect estimates had to be made from the published figures for commercial mussel production. And the abundances of organisms other than mussels on these plots had to be estimated by analogy with adjacent, uncultivated areas.

Table 8.3

SPECIES OF MACROBENTHOS SAMPLED IN OPEN GREVELINGEN

Ecological Group	Common Name	Scientific Name
Cockles and limpets	Cockles Limpets	*Cardium edule* *Capitella*
Mussels and oysters	Mussels Oysters	*Mytilus edulis* *Ostrea edulis*
Selective deposit feeders with pelagic larvae		*Macoma balthica* *Scrobularia plana* *Angulus*
Deposit feeders with nonpelagic larvae and suspension-feeding worms		*Scolopolos armiger* *Tharix marioni* *Heteromastus filiformis* *Arenicola marina* *Corophium* (diverse species)
Omnivores and infaunal predators		*Nereis diversicolor* *Gammarus* (diverse species) *Harmothoes* species *Etiona longa* *Anaitides maculata* *Nephthys hombergi*
Benthic grazers	Periwinkle	*Littorina littorea* *Hydrobia ulvae*
Epifaunal predators	Shore crab Brown shrimp	*Carcinus maenas* *Crangon crangon*

The final problem with these data was that the major sampling effort had taken place in the Grevelingen before it was closed (May 1971), and not in the Oosterschelde. Estimating abundances in the Oosterschelde therefore involved modification of the measurements from the Grevelingen. However, the few samples of organisms that have been taken in the Oosterschelde suggested that they are not very dissimilar from those found in the Grevelingen. (See the Addendum to this volume for further discussion.)

8.5. MICROBENTHOS

Very little is known about microbenthic organisms. The Hydrobiological Institute, Yerseke, is supporting research on these organisms, and the actual research is being carried out by the University of Ghent, Belgium. Organisms of this kind are obtained from carefully sifted core samples taken from the water bottom. It is known that their distribution is highly nonuniform, but so little is known of their preferences and habits that proper design of a sampling program for our needs is impossible. However, it is thought that they mostly eat and are eaten by one another, except for an occasional meal of detritus. Thus, we have interpreted their net participation in the ecology of the Oosterschelde as contributing only to the rate of disappearance of detritus.

8.6. PLANKTON

Data on plankton came from the Hydrobiological Institute, Yerseke, and the Netherlands Institute for Sea Research, Texel. Organisms considered in this group are phytoplankton, zooplankton, and the planktonic larvae of various (usually macrobenthic) organisms. The method for measuring the abundances of these organisms was to count individual organisms in water samples under a microscope.

One problem with estimating plankton abundances is that a highly skilled technician must examine the microscope slides. Such people are in short supply. Furthermore, their work must be carefully controlled for quality, lest species be miscounted, misidentified, or omitted. Such control slows an already slow process; consequently our knowledge about the abundances of planktonic organisms in the Oosterschelde is very incomplete.

Other problems are that estimating the size (especially the ash-free dry weight) of plankton is difficult, and that the abundance of plankton changes rapidly throughout the year. Phytoplankton blooms occur at certain periods of the year, zooplankton respond rapidly to changes in their food supply, and planktonic larvae of a particular species may be present only during a very brief reproductive period.

8.7. DETRITUS

Wolff (1973) reported that the detritus content of the sediments in the Oosterschelde is between 0.1 percent and 1 percent by volume. This content was measured by inferring the organic matter content from oxygen uptake experiments. The technique is essentially the same as the one by which ash-free dry weight is measured (see Sec. 2.3), except that here one measures the ash-free dry weight of the sediment, rather than of a specific organism.

Wolff's value may seem low, but it is equivalent to an enormous mass of organic material. For example, consider only the top 30 cm of the sediments. The area of the Oosterschelde is approximately 400 sq km, and so this 30-cm layer represents 120 million cu m of sediments. If the volume were 0.1 to 1 percent organic material with specific gravity 1.0, there would be between 120000 and 1.2 million metric tons of organic material in the sediments of the Oosterschelde. In comparison, the total ash-free dry biomass in the present Oosterschelde probably does not exceed 30000 metric tons (see Table 8.4).

Suspended detritus is measured in water samples taken in the same fashion as for measurements of planktonic organisms. Often, in fact, the same samples are used. The sample is filtered, dried, and heated in a furnace to determine ash-free dry weight. Our estimates of suspended detritus were calculated as 5 percent of the suspended matter concentration. This concentration was measured by the Environmental Division of the Delta Service, Rijkswaterstaat. The estimate that 5 percent of suspended matter is organic is from Manuels and Postma (1974).

8.8. INITIAL ABUNDANCE ESTIMATES FOR THE OOSTERSCHELDE

Table 8.4 contains the initial abundance estimates we have used in our model of the Oosterschelde. Detailed information regarding the data and assumptions

Table 8.4

INITIAL ABUNDANCE ESTIMATES FOR THE OOSTERSCHELDE

(In metric tons afdw)

Ecological Group	Segment			
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms	Shellfish Culture Plots
Photosynthetic organisms	1300.0	7770.0	--	--
Detritus/microbenthos	25100.0	77500.0	55900.0	7250.0
Zooplankton/pelagic larvae	563.0	--	--	--
Mussels/oysters	--	--	--	1200.0
Cockles/limpets	--	9255.0	200.0	--
Selective deposit feeders with pelagic larvae	--	594.0	17.0	77.0
Crabs/shrimp	--	14.3	19.8	12.7
Sea stars	--	--	24.0	19.0
Deposit feeders with nonpelagic larvae	--	2100.0	0.116	272.0
Omnivores/predator worms	--	12.0	1.92	1.56
Benthic grazers	--	4620.0	--	432.0
Planktivorous fish	250.0	--	--	--
Benthos-eating fish	1600.0	--	--	--
Fish-eating fish	316.0	--	--	--
Plant-/detritus-eating fish	30.0	--	--	--
Fish-eating birds	0.0462	--	--	--
Plant-eating birds	--	0.074	--	--
Benthos-eating birds	--	9.5	--	--

from which each estimate was derived will be found in the Addendum to this volume.

Remember that our eventual purpose in this part of the report is to calibrate our model to the present Oosterschelde. This means that, given as inputs, the external mass transfer rates that characterize the present Oosterschelde, the model should produce, as outputs, our estimates of the long-term average abundances of the organisms characteristic of the present Oosterschelde. As we will explain later (in Chap. 10), the abundances given in Table 8.4 are not our final estimates of the long-term average abundances in the present Oosterschelde. They must first be adjusted to conform with the balance requirement. However, the abundances in Table 8.4 will serve as the starting point for the calibration procedure.

8.9. COMMENTARY ON ABUNDANCE DATA

Table 8.5 summarizes the availability of abundance data. It reveals how incomplete they are for the Oosterschelde. Indeed, inadequate quality and quantity of abundance data have been the worst impediments to this study.

Table 8.5

SUMMARY OF AVAILABLE ABUNDANCE DATA

	Data Collected at			
Community	Oos.	Open Grevelingen	Closed Grevelingen	Other
Plankton	(X)			(X)
Microbenthos				(X)
Macrobenthos	(X)	X	(X)	
Fish	X	X		
Birds	(X)	X	X	

NOTE: X = fairly complete data; (X) = incomplete data.

Not only are abundance data incomplete, but they are also very uncertain. Even direct measurements of abundances in the Oosterschelde have a high variance. For example, as explained above, measurements of benthos-eating fish depend on assumptions about gear efficiencies that are largely arbitrary. As another example, the extremely nonuniform distribution of macrobenthos magnifies the variance of their abundance estimates.

Of course, indirect abundance estimates are even more uncertain. We were compelled to infer some abundances from data on commercial yields. This is true for both mussels, which are cultured, and various species of fish, whose uncultured populations are simply exploited. The difficulties of this approach were discussed in Sec. 8.3.

We indirectly estimated other abundances in the Oosterschelde by transferring measurements made in other places (the Grevelingen or the Waddensea). This was the case for most macrobenthic organisms, which were most completely sampled in the Grevelingen. We also made transfers of this kind from one part of the Oosterschelde to another. For example, since we had no data on macrobenthos on mussel culturing plots, we had to infer their abundances there from our estimates of their abundances on shallow bottoms and tidal flats.

To transfer an abundance estimate from one place to another, one must assume that biomass densities in the two places are similar or one must devise a rule for scaling the measurements from the one place to the other. For example, we assumed that the abundances of organisms on the mussel plots were in the same ratio to mussels as were the abundances of the same organisms on the shallow bottoms and tidal flats to the abundances of cockles. This was because cockles appear to occupy the same position in the food web as mussels, and therefore cockles might be in the same numerical relationship to their predators as are mussels. We believe this assumption to be reasonable though unproved.

Our situation is not unique. All investigators attempting to inventory an entire ecosystem have been forced to make unsupported assumptions and questionable inferences. For example, when we first began to construct our model, we were advised that only cultured mussels were found in Zeeland, i.e., no wild mussels could be found there. To us, as to our advisers, this implied that the closed Grevelingen contained no mussels, and that mussels in the Oosterschelde were found only on the shellfish culture beds. We embodied this assumption in our model. Later (too late to change the model), R.I.V.O. carried out a mussel-fishing experiment in the closed Grevelingen that recovered 10000 tons of mussels, about one-fifth the abundance of cultured mussels in the Oosterschelde.

We speculate that this error arose because in the Grevelingen, when it was open, and to a lesser extent in the present Oosterschelde, wild mussels were and are suppressed. Whenever mussels are found in significant numbers, they are transferred to the mussel plots. Also, the areas where their spat can thrive are located and used by the mussel growers in their culturing operations. Thus, one should expect that if mussel culturing operations ceased in the Oosterschelde, the mussel population would remain large.

A second example of a disproven assumption concerns cockles. Initially, we estimated the abundance of cockles in the Oosterschelde based on their abundance in the Grevelingen. People at R.I.V.O., not having the Grevelingen measurements available, estimated the abundance of cockles in the Oosterschelde from the commercial yield. There was a thirtyfold difference between the two estimates, our estimate being the higher.

It was important to determine which of these estimates was more nearly correct. If R.I.V.O.'s estimate were correct, cockles would be only a minor species in the Oosterschelde. If we were correct, cockles would be the most abundant single species. The difference in the estimates had profound implications for the total amount that the organisms in the Oosterschelde would eat, and therefore what the net rate of detritus import had to be. So, we asked the Environmental Division of the Delta Service to conduct a special cockle-sampling program.

The program was carried out during February 1976, a time when the biomass of cockles should be about half of its annual average (judging from the monthly measurements in the Grevelingen). From the program's findings, we estimated that the biomass density was 19.3 gm/sq m on shallow bottoms and tidal flats. The similar figure for the open Grevelingen in February was 16.3 gm/sq m. This suggests that our estimate, rather than R.I.V.O.'s, is more nearly correct.

Finally, remember that our model deals with long-term average abundances, and not with the abundances of organisms at any particular instant in time. The instantaneous abundances will vary systematically from season to season, because many species migrate or spawn or exhibit other behaviors according to seasonally correlated stimuli. Instantaneous abundances will also vary randomly from one year to the next, as demonstrated in Fig. 8.1. To obtain the information our model needs, these instantaneous abundances must be measured frequently enough to capture the seasonal variations, and must be averaged over a long enough period to smooth out the yearly fluctuations. One can question how well the available measurements fulfill these criteria. In other words, the abundances shown in Table 8.4, which will serve as the starting point for calibrating our model to the present Oosterschelde, may correspond to an ecological state considerably different from the long-term average state at which we are aiming.

In spite of their shortcomings, however, these data still have value. They contain information, albeit far from perfect. We ought to be better off if we use this information judiciously than if we ignore it altogether.

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Chapter 9

PARTITIONING ABUNDANCES OF HETEROTROPHS BY DIET ITEM

9.1. THE PARTITIONING PRINCIPLE

What we have done in Chap. 8 is to estimate the abundances of each AQ in every segment. (AQ means "accounting quantity"; see Sec. 2.5.) Now let $V_{j,s}$ be the abundance of AQ j in segment s. (Table 8.4 contains our initial estimates of these quantities $V_{j,s}$.) These abundances are related to the variables $x_{i,j,s}$ according to the equation

$$V_{j,s} = \sum_{i} x_{i,j,s} \ . \tag{9.1}$$

For detritus and photosynthetic AQs, the summation on the right-hand side of Eq. (9.1) contains only a single term (see Secs. 3.6 and 3.7). However, for heterotrophs, there may be several terms in this sum.

Thus, knowing the abundance of each heterotroph in every segment is not enough. We must partition the abundance of each heterotroph into terms for each of its diet items to find initial estimates for each of the variables $x_{i,j,s}$. That is, for each AQ j in every segment s, we must estimate what fraction of its diet consists of AQ i. Since data for making these estimates are generally unavailable, we must employ an assumption. The assumption we choose to make is that the amount of each AQ i that an AQ j in segment s will eat will be proportional to the abundance of AQ i available as food to AQ j in segment s, an assumption we will try to justify below.

In our model, not all of an AQ i need be available as potential food to a heterotrophic AQ j in segment s. However, we assume that all of AQ i in one or more segments will be available, depending upon how mobile AQs i and j are. If AQ j, for example, is very mobile, then it may feed on AQ i in every segment where AQ i is found. In our model, this is the case for benthos-eating fish. Each individual fish can swim rapidly from any area of the bottom to any other, and thus every benthic organism is available as food to every benthos-eating fish.

On the other hand, if AQ j is relatively immobile, then the only individuals of AQ i available to it are those that live in the same segment s, or which happen to swim or be swept close to AQ j. In our model, for example, we consider omnivores to be sufficiently immobile that they can only feed on organisms that happen to be in the same segment. Of course, there are omnivores in every benthic segment, so that if omnivores eat an AQ i anywhere, some omnivores will eat AQ i wherever AQ i can be found. But no single omnivore can do so.

Now, we will offer such support as we can for our assumption of proportionality in diet selection. Such direct measurements of food preferences as have been made tend to support our assumption, at least for nonherbivorous species. Stomach contents of plaice and other demersal fish (Thijssen et al., 1974; Edwards and Steele, 1968; Braber and DeGroot, 1973; and McIntyre and Eleftherion, 1968), and of cod (Daan, 1975), generally reflect the abundances of appropriately sized prey in the region of capture. (In our model, the matter of the size preference for food items is dealt with in the food web. Each ecological group has been chosen to contain organisms of roughly the same size. If the food web specifies that AQ j eats AQ i, then we have determined that organisms in AQ i are of the right size for AQ j to eat.) Ursin (1973) constructed a model based on the assumption that carnivorous fish choose their prey on the basis of size and abundance alone. That is, he assumed that two different prey species of similar size will be consumed in the same ratio as their local abundances. Data on cod and dab diets seem to fit this model fairly well.

There are, of course, some conflicting data. Ellis et al. (1976) review some reports that herbivores, especially terrestrial herbivores, may exercise considerable discrimination among available food sources. (This is of limited importance for our model, because we have not distinguished among photosynthetic species beyond separating planktonic from benthic forms.) Ivlev (1961) reported that fish generally, and carp in particular, exercise little discrimination among appropriately sized food items until they become partly satiated. But then they may begin to show a marked preference for relatively rare food items.

In addition, the proportionality rule for diet selection applies only at each instant in time, for it is derived from moment-to-moment observations. It does not apply when averaged over long periods. For example, a migratory predator and its migratory prey might both be present in the Oosterschelde only during the winter, while a second, resident prey species is present during that time in below-average numbers. (Typically, the abundance of a resident species reaches its annual minimum in winter.) Even if each meal consumed by the predator includes the two prey species in proportion to their current abundances, the predator will appear to overconsume the migratory prey, and underconsume the resident prey, from the point of view of long-term average abundances.

Nevertheless, we feel that the proportionality rule for diet selection is probably a fair approximation of the average situation. Most of the species in the Oosterschelde are resident species, and show similar seasonal patterns of abundances. The most abundant migratory ecogroup, benthos-eating fish, is represented in the Oosterschelde in every season by at least one species. In any case, in order to implement the general ecomodel, we must obtain estimates of every variable $x_{i,j,s}$ in the present Oosterschelde. Given the limitations of the data, we can think of no better way to do this than to assume the proportionality rule for diet selection.[1]

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[1] In Sec. 2.7.1, we rejected the proportionality rule for diet selection as the means for predicting the stable ecostate. Now, for purposes of calibration, we assume that the present Oosterschelde ought to obey this rule, at least approximately. Thus, it is only reasonable that every other case should obey it as well. In fact, we have found that they do; for example, in case D4 (the closed case with compartment design "4"), among the most important variables—which constitute over 99 percent of the total biomass—only one deviated from the rule by more than 25 percent.

However, our calibration process, which uses this diet selection rule, is imperfect; the degree of imperfection can be estimated by the following experiments. We recalibrated the model to the abundances it predicted for two of the reduced-tide cases, one with each compartment design, and then used the two recalibrated models to "predict" abundances for the present Oosterschelde. If the calibration were perfect, the "predicted" present Oosterschede would match the initial calibrated state exactly. In both experiments, the match was close but not exact: Only one or two of the "predicted" abundances in each case differed by more than 17 percent from their calibrated values; these outliers were always less abundant ecogroups (shrimp and crab, and omnivores). However, in a similar experiment carried out for case D4, the predictions frequently differed from the calibrated abundances by a factor of 2. The D4 results are so different because D4 has an *extreme* ecostate, in which some of the abundances are

9.2. THE PARTITIONING METHODOLOGY

Having enunciated the principle for partitioning the abundances of heterotrophs by diet item, we now describe the general rules of application. First we will show how to describe which organisms are available as food to each heterotroph in every segment. Then, we will derive the equation that uses this information, together with estimates of the abundances, to implement the partitioning.

To specify which individuals of AQ i are available to a heterotrophic AQ j in segment s, we construct the following matrix. Each column of this matrix corresponds to a heterotrophic AQ j in a segment s. For example, since omnivores can be found in three segments (shallow bottoms and tidal flats, deep bottoms, and shellfish culture plots), there are three columns of this matrix corresponding to omnivores. Similarly, each row of this matrix will correspond to an AQ i in a segment s. That is, there are three rows for omnivores, just as there are three columns. Finally, there are rows for detritus AQs and photosynthetic AQs, but no columns for these nonheterotrophic AQs.

Next, using the considerations suggested in Sec. 9.1, we fill in the matrix with zeros and ones. For example, consider the element of the matrix in the column corresponding to fish-eating fish in the pelagic segment, and the row corresponding to shrimp and crab in the shallow and intertidal segment. This element is "1" because shrimp and crab are a diet item of fish-eating fish, and, in addition, shrimp and crab in the shallow and intertidal segment are available as food to fish-eating fish in the pelagic segment. Conversely, fish-eating fish do not eat omnivores in the shallow and intertidal segment, and so the element in the corresponding column and row is zero. When the matrix is complete, every heterotroph in every segment will have had described for it which AQs in what segments are available as food.

We now denote the elements of this matrix as

$$D_{i,r;j,s} = \begin{cases} 1 \text{ if AQ j in segment s} \\ \quad \text{eats AQ i in segment r.} \\ 0 \text{ if AQ j in segment s does} \\ \quad \text{not eat AQ i in segment r.} \end{cases} \tag{9.2}$$

The matrix $D_{i,r;j,s}$ that we actually used in our model is presented as Table 9.1. For ease in reading, we have suppressed the zeros and replaced the ones with dots.

In our model, we assumed that the amount of AQ i in segment r available as food to AQ j in segment s is the product, $V_{i,r}D_{i,r;j,s}$. Thus, the total amount of AQ i available to AQ j in segment s is

$$\begin{matrix}\text{Total AQ i available} \\ \text{to AQ j in segment s}\end{matrix} = \sum_r V_{i,r}D_{i,r;j,s} \; .$$

---

near the minimum values allowed by the mass-balance constraints. The reduced-tide cases and the present Oosterschelde, by contrast, have *moderate* ecostates.

These observations argue that when the model is calibrated to a moderate ecostate, its predictions are insensitive to modest changes in the calibration state. (This will not be true, however, when the model is calibrated to an extreme state, such as D4.) These observations also suggest that our imperfect calibration procedure, applied to the moderate ecostate of the present Oosterschelde, has not appreciably affected the model's predictions for other cases, certainly not enough to influence our policy conclusions.

Table 9.1

AVAILABILITY OF PREY TO HETEROTROPHIC AQs

	Predator																										
	Pelagic						Shallow/Intertidal								Deep Bottoms						Shellfish Culture						
Prey	3. Zooplankton	12. Planktivorous fish	13. Benthos-eating fish	14. Fish-eating fish	15. Plant-/detritus-eating fish	16. Fish-eating birds	5. Cockles/limpets	6. Selective deposit feeders with pelagic larvae	7. Shrimp/crab	9. Deposit feeders with nonpelagic larvae	10. Omnivores	11. Benthic grazers	17. Plant-eating birds	18. Benthos-eating birds	5. Cockles/limpets	6. Selective deposit feeders with pelagic larvae	7. Shrimp/crab	8. Sea stars	9. Deposit feeders with nonpelagic larvae	10. Omnivores	4. Mussels/oysters	6. Selective deposit feeders with pelagic larvae	7. Shrimp/crab	8. Sea stars	9. Deposit feeders with nonpelagic larvae	10. Omnivores	11. Benthic grazers
Pelagic																											
1. Phytoplankton	●						●								●						●						
2. Suspended detritus	●						●								●						●						
3. Zooplankton	●	●	●																								
12. Planktivorous fish				●		●																					
13. Benthos-eating fish				●		●																					
14. Fish-eating fish				●																							
15. Plant-/detritus-eating fish																											
16. Fish-eating birds																											
Shallow/Intertidal																											
1. Sea grass/seaweed; benthic diatoms					●			●		●	●	●	●														
2. Organic sediments					●			●		●	●	●	●														
5. Cockles/limpets			●						●					●			●						●				
6. Selective deposit feeders with pelagic larvae			●						●					●			●						●				
7. Shrimp/crab			●	●					●					●			●						●				
9. Deposit feeders with nonpelagic larvae			●						●		●			●			●						●				
10. Omnivores			●						●		●			●			●						●				
11. Benthic grazers			●						●					●			●						●				
17. Plant-eating birds																											
18. Benthos-eating birds																											
Deep Bottoms																											
2. Organic sediments																●			●	●							
5. Cockles/limpets			●						●								●	●					●				
6. Selective deposit feeders with pelagic larvae			●						●								●						●				
7. Shrimp/crab			●	●					●								●						●				
8. Sea stars			●																								
9. Deposit feeders with nonpelagic larvae			●						●								●			●			●				
10. Omnivores			●						●								●			●			●				
Shellfish Culture																											
2. Organic sediments					●																	●			●	●	●
4. Mussels/oysters			●						●					●			●						●	●			
6. Selective deposit feeders with pelagic larvae			●						●								●						●				
7. Shrimp/crab			●	●					●								●						●				
8. Sea stars			●																								
9. Deposit feeders with nonpelagic larvae			●						●								●						●			●	
10. Omnivores			●						●								●						●			●	
11. Benthic grazers			●						●								●						●	●			

The complete amount of food of all types available to AQ j in segment s should be

$$\text{Food available to AQ j in segment s} = \sum_i \sum_r V_{i,r} D_{i,r;j,s} \ .$$

Note that in principle, $D_{i,r;j,s}$ need not be zero or 1, but may have any value in between. For example, if only 50 percent of the shrimp and crab in the shallow and intertidal segment were available to fish-eating fish in the pelagic segment, then one could signify this by setting $D_{i,r;j,s}$ equal to 0.5. Similarly, if the fish-eating fish showed an aversion to eating shrimp and crab, as compared with eating other fish, the elements corresponding to fish-eating fish consuming shrimp and crab could be reduced. However, as explained in Sec. 9.1, we found no sound reason for assuming that when two different AQs in the same or different segments were each available to some degree as food for AQ j in segment s, different fractions of the two should be available. We therefore assumed initially that all of these fractions were the same, unless they were zero. Choosing the elements $D_{i,r;j,s}$ to be either zero or 1 implements this assumption.

Note that the matrix with elements $D_{i,r;j,s}$ can be regarded as a representation of the food web. As we represented it before in our small example (see Figs. 2.1, 4.1, and 4.5), the food web was a network with a node for each ecogroup, and an arc from a node i to a node j only if ecogroup i was preyed upon by ecogroup j. In matrix D, there is a row for each ecogroup in each segment, and ecogroup i is preyed upon by ecogroup j if for some pair of segments r and s (possibly the same segment, i.e., r = s), the quantity $D_{i,r;j,s}$ is positive. However, the matrix D contains more information than the food web. First of all, it can specify that some segments act as protective shelters for some species, since an ecogroup j may not find that those members of ecogroup i in segment r are among its available food supply. Second, if values of $D_{i,r;j,s}$ other than zero and 1 are used, the matrix can specify the relative desirability of different prey species, and the relative protection that they enjoy in the various segments. Representing the food web as a network omits all such quantitative information.

In Sec. 3.2, we defined $y_{i,j,s}$ to be the daily amount of AQ i that is consumed by individuals of AQ j that are found in segment s. Thus, the total food intake of AQ j in segment s is

$$\text{Food intake by AQ j in segment s} = \sum_i y_{i,j,s} \ .$$

According to the principle that a heterotroph eats each diet item in proportion to the latter's availability, the ratio of the variable $y_{i,j,s}$ to the total food intake by AQ j in segment s should be the same as the ratio of the total AQ i to the grand total of all food available to AQ j in segment s. That is,

$$\frac{y_{i,j,s}}{\sum_i y_{i,j,s}} = \frac{\sum_r V_{i,r} D_{i,r;j,s}}{\sum_i \sum_r V_{i,r} D_{i,r;j,s}} \ . \qquad (9.3)$$

In Sec. 3.5. we related the variables $x_{i,j,s}$ to the quantities $y_{i,j,s}$ according to the equation

$$x_{i,j,s} = \frac{(1 - f_i)y_{i,j,s}}{r_j} , \qquad (9.4)$$

where f_i is the proportion of AQ i that cannot be assimilated, and will therefore be excreted as feces, and r_j is the amount of food that AQ j must assimilate to live and grow normally. By combining Eqs. (9.3) and (9.4), we derive the following expression for the variable $x_{i,j,s}$:

$$\frac{x_{i,j}}{V_{j,s}} = \frac{\sum\limits_{r} (1 - f_i)V_{i,r}D_{i,r;j,s}}{\sum\limits_{i}\sum\limits_{r} (1 - f_i)V_{i,r}D_{i,r;j,s}} . \qquad (9.5)$$

In our model of the Oosterschelde, we used the matrix $D_{i,r;j,s}$ shown in Table 9.1. How to read this matrix has been explained in the text above. We have used this matrix, together with the abundance estimates from Table 8.4, to obtain initial estimates for each of the variables $x_{i,j,s}$ according to Eq. (9.5). The results are not shown here, because we have no data with which to compare them.

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Chapter 10

DETERMINING BALANCED ESTIMATES OF THE VARIABLES

10.1. INTRODUCTION

The true values of the variables $x_{i,j,s}$ should satisfy the balance constraints. In general, however, our initial estimates of these variables do not—i.e., our initial estimates are unbalanced. Considering the uncertainties in the initial abundance estimates, it would be a most unlikely coincidence if they were balanced. The next step of the calibration produces adjusted estimates of the variables that are balanced: They satisfy the balance constraints, and (because we have no better guide to their true values) they are close to the initial estimates. That is, the next step of calibration yields an associated pair of estimates of the variables: an initial unbalanced estimate and an adjusted balanced estimate.

Some mass transfers to and from outside the ecosystem may be unknown, or poorly known. This is especially true for detritus. We can estimate these unknowns by not requiring that the adjusted, balanced estimates of the variables satisfy their associated balance constraints. We then estimate values for the $x_{i,j,s}$'s that satisfy the remaining balance equations. These $x_{i,j,s}$'s can be substituted into the balance equations whose external mass transfers are unknown, and the external mass transfers can be chosen so that these balance equations, too, are satisfied.

Usually the results of this operation are unsatisfactory. Even though our technique for finding balanced estimates ensures that they will be as close as possible to the initial but unbalanced estimates of the variables, still the balanced estimates may bear scant similarity to the associated unbalanced estimates. When this happens, we take it to signify that the original unbalanced estimates were incorrect, which is not an unexpected finding, since the original estimates were largely conjectures derived from hypotheses based on assumptions. When the original estimates turn out to be far afield, one can feel justified in modifying or replacing some of the least tenable of the assumptions, and in re-estimating one or more of the variables. This balancing act generates a succession of associated pairs of estimates of the variables: an initial unbalanced estimate and its associated balanced estimate; a revised unbalanced estimate and its associated balanced estimate; and so forth. In calibrating the model of the Oosterschelde, we changed the initial unbalanced estimates of the variables approximately twenty times before we arrived at satisfactory balanced estimates.

10.2. METHODOLOGY FOR FINDING BALANCED INITIAL ESTIMATES OF THE VARIABLES $x_{i,j,s}$

In this section we address the problem of finding balanced estimates of the variables $x_{i,j,s}$ that are as close as possible to given unbalanced estimates. As explained above, we seek to solve this problem for a succession of different unbalanced estimates, starting from the estimates given in Table 8.4. Later estimates in the sequence will be obtained from earlier ones by judicious adjustments designed to produce more nearly balanced estimates.

As stated, our problem is a standard mathematical programming problem: We wish to minimize a function of our variables subject to known constraints. In this case, the function to be minimized is some measure of the distance between a specified unbalanced estimate and the balanced estimate we are calculating. The constraints, of course, are the balance conditions and the common-sense requirement that each variable be positive or (at worst) zero.

An extensive literature exists on how such problems can be solved (Abadie, 1967; Fiacco and McCormick, 1968; Rosen, 1960), and so we need not discuss methods of solution here. However, there remains the question of what measure of distance from the specified unbalanced estimate to any other estimate of the variables we should use. In one sense, the choice is not critical, since we repeatedly revise our specified unbalanced estimate until it becomes nearly balanced. Any measure of distance should suffice, because it will achieve its minimum at a balanced estimate that by any standard is very close to the revised unbalanced estimate that is now nearly balanced.

In another sense, however, our choice of a distance function is important, because when our unbalanced estimates of the variables are very far from being balanced, we desire that the balanced estimates closest to them guide us in revising the unbalanced estimates. For example, if we were to find that the balanced estimates of the variables gave us an abundance of sea stars in the shellfish culture plots of 50 metric tons, instead of our old estimate of 19 metric tons, we would like to be able to interpret this outcome as reason to revalue our estimate of sea star abundance upward. We want to avoid a distance measure for which this same outcome would more likely imply that a competitor of sea stars should be adjusted slightly downward. (We should mention that we have not found a distance measure that is entirely satisfactory from this standpoint.)

We tried two different distance measures to begin with. The first measure took the distance from the vector of variables x (containing components $x_{i,j,s}$) and the vector u (with components $u_{i,j,s}$) to be

$$M(x,u) = \sum_{i} \sum_{j} \sum_{s} \left(x_{i,j,s} - u_{i,j,s} \right)^2 .$$

This measure was unsatisfactory, because a discrepancy of 1 metric ton in a variable corresponding to a very abundant organism counted just as heavily as the same discrepancy of 1 ton in a very rare organism. For example, according to this distance function, it is no worse to overestimate the number of cockles by 1 ton (we think there are over 9000 tons of cockles present) than to overestimate fish-eating birds by the same 1 ton (there is probably less than 0.1 ton of these birds present).

Next, we tried a distance measure that measured a relative discrepancy rather than an absolute difference. By letting the vector u, above, be the unbalanced estimate we start with, and the vector x, above, be the balanced estimate we seek, then the distance from x to u can be measured by

$$M(x,u) = \sum_i \sum_j \sum_s \frac{\left(x_{i,j,s} - u_{i,j,s}\right)^2}{u_{i,j,s}^2} . \tag{10.1}$$

This distance measure was much superior to the first, so we used it in most of our work. Nevertheless, the second measure appears to overcompensate for the faults of the first. We were dissatisfied with the first measure because errors in variables estimated to have small values were being too lightly weighted in comparison with errors in variables estimated to be large. Although an improvement, the second measure causes errors in small variables to be too heavily weighted compared with errors in large variables. While we may tolerate a 50 percent or even a 100 percent error in a small variable—e.g., one corresponding to a rare ecological group, such as omnivores and predatory worms—we would be very reluctant to permit such a discrepancy to persist in a large variable, one that might, for example, correspond to an abundant group such as cockles or benthic grazers.

We therefore continued to seek a better choice for a distance measure. An obvious measure to use, because it is a compromise between the first two, is

$$M(x,u) = \sum_i \sum_j \sum_s \frac{\left(x_{i,j,s} - u_{i,j,s}\right)^2}{u_{i,j,s}} . \tag{10.2}$$

Another possible measure is the Gibbs function. To employ this measure, we would simply set the parameters $c_{i,j,s}$ to be

$$c_{i,j,s} = -\log \frac{u_{i,j,s}}{\bar{u}_s} . \tag{10.3}$$

With these values for its parameters, the Gibbs function becomes

$$M(x,u) = \sum_i \sum_j \sum_s x_{i,j,s} \log \frac{x_{i,j,s}}{u_{i,j,s}} - \sum_s \bar{x}_s \log \frac{\bar{x}_s}{\bar{u}_s} . \tag{10.4}$$

These two possibilities are very similar. In fact, in the limit, as the nominal values of the segment parameters Z_s become infinitely large, the distance measure defined in Eq. (10.2) becomes equal to the quadratic Taylor's approximation of the Gibbs function defined by Eq. (10.4), where the approximation is made at the point u (the vector with components $u_{i,j,s}$).

Because of this similarity, we investigated only one of these functions, the Gibbs function. This choice was attractive on practical grounds because the same computer code that our model uses to predict responses of the Oosterschelde ecology to changes in segment sizes or external mass transfers can also help us find initial balanced estimates for the variables. It is also attractive on theoretical grounds related to statistical estimation theory. (See Jaynes, 1967, 1962, and 1968.)

According to this work, we can regard the ratio $u_{i,j,s}/\bar{u}_s$ as the prior probability of finding an organism j supporting itself on organism i in a small sample from segment s. (Of course, any individual organism will eat some of every diet item available to it. Thus, this ratio can be interpreted as the prior probability of finding the organism, times the fraction of its diet that is organism i.) Similarly, the balanced estimates that we derive by minimizing this function yield ratios $x_{i,j,s}/\bar{x}_s$, which can be interpreted as the corresponding posterior probabilities.

10.3. FINDING INITIAL BALANCED ESTIMATES OF THE VARIABLES $x_{i,j,s}$

In this and several following sections, we will describe the sequence of operations we used to calibrate the model to the present state of the Oosterschelde ecology. The sequence we report, however, is not a faithful rendering of the sequence we actually followed. In the actual sequence, we frequently made adjustments to such parameters as the initial estimates of ecogroup abundances, later to be revised a second or a third time, or even restored to their original values. In our description below, such steps are omitted.

In addition, we performed the calibration procedure twice, once using the distance measure defined by Eq. (10.1), and once using the Gibbs function defined as in Eq. (10.4). The calibration sequence described here used the Gibbs function as its distance measure. But, much of our work was done using the model as calibrated with Eq. (10.1) as the distance measure. Thus, when recalibrating with the Gibbs function, we were motivated to produce essentially the same calibrated model as we had with Eq. (10.1).

Fortunately, a replication could be readily achieved. To this end, at some points in the calibration sequence we changed certain parameters specifically to make the second calibration arrive at the same state as the first. Our justification was that there is a range of plausible calibrated models that will reproduce the ecogroup abundances in the present Oosterschelde within the certainty with which they are known. We had to choose one such plausible calibrated state, in the full knowledge that it might be considerably different from the true (but unknown) state of the present Oosterschelde. We could see no advantage in picking another, unless the second calibration procedure had for some reason shown the first to be implausible.

The fact that we have chosen one calibrated state does not mean we have ignored the existence of other plausible calibrations. We have tried, in drawing our conclusions, to avoid those that depend strongly on the calibrated state of the model. Rather, we have based our conclusions on comparisons between states that we expect would hold for any reasonable calibrated state.

As we have pointed out, finding acceptable balanced estimates of the variables —i.e., estimates that satisfy the balance constraints—cannot be a completely automated process. To illustrate this point, suppose that we carry out the procedure as we have described it so far. That is, we start with the abundance estimates given in Table 8.4 and with the food availability matrix shown in Table 9.1. To these we apply Eq. (9.5), obtaining our initial unbalanced estimates of the variables. Finally, we find new balanced estimates of the variables that minimize the distance function given by Eq. (10.4). If we collect these balanced estimates of the variables into estimates for the abundances of each AQ in every segment, we obtain the abundances shown in Table 10.1. (In this table, the first line of numbers opposite an ecological group's name is the new balanced abundance estimates. We have included as a second line, in parentheses, the abundance estimates from Table 8.4.)

Table 10.1

COMPARISON BETWEEN INITIAL UNBALANCED ABUNDANCE ESTIMATES AND INITIAL BALANCED ESTIMATES

(In metric tons afdw)

Ecological Group	Segment			
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms	Shellfish Culture Plots
Photosynthetic organisms	1119.0 (1300.0)	7675.0 (7770.0)	--	--
Detritus/microbenthos	25100.0 (25100.0)	77500.0 (77500.0)	55900.0 (55900.0)	7250.0 (7250.0)
Zooplankton/pelagic larvae	572.9 (563.0)	--	--	--
Mussels/oysters	--	--	--	1306.0 (1200.0)
Cockles/limpets	--	9007.0 (9255.0)	194.7 (200.0)	--
Selective deposit feeders with pelagic larvae	--	532.0 (594.0)	15.3 (17.0)	69.5 (77.0)
Crabs/shrimp	--	32.5 (14.3)	45.1 (19.8)	28.9 (12.7)
Sea stars	--	--	29.9 (24.0)	16.7 (19.0)
Deposit feeders with nonpelagic larvae	--	1949.0 (2100.0)	0.108 (0.116)	254.0 (272.0)
Omnivores/predator worms	—	11.2 (12.0)	1.63 (1.92)	1.54 (1.56)
Benthic grazers	--	3936.0 (4620.0)	--	373.0 (432.0)
Planktivorous fish	238.4 (250.0)	--	--	--
Benthos-eating fish	2262.0 (1600.0)	--	--	--
Fish-eating fish	202.8 (316.0)	--	--	--
Plant-/detritus-eating fish	30.0 (30.0)	--	--	--
Fish-eating birds	0.0462 (0.0462)	--	--	--
Plant-eating birds	--	0.074 (0.074)	--	--
Benthos-eating birds	--	9.5 (9.5)	--	--

10.4. FINDING REVISED BALANCED ESTIMATES: FIRST ITERATION

The AQ whose abundance matched least acceptably in Table 10.1 was the benthic grazers in the shallow bottom and tidal flat segment. (Even though other AQs show a greater percentage difference, we single out benthic grazers because we have a considerable amount of data to support our estimate of their abundance —at least in the Grevelingen—and because their abundance is so large.) Consequently, we reexamined our original estimates of benthic grazers. (Benthos-eating fish also matched poorly, but for simplicity we leave them until later).

Originally, we estimated the abundance of benthic grazers on the tidal flats and shallow bottoms of the Oosterschelde by assuming their density to be the same as that found on the tidal flats in the Grevelingen. However, benthic grazers are not found much in permanently submerged areas (Wolff, 1973). Since the tidal flats make up only 58 percent of the shallow bottom and tidal flat segment, we felt justified in reducing our estimate to 58 percent of its original value.

Furthermore, according to Wolff, benthic grazers are not abundant where wave action is prevalent. But the tidal flats in the western part of the Oosterschelde are subjected to considerable wave action. We have therefore further reduced our estimate of benthic grazers on shallow bottoms and tidal flats to 40 percent of the value found in Table 8.4.

For much the same reasons, we altered the abundance estimate of selective deposit feeders with pelagic larvae in the shallow bottom and tidal flat segment. The original estimate assumed that these organisms were found in the same density on the tidal flats and shallow bottoms of both the Grevelingen (where they were measured) and the Oosterschelde. Once again, however, there is reason to believe that the shallow areas of the Grevelingen and Oosterschelde are not as similar as we had first thought.

Of the species among the selective deposit feeders, *Macoma balthica* is the most abundant. According to Wolff, *Macoma* dwells on mud flats. But mud flats are more prevalent in the Grevelingen than in the Oosterschelde, as a fraction of total tidal flat area. A large fraction of the Oosterschelde's tidal flats are composed of sediments coarser, and with less organic material, than mud. We thus reduced (somewhat arbitrarily) our estimate of selective deposit feeders on shallow bottoms and tidal flats to 50 percent of the value in Table 8.4.

Having changed our abundance estimates, we recalculated estimates of the variables according to Eq. (9.5) and recalculated balanced estimates of the variables by minimizing the distance function, Eq. (10.4), subject to the balance constraints. The results are shown in Table 10.2.

10.5. FINDING REVISED BALANCED ESTIMATES: SECOND ITERATION

Note in Table 10.2 the improved matching between the initial unbalanced and balanced estimates. For benthic grazers in the shallow bottom and tidal flat segment, the discrepancy (comparison between the balanced estimate and the unbalanced estimate from which it was derived) changed from -15 percent to -9

Table 10.2

FIRST REVISION OF ABUNDANCES: COMPARISON BETWEEN REVISED UNBALANCED ABUNDANCE ESTIMATES AND REVISED BALANCED ESTIMATES

(In metric tons afdw)

Ecological Group	Segment			
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms	Shellfish Culture Plots
Photosynthetic organisms	1240.0 (1300.0)	7740.0 (7770.0)	--	--
Detritus/micro-benthos	25100.0 (25100.0)	77500.0 (77500.0)	55900.0 (55900.0)	7250.0 (7250.0)
Zooplankton/pelagic larvae	581.0 (563.0)	--	--	--
Mussels/oysters	--	--	--	1329.0 (1200.0)
Cockles/limpets	--	9205.0 (9255.0)	198.9 (200.0)	--
Selective deposit feeders with pelagic larvae	--	281.3 (300.0)	16.0 (17.0)	72.4 (77.0)
Crabs/shrimp	--	19.8 (14.3)	27.5 (19.8)	17.6 (12.7)
Sea stars	--	--	26.5 (24.0)	14.4 (19.0)
Deposit feeders with nonpelagic larvae	--	2014.0 (2100.0)	0.111 (0.116)	261.0 (272.0)
Omnivores/predator worms	--	11.3 (12.0)	1.74 (1.92)	1.51 (1.56)
Benthic grazers	--	1683.0 (1848.0)	--	395.2 (432.0)
Planktivorous fish	238.7 (250.0)	--	--	--
Benthos-eating fish	1824.0 (1600.0)	--	--	--
Fish-eating fish	170.9 (316.0)	--	--	--
Plant-/detritus-eating fish	30.0 (30.0)	--	--	--
Fish-eating birds	0.0462 (0.0462)	--	--	-
Plant-eating birds	--	0.074 (0.074)	--	--
Benthos-eating birds	--	9.5 (9.5)	--	--

percent. For selective deposit feeders, the change was from −10 percent to −6 percent.

There were also improvements in such ecological groups as benthos-eating fish (which changed from a discrepancy of +41 percent to +14 percent), photosynthetic organisms in the pelagic segment (−14 percent to −5 percent), and deposit feeders with nonpelagic larvae on shallow bottoms and tidal flats (−7 percent to −4 percent). These improvements are in the prey (photosynthetic organisms), the competitors (deposit feeders with nonpelagic larvae), and the predators (benthos-eating fish) of the organisms whose abundance estimates we changed. This suggests that we might effect further improvement in benthic grazers and selective deposit feeders by altering our estimates of the abundances of these other ecological groups.

In our model, each ecological group must be in balance. This means that enough of each group must be consumed by its predators to prevent net growth. If there are too few predators to consume a given abundance of benthic grazers, the model will react by reducing the abundance of benthic grazers. It may be that we can change this reaction by increasing our estimates of the predators of benthic grazers.

In particular, we will reestimate the abundance of benthos-eating fish. This group is an important predator, not only of benthic grazers and selective deposit feeders, but of omnivores and deposit feeders with nonpelagic larvae as well. The most abundant of these prey of benthos-eating fish are now being underestimated, perhaps because of insufficient predation. This possibility is borne out by the fact that benthos-eating fish are predicted by the model to eat about 40 percent more of selective deposit feeders, deposit feeders with nonpelagic larvae, and benthic grazers than is justified by their abundance, according to the proportionality rule for diet selection. (We have not shown the diet choices calculated for either the balanced or the unbalanced estimates. Aside from the use of diets that we have made here—namely to judge whether a balanced estimate is satisfactory—diets have only served as intermediate variables for the calculation of abundances.)

The estimate of benthos-eating fish given in Table 8.4 assumes that these fish are three times more dense over the shallow bottoms and (at high tide) the tidal flats than they are over the deep bottoms. Now we change that ratio to five. (This ratio is speculation in any case.) We also increase the estimate slightly to account for the species goby, which were not reported by R.I.V.O. because their small size enables them to frequently escape the sampling net, and because they are not commercially interesting (R.I.V.O.'s main work concerns the proper management and exploitation of commercial fisheries). The new estimate of benthos-eating fish is 2200 tons afdw.

We note that predation of mussels by benthos-eating fish is being underestimated by a factor of 2 (i.e., the balanced estimate is only one-half of the corresponding unbalanced estimate). We can improve this estimate either by decreasing the abundance estimate of benthos-eating fish or by increasing the estimate of mussels. In view of our earlier decision to increase the estimate of benthos-eating fish, we must select the latter course.

Our initial estimate of this mussel abundance was derived from data on the commercial production of mussels. According to these data, only one-third of the growth and reproduction of mussels is consumed by predators; the other two-thirds are harvested by man. We do not believe that the mussel growers can be this efficient in preventing other organisms from preying on their mussels. But, if man takes a smaller fraction of the mussel growth, as we believe he does, then there must be a larger standing stock of mussels than we have estimated in Table 8.5. The rationale is that the smaller fractional "take," multiplied by the (necessarily) larger total growth, must equal a known harvest. And this larger total growth requires a larger standing stock to support it. We therefore increased our estimate of mussel abundance from its value of 1200 tons in Table 8.4 to 2000 tons.

Having changed our abundance estimates, we recalculated estimates of the variables according to Eq. (9.5), and recalculated balanced estimates of the variables by minimizing the distance function, Eq. (10.4), subject to the balance constraints. The results are shown in Table 10.3.

10.6. FINDING REVISED BALANCED ESTIMATES: THIRD ITERATION

Table 10.3 shows modest improvements in the comparisons between many balanced and unbalanced pairs of estimates. Benthos-eating fish improved from a 14 percent overestimate in Table 10.2 to a 6 percent underestimate in Table 10.3. (This improvement is actually insignificant, because our knowledge of these abundances is not accurate to within 14 percent. However, their diet match improved greatly.) Selective deposit feeders, deposit feeders with nonpelagic larvae, and benthic grazers all improved slightly; but there remain some instances of poor matches, notably zooplankton and fish-eating fish.

The latter matches are poor, not because the balanced estimates of the abundances compare poorly with the corresponding unbalanced estimates, but because the balanced estimates of their diets differ considerably from the unbalanced diet estimates. In particular, both zooplankton and fish-eating fish are cannibalistic, but the latest balanced estimates require that these organisms have a very pronounced aversion toward eating members of their own ecogroups.

To improve the match of the fish-eating fish diet, we reduced our estimate of their abundance from 316 tons to 200 tons. We reasoned that since fish-eating fish are the only predators of fish-eating fish, the amount of themselves that the balanced estimate predicts they eat will be proportional to their own abundance. But the unbalanced estimate of their self-consumption contains their own abundance as a factor twice, once because the total amount they eat is proportional to their abundance, and once because the fraction of their diet made up of themselves depends on how abundant they are relative to other diet items. Therefore, reducing our estimate of their abundance should reduce the unbalanced estimate of their cannibalism more than the balanced estimate.

To improve the match for zooplankton cannibalism, we could similarly increase our estimate of their abundance. However, we chose instead to reduce our estimate of the abundance of their most important predator, planktivorous fish. Here is a point at which we could no doubt have chosen otherwise, and thus have arrived at a different calibrated state of the model. But, when we calibrated the model using Eq. (10.1) as our distance measure, we reduced the abundance estimate of planktivorous fish (the option of increasing the abundance estimate of zooplankton did not appear to be as attractive in that case). Therefore, of what appear, in this second calibration sequence, to be two equally good alternatives, we again chose the one

Table 10.3

SECOND REVISION OF ABUNDANCES: COMPARISON BETWEEN REVISED UNBALANCED ABUNDANCE ESTIMATES AND REVISED BALANCED ESTIMATES

(In metric tons afdw)

Ecological Group	Segment			
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms	Shellfish Culture Plots
Photosynthetic organisms	1221.0 (1300.0)	7732.0 (7770.0)	--	--
Detritus/microbenthos	25100.0 (25100.0)	77500.0 (77500.0)	55900.0 (55900.0)	7250.0 (7250.0)
Zooplankton/pelagic larvae	581.0 (563.0)	--	--	--
Mussels/oysters	--	--	--	2145.0 (2000.0)
Cockles/limpets	--	9447.0 (9255.0)	204.1 (200.0)	--
Selective deposit feeders with pelagic larvae	--	291.0 (300.0)	16.5 (17.0)	75.0 (77.0)
Crabs/shrimp	--	13.2 (14.3)	18.3 (19.8)	11.7 (12.7)
Sea stars	--	--	22.4 (24.0)	14.4 (19.0)
Deposit feeders with nonpelagic larvae	--	2074.0 (2100.0)	0.115 (0.116)	269.4 (272.0)
Omnivores/predator worms	--	11.4 (12.0)	1.82 (1.92)	1.50 (1.56)
Benthic grazers	--	1753.0 (1848.0)	--	412.4 (432.0)
Planktivorous fish	231.5 (250.0)	--	--	--
Benthos-eating fish	2064.0 (2200.0)	--	--	--
Fish-eating fish	186.5 (316.0)	--	--	--
Plant-/detritus-eating fish	30.0 (30.0)	--	--	--
Fish-eating birds	0.0462 (0.0462)	--	--	--
Plant-eating birds	--	0.074 (0.074)	--	--
Benthos-eating birds	--	9.5 (9.5)	--	--

of reducing the abundance estimate of planktivorous fish. Accordingly, we reduced our estimate of planktivorous fish from its value of 250 tons in Table 8.4 to 125 tons.

Having changed our abundance estimates, we recalculated estimates of the variables according to Eq. (9.5), and recalculated balanced estimates of the variables by minimizing the distance function, Eq. (10.4), subject to the balance constraints. The results are shown in Table 10.4.

Table 10.4

THIRD REVISION OF ABUNDANCES: COMPARISON BETWEEN REVISED UNBALANCED ABUNDANCE ESTIMATES AND REVISED BALANCED ESTIMATES

(In metric tons afdw)

Ecological Group	Segment			
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms	Shellfish Culture Plots
Photosynthetic organisms	1226.0 (1300.0)	7734.0 (7770.0)	--	--
Detritus/microbenthos	25100.0 (25100.0)	77500.0 (77500.0)	55900.0 (55900.0)	7250.0 (7250.0)
Zooplankton/pelagic larvae	559.0 (563.0)	--	--	--
Mussels/oysters	--	--	--	2139.0 (2000.0)
Cockles/limpets	--	9418.0 (9255.0)	203.5 (200.0)	--
Selective deposit feeders with pelagic larvae	--	289.8 (300.0)	16.5 17.0)	74.6 (77.0)
Crabs/shrimp	--	13.6 (14.3)	18.9 (19.8)	12.1 (12.7)
Sea stars	--	--	22.9 (24.0)	14.7 (19.0)
Deposit feeders with nonpelagic larvae	--	2066.0 (2100.0)	0.114 (0.116)	268.4 (272.0)
Omnivores/predator worms	--	11.4 (12.0)	1.81 (1.92)	1.5 (1.56)
Benthic grazers	--	1745.0 (1848.0)	--	410.2 (432.0)
Planktivorous fish	123.2 (125.0)	--	--	--
Benthos-eating fish	2054.0 (2200.0)	--	--	--
Fish-eating fish	171.2 (200.0)	--	--	--
Plant-/detritus-eating fish	30.0 (30.0)	--	--	--
Fish-eating birds	0.0462 (0.0462)	--	--	--
Plant-eating birds	--	0.074 (0.074)	--	--
Benthos-eating birds	--	9.5 (9.5)	--	--

10.7. FINDING REVISED BALANCED ESTIMATES: FOURTH ITERATION

In Table 10.4, all the balanced abundances match very well with the corresponding unbalanced estimates. A few of the less abundant ecogroups have diets whose balanced and unbalanced estimates do not match too well, but for the more important groups, both the abundances and the diets are in very good agreement. We might stop further calibration at this point.

However, when we calibrated with Eq. (10.1) as our distance measure, we found it desirable to adjust the abundance estimates of omnivores. For no other reason than to obtain the same calibration in this case, we will also change the omnivore abundance estimates. Accordingly, the values in Table 8.4 become the following: on shallow bottoms and tidal flats, 4.0 tons; on deep bottoms, 1.14 tons; and on the shellfish culture plots, 0.95 ton.

Having changed our abundance estimates, we recalculated estimates of the variables according to Eq. (9.5), and recalculated balanced estimates of the variables by minimizing the distance function, Eq. (10.4), subject to the balance constraints. The results are shown in Table 10.5.

10.8. SOME FINAL COMMENTS ON FINDING ACCEPTABLE BALANCED ESTIMATES

In this chapter, we have described the process by which one can obtain acceptable, balanced estimates of the abundances of each ecological group in every segment. This description is not a recreation of our original path to an acceptable balanced estimate, although our original path ended where our illustration did (i.e., at the abundances given in Table 10.5). Our route was much more tortuous, taking about twenty iterations rather than the four or five shown here. For example, we began with very different estimates for the abundance of detritus than are found in Table 8.4. The abundance estimates of sea stars had to be revised during this process because new data were uncovered. Indeed, many of the initial abundance estimates were revised because of the acquisition of new data, making it necessary to repeat much of this process several times.

During this revision process, we changed more parameters than merely the abundance estimates. For example, at one time we thought it would be necessary to adjust the prey availability matrix, $D_{i,r,js}$. We also had to search for intrinsic mortality rates for phytoplankton and for benthic photosynthetic organisms (sea grass, seaweed, and benthic diatoms). (It later became clear that this is not a very important parameter. If a photosynthetic organism dies, it is still available to its consumers as food in the form of detritus.) As another example, we had to choose a rate of detritus mineralization.

In one sense, the mineralization rate is unimportant. During the entire process of finding acceptable balanced estimates, we allowed the rate of detritus import to float—i.e., to assume whatever value that would allow the distance from the unbalanced estimate to its balanced counterpart to be minimized. (This, incidentally, is why in all of our revisions of the abundances, the balanced estimates of detritus abundances match the unbalanced estimates perfectly.) We found that the rate of detritus import that minimized the distance between the final unbalanced esti-

Table 10.5

FOURTH REVISION OF ABUNDANCES: COMPARISON BETWEEN REVISED UNBALANCED ABUNDANCE ESTIMATES AND REVISED BALANCED ESTIMATES

(In metric tons afdw)

Ecological Group	Segment			
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottom	Shellfish Culture Plots
Photosynthetic organisms	1226.0 (1330.0)	7734.0 (7770.0)	--	--
Detritus/microbenthos	25100.0 (25100.0)	77500.0 (77500.0)	55900.0 (55900.0)	7250.0 (7250.0)
Zooplankton/pelagic larvae	559.0 (563.0)	--	--	--
Mussels/oysters	--	--	--	2139.0 (2000.0)
Cockles/limpets	--	9418.0 (9255.0)	203.5 (200.0)	--
Selective deposit feeders with pelagic larvae	--	289.8 (300.0)	16.5 (17.0)	74.7 (77.0)
Crabs/shrimp	--	13.6 (14.3)	18.9 (19.8)	12.1 (12.7)
Sea stars	--	--	22.9 (24.0)	14.7 (19.0)
Deposit feeders with nonpelagic larvae	--	2066.0 (2100.0)	0.114 (0.116)	268.3 (272.0)
Omnivores/predator worms	--	3.8 (4.0)	1.07 (1.14)	0.91 (0.95)
Benthic grazers	--	1745.0 (1848.0)	--	410.2 (432.0)
Planktivorous fish	123.2 (125.0)	--	--	--
Benthos-eating fish	2054.0 (2200.0)	--	--	--
Fish-eating fish	171.2 (200.0)	--	--	--
Plant-/detritus-eating fish	30.0 (30.0)	--	--	--
Fish-eating birds	0.0462 (0.0462)	--	--	--
Plant-eating birds	—	0.074 (0.074)	--	--
Benthos-eating birds	--	9.5 (9.5)	--	--

mates and their balanced counterparts was approximately 500 metric tons/day, plus the rate at which detritus was lost from the ecosystem by mineralization. Consequently, if we assumed a high rate of detritus mineralization, the ecosystem required an incredibly high rate of detritus import.

At first we assumed that the mineralization rate was 10 percent per day. But, given the detritus abundances we have estimated (a total of 165750 tons), this would have implied that 16575 tons of detritus must be mineralized each day. But if this much is mineralized, and if at the same time the abundance of detritus remains roughly constant (this is our stationarity assumption), then 16575 tons of detritus must be replaced from somewhere—along with the 500 tons of detritus consumed daily by the various ecological groups. In the appendix, we point out that even 500 tons/day of detritus import is difficult to explain, or even to accept. How much more difficult it would be to accept a detritus import rate of 17000 tons/day!

Consequently, we reduced the mineralization rate from 10 percent per day to 0.12 percent per day. We support this choice as follows. First, we found that the rate of 10 percent per day applied to sewage treatment plants, and not to natural situations (Bigelow and De Haven, 1977, and references therein). Observations of mineralization in nature suggested it was much slower there. For example, inferences of turnover time for organic molecules in the deep oceans suggested a mineralization rate of 0.1 percent per year or less (Parsons and Takahashi, 1973, p. 136). Thinking that mineralization ought to occur more rapidly in the biomass-rich Oosterschelde than in the deep oceans, we compromised on the value of 0.12 percent per day for a mineralization rate. This added only 200 tons/day to the requirement for detritus import.

Still other parameters we considered adjusting were the fraction of the production of an ecological group that was lost from the Oosterschelde by migration, and the fraction of the daily ration that was used for production. Reducing this latter fraction is one way of "aging" a population. (Older organisms grow more slowly than younger ones.) However, we found that much the same effects could be produced by adjusting the abundances, or in some cases the external mass transfers, and so we abandoned this line of attack.

10.9. INSIGHTS DEVELOPED DURING CALIBRATION

One of the most valuable benefits arising from the process of finding acceptable balanced estimates is the opportunity it affords for gaining insights into the quantitative relationships among the different ecological groups. For example, we found that a very large rate (500 tons/day plus the amount of mineralization per day) of detritus import is required to support the biomass in the present Oosterschelde. As we have pointed out in the appendix, such a conclusion could hardly have been derived from any existing method and data other than those we used, namely, the method of calculating a balanced ecostate from the existing abundance data.

Yet another insight involves mussels. Previous studies of mussels in the Oosterschelde concentrated on the commercial aspects of the mussel culture. It was natural, therefore, that estimates of mussel abundances were based solely on the mussel harvest. By contrast, our work forced us to realize that so large a standing stock of mussels must suffer heavy predation by their natural enemies, such as sea stars and benthos-eating fish. To express it in another way, previous estimates assumed that the mussel culture was ecologically separated from the "wild" parts of the Oosterschelde. But our work forced us to consider the mussel culture plots as only one part of a larger ecosystem, interrelated with all the other parts. This implies that previous estimates of mussel production must be significantly lower than the production (growth plus reproduction) that actually occurs.

Other examples of insights abound. We discovered, for example, that benthos-eating fish are very important predators of many bottom species, so important that without them the ecostate would be very different from what it is at present. If all benthos-eating fish were suddenly to disappear from the Oosterschelde, there would be little influence left to restrain the explosive growth of their prey. Selective deposit feeders, cockles, benthic grazers, and other benthic animals would initially experience a population explosion, but would quickly outgrow their food supplies. If no organism were able to replace benthos-eating fish as a major predator of benthic creatures, the total production—reproduction plus growth—of these creatures would have to decline. Either the biomass of benthic creatures would have to drop, or the production per unit biomass would have to decline. (This decline could be accomplished if the populations of these organisms came to be composed of mostly old and large individuals; see Chap. 6.)

One can speculate that because there would be ample food for a large biomass of old benthic organisms, the ecosystem would evolve toward this option. But it seems likely that old populations of organisms would be inherently less stable than populations containing a large fraction of younger members. For example, suppose that conditions altered in such a way as to encourage an increase in the biomass of a particular organism. In an old population, a greater part of any change in the biomass must occur because of reproduction, which involves an extended delay, instead of growth, which can occur with almost no delay. It is well known that dynamic systems involving time delays are generally less stable than systems that respond immediately to stimuli. One can therefore argue that in the Oosterschelde, benthos-eating fish are an important stabilizing influence.

Carrying this speculation still farther, we realize that what is true of benthic animals when their numbers are not controlled by predation will be equally true of any other species that stands at the top of the food web. This fact is important, because some ecological groups may disappear if the Oosterschelde is severed from the North Sea by means of a closure dam. Examples are fish-eating fish and many migratory species of benthos-eating fish. (Eel would remain as a resident benthos-eater, and might become abundant enough to replace these migratory species as a predator, but the present species of fish-eating fish would probably disappear completely.) This implies that benthos-eating fish—whose numbers are now at least partly controlled (and according to our speculation stabilized) by fish-eating fish—would then be at the top of the food web. Thus, one might look for greater instabilities in their population in a closed Oosterschelde than is true in the present Oosterschelde. Alternatively, one might search for new species of fish-eating fish that could thrive in a closed Oosterschelde, hoping thereby to maintain its present ecological stability.

Admittedly, our insights are somewhat speculative. Nevertheless we believe that they illustrate benefits from the process of finding acceptable balanced estimates of the abundances. The process sets one to thinking of the ecosystem as a system, with all of its parts interacting, rather than as a collection of parts that can be considered separately. Having an explicit, formal model that contains many of these interactions, and has been placed on the computer, means that a tool is available for investigating the quantitative implications of the interactions. With model and computer code available, we can trace the impact of a changed abundance or an altered fishing rate on the entire food web. Without it, we can only agree—impotently—that some impact will propagate itself through the ecosystem.

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Chapter 11

MODEL VALIDATION

11.1. APPROACH TO VALIDATION

With the model calibrated as we have described, it will reproduce our balanced estimates of the variables when given our best estimates of the inputs (the nominal segment parameters Z_s, and the nominal values for external mass transfer rates). However, to appreciate how reliable are the model's results, we must validate the model.

Earlier (in Sec. 4.5) we reported on an exercise that tested the reasonableness of our model when it was applied to a simple exemplary ecosystem consisting of plants, detritus, a herbivore, an omnivore, and a carnivore in a single segment. We ascertained that the responses of this ecosystem to a variety of stresses imposed from outside was qualitatively reasonable (quantitative judgments were of course impossible in the absence of actual data with which to compare our results). This exercise was a limited validation.

Our calibration procedure, as reported in Chap. 10, can be viewed as a similar exercise. During calibration, we gained further confidence that the model was at least reasonable in its responses. This validation technique is weak, however, and must be buttressed by other tests. So we tried to validate the model by testing it against data pertaining to the Grevelingen.

The Grevelingen is a lake, just to the north of the Oosterschelde, that was separated from the North Sea by a barrier dam in May 1971 (see Fig. 1.1). Prior to that time, it was a sea arm very similar to the present Oosterschelde. A considerable amount of data were collected concerning the abundances of various ecological groups in the Grevelingen, both before and after closure. Some of these data (e.g., densities of macrobenthos) were used to help estimate abundances of ecogroups in the Oosterschelde.

Two methods of validating the model, using the Grevelingen data, suggest themselves. First, we could use the model, calibrated to the Oosterschelde, to estimate what the abundances of organisms ought to have been in the Grevelingen both before and after closure. This approach assumes that the present Oosterschelde is simply a reproportioned open Grevelingen, i.e., that the only differences between the present Oosterschelde and the open Grevelingen are the sizes of the segments, and the external mass transfer rates.

Such an assumption is highly questionable, as is suggested by some of our difficulties during calibration. We found it necessary, for example, to assume densities for benthic grazers in the Oosterschelde that were very different from those in the open Grevelingen. In addition, the mussel culture in the open Grevelingen was carried on within a different area and with a different intensity. In fact, when we reproportioned the Oosterschelde model to obtain an estimate of the abundances in the open Grevelingen, these were exactly the points at which the model's predictions matched the data least well. Of course, this outcome should be expected on other grounds, namely the grounds that forced us, because of a lack of data measured in the Oosterschelde itself, to assume that the densities of organisms, particularly of macrobenthos, were the same in the Oosterschelde as in the open Grevelingen. This is very similar to assuming that the Oosterschelde is a reproportioned open Grevelingen, the only exceptions being those abundances that we modified during the calibration procedure, and which the reproportioned Oosterschelde model predicted poorly.

We therefore took another approach to validation, using the Grevelingen data: We calibrated the model to reflect the observed situation in the open Grevelingen, and then tried to reproduce the observed abundances in the closed Grevelingen.

In the sections that follow, we will describe the steps involved in carrying out this attempt at validation. First, we will present our estimates of the segment sizes and external mass transfer rates that characterize the open and closed Grevelingen. Next, we will give our estimates of the abundances of the various ecogroups in both the open and closed Grevelingen. Third, we will calibrate the model to our estimates of abundances in the open Grevelingen. Fourth, we will change the segment sizes and external mass transfer rates to reflect the closed Grevelingen, and compare the model's predictions with the independent measurements of abundances there. A discussion of what implications this comparison has for our interpretation of the predictions of the model concludes the chapter.

11.2. SEGMENT SIZES AND EXTERNAL MASS TRANSFER RATES FOR THE GREVELINGEN

11.2.1. Segment Sizes in the Grevelingen

The size of the pelagic segment is the mean volume of water in the salt basin; the sizes of the three benthic segments are the areas covered by the appropriate depths of water at different parts of the tidal cycle. (The benthic segments were defined previously as follows: The *deep bottom segment* consists of the areas of the bottom that are submerged to a depth of at least 3 m even at mean low water (i.e., at the average low tide). Areas of the bottom that are below mean high water (i.e., submerged by an average high tide), but are above the deep bottoms, are either in the *shallow bottom and tidal flat segment*, or in the *shellfish culture plot segment.* What fraction of this area consists of shellfish culture plots was determined from Wolff (1977). The shallow bottom and tidal flat segment consists of the remainder of this shallow area.)

Our method for evaluating segment sizes involves measuring areas within depth contours on a map of the bottom of the Grevelingen. From the depth contours, we can obtain the areas of the benthic segments directly. Appropriately integrated, they also give the volume of water in the basin. Table 11.1 shows the nominal segment sizes that we have assumed for the open and closed Grevelingen and, for comparison, segment sizes for the present Oosterschelde as well.

Note that the area (calculated as the sum of the areas of the three benthic segments) of the closed Grevelingen is smaller than the area of the open Grevelingen. This is not an error, but is due to the fact that there is no tide in the closed Grevelingen. The mean high water level is therefore lower than in the open Grevelingen. (In fact, mean high water, mean low water, and the overall mean water level are all the same.) Consequently, less area is covered at mean high water in the closed Grevelingen than in the open Grevelingen.

Recall that segment sizes are reflected in the model by the parameters Z_s for each segment s (see Sec. 4.2). The values of the parameters Z_s that we have chosen to use can be obtained from the segment sizes in Table 11.1 as follows. For the pelagic segment, multiply the number of million cubic meters of water by 1000. For example, in the present Oosterschelde, the size of the pelagic segment is 3156 million cu m, so $Z_{pelagic} = 3.156 \times 10^6$. For the benthic segments, multiply the size in square kilometers by 10^4. In the present Oosterschelde, for example, the size of the deep bottom segment is 200.4 sq km, so $Z_{deeps} = 2.004 \times 10^6$. By this means, the value of each Z_s is made large enough to far exceed the total biomass within the corresponding segment s. This being the case, the behavior of the model is virtually independent of the precise sizes of the parameters Z_s.

Table 11.1

NOMINAL SEGMENT SIZES FOR THE OOSTERSCHELDE AND THE GREVELINGEN

Segment	Segment Size		
	Present Oos.	Open Grevelingen	Closed Grevelingen
Pelagic segment (million cm)	3156	601	579
Benthic segments (sq km)			
Shallow	251.0	76.5	53.9
Deep	200.4	33.4	52.8
Shellfish culture	25.0	20.3	0.0

11.2.2. Fishing and Migration Rates in the Grevelingen

Fishing and migration rates, except for the mussel and cockle fishing rates, are as poorly known for the Grevelingen as they are for the Oosterschelde. We thus assumed the same rates for the Grevelingen as for the present Oosterschelde. According to Wolff (1977), the mussel fishing rate in the open Grevelingen is 15 million kg/yr live weight, or 1.64 tons afdw/day. Since mussels are not cultivated in the closed Grevelingen, and cockles have never been fished in the Grevelingen, open or closed, the fishing rates are zero. Table 11.2 shows the nominal fishing and migration rates that we have assumed for the open and closed Grevelingen.

11.2.3. Photosynthesis and Detritus Import in the Grevelingen

As we argued in Chap. 7, we assumed that the rate of photosynthesis is proportional to the area exposed to solar radiation at mean high tide. The proportionality

Table 11.2

NOMINAL FISHING AND MIGRATION RATES IN EACH ALTERNATIVE CASE

	Alternative Cases	
	Open Grevelingen	*Closed Grevelingen*
Fishing or Harvest Rates (tons afdw/day)		
Mussels and oysters	1.64	0.0
Sea stars[a]	0.0529	0.0
Cockles	0.0	0.0
Planktivorous fish	0.079	0.079
Benthos-eating fish	0.3584	0.3584
Fish-eating fish	0.00373	0.00373
Migration Rate (tons afdw/day/ton biomass)		
Planktivorous fish	0.00225	0.0
Benthos-eating fish	0.002	0.0
Fish-eating fish	0.0008	0.0
Shrimp	0.0016	0.0

---

[a] Sea stars are a major predator of mussels and are controlled by mussel growers to limit damage to the mussel crop.

constant is 180 gC/sqm/yr. Given the areas from Table 11.1, we can compute primary production rates of 122 tons afdw/day for the open Grevelingen, and 100 tons afdw/day for the closed Grevelingen.

Detritus is not imported into the present, closed, Grevelingen at all since there is no tide. However, detritus was certainly imported into the Grevelingen while it was open to the North Sea. Wolff (in preparation), using a method developed by Postma (1954) to estimate the rate of detritus import into the open Grevelingen, arrived at 135 to 200 tons afdw/day. By comparing this rate with our estimate for detritus import into the Oosterschelde, we obtained an essentially identical estimate of 190 tons afdw/day. (This estimate assumes that detritus import per unit area was the same in the two sea arms.) We therefore took 190 tons afdw/day as our nominal rate.

Table 11.3 shows the rates of photosynthesis and detritus import that we have selected as nominal for the Grevelingen.

Table 11.3

RATES OF PHOTOSYNTHESIS AND DETRITUS IMPORT
IN OPEN AND CLOSED GREVELINGEN

(In tons afdw per day)

	Detritus Import	*Photosynthesis*
Open Grevelingen	190	122
Closed Grevelingen	0	100

11.3. ABUNDANCES IN THE OPEN AND CLOSED GREVELINGEN

Our abundance estimates of the various ecogroups in the open Grevelingen are given in Table 11.4 and those for the closed Grevelingen, in Table 11.5. Detailed information regarding the data and assumptions from which each estimate was derived is given in the Addendum to this volume. Certain general comments should be made at this time, however.

Most of the abundances of macrobenthic ecogroups were originally measured in the open Grevelingen, and the organisms were then assumed to occur in the same densities in the Oosterschelde. Hence, in Table 11.4, most of the estimates for the deep bottom and shallow bottom segments are in the same ratio to the corresponding initial abundance estimates for the Oosterschelde as are the Grevelingen segment sizes to the Oosterschelde segment sizes. Recall, however, that some of the initial estimates of abundances in the Oosterschelde were modified in the course of calibration, notably selective deposit feeders and benthic grazers. Thus, although

Table 11.4

ABUNDANCE ESTIMATES FOR OPEN GREVELINGEN

(In metric tons afdw)

Ecological Group	Segment			
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms	Shellfish Culture Plots
Photosynthetic organisms	247.0	2460.0	--	--
Detritus/micro-benthos	4780.0	23620.0	9320.0	5890.0
Zooplankton/pelagic larvae	107.0	--	--	--
Mussels/oysters	--	--	--	1000.0
Cockles/limpets	--	2510.0	92.0	--
Selective deposit feeders with pelagic larvae	--	170.0	2.94	38.5
Crabs/shrimp	--	4.1	3.3	6.4
Sea stars	--	--	4.0	9.5
Deposit feeders with nonpelagic larvae	--	600.0	0.02	136.0
Omnivores/predator worms	--	1.14	0.19	0.48
Benthic grazers	--	1318.0	--	216.0
Planktivorous fish	34.0	--	--	--
Benthos-eating fish	600.0	--	--	--
Fish-eating fish	54.0	--	--	--
Plant-/detritus-eating fish	50.0	--	--	--
Fish-eating birds	0.0124	--	--	--
Plant-eating birds	--	0.126	--	--
Benthos-eating birds	--	2.74	--	--

Table 11.5

ABUNDANCE ESTIMATES FOR CLOSED GREVELINGEN

(In metric tons afdw)

Ecological Group	Segment[a]		
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms
Photosynthetic organisms	400.0	3425.0	--
Detritus/microbenthos	(b)	(b)	(b)
Zooplankton/pelagic larvae	10.8	--	--
Mussels/oysters	--	--	--
Cockles/limpets	--	300.0	28.0
Selective deposit feeders with pelagic larvae	--	8.29	0.816
Crabs/shrimp	--	(b)	(b)
Sea stars	--	--	(b)
Deposit feeders with nonpelagic larvae	--	(b)	(b)
Omnivores/predator worms	--	(b)	(b)
Benthic grazers	--	(b)	--
Planktivorous fish	(b)	--	--
Benthos-eating fish	(b)	--	--
Fish-eating fish	(b)	--	--
Plant-/detritus-eating fish	(b)	--	--
Fish-eating birds	0.273	--	--
Plant-eating birds	--	1.87	--
Benthos-eating birds	--	0.637	--

[a] Note that in closed Grevelingen there is no shellfish culture segment.

[b] Unknown.

we had initially assumed that the Oosterschelde was simply a reproportioned open Grevelingen, we do not assume this in our final, calibrated model of the Oosterschelde.

Abundances in the shellfish culture segment of the open Grevelingen were obtained from our model of the present Oosterschelde by scaling them in the same fashion as the abundance of mussels. In our model of the present Oosterschelde, we assume there are 2000 tons of mussels on the culture plots; in the open Grevelingen, their abundance is 1000 tons. The abundances of other organisms on the shellfish culture plots of the Grevelingen are consequently also half that of their abundance in the Oosterschelde.

Birds have been counted in both the open and closed Grevelingen, and our abundance estimates derive from these observations. For validation, it is unfortunate that our model uses the abundances of birds as inputs instead of providing them as outputs, because these abundances are better known than most others.

To obtain abundance estimates of fish in the open Grevelingen, we have assumed biomasses per square meter of surface equal to those found in the Oosterschelde. This assumption appears to be borne out by data reported in the R.I.V.O.'s semiannual surveys (Demersal Surveys). The only exception is for plant- and detritus-eating fish, whose abundance we have taken to be in the same ratio to plant-eating birds as in our model of the Oosterschelde.

Regarding our abundance estimates for the closed Grevelingen (Table 11.5), we have the following comments. First, few measurements have been made in the closed Grevelingen, thus leaving our estimates incomplete. We have left them incomplete, instead of completing them by making comparisons with other, similar basins, because we propose to use these data for validation only, and not for calibration. In this respect, our use of the closed Grevelingen differs from our use of both the Oosterschelde and the open Grevelingen. Both of these basins were used as calibration points, and hence it was necessary to have complete abundance estimates for each.

The estimate of the abundance of fish-eating fish in the closed Grevelingen deserves some comment. It is expected that the fish-eating fish species now found in the closed Grevelingen will eventually disappear, since they are not able to reproduce there. However, their ecological function is now being performed by those fish-eating fish who have survived since the date of closure. Further, we expect that these fish will be replaced by other species, given enough time for those other species to discover the favorable (to them) situation in the closed Grevelingen. Failing this, the Dutch may decide to stock the Grevelingen with new species of fish-eating fish in order to enhance sport fishing. We therefore recorded their abundance as unknown in Table 11.5, instead of estimating it as zero.

Finally, we should explain why the abundance of selective deposit feeders with nonpelagic larvae in the shallow segment of the closed Grevelingen is unknown. This is surprising, in view of this ecogroup's high abundance in the shallow and intertidal segment of the open Grevelingen. One would expect these organisms to remain at least moderately abundant in the shallows of the Grevelingen after closure. However, since closure, sampling in the shallows has taken place only at three points with very similar characteristics. Because none of this ecogroup has ever been reported at any of these locations, either before or after closure, we are unable to form a direct estimate of their abundance in the shallows of the closed Grevelingen.

11.4. CALIBRATING THE MODEL TO THE OPEN GREVELINGEN

Using the initial abundance estimates shown in Table 11.4, and the inputs from Tables 11.1, 11.2, and 11.3 for the open Grevelingen, we carried out the procedure described in Chap. 9 and in Sec. 10.2 to find balanced estimates of all the variables $x_{i,j,s}$. We then attempted to modify these inputs in order to obtain a better comparison between the balanced and unbalanced estimates. However, we quickly found that the major factor preventing a better match was the detritus import rate. (Actually, of course, the rate of primary production would do as well; the two rates are largely interchangeable in their effect on the ecosystem.) We therefore decided not to alter any of the abundance estimates to seek a better calibration.

A comparison of the initial unbalanced abundance estimates (also shown in Table 11.4) with the balanced estimates derived from them is shown in Table 11.6. In this comparison, the balanced estimates of the abundance of an ecogroup are shown on the first line of the table, and the initial, unbalanced estimates are shown in parentheses in the line below.

Table 11.6

COMPARISON BETWEEN UNBALANCED AND BALANCED ABUNDANCE ESTIMATES FOR OPEN GREVELINGEN, ASSUMING A DETRITUS IMPORT RATE OF 190 TONS afdw PER DAY

	Segment			
Ecological Group	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms	Shellfish Culture Plots
Photosynthetic organisms	262.0 (247.0)	2468.0 (2460.0)	--	--
Detritus/microbenthos	4751.0 (4780.0)	23444.0 (23620.0)	9263.0 (9320.0)	5848.0 (5890.0)
Zooplankton/pelagic larvae	62.6 (107.0)	--	--	--
Mussels/oysters	--	--	--	906.0 (1000.0)
Cockles/limpets	--	2099.0 (2510.0)	77.0 (92.0)	--
Selective deposit feeders with pelagic larvae	--	127.0 (170.0)	2.18 (2.94)	28.6 (38.5)
Crabs/shrimp	--	4.29 (4.1)	3.46 (3.3)	6.7 (6.4)
Sea stars	--	--	6.87 (4.0)	10.8 (9.5)
Deposit feeders with nonpelagic larvae	--	481.0 (600.0)	0.016 (0.02)	108.0 (136.0)
Omnivores/predator worms	--	0.77 (1.14)	0.12 (0.19)	0.32 (0.48)
Benthic grazers	--	806.0 (1318.0)	--	131.0 (216.0)
Planktivorous fish	35.1 (34.0)	--	--	--
Benthos-eating fish	602.0 (600.0	--	--	--
Fish-eating fish	26.7 (54.0)	--	--	--
Plant-/detritus-eating fish	50.0 (50.0)	--	--	--
Fish-eating birds	0.0124 (0.0124)	--	--	--
Plant-eating birds	--	0.126 (0.126)	--	--
Benthos-eating birds	--	2.74 (2.74)	--	--

In Table 11.6, we see that the balanced estimates generally fall below the initial, unbalanced ones. There are a few ecogroups for which this is not true, e.g., benthos-eating fish, shrimp and crab, and sea stars. And for most other groups, the underestimate is not serious. Mussels, for example, are underestimated by less than 10 percent, cockles by 16 percent, deposit feeders with nonpelagic larvae by 20 percent, and selective deposit feeders with pelagic larvae by 26 percent. Neither are the underestimates of zooplankton (by 40 percent) and fish-eating fish (by 50 percent) serious, since the original estimates of these abundances were little better than guesses.

However, one can begin to argue that an underestimate of benthic grazers by 39 percent may be significant. And in any case, we think it is significant that virtually all of the balanced estimates are lower than their corresponding unbalanced estimates. Therefore, we recalibrated the model to the open Grevelingen, this time letting the detritus import rate adjust itself to whatever level would yield the best match between balanced and unbalanced estimates. The results are shown in Table 11.7, in the same format as that of the first calibration results. The detritus import rate that accomplished this was 270 tons afdw/day.

Changing the rate of detritus import from 190 to 270 tons afdw/day has had a profound effect upon the match between the balanced and unbalanced estimates. The abundances of a few ecogroups match less well, but these are generally ecogroups with very low abundances, such as shrimp and crab (now overestimated by 86 percent) and sea stars (now overestimated by 34 percent). Essentially the only major ecogroup whose match became worse was benthos-eating fish. With a detritus import of 190 tons afdw/day its match was perfect; with a 270 ton day import, it was overestimated by 29 percent. However, there is easily an uncertainty of 30 percent in our knowledge of the true value.

There was uniform improvement in the matches for all other ecogroups. Zooplankton were previously underestimated by 40 percent; now they match exactly. Mussels have improved from -9 percent to $+4$ percent. Cockles have moved from -16 percent to -2 percent; selective deposit feeders, from -26 percent to -9 percent; and benthic grazers, from -39 percent to -13 percent.

This improvement, however, was accomplished by increasing the rate of detritus import beyond our earlier estimate of 190 tons afdw/day. We mentioned that our estimate of detritus import into the Oosterschelde has been criticized as being too high. An estimate of detritus import into the open Grevelingen as high as 270 tons afdw/day would be similarly criticized.

It is thus impossible for us to choose between these two calibrations. The first presents an acceptable, if not exceptional, match between the observations and the balanced abundance estimates, while assuming a high but (relatively) uncontroversial rate of detritus import. The other assumes a controversially high detritus import rate, but presents a very close match between observations and the balanced estimates.

Fortunately, for our purpose it is immaterial which calibration we choose. After all, our purpose in calibrating to the open Grevelingen is to provide a starting point from which we can make predictions about abundances in the closed Grevelingen, which we will then compare with observed abundances there. But these predictions can only depend on the values of all the parameters provided for our model of the closed Grevelingen, these parameters being the mass-balance matrix A, the seg-

Table 11.7

COMPARISON BETWEEN UNBALANCED AND BALANCED ABUNDANCE ESTIMATES FOR OPEN GREVELINGEN, ASSUMING A DETRITUS IMPORT RATE OF 270 TONS afdw PER DAY

Ecological Group	Segment			
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms	Shellfish Culture Plots
Photosynthetic organisms	231.0 (247.0)	2446.0 (2460.0)	--	--
Detritus/micro-benthos	4781.0 (4780.0)	23612.0 (23620.0)	9320.0 (9320.0)	5890.0 (5890.0)
Zooplankton/pelagic larvae	108.4 (107.0)	--	--	--
Mussels/oysters	--	--	--	1042.0 (1000.0)
Cockles/limpets	--	2456.0 (2510.0)	90.0 (92.0)	--
Selective deposit feeders with pelagic larvae	--	155.0 (170.0)	2.70 (2.94)	35.3 (38.5)
Crabs/shrimp	--	7.65 (4.1)	6.16 (3.3)	11.9 (6.4)
Sea stars	--	--	6.49 (4.0)	11.6 (9.5)
Deposit feeders with nonpelagic larvae	--	566.0 (600.0)	0.019 (0.02)	129.0 (136.0)
Omnivores/predator worms	--	1.05 (1.14)	0.16 (0.19)	0.45 (0.48)
Benthic grazers	--	1152.0 (1318.0)	--	190.0 (216.0)
Planktivorous fish	39.1 (34.0)	--	--	--
Benthos-eating fish	772.0 (600.0)	--	--	--
Fish-eating fish	40.8 (54.0)	--	--	--
Plant-/detritus-eating fish	50.0 (50.0)	--	--	--
Fish-eating birds	0.0124 (0.0124)	--	--	--
Plant-eating birds	--	0.126 (0.126)	--	--
Benthos-eating birds	--	2.74 (2.74)	--	--

ment parameters Z_s, external mass transfer rates (fishing and harvest rates, detritus import rate, rate of photosynthesis, and migration rates), and the parameters $c_{i,j,s}$.

None of the values of these parameters for the closed Grevelingen depend on which calibration to the open Grevelingen we choose. The matrix A depends on the quantities given in Table 6.6 and the predator-prey relations described in Table 9.1. The segment sizes and external mass transfer rates for the closed Grevelingen are given in Tables 11.1, 11.2, and 11.3. And the values of the parameters $c_{i,j,s}$ are calculated from the initial unbalanced abundances in the open Grevelingen by using Eqs. (9.5) and (10.3). (The values of the $c_{i,j,s}$'s will be the same for the closed Grevelingen as for the open Grevelingen.) Since the initial estimates of abundances are the same for both calibrations to the open Grevelingen, the parameters $c_{i,j,s}$ must also be the same. It follows that the model's predictions of abundances in the closed Grevelingen will not depend on which calibration to the open Grevelingen we choose.

11.5. VALIDATING THE MODEL AGAINST THE CLOSED GREVELINGEN

To validate the model, we started with the model calibrated to the open Grevelingen and then changed its segment-size parameters and external mass transfer rates to reflect the closed Grevelingen. The values of these parameters for the closed Grevelingen can be found in Tables 11.1, 11.2, and 11.3. The model's predictions are compared in Table 11.8 with the few measurements we have of abundances in the closed Grevelingen Again, the model's predictions of the abundances of an ecogroup appear in the first line and the measured values, if known, appear in the following line in parentheses.

In Table 11.8, we see that most predicted abundances are considerably lower than they were in our model of the open Grevelingen. This is also the case for those few abundances for which we have data. Thus, our model appears qualitatively to have correctly predicted the impact of closing the Grevelingen.

The one exception to this observation is photosynthetic organisms in the shallow bottom and tidal flat segment. For these organisms, the model predicted a decrease in abundance, whereas an increase was actually observed. (Lest the reader think that the model must necessarily have predicted decreases in all abundances, we point out that photosynthetic organisms in the pelagic segment were predicted to increase, which they were observed to do after the closure of the Grevelingen.)

The reason that benthic photosynthetic organisms decreased in the model may have been that, in the open Grevelingen, most of these organisms were benthic diatoms. Thus, the parameters describing this variable—metabolic fraction and mortality—reflected the characteristics of benthic diatoms much more than sea grasses and seaweeds, which are the other benthic photosynthetic organisms. When the Grevelingen was closed, benthic diatoms were indeed observed to decrease moderately, but sea grasses and seaweeds increased dramatically at the same time, resulting in a net increase in this abundance. We can speculate that if we had included both kinds of organisms in the model separately, then the model might have predicted an increase in sea grasses and seaweeds.

Table 11.8

COMPARISON BETWEEN MEASURED ABUNDANCES AND MODEL PREDICTIONS FOR CLOSED GREVELINGEN

	Segment		
Ecological Group	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms
Photosynthetic organisms	329.0 (400.0)	1769.0 (3425.)	--
Detritus/microbenthos	4434.0 (a)	15958.0 (a)	14184.0 (a)
Zooplankton/pelagic larvae	27.0 (10.8)	--	--
Mussels/oysters	--	--	--
Cockles/limpets	--	697.0 (300.0)	57.5 (28.0)
Selective deposit feeders with pelagic larvae	--	31.6 (8.29)	1.21 (0.816)
Crabs/shrimp	--	0.1 (a)	0.18 (a)
Sea stars	--	--	1.55 (a)
Deposit feeders with nonpelagic larvae	--	154.0 (a)	0.011 (a)
Omnivores/predator worms	--	0.12 (a)	0.045 (a)
Benthic grazers	--	97.1 (a)	--
Planktivorous fish	15.8 (a)	--	--
Benthos-eating fish	142.7 (a)	--	--
Fish-eating fish	3.24 (a)	--	--
Plant-/detritus-eating fish	50.0 (a)	--	--
Fish-eating birds	0.273 (0.273)	--	--
Plant-eating birds	--	1.87 (1.87)	--
Benthos-eating birds	--	0.637 (0.637)	--

[a] Unknown.

Quantitatively, our predictions do not appear to be accurate, but they may turn out to be so. For example, our model has predicted that zooplankton should have declined to an abundance of 27 tons in the closed Grevelingen, instead of the observed 10.8 tons. But, the abundance estimates of zooplankton in both the open and closed Grevelingen are so uncertain, and based on such scanty data, that our prediction might easily be closer to the true long-term average abundance than are the observed 10.8 tons.

In fact, all of our abundance estimates for the closed Grevelingen are based on only a few samples. They are not widely enough separated in space to constitute a representative sampling from the highly nonuniform distributions of many organisms (especially macrobenthos such as cockles, worms, etc.). They are too infrequent to account for seasonal variations. They have not been continued long enough to smooth out year-to-year fluctuations, even if one believes that the Grevelingen, which was closed only in May 1971, has ceased to evolve in response to closure. Although we have tried to correct as best we could for these biases, our abundance estimates for the closed Grevelingen almost surely do not represent long-term average abundances.

This point also applies to our prediction of the abundance of selective deposit feeders in the shallow segment of the closed Grevelingen. Our estimate for their abundance of 8.29 tons was based on samples taken at three very similar points, at which these organisms had been found only in low densities prior to closure. The locations in which these organisms had been found abundantly before closure have not been sampled since that event. Thus, our estimate of this abundance is very uncertain indeed.

This point can be made even more strongly in the case of cockles and limpets. It would appear that our model has overpredicted cockles in the closed Grevelingen. But once again, cockles have been sampled at only three very similar points since closure, the same points at which selective deposit feeders were sampled. Furthermore, the findings from even these few samples are bound to be misleading, because we have made no provision in the model for mussels to occupy any segment other than the shellfish culture segment.

Now, mussels and cockles are members of different superspecies only because they live in different segments. Their diets and their predators are essentially the same. Thus the model is saying that the abundance of cocklelike creatures (such as cockles, mussels, and oysters) in the closed Grevelingen ought to be higher than the abundance of cockles that has been observed there. In fact, we do find them. They are not all cockles, of course. They include many mussels as well. Recently, the R.I.V.O. conducted a mussel fishing experiment in which, we were told, they collected 10000 tons live weight of mussels from the closed Grevelingen. This amounts to 400 tons afdw, which is the difference between our prediction and the observation of cockle abundance. If anything, then, we appear to have underpredicted, and not overpredicted, the abundance of cocklelike organisms in the closed Grevelingen.

We conclude, therefore, that our model has been verified as well as the available data permit. Uncertainties in the data concerning abundances in both the open and closed Grevelingen make it impossible to distinguish realistically between our estimates of the abundances in the closed Grevelingen and the predictions of the model.

11.6. IMPLICATIONS FOR OTHER PREDICTIONS BY THE MODEL

The results of this validation exercise have implications for any predictions the model can make regarding the Oosterschelde (which is our primary concern in this study), and any conclusions we may draw from these predictions. Briefly, there are two implications: (1) Predictions by the model have large uncertainties, which reflect the uncertainties and deficiencies of the available data; and (2) nevertheless, the model can usefully distinguish between two alternatives if its predictions are very different.

The same arguments support both of these implications. First, the large uncertainties in our abundance estimates preclude the model from making precise predictions. That is, in the same way that we cannot expect close agreement between model outputs and measured values during validation, we cannot expect close agreement between the model's predictions and any measurements that may later be made. Second, it should be remembered that our model predicts long-term average abundances and diets, whereas individual measurements give information about instantaneous abundances only. Even if measurements allowed us to estimate instantaneous abundances exactly, we should not expect perfect agreement between any measured abundance and the predictions of the model. Random variations from year to year, and systematic seasonal variations, are too great. It would require a long series of measurements to obtain observed long-term averages to compare with the model's predictions.

However, our model has predicted the directions in which abundances have changed since the Grevelingen was closed, and, in addition, it has been in rough agreement with the magnitudes of those changes. We conclude, therefore, that because of data limitations, and natural yearly variations in abundances, predictions by the model are much more significant in a relative rather than in an absolute sense. In other words, large changes from case to case are significant, whereas small changes are probably not significant. And, of course, the direction of a large change is significant.

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PART III

RESULTS AND CONCLUSIONS

Chapter

Chapter 12

ALTERNATIVE CASES CONSIDERED AND THEIR INPUTS

12.1 DESCRIPTION OF CASES

One can conceive of a wide variety of different project types and designs to improve the safety of lands bordering the Oosterschelde. Each possible design is potentially another case for study, but we do not intend to study them all. Rather, we selected a menu of cases for evaluation that would bracket the range of possible ecological impacts. These cases are described in Table 12.1. We will also refer to them as *alternatives*, since from among them, one will eventually be chosen as the final design for the Oosterschelde.

Each case consists of two parts: a proposal about what to do to the mouth of the Oosterschelde, indicated by a letter (A, C, or D); and a proposal about how to partition the Oosterschelde basin into saltwater and freshwater parts with compartment dams, indicated by a number (3 or 4). The different cases thus have designations such as A3 or C3 or D4.

The numerals "3" and "4" refer to the compartment designs shown in Fig. 12.1. Compartment design "3," shown in Fig. 12.1a, has a small, freshwater eastern lake (the Zoommeer), separated from the large, saltwater western basin by the Oesterdam. Design "4," shown in Fig. 12.1b, has a larger freshwater eastern lake, separated from the saltwater western basin by the Wemeldingedam. In both designs, there is a second dam, called the Philipsdam, that separates the northern Volkerak region from the saltwater basin. Our model deals with only the saltwater basin. It is not concerned with either the freshwater Zoommeer or the freshwater lake to be created in the Volkerak.

The letters designate what is to be done to the mouth of the Oosterschelde. The letter "A" denotes an Oosterschelde whose mouth remains in the present, unobstructed condition. To achieve safety from flooding in cases with an "A" designation, the dikes around the shores of the Oosterschelde would be greatly reinforced. The letter "D" denotes an Oosterschelde whose mouth is entirely closed by a permanent dam, although there might be sluices or shipping locks in the dam that would permit some exchange of saltwater between the Oosterschelde basin and the North Sea. This dam would, by itself, provide safety from flooding to the Oosterschelde region.

The final letter designation, "C," indicates that a storm-surge barrier is to be built across the mouth of the Oosterschelde. This is a dam with gates in it. In a storm, the gates would be closed and there would be only a slow leakage of water between the Oosterschelde and the North Sea. Then the barrier would act almost like the dam of the cases with designation "D." In good weather, the gates would be left open, allowing enough water to flow between the Oosterschelde and the North Sea so that there would be a significant tide in the basin.

How great a tide would be observed in the basin depends on the effective aperture (called the μA) in the storm-surge barrier through which water can flow. The effective aperture may differ from the geometric aperture because of frictional

Table 12.1

DIFFERENT CASES CONSIDERED

Case Designation	Description
Present Oosterschelde	Mouth of Oosterschelde unobstructed, allowing maximum tide in basin. Basin not partitioned, so saltwater basin has maximum size.
A3	Mouth unobstructed, maximum tide. Basin partitioned into small eastern and northern freshwater lakes, large saltwater basin.
C3, $\mu A = 20000$	Mouth obstructed, reducing tide slightly. Saltwater basin is large.
C3, $\mu A = 11500$	Mouth obstructed, reducing the tide moderately. Saltwater basin is large.
C3, $\mu A = 6500$	Mouth obstructed, reducing the tide considerably. Saltwater basin is large.
C3, $\mu A = 3250$	Mouth obstructed, reducing tide greatly. Saltwater basin is large.
D3	Mouth completely obstructed, eliminating tide. Saltwater basin is large.
A4	Mouth unobstructed, maximum tide. Basin partitioned into large eastern and northern freshwater lakes, small saltwater basin.
C4, $\mu A = 11500$	Mouth obstructed, reducing tide slightly. Saltwater basin is small.
C4, $\mu A = 6500$	Mouth obstructed, reducing tide moderately. Saltwater basin is small.
D4	Mouth completely obstructed, eliminating tide. Saltwater basin is small.

effects. The tidal range (difference between mean high water and mean low water) also depends on how large a basin must be filled by the water flowing through the barrier, and hence on the compartment design. Figure 12.2 shows the relation between effective aperture and tidal range at a selected reference point, Zierikzee, for both compartment designs "3" and "4."

These changes in tidal range are reflected in the model by their influence on the sizes of the benthic segments. When the tidal range is reduced, the mean low water level rises and the mean high water level falls. The fall in mean high water means that a smaller area is submerged at high tide, and therefore the total size

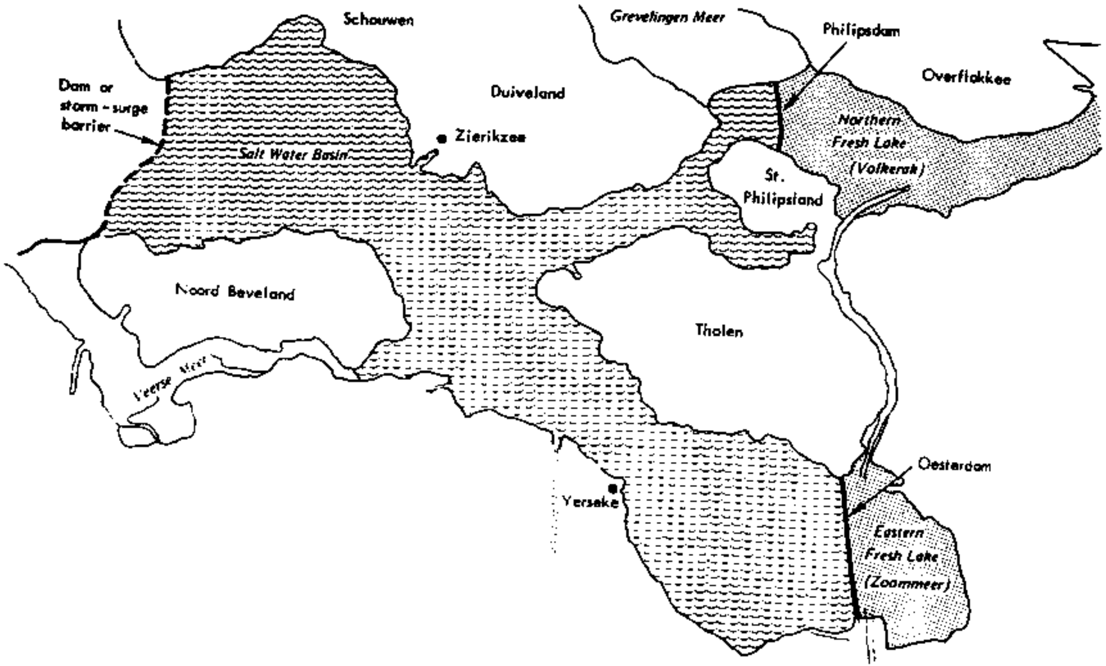

Fig. 12.1a — Compartment design "3"

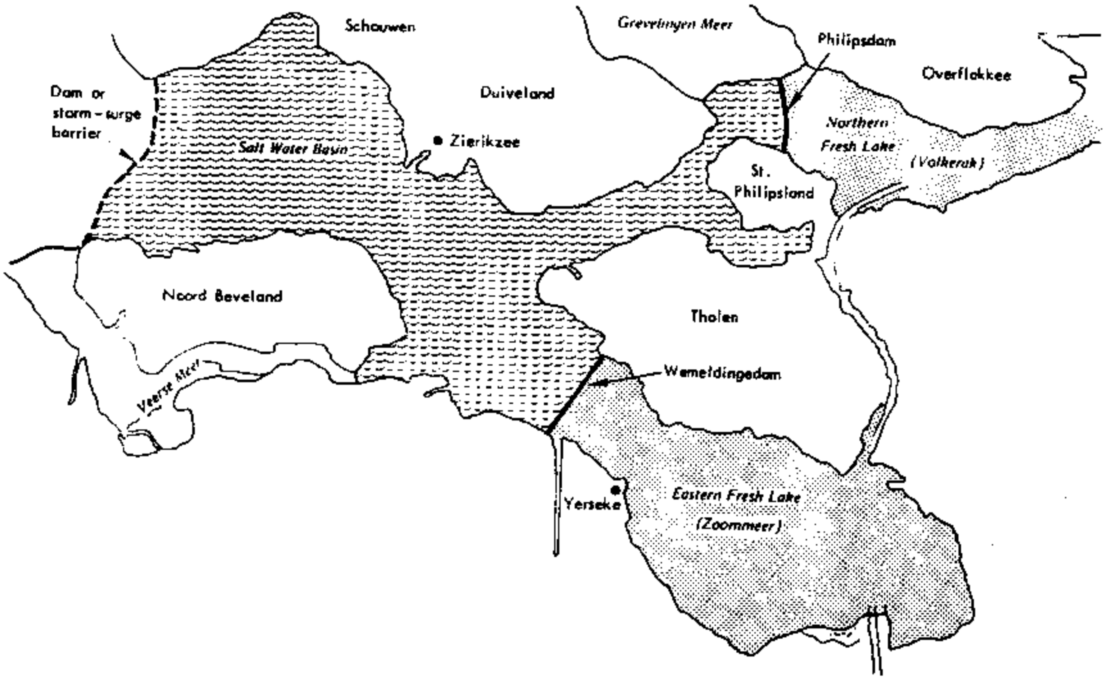

Fig. 12.1b — Compartment design "4"

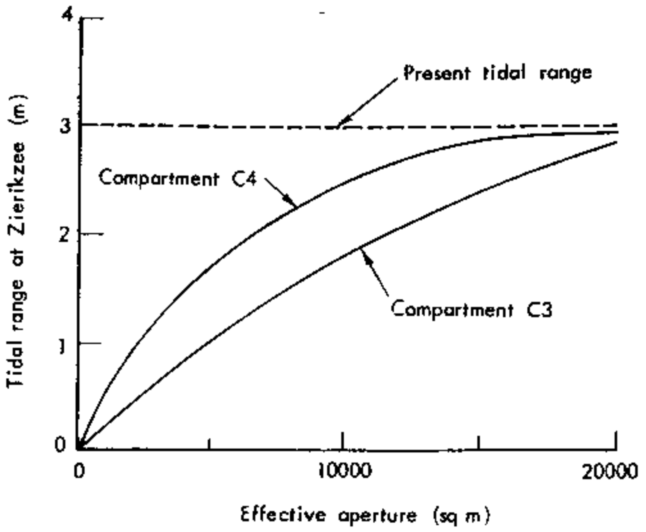

Fig. 12.2 — Relation between the effective aperture and the tidal range at Zierikzee for both the C3 and C4 compartments

of all the benthic segments must decline. However, because the mean low water level rises, a greater area is submerged at mean low water to a depth exceeding 3 m. As the reader may recall, this qualifies an area to be included in the deep bottom segment, which accordingly increases in size as the tidal range decreases. Thus, the shallow bottom and tidal flat segment, or the shellfish plot segment, or both, must diminish in size with decreasing tidal range.

Not all of these cases are nominal alternatives. Some are treated as excursions to highlight the importance of an assumption or a design factor. Reasons for distinguishing certain cases as nominal are explored later, in Sec. 14.1. Aside from the present Oosterschelde case (for calibration), the nominal cases are

A3
C3, $\mu A = 20000$ sq m
C3, $\mu A = 11500$ sq m
C3, $\mu A = 6500$ sq m
D4

In addition, to investigate further the importance of the tidal range on the results, we consider case C3, $\mu A = 3250$ sq m. To show the importance of one's choice of compartmentation, we make detailed comparisons of D3 with D4, and A3 with A4. To further highlight the influence of compartmentation, we present results for C3, $\mu A = 20000$ sq m, and C4, $\mu A = 11500$ sq m (they have essentially the same tidal range), and for C3, $\mu A = 11500$ sq m, and C4, $\mu A = 6500$ sq m (again, these have the same tidal range).

12.2. SEGMENT SIZES

The sizes of the four segments are as follows: for the pelagic segment, the mean volume of water in the salt basin; and for the benthic segments, the areas covered by the appropriate depths of water at different parts of the tidal cycle. The benthic segments were defined previously as follows: The deep bottom segment consists of the areas of the bottom that are submerged to a depth of at least 3 m even at mean low water (i.e., at the average low tide). Areas of the bottom that are below mean high water (i.e., submerged by an average high tide), but that are above the deep bottoms, are either in the shallow bottom and tidal flat segment or in the shellfish culture plot segment. The part of this area that consists of potential shellfish culture plots is shown in Fig. 12.3. (Only 25 sq km are presently used for shellfish culture, mostly the areas near Yerseke.) The shallow bottom and tidal flat segment consists of the remainder of this shallow area. Our method for evaluating segment sizes involved measuring areas within depth contours on maps of the bottom of the Oosterschelde. These maps were marked to show the boundaries of the salt basin for both the "3" and "4" compartment designs, as well as the boundaries of the present-day shellfish culture plots. From the depth contours, we could determine the areas of the benthic segments directly. Appropriately integrated, the depth contours also give the volume of water in the basin.

These segment sizes will depend on the case considered. The size of the pelagic segment will depend only on whether the compartment design is "3" or "4." It will not depend on the reduction in the tidal range. The reason is that no matter what the tidal range, the mean water level will remain approximately the same; and to a very good approximation, it is the mean water level that determines the mean volume of water in the basin.

The shellfish culture area depends on the compartment design. If compartment design "3" is chosen, the culture area will remain as it is today, approximately 2500 ha. If compartment design "4" is chosen, all the oyster banks and 30 percent of the mussel beds presently in use will be annihilated. But because of its depth, this segment is not affected by changes in the tidal range.

The shallow bottom segment will depend not only on the compartment design, but on the tidal range as well. Recall that this segment includes the area of the bottom that is no more than 3 m deep at mean low water, plus the area that is covered by water during only part of the tidal cycle—the tidal flats—minus the shellfish culture area. If the tidal range is reduced, the area of the tidal flats will also be reduced, and with it the size of the shallow bottom segment.

The deep bottom segment will also depend on both the compartment design and the tidal range. This segment includes the area that is covered by at least 3 m of water at mean low tide. If the tidal range is reduced, then the mean low water mark will rise (as the mean high water mark falls). All areas of the bottom below the old mean water level will thus be under more water, and some areas will therefore cease to be shallow bottoms and become deep bottoms.

Of course, man might cause other changes in segment sizes than we consider here. The most likely would be either to abandon shellfish culture, or to increase the area devoted to it. These changes would redistribute some of the shallow bottom area between the culture plots and the shallow bottom and tidal flat segment. The nominal segment sizes that we have assumed for each case are shown in Table 12.2.

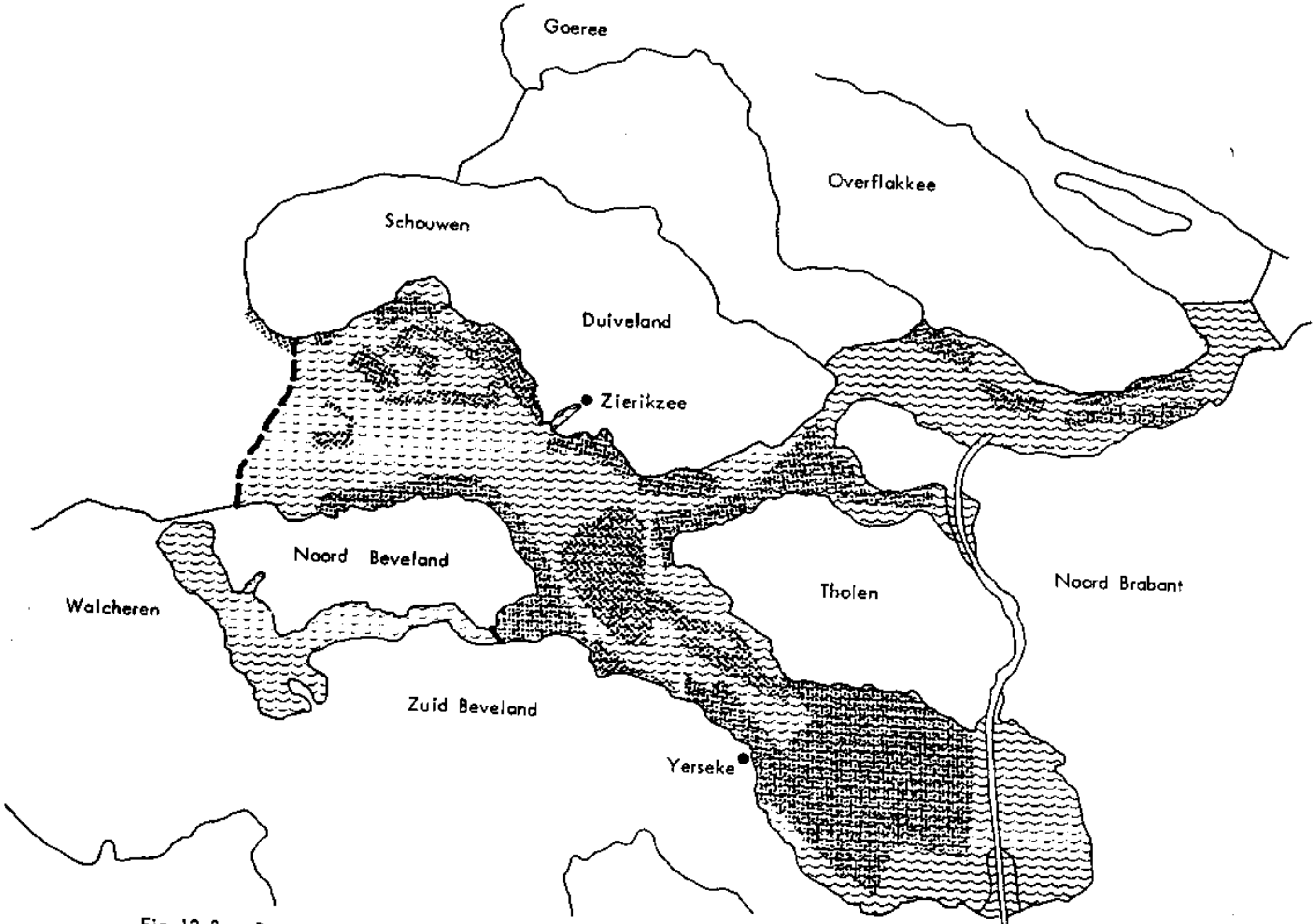

Fig. 12.3 — Potential shellfish culture plots in the Oosterschelde (only 25 sq km are actually in production)

Table 12.2

NOMINAL SEGMENT SIZES FOR EACH ALTERNATIVE CASE CONSIDERED

Case	Pelagic Segment (millions of cu m)	Benthic Segments		
		Shallow (sq km)	Deep (sq km)	Shellfish Culture (sq km)
Present Oosterscheide	3156	251.0	200.4	25.0
A3	2898	174.0	170.5	25.0
C3, $\mu A = 20000$	2898	169.4	174.9	25.0
C3, $\mu A = 11500$	2898	154.6	184.9	25.0
C3, $\mu A = 6500$	2898	134.8	192.6	25.0
C3, $\mu A = 3250$	2898	113.3	199.7	25.0
D3	2898	131.3	201.4	0.0
A4	2386	99.7	120.5	10.7
C4, $\mu A = 11500$	2386	94.2	125.3	10.7
C4, $\mu A = 6500$	2386	87.0	129.1	10.7
D4	2386	62.9	139.0	0.0

Recall that segment sizes are reflected in the model by the parameters Z_s for each segment s (see Sec. 4.2). The values of the parameters Z_s that we have chosen to use can be obtained from the segment sizes in Table 12.2 as follows. For the pelagic segment, multiply the number of million cubic meters of water by 1000. In the present Oosterschelde, for example, the size of the pelagic segment is 3156 million cubic meters, so $Z_{pelagic} = 3.156 \times 10^6$. For the benthic segments, multiply the size in square kilometers by 10^4. The size of the deep bottom segment in the present Oosterschelde, for example, is 200.4 square kilometers, so $Z_{deeps} = 2.004 \times 10^6$. By this means, the value of each Z_s is made large enough to far exceed the total biomass within the corresponding segment s. This being the case, the behavior of the model is virtually independent of the precise sizes of the parameters Z_s.

12.3. FISHING AND MIGRATION RATES, AND ABUNDANCES OF BIRDS

In this section, we discuss the fishing and migration rates, and the abundances of birds, that may characterize the alternative cases for the Oosterschelde. These rates and abundances correspond to the model parameters MIG_j and b_j for heterotrophic ecological groups. We defer discussion of the parameters b_j for photosynthetic organisms and detritus to the next section.

Neither migration and fishing rates nor abundances of birds can be predicted for the analysis cases. First, migration rates are largely unknown even for historical situations. Second, migration and fishing rates, as well as abundances of birds, depend mostly on factors external to the Oosterschelde.

Our strategy is therefore to investigate the sensitivity of the model outputs to different assumptions about these quantities. For example, the model cannot predict the actual abundances of birds. If the Oosterschelde does not suit them, they can readily fly elsewhere. Instead, we investigate potential abundances. We vary the abundance of a bird species by varying its migration rate, and note the effect of this variation on other species.

Nor can the model predict the actual mussel or cockle harvest. New techniques may make greater harvests economically feasible. The harvest may vary with market conditions. Instead, we investigate the potential range of harvests. We vary the assumed harvest, and then note the effects on other species.

However, it is desirable to have certain reasonable rates specified as nominal. We show these nominal rates in Table 12.3. Note that in the open cases A3 and A4, and in the cases with a storm-surge barrier (C3 and C4), the nominal rates are assumed to be the same as we have estimated them to be today. In the closed cases (D3 and D4), however, we have nominally assumed that oysters and mussels have ceased to be cultured, and that cockles are no longer fished. These rates, therefore, are made equal to zero. We assume, however, that planktivorous fish, benthos-eating fish, and fish-eating fish are caught in the same quantities in the closed cases as they are in the present Oosterschelde. These rates are rather low, and we expect that any commercial fishing discontinued after closure would be replaced by recreational fishing. We base this expectation on the observed increase in recreational fishing that occurred in the Grevelingen after it was closed. Moreover, we have assumed in the closed cases that migration is no longer possible, and so all the parameters MIG_j are also set to zero.

Table 12.3

NOMINAL FISHING AND MIGRATION RATES
IN EACH ALTERNATIVE CASE

Ecological Group	Case Open and Storm-surge Barrier	 Closed (D3 and D4)
Fishing or Harvest Rates (Tons afdw per day)		
Mussels and oysters	3.34	0.0
Sea stars[a]	0.0529	0.0
Cockles	3.07	0.0
Planktivorous fish	0.079	0.079
Benthos-eating fish	0.3584	0.3584
Fish-eating fish	0.00373	0.00373
Migration Rate (Tons afdw per day per ton biomass)		
Planktivorous fish	0.00225	0.0
Benthos-eating fish	0.002	0.0
Fish-eating fish	0.0008	0.0
Shrimp	0.0016	0.0

[a] Sea stars are a major predator of mussels and are controlled by mussel growers to limit damage to the mussel crop.

The reader will note that we have not specified migration rates for birds, or a migration or fishing rate for plant- and detritus-eating fish. This is in spite of the fact that birds are migratory organisms, and plant- and detritus-eating fish are certainly fished in the Oosterschelde. The reason we have not specified these rates has been explained in Sec. 7.2.8, but to review, it is due to the following interesting feature of our model.

If one examines the prey availability matrix shown in Fig. 9.1 (which is one way of representing the food web in our model), one will notice that birds and plant- and detritus-eating fish are not preyed upon by any ecological group. This is not to say that these organisms never die in the Oosterschelde. For example, from time to time a disease such as botulism may kill significant numbers of some birds.[1] But their numbers are not controlled by predation in the Oosterschelde.

The consequence is that in the model the balance equations for these ecogroups contain only terms relating to these ecogroups eating other AQs, and hence (see Sec. 3.8) all the nonzero coefficients in one of these balance equations are the same, and equal to $g_jr_j - MIG_j$. This equation is thus equivalent to a prescription of the abundance of ecogroup j. In fact, if one chooses MIG_j appropriately, as we have done, one can make this equation read

$$\sum_i \sum_s x_{i,j,s} = b_j \ .$$

The fact that these equations prescribe the abundances of the corresponding ecogroups means that the model cannot predict their abundances. They are input, and cannot also be outputs. But if we use the model outputs in conjunction with one or another assumption, we can arrive at reasonable estimates of the effect of each alternative on these abundances.

12.4. RATES OF PHOTOSYNTHESIS AND DETRITUS IMPORT

12.4.1. Rates of Photosynthesis

As explained in Part II, Chap. 7, we assumed that the rate of photosynthesis in the Oosterschelde basin is proportional to its area. We estimated the constant of proportionality to be 180 gC/sqm/yr, or a bit less than 1 g ash-free dry weight of organic substance synthesized on each square meter during the average day.

In Chap. 7, we argued that photosynthesis in the Oosterschelde took place in basically three different kinds of areas. In areas covered by deep water, all the photosynthesis was due to phytoplankton, which produced at the rate of 180 gC/sqm/yr in the Waddensea (Cadee and Hegeman, 1974b), in the open Grevelingen (Vegter, 1975a,b), and, as far as we can tell, in the closed Grevelingen as well (Vegter, 1975b). In most areas covered by shallow water, and on the tidal flats, production is by a combination of phytoplankton and benthic diatoms. We can

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[1] We pointed out earlier (see Sec. 7.2.8) that the death rate of these organisms can be modeled by including them in the rate of detritus import. Because these death rates are insignificant compared with the uncertainty in the rate of detritus import, this procedure even makes it unnecessary to estimate the death rates.

approximate the production by phytoplankton in these areas to be one-half of the production in deeper areas, because the phytoplankton are only in these areas in substantial numbers when the tide is high—i.e., one-half of the time. Added to the 90 gC/sqm/yr obtained in this way, however, is the production of approximately 100 gC/sqm/yr by benthic diatoms (Cadee and Hegeman, 1974a). Finally, there is a small area covered by sea grasses, which, according to Nienhuis (1976), produces at a rate similar to the other areas. Thus, regardless of the kind of area considered, the production is about the same.

We also argued that changing the Oosterschelde from open to closed (or anything in between) should not significantly alter the production rate per unit area. Our reasoning was twofold. First, it has been found (Brylinsky and Mann, 1973) that the productivity of a lake is very well predicted ($r = 0.71$) from its location and the energy parameters (solar intensity and cloud cover) that characterize its location. Second, what scanty information we have about productivity in both the open and closed Grevelingen suggests that not much change has occurred.

This insensitivity of production to closure was not expected, because it was felt that after closure, the turbidity of the water should decrease. And, indeed, a decrease in turbidity was observed. However, this decrease occurred only during the stormy winter months, and not during the growing season. Thus turbidity, which many investigators believe important (Gieskes and Kraay, 1975; Murphy, 1962), appears not to play a significant role.

Because of this reasoning, we assumed that in every alternative case the rate of photosynthesis would be proportional to the area of the basin. But the area of the basin is just the sum of the areas of the benthic segments, which have been given in Table 12.2. To obtain the rate of photosynthesis for a case, we simply multiply the area of the basin in that case (from Table 12.2) by 0.9534 g afdw/sqm/day, which is equivalent to 180 gC/sqm/yr.

12.4.2. Detritus Import in the Open and Closed Alternatives

As explained in Part II, we estimated detritus import in the present Oosterschelde during the model implementation and calibration procedure. Our estimate was that 704 tons/day of detritus are being imported. As discussed in the appendix, it was necessary to estimate detritus import in this way because there existed neither direct measurements of this import rate (they are only now being started) nor any better indirect method of estimation. This is not only a problem in determining today's rate of import, but also in predicting the rate of detritus import in the various alternative cases.

We first deal with the problem for the easiest alternatives, the closed cases. If we dam off the Oosterschelde entirely, as in alternatives D3 and D4, nominal detritus import will drop to zero. However, some possibility for achieving detritus import from the North Sea through sluices will still exist. The import that could be achieved in this way can be estimated as follows.

According to Parsons (1963), the North Sea contains about 1.5 g/cu m of particulate organic matter.[2] Thus, a sluice that brought in water at a rate of 100 cu m/sec

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[2] We consider particulate organic matter alone because it can be trapped in the Oosterschelde by sedimentation. By contrast, there is no obvious mechanism to entrap a large fraction of dissolved organic matter. (See the appendix for further discussion.)

could import with it a theoretical maximum of only 13 tons of organic material (i.e., detritus) each day.

However, this assumes that the flow of 100 m/sec is the average flow. If the sluice merely has a capacity of 100 cu m/sec, it will only carry that much into the Oosterschelde when the tide is high. The rest of the time it will carry in less than this amount, and for half of the time, it must carry water out of the Oosterschelde. In addition, as the sluice carries the water out, it will carry organic material with it in the concentration found inside the Oosterschelde. This, too, will reduce the amount of detritus imported by a sluice to less than its theoretical maximum.

We believe that these two factors must reduce the detritus import through a sluice to no more than one-third of the theoretical maximum, or 4 tons/day imported per 100 cu m/sec capacity. Thus, to approximate the present-day detritus import using sluices would require a capacity of 15000 to 20000 cu m/sec. This is very large, but it is possible. The Haringvliet sluices have a capacity of 6000 cu m/sec. However, such large sluices would be hard to distinguish from a storm-surge barrier, and with such large sluices in place, the "closed" alternatives would be difficult to distinguish from alternatives with a reduced tide.

It is also easy to compute detritus import for the open alternatives, A3 and A4. These differ from the present Oosterschelde only because eastern and northern lakes are separated from the larger basin by the Oesterdam (in alternative A4, the Wemeldingedam) and the Philipsdam (see Fig. 12.1). There seems to be no reason why the concentration of detritus in the salt basin should decrease as a result of compartmentation. Thus, the detritus import would change only as the volume of water flowing in and out with the tide changed. For the open cases, therefore, we assume that detritus import changes from the present situation proportionately with tidal volume.

12.4.3. Detritus Import in the Storm-Surge Barrier Alternatives

To estimate detritus import in the alternatives with a storm-surge barrier was much more problematic. We originally assumed that detritus import in the reduced-tide cases would also be proportional to tidal volume. But, in a personal communication, J.H.J. Terwindt, then director of the Environmental Division of the Delta Service, Rijkswaterstaat, challenged this assumption. He argues that as the barrier aperture is decreased, the consequent reduction in the tide and in current velocities would permit a larger fraction of the suspended organic matter to settle to the bottom of the Oosterschelde. He feels that this effect would be pronounced enough that the import of particulate matter—he supposes most detritus import to be particulate—would increase, at least for apertures in excess of 5000 sq m.

Terwindt did not supply actual estimates of detritus import rates for the storm-surge barrier cases. To produce these needed estimates in a manner consistent with Terwindt's hypothesis, we constructed the following simple model of detritus import by tidal action. First, it is logically necessary that the import of particulate matter be proportional to tidal volume and to the difference in the concentration of particulate matter in the incoming and outgoing waters. The incoming waters, which we take to be of the same composition as the North Sea coastal waters, have a particulate organic content of about 1.5 g/cu m (Parsons, 1963).

We assume—and this is the only point on which we must make an assumption—that for a constant basin size but varying tidal range, the concentration of organic particulate matter in the outgoing waters is proportional to tidal volume. This is consistent with Terwindt's hypothesis that the concentration of suspended organic matter should diminish. Thus, our model (for constant basin size) is

$$D = V(1.5 - AV) , \tag{12.1}$$

where D is detritus import per tidal cycle (taken as one-half the daily import), V is tidal volume, and A is an unknown constant of proportionality.

To evaluate A, we assume that detritus import per unit tidal volume in alternative A3 is the same as it is in the present Oosterschelde. This is equivalent to assuming that the particulate content of the waters of the Oosterschelde is not changed by the construction of the Oesterdam and the Philipsdam. According to this assumption, A3 should have a detritus import of 546 tons/day. Since the tidal volume in case A3 should be approximately 1113 million cu m per tidal cycle, we obtain a value for A of

$$A = 1.127 \cdot 10^{-9} .$$

By substituting this value of A into the formula, we can calculate detritus import rates for all the C3 cases.

We can do the same for the C4 cases. That is, we determine that detritus import in case A4 is 341.2 tons/day, and so we must have

$$A = 1.8 \cdot 10^{-9} .$$

As we have explained, Eq. (12.1) was obtained by assuming that the concentration of organic matter in the outgoing water is proportional to the tidal volume. This assumption may be challenged. For example, there will surely be some organic matter in suspension even if the tide is reduced to zero, as is demonstrated by the experience in the Grevelingen. Thus, at least for small tidal volumes, the concentration of organic matter in the outgoing water will be larger than assumed here, and hence the rate of detritus import will be smaller.

In Fig. 12.4, we illustrate several different assumed relations between the concentration of organic matter in the outgoing water and the tidal volume. All of these relations predict the same detritus import rate at a tidal volume characterizing the open alternative A3, and all of them are monotone increasing functions. That is, one expects that the concentration will increase as the tidal volume increases, and decline as the tidal volume declines. However, as can be seen, there is a wide range of relations that satisfy both of these constraints.

We do believe, however, that the upper and lower curves in this figure represent the extremes of the relations one might reasonably assume. Further, based on conversations with Terwindt, we think that the actual relation will be closer to the lower curve (which implies a high detritus import rate), at least for moderate-to-large tidal volumes, than to the upper curve. Therefore, as explained above, we have adopted this lower relation as our nominal assumption.

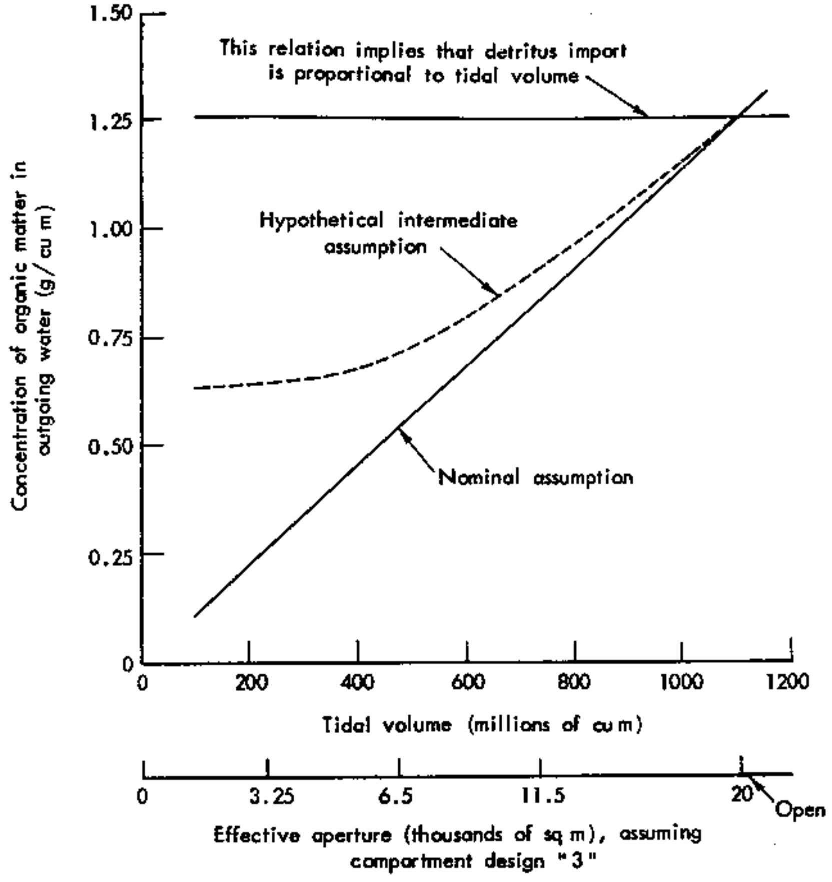

Fig. 12.4 — Alternative relations between the concentration of organic matter in outgoing water and the tidal volume for compartment design "3"

12.4.4. Summary of Rates of Detritus Import and Photosynthesis

Detritus import rates and rates of photosynthesis for each alternative case appear in Table 12.4. In the first column, the rates of detritus import were calculated by assuming that detritus import is proportional to tidal volume, which was our original assumption. We have retained the results arising from this assumption to demonstrate the extreme importance of detritus import to the Oosterschelde ecology. In the second column, the rates were calculated by using Eq. (12.1). These rates will be used in our nominal cases. The photosynthetic rates shown in the third column were calculated by assuming that the rate of photosynthesis is proportional to the area of the basin.

Recent measurements by the Environmental Division of the Delta Service, Rijkswaterstaat, suggest that the concentration of particulate organic matter in waters entering the Oosterschelde from the North Sea may be as high as 3 g/cu m, instead of 1.5 g/cu m. Under this alternative assumption, we repeated our

Table 12.4

RATES OF DETRITUS IMPORT AND PHOTOSYNTHESIS
FOR EACH ALTERNATIVE CASE

(Tons per day)

Case	Detritus Import		Photosynthesis
	Proportional to Tidal Volume	Using Eq. (12.1)	
Present Oosterschelde	704.0	704.0	455.0
A3	546.0	546.0	352.9
C3, $\mu A = 20000$	522.0	640.0	352.7
C3, $\mu A = 11500$	359.2	990.0	348.1
C3, $\mu A = 6500$	232.8	916.0	346.1
C3, $\mu A = 3250$	108.6	570.0	322.8
D3	0.0	0.0	317.8
A4	341.2	341.2	220.5
C4, $\mu A = 11500$	304.8	471.2	219.9
C4, $\mu A = 6500$	222.5	618.6	216.6
D4	0.0	0.0	193.8

calculation of detritus import in case C3, $\mu A = 11500$ sq m. This involved reestimating the constant A in Eq. (12.1), so that detritus import in case A3 would remain at 546 tons/day. The new estimate of detritus import in case C3, $\mu A = 11500$ sq m, was 1740 tons/day.

In the appendix, we discuss the arguments that support a detritus import as large as 700 tons/day in the *present* Oosterschelde and those that oppose it. We conclude that the arguments opposing so large an import have considerable force. They would have equal force in an Oosterschelde with a storm-surge barrier. Thus, we cannot accept a detritus import as large as 1740 tons/day in a storm-surge barrier case.

This is not meant to deny that the concentration of particulate organic matter in inflowing water is as high as 3 g/cu m. But, if it is this high, then we strongly doubt that the concentration inside the basin is proportional to tidal volume. Rather, we would replace the proportionality assumption by one more like the hypothetical intermediate assumption shown in Fig. 12.4.

12.5. ABUNDANCE OF BENTHIC DETRITUS EATERS

In a reduced-tide Oosterschelde, suspended matter should decrease. The water will become clearer because more of the particulate matter (organic + inorganic) will settle to the bottom. One can therefore argue that deposit feeders (benthic detritus eaters) should receive a larger share of total detritus.

However, because of the manner in which we formulated our model, this did not occur. In the model, we had only one accounting quantity (AQ) corresponding to detritus. Consequently, all detritus was available to all creatures, whether they could eat benthic detritus or only detritus suspended in the pelagic segment. When we increased detritus import in accordance with Terwindt's advice, this feature of the model caused it to predict an increase in all detritus eaters, both pelagic and benthic.

To simulate this increased sedimentation of detritus, we altered various of the parameters $c_{i,j,s}$ to increase the abundances of benthic detritus eaters beyond what the model would otherwise have predicted. Then we let the model decide by how much the abundances of other detritus eaters (especially pelagic) would change.

Because the parameters $c_{i,j,s}$ are not related in any simple way to any directly observable quantity, such as an abundance, we found it desirable to carry out our changes of these parameters indirectly. We made assumptions about how a barrier of a given aperture would affect the abundances of the most important benthic detritus eaters, and employed the mathematical device of Lagrange multipliers to find the values of the parameters $c_{i,j,s}$ that corresponded to these assumptions.

In more detail, our procedure was as follows: First, we imposed three new constraints on the model, which prescribed the abundances of selective deposit feeders with pelagic larvae, deposit feeders with nonpelagic larvae and suspension-feeding worms, and benthic grazers, respectively. These three ecogroups make up virtually all of the biomass of organisms that eat benthic detritus in the present Oosterschelde. Such a new constraint would take the form of Eq. (12.2) below:

$$\sum_i \sum_s x_{i,j,s} = \text{Desired abundance of ecogroup } j \,. \qquad (12.2)$$

By adjusting the right-hand sides of these new constraints, we can ensure that the abundances of these organisms, and hence the amount of detritus (and other things) that they eat, are equal to any values we want to assume for a given alternative. Then, we can set each of the segment sizes and external mass-transfer rates to the values that characterize that alternative, and solve the model to find the abundances of all the other, still unconstrained, ecogroups. In addition to calculating the abundances, the solution procedure also calculates the Lagrange multiplier for each constraint, including the new ones.

Given the Lagrange multipliers, one may create a new problem that will have the same solution as the old one, but will not have the additional constraints. The objective function of the new problem—in our case the Gibbs function (see Eq. (4.3) in Sec. 4.2)—is obtained from the old one by subtracting from it one or more of the constraint equations, each multiplied by its corresponding Lagrange multiplier. This has the effect of subtracting a linear function of the variables $x_{i,j,s}$ from the objective function. But, since the Gibbs function is already the sum of a nonlinear function and a linear function—the latter being the sum of the $c_{i,j,s}$'s times the $x_{i,j,s}$'s—subtracting another linear function is equivalent to changing the parameters $c_{i,j,s}$.

Only one difficulty remains, but it is the most important one of all. This is the difficulty of choosing what abundances of benthic detritus eaters ought to characterize the various alternatives. We resolved this very uncertain matter by choosing what appear to us to be reasonable abundances as our nominal assumptions, and later investigating the sensitivity of our results to changes in these assumptions. The nominal assumptions are as follows.

We assumed that the parameters $c_{i,j,s}$ would be the same in all alternatives in which the Oosterschelde is open. As a result we can calculate the abundances of benthic detritus eaters in alternatives A3 and A4 by using the same $c_{i,j,s}$'s that apply in the present Oosterschelde. Given the abundances in one of these open alternatives, we multiply them all by the same factor to arrive at estimates of abundances for an alternative with the same compartmentation design but a different aperture. That is, we assume that all benthic detritus eaters will benefit equally. The question then becomes, What should this factor be?

For cases in which the aperture of the storm-surge barrier equaled or exceeded the aperture giving the maximum detritus import, we chose the value of this factor so that suspension feeders (cockles, mussels, and oysters), who feed on suspended detritus and phytoplankton just above the bottom, would neither suffer nor benefit, as compared with the open case with the same compartment design. We reason that turbulence caused by winds and waves should repeatedly bring detritus that has settled to the bottom back into suspension in the water close to the bottom, where it is accessible to suspension feeders. For cases with smaller apertures, we maintained the values of the $c_{i,j,s}$'s equal to those that obtained for the cases whose apertures gave the maximum detritus imports for their respective compartment designs.

We are aware that the grounds for this assumption are tenuous. But we think it preferable to make such an assumption and later determine whether our policy conclusions are sensitive or insensitive to it. If insensitive, we contend that the conclusions will stand in spite of many uncertainties in the assumptions.

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Chapter 13

RESULTS FOR THE NOMINAL ASSUMPTIONS

This chapter will discuss the ecological impacts we have estimated from the general ecomodel outputs. What are these impacts? Why did we choose to estimate them and not others? In particular, we shall identify questions of interest about the Oosterschelde that each impact illuminates.

13.1. BIOMASS

The output quantities of the model are measures of the biomass of the various ecological groups. In Figs. 13.1 and 13.2, we present these outputs for all the alternative cases under the nominal assumptions. To remind the reader, the nominal assumptions are that

1. The rate of photosynthesis is proportional to the total area that is submerged at mean high tide. This, of course, is just the sum of the areas of the three benthic segments. The nominal photosynthetic rates for the different alternatives can be found in Table 12.4.
2. The rates of detritus import for the different alternatives can be determined from Eq. (12.1), which was, in turn, based on the Terwindt thesis, that most imported detritus is particulate. In the storm-surge barrier alternatives (i.e., those with a reduced tide), a larger fraction of the particulate matter brought in with the tide should settle to the bottom and thus be trapped in the Oosterschelde. This implies that for all but the most severe reductions in the tide, detritus import should increase over its present rate. The nominal rates of detritus import for the different alternatives can be found in Table 12.4.
3. Benthic detritus eaters benefit from the simultaneous increases in detritus import and sedimentation that the Terwindt thesis predicts for the reduced-tide alternatives with the larger apertures. The degree to which they benefit is just sufficient so that suspension feeders neither benefit nor suffer, as compared with an open alternative with the same compartment design. For smaller apertures, all detritus eaters suffer.
4. In all the alternative cases with a tide, however much reduced, migration and fishing continue to occur at the same rates as they do at present. In the cases with no tide—the two closed alternatives, D3 and D4—we assumed that there is no harvesting of shellfish and no migration, but that fishing continues without change. We have thus eliminated the shellfish culture segment in D3 and D4. However, even though migratory species can no longer enter and leave the Oosterschelde once it is closed, we assume that these species are replaced by ecologically equivalent resident species. Consequently, we have retained the same food web in D3 and D4 as in all the other alternatives.

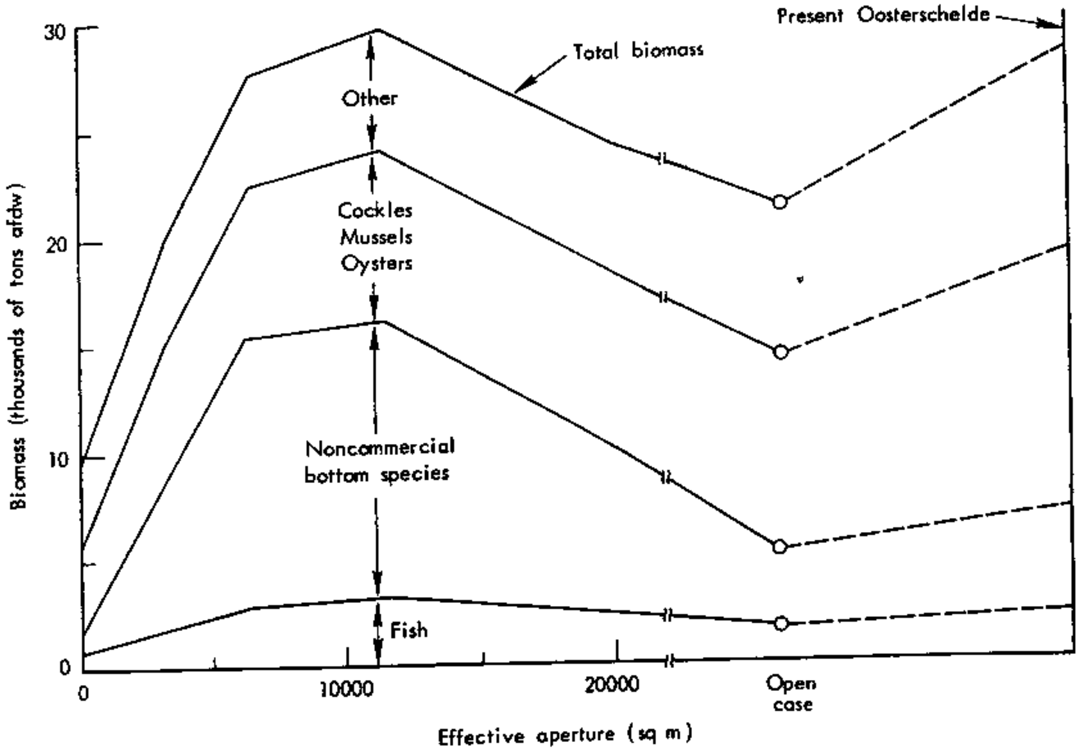

Fig. 13.1 — Biomass by component for all alternative cases with compartment design "3"

The total biomass in Figs. 13.1 and 13.2 has been broken down into four components: fish; noncommercial bottom species, such as worms and snails; cockles, mussels, and oysters (commercial bottom species); and all other ecological groups. The last category includes the birds and all the planktonic organisms.[1] We have separated fish and the commercial bottom species because of the great social and/or commercial interest in them, and we have partitioned the remaining groups into two categories because, by doing so, we can better highlight the major differences in the ecological impacts of the different alternatives.

In Fig. 13.1 we see that construction of the Philipsdam and the Oesterdam has the effect of reducing the total biomass by about 25 percent, without much changing the proportion of that total that corresponds to each of the four components. (Note that on the right-hand margin of Fig. 13.1, we have included the present ecological state of the Oosterschelde for easy comparison.) This result is to be expected, since the only effect of building these dams is to reduce all the segments, as well as the rates of photosynthesis and detritus import, by approximately the same 25 percent.

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[1] Birds are not presented here as a separate component of biomass because their biomass is too small to show on the scale in Figs. 13.1 and 13.2. Changes in the bird population are dealt with as separate impacts in Sec. 13.2 below.

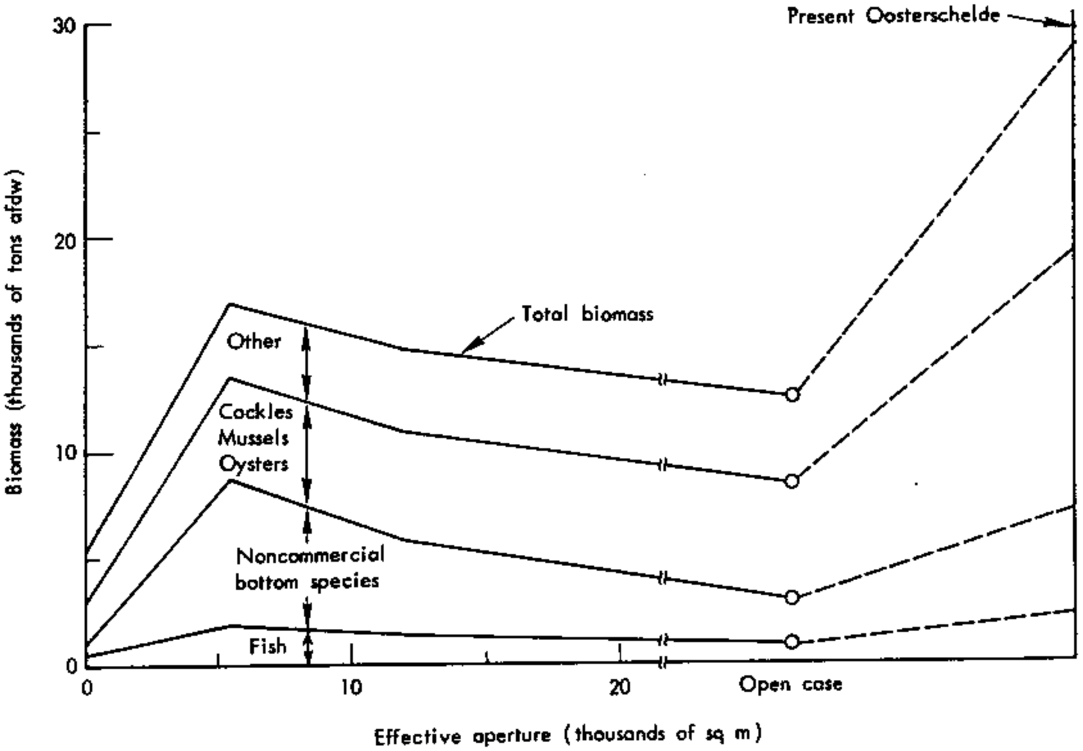

Fig. 13.2—Biomass by component for all alternative cases with compartment design "4"

By building these dams and doing nothing else, one would, of course, be implementing alternative A3.

But if, in addition, one builds a storm-surge barrier, then one will be implementing one of the C3 alternatives. In these cases, the ecological impacts will depend on the effective size of the aperture in the barrier. As the aperture is reduced from the present open state (80000 sq m) to approximately 11500 sq m, the total biomass will continually increase. For apertures smaller than 11500 sq m, the total biomass will begin to decrease as the aperture is made smaller. This effect is, of course, a consequence of the Terwindt thesis. According to our interpretation of the thesis, the detritus import should increase as the aperture decreases until it reaches a maximum near 11500 sq m. For smaller apertures, the detritus import will reverse its trend.

However, these changes in total biomass are not always distributed among the four components of biomass in the same way. According to our model, changes in the aperture should influence the abundance of noncommercial bottom species most. Indeed, the other components hardly respond at all to changes in the aperture until it is made very small. And by the time it is zero (alternative D3), the four biomass components have returned to proportions similar to those in the present Oosterschelde, but at a total biomass that is only one-third as great.

It should not surprise us that these changes in the aperture would affect noncommercial bottom species more than any other component of biomass. These are the species that live on benthic detritus. According to the Terwindt thesis, therefore, they should receive the greatest benefit from the increase in detritus import and sedimentation that would accompany a reduction in the aperture.

In Fig. 13.2, we can see the effects of creating the small saltwater basin that characterizes alternative A4. Again, the total biomass is reduced whereas the proportions of each component remain roughly the same. Now, however, the reduction is in excess of 50 percent, rather than 25 percent, as the model estimated for alternative A3. Nor is this surprising, since according to our nominal assumptions, the smaller basin should have both less photosynthesis and less detritus import than the larger one.

Again, if a storm-surge barrier is built, its ecological impacts will depend on the effective size of the aperture. If the aperture is made very large, there will be no greater effect from building the barrier than from building the compartmentation dams alone. However, as the aperture is reduced, the total biomass should become first larger, and then smaller. According to Eq. (12.1), detritus import should reach a maximum when the tidal volume is about 415 million cu m, compared with almost 700 million cu m in alternative A4. This corresponds to an aperture of approximately 6000 sq m, which is essentially the point at which the total biomass in Fig. 13.2 achieves its maximum. Once again, noncommercial bottom species derive the greatest benefit from increases in detritus import and sedimentation that accompany reductions in the aperture.

The most evident difference between Figs. 13.1 and 13.2 is that the biomasses in Fig. 13.2—corresponding to alternatives with compartment design "4"—are much smaller than the biomasses in Fig. 13.1—which correspond to alternatives with compartment design "3." The reason is that the smaller saltwater basin of compartment design "4" supports less detritus import and less photosynthesis than the large saltwater basin of compartment design "3." In fact, the single most important difference between any two alternatives is the difference between the sum of the photosynthesis and detritus import.

Figure 13.3 illustrates this point. In this figure, we plotted the total primary food available, calculated as detritus import plus photosynthesis, against total biomass for every alternative under the nominal assumptions. We also plotted the points corresponding to all the storm-surge barrier alternatives but in which we assume that detritus import is proportional to tidal volume instead of obeying the Terwindt thesis. (The detritus import rates assumed for these cases can be found in Table 12.4.) Among these points are cases with three different compartmentations (the present, and designs "3" and "4"), and widely varying primary food supplies (from less than 200 tons/day to more than 1300 tons/day). In all of these cases, the model estimates that total biomass should be approximately twenty-three times the daily availability of detritus plus photosynthesis.

This result should have been anticipated. In Sec. 3.10 of Part I, we developed an overall system balance equation that very clearly points out the dependence of the ecosystem on detritus import plus photosynthesis. If isolated, the ecosystem would irreversibly dissipate its biomass through metabolic processes. It is only because these metabolic losses are replaced by photosynthesis and detritus import

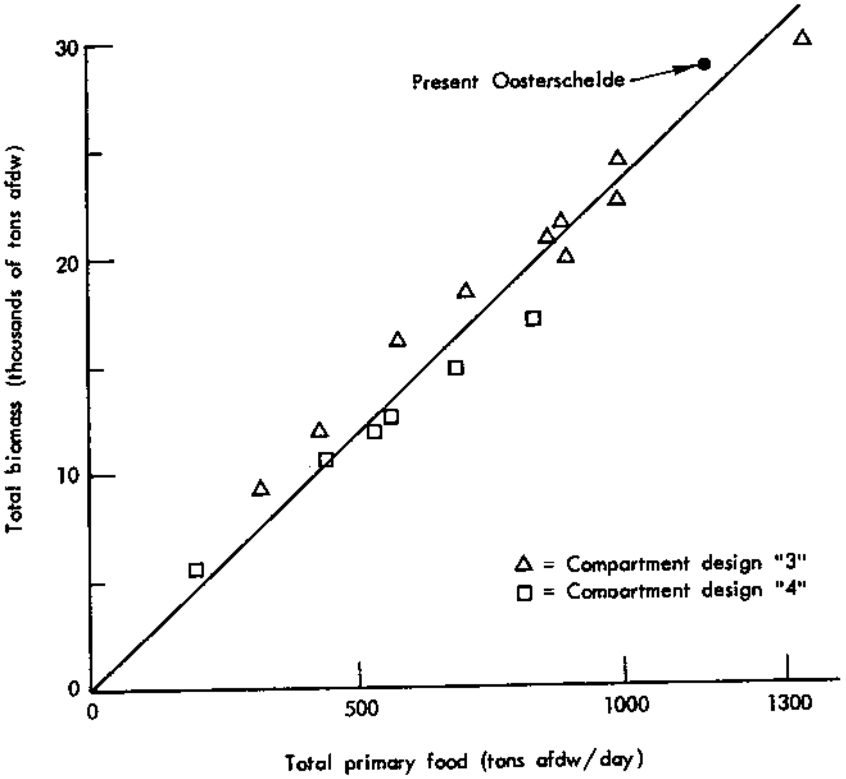

Fig. 13.3 — Primary food availability (detritus import + photosynthesis) as a predictor of total biomass

that the ecosystem can continue. What might not have been anticipated was that detritus import plus photosynthesis is such a good predictor of the model's estimates of total biomass.

13.2. POTENTIAL ABUNDANCE OF BIRDS

13.2.1. The Handling of Birds in the Model

As we have stated previously, there are three ecological groups in the model that represent birds. These are benthos-eating birds, fish-eating birds, and plant-eating birds. These groups include the species given in Table 8.1 of Chap. 8.

The reader should recall that no ecogroup in our model preys upon birds, and that therefore, as explained in Sec. 7.2.8, and reviewed in Sec. 12.3, the bird balance equations are prescriptions of the abundances of the various bird ecogroups. The abundances of birds are thus inputs to our model, and not outputs.

As a consequence of their being inputs, our model cannot predict the actual bird abundances that would be observed in any alternative case. Instead, to make an estimate of these abundances, we investigate the influence of a range of assumed abundances on other ecogroups. Based on these influences, we try to make reasonable estimates for the bird abundances. The next several sections describe how this program was put into practice.

13.2.2. Benthos-Eating Birds

We used two different notions to obtain two different estimates of the abundance of benthos-eating birds in the various alternative cases. The first is that their numbers are limited by competition for a limited food supply. This is a notion that our model can help to investigate directly. To do so, we ran our model for a wide range of possible abundances of benthos-eating birds. In Fig. 13.4, we show the only significant consequence of this exercise, namely that as benthos-eating birds become more abundant, they replace some benthos-eating fish, and this replacement occurs in such a way that the total consumption by benthos-eating fish and birds remains constant.

We did a similar experiment for alternative D4, which is as different from the present Oosterschelde as any of our alternative cases. As shown in Fig. 13.5, we obtained similar results. Once again, the only significant result was that as benthos-eating birds increased, they replaced benthos-eating fish at such a rate that the total food consumption by both groups remained approximately constant. In alternative

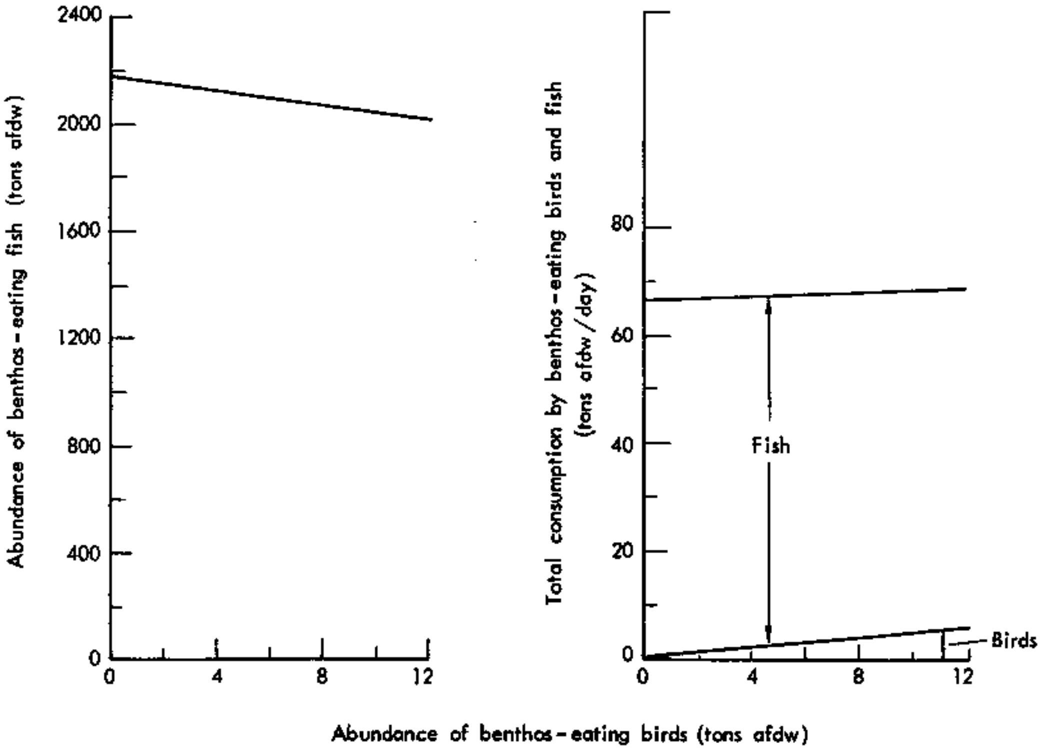

Fig. 13.4 — The effect of a change in the abundance of benthos-eating birds on benthos-eating fish in the present Oosterschelde

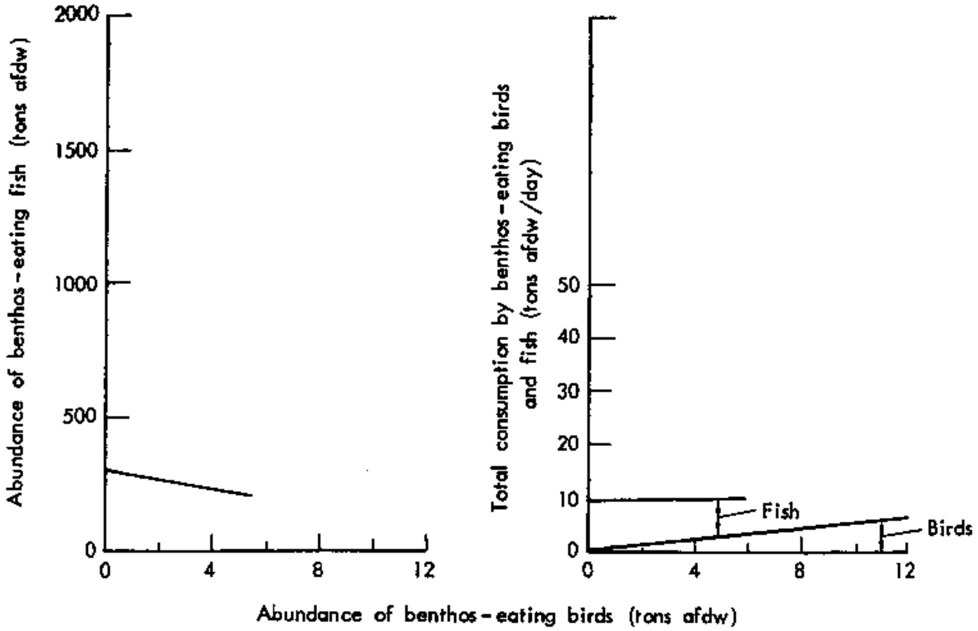

Fig. 13.5 — The effect of a change in benthos-eating birds on benthos-eating fish in alternative D4

D4, however, that total combined consumption was much smaller than in the present Oosterschelde.

To use the competition idea to estimate the abundance of benthos-eating birds in each alternative, we assumed that in every alternative, fish and birds would have the same comparative success in competing for food but that their actual numbers would rise and fall in proportion to their combined consumption. Because the model estimates that their combined consumption is independent of their relative abundances, we can calculate the combined consumption for an alternative by running the model of that alternative with any reasonable value for the right-hand side parameter b_j for benthos-eating birds. Then the abundance of benthos-eating birds will change from the present abundance by the same factor as the combined consumption of benthos-eating fish and birds has changed. Based on this principle, we calculated abundances of 7.3 tons, 13.0 tons, and 1.3 tons in the nominal cases A3, C3 with $\mu A = 11500$ sq m, and D4.

The other notion we used for estimating benthos-eating birds was that they were limited, not by the availability of food, but by the area on which they could feed. Most benthos-eating birds are waders and cannot feed in water deeper than about 30 cm. The only areas that are ever within 30 cm of the surface are the tidal flats and the area between mean low water and mean low water minus 30 cm. The feeding areas available to benthos-eating birds in each alternative case are shown in Table 13.1.

These areas are approximated as follows. We know that the shallow bottom segment extends from mean high water to mean low water minus 30 cm. If the slope

Table 13.1

AREAS ON WHICH WADING BIRDS MAY FEED
FOR EACH ALTERNATIVE CASE

Case	Tidal Range at Zierikzee (cm)	Shallow Bottom Area (sq km)	Waders' Feeding Area (sq km)
Present Oosterschelde	301.3	251.0	138.3
A3	301.3	174.0	95.9
C3, $\mu A = 20000$	288.2	169.4	91.9
C3, $\mu A = 11500$	200.9	154.6	71.3
C3, $\mu A = 6500$	131.0	134.8	50.4
C3, $\mu A = 3250$	68.0	113.3	30.2
D3	0.0	106.3	10.6
A4	301.3	99.7	54.9
C4, $\mu A = 11500$	270.0	94.2	49.6
C4, $\mu A = 6500$	200.0	87.0	40.0
D4	0.0	53.2	5.3

of these bottom areas is the same, on the average, whether they lie above or below mean low water minus 30 cm, then the fraction of this segment in which wading birds may feed is equal to the fraction of the vertical range of this segment that lies above mean low water minus 30 cm. This fraction is

$$F = \frac{(\text{Tidal range}) + 30 \text{ cm}}{(\text{Tidal range}) + 300 \text{ cm}} .$$

To apply this notion, we assume that the abundance of benthos-eating birds is proportional to their feeding area. Thus, because the feeding area of these birds is approximately one-half as large in case C3, $\mu A = 11500$ sq m, as it is in the present Oosterschelde, this notion predicts that benthos-eating birds should only be one-half as abundant in C3, $\mu A = 11500$ sq m. In general, this notion predicts lower abundances of benthos-eating birds than the competition model: 6.6 tons in A3, 4.9 tons in C3, $\mu A = 11500$ sq m, and 0.36 tons in D4.

In Table 13.2, we give abundance estimates of benthos-eating birds for each alternative case. Considering the quality of the data on abundances from which we calibrated the model, we cannot say that the two methods give significantly different results. The only experimental evidence we have regarding how benthos-eating birds might react in the various alternatives fails to differentiate between the two estimates. This evidence is that after the Grevelingen was closed in May 1971, the abundance of benthos-eating birds was observed to decline approximately fivefold (Wolff et al., 1975). Both of our estimation methods predict a substantial decline in benthos-eating birds after closure.

Based on these estimates, the most we can say is that we would expect the abundance of benthos-eating birds to decline dramatically if the Oosterschelde were closed (alternatives D3 and D4), and to decline somewhat in any alternative with compartment design "4." But any alternative with compartment design "3," and some tide in the basin, will hardly influence the abundance of benthos-eating birds at all.

Table 13.2

ABUNDANCE ESTIMATES OF BENTHOS-EATING BIRDS
FOR EACH ALTERNATIVE CASE

(Tons afdw)

Case	Biomass Estimates Based On—	
	Competition	Feeding Area
Present Oosterschelde	9.5	9.5
A3	7.3	6.6
C3, μA = 20000	9.7	6.3
C3, μA = 11500	13.0	4.9
C3, μA = 6500	11.7	3.5
C3, μA = 3250	8.1	2.1
D3	2.5	0.73
A4	4.1	3.8
C4, μA = 11500	5.9	3.4
C4, μA = 6500	7.5	2.7
D4	1.4	0.36

13.2.3. Fish-Eating Birds

We estimated the abundance of fish-eating birds using only the competition notion. To investigate, we ran the model for the present Oosterschelde with a wide range of abundances of fish-eating birds. (Recall that in our model, we are forced to prescribe their abundance.) Figure 13.6 shows the only significant result of this experiment: As fish-eating birds become more abundant, they replace fish-eating fish in such a way that the total consumption of food by the combined groups remains constant.

We did a similar experiment for alternative D4, which is as different from the present Oosterschelde as any of our alternative cases. As shown in Fig. 13.7, we obtained similar results. Once again, the only significant result was that as fish-eating birds increase, they replace fish-eating fish at such a rate that the total food consumption by both groups remains approximately constant. In alternative D4, however, that total combined consumption was much smaller than in the present Oosterschelde.

We used the competition notion to estimate fish-eating bird abundances for each alternative in much the same way as we used it to estimate benthos-eating bird abundances. We assumed that fish and birds would have the same relative success in competing with each other for food in all the alternative cases with a tide, and therefore that the ratio of fish-eating birds to total consumption by both the birds and the fish would be the same for all of these cases as it is in the present Oosterschelde. However, there are no resident fish-eating fish in the present Oosterschelde that could replace the migratory species in this ecogroup there. Thus, we expect that in closed alternatives D3 and D4 all of these fish will disappear. Fish-eating birds would therefore be expected to increase enormously to take advantage of the increased food supply. In fact, this phenomenon has been observed in the Grevelingen, where fish-eating birds have increased twentyfold since closure (Wolff et al., 1975).

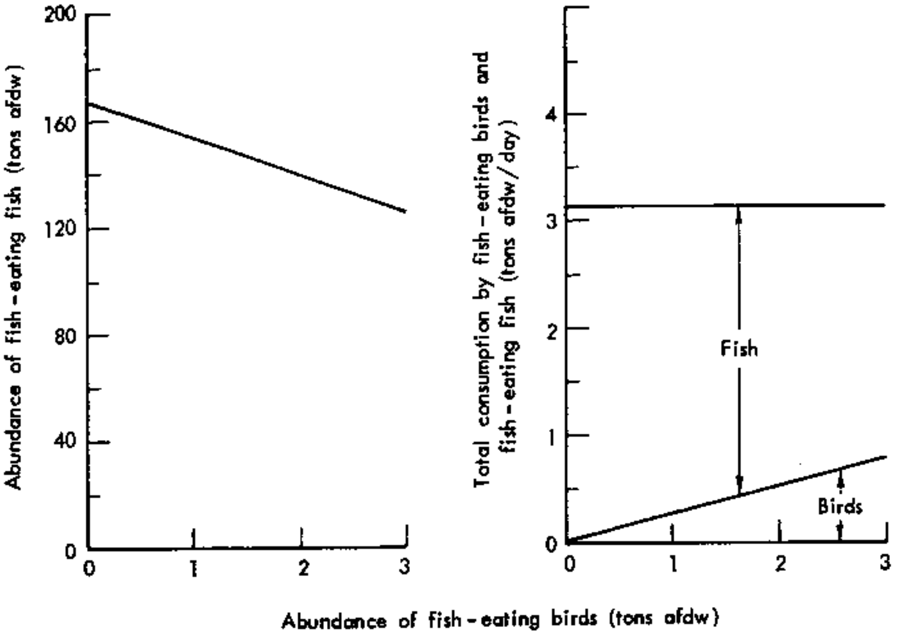

Fig.13.6 — The effect of a change in abundance of fish-eating birds on fish-eating fish in the present Oosterschelde

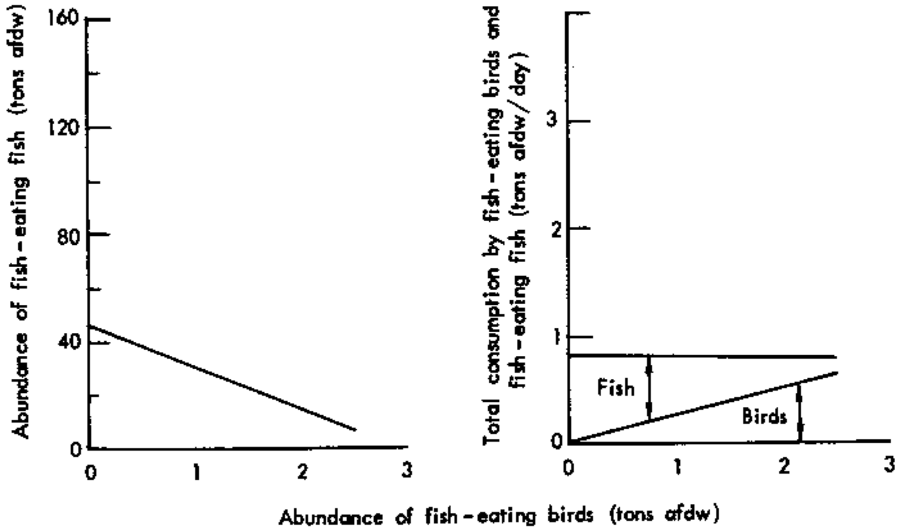

Fig.13.7 — The effect of a change in abundance of fish-eating birds on fish-eating fish in alternative D4

In Table 13.3, we list our abundance estimates of fish-eating birds for each alternative case. These have been calculated by running the model for each case with an arbitrary but reasonable value for the right-hand side parameter b_j for fish-eating birds. From the abundances of fish-eating birds and fish predicted in each of these runs, and from our estimates of the daily rations of these organisms, we calculated the combined daily food consumption by the two groups. This we compared with the combined consumption in the present Oosterschelde; and for the cases with a tide, we estimated the change in the abundance of fish-eating birds to be proportional to the change in the combined consumption. For cases D3 and D4, however, we estimated fish-eating birds to be sufficiently abundant to require the entire combined food consumption calculated from the corresponding runs of the model.

Table 13.3

ABUNDANCE ESTIMATES OF FISH-EATING BIRDS
FOR EACH ALTERNATIVE CASE

(Tons afdw)

Case	*Biomass Estimates Based on Competition*
Present Oosterschelde	0.0462
A3	0.0345
C3, μA = 20000	0.0445
C3, μA = 11500	0.063
C3, μA = 6500	0.0566
C3, μA = 3250	0.0382
D3	6.85
A4	0.0179
C4, μA = 11500	0.0268
C4, μA = 6500	0.0348
D4	3.94

We mentioned above that once the Grevelingen was closed, fish-eating birds increased twentyfold. This fact appears to us to support the idea that competition for food is what limits the numbers of these birds in the present Oosterschelde. However, a second explanation has been suggested: When the Grevelingen was closed, the water became clearer, so that birds could see their prey better and were therefore more successful predators of fish.

We do not find this explanation entirely convincing. The seeing depth in the present (closed) Grevelingen has been found to be about 3 m on the average, whereas the seeing depth in the present Oosterschelde averages 1.8 m. Assuming that the open Grevelingen had the same seeing depth as the present Oosterschelde, this improvement in seeing does not seem to us sufficient to explain the enormous increase in fish-eating birds. After all, these birds feed near the surface of the water, where seeing was moderately good even in the open Grevelingen. Furthermore, the improvement in seeing has not occurred uniformly throughout the year. There has been no improvement at all during the growing season (May through October). Improvement in seeing has occurred only during the stormy winter months, when fish-eating birds have migrated to other areas. The birds have thus experienced less than the average increase in seeing depth. The modest increase in seeing depth that we think occurred when the Grevelingen was closed would not have improved the birds' feeding ability enough to result in a twentyfold increase in their abundance.

We do not mean to imply that the increase in seeing depth has had no effect on the abundance of fish-eating birds in the Grevelingen, or that it will have no effect in the Oosterschelde. However, we believe this effect to be secondary to the influence of competition with fish-eating fish.

We mentioned earlier that large sluices could be built into the closure dam in alternative D3 or D4. If these sluices were thousands of square meters in area, it seems very probable that fish could still migrate into the Oosterschelde from the North Sea. In this case, competition with fish-eating fish might keep the abundance of fish-eating birds near its present low level. This would also apply if the closed Oosterschelde were artificially stocked with fish-eating fish.

13.2.4. Plant-Eating Birds

In an attempt to discover a principle on which to base an estimate of the abundance of plant-eating birds in the various alternatives, we ran the model for a wide range of different right-hand side parameters b_j—i.e., for a range of assumed abundances—and observed the influence of this change on the other ecological groups. The model predicts no substantial effect from changes in assumed abundances, unless the assumed abundances are many tens of thousands of times greater than the present abundance. Thus, at present, the availability of food imposes no limitation on the abundance of plant-eating birds, and no such limitation can be expected in any of the alternatives we have considered for the Oosterschelde. Our model, therefore, offers no insight into the response of plant-eating birds to the different alternatives.

To estimate the impacts of the various cases on the abundance of plant-eating birds, we therefore resorted to a comparison based on experience in the Grevelingen. There, the abundance of plant-eating birds increased fifteenfold after closure. This could have been due to an increase in the sea-grass beds, which, in turn, provided a larger nesting area. Or it could be that only a small fraction of the sea grasses is a suitable food for these birds, and this selectivity makes the actual food supply much less than the apparent supply. Whatever the explanation, we assumed that the abundance of plant-eating birds would be correlated with the size of the sea-grass beds.

Sea grasses can grow only in shallow areas that are not subject to fast currents. In fast currents, their seeds are washed away before they can sprout and take root. In deep areas, they cannot receive enough solar energy to survive. Because there are relatively few areas with these characteristics in the present Oosterschelde, only a small area is presently covered with sea grasses.

Much of this area lies in the extreme eastern end of the Oosterschelde. Some of the area would be behind the Oesterdam if an alternative with compartment design "3" were selected, and more would be behind the Wemeldingedam if an alternative with compartment design "4" were selected. Thus, alternatives with compartment design "4" would be worse for plant-eating birds than alternatives with compartment design "3." However, because a reduction in the tide would also reduce current velocities, it is not clear that all the alternatives would be worse for plant-eating birds than the present Oosterschelde. In fact, if the tide were reduced enough, and certainly if the Oosterschelde were closed, the abundance of plant-eating birds should increase.

13.3. POTENTIAL SHELLFISH CULTURE

13.3.1. Issues Concerning Shellfish Culture

The Oosterschelde is the site of a large mussel and oyster culturing industry. Each year, 30000 tons (live weight) of mussels, and 1000 tons (live weight) of oysters are harvested. Converting these rates to the units we are using in our model, we find that 3.34 tons afdw are harvested on the average day.

Mussels are fished from the production plots with a special dredging net. During this operation, their shells are still open, and they take up sand and silt. This sand and silt make the mussels unfit for direct consumption, and so they must be cleaned before they can be marketed.

In the Oosterschelde, special plots characterized by a very firm bottom (almost no sand or silt) and a moderately strong current are used for cleaning, or rewatering, the mussels grown there. Mussels grown in the Waddensea are also transported to rewatering plots in the Oosterschelde, where they are cleaned and stored before sale. In recent years, 70000 tons live weight of mussels per year have passed through the Oosterschelde rewatering plots on their way to market. At any time, one could find about 10000 tons of mussels on these plots.

There are two questions concerning shellfish culture that we wish to shed light on. (1) Which of the alternative cases will preserve the shellfish culture? (2) Which of the alternatives will permit the Waddensea mussels to continue to be rewatered in the Oosterschelde?

13.3.2. Maximum Feasible Shellfish Harvest for Each Alternative

For a variety of reasons, we are unable to predict the actual mussel harvest. New techniques may make greater harvests economically feasible, and the harvest may vary with market conditions. Instead, we used the model to investigate the potential harvest. In a sequence of runs of the model, we varied the assumed harvest and noted the effects on the abundances of the various ecological groups.

Figure 13.8 shows the results of such an experiment for the present Oosterschelde. Basically, we found that the larger the mussel harvest, the larger the standing stock needed to sustain it. Also, the larger the harvest of mussels and oysters, the more it is necessary to control their predators. These results were anticipated in the simple exemplary ecosystem that we investigated in Sec. 4.4 of Part I (see especially Fig. 4.7). A final observation is that increasing the harvest by as much as a factor of three had no significant effect on any ecogroup except mussels and oysters, and their predators.

Note the sensitivity, in Fig. 13.8, of both shellfish abundance and predator control to the assumed harvest. At the point that characterizes the present Ooster-

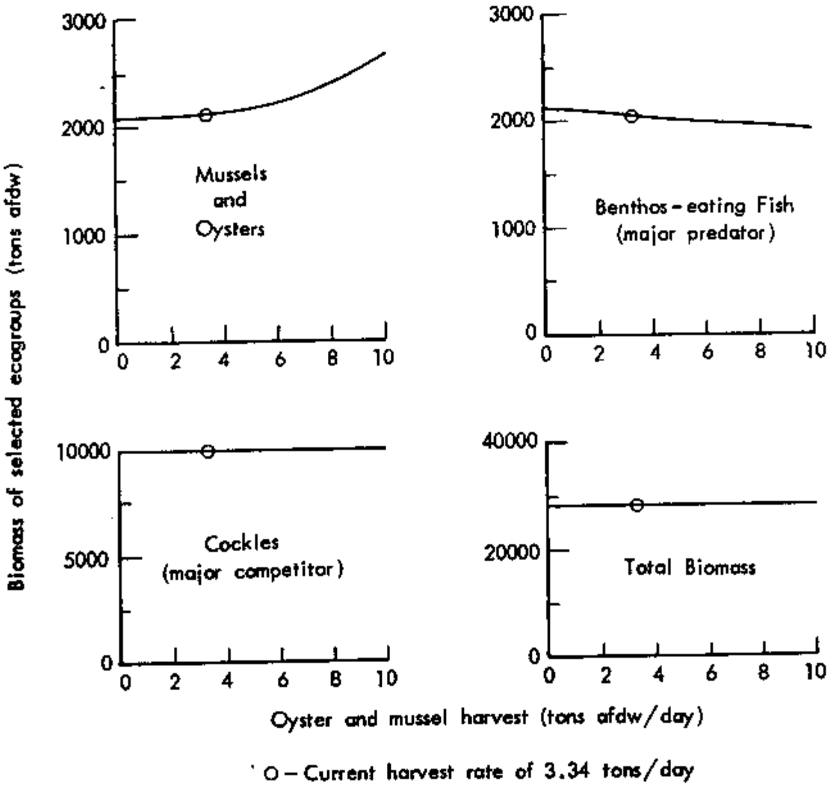

Fig. 13.8 — Effect of variations in the mussel harvest on the present Oosterschelde

schelde, however, even these two quantities are quite insensitive to the harvest. On the other hand, tripling the harvest would require significant increases in the abundance of cultured shellfish, and significant control of their predators.

We argue that changes such as these would require substantial changes in the techniques now being used for shellfish culture in the Oosterschelde. These changes would probably be expensive and difficult. Thus, if shellfish culture is to continue under economic conditions similar to those of today, the sensitivity of shellfish abundance and of their predators to variations in the harvest cannot be much greater than observed at present.

This principle enables us to forecast whether the existing shellfish culture industry could continue under the alternatives we are investigating. We vary the harvest rate for mussels and oysters for each alternative, and we note whether the sensitivity of shellfish abundance and their predators appears to be much greater than it is in the present Oosterschelde. If the sensitivity of either one is much greater in a case than it is in the present Oosterschelde, we doubt the possibility of continuing commercial shellfish culture activities on the same scale and in the same manner as today. But, if the sensitivity of the abundances of either mussels or their predators appears to be smaller than or similar to those of today's industry, then we see no obstacle to a continuing commercial shellfish culture industry in that case.

Figure 13.9 shows the results of this experiment for the alternatives with compartment design "3." For comparison, we have also included the result for the present Oosterschelde. Note that the dependence of mussel and oyster abundance on the harvest rate of mussels and oysters appears to be much the same in all cases with a tide. In these same alternative cases, benthos-eating fish—the major predators of mussels and oysters—are also not very differently sensitive to changes in the harvest rate. According to our principle, then, we can expect that mussel and oyster culture, on the same scale as it is carried on at present, will remain commercially feasible in alternative A3, and alternatives C3 in which the effective apertures are greater than 3250 sq m.

The closed alternative, D3, is different. The abundances of both mussels and oysters, and of benthos-eating fish, are generally much lower in this case than in any case with a tide. Further, this is true for all rates of mussel and oyster harvest. It appears unlikely, therefore, that commercial culturing of oysters and mussels could continue if alternative D3 were chosen.

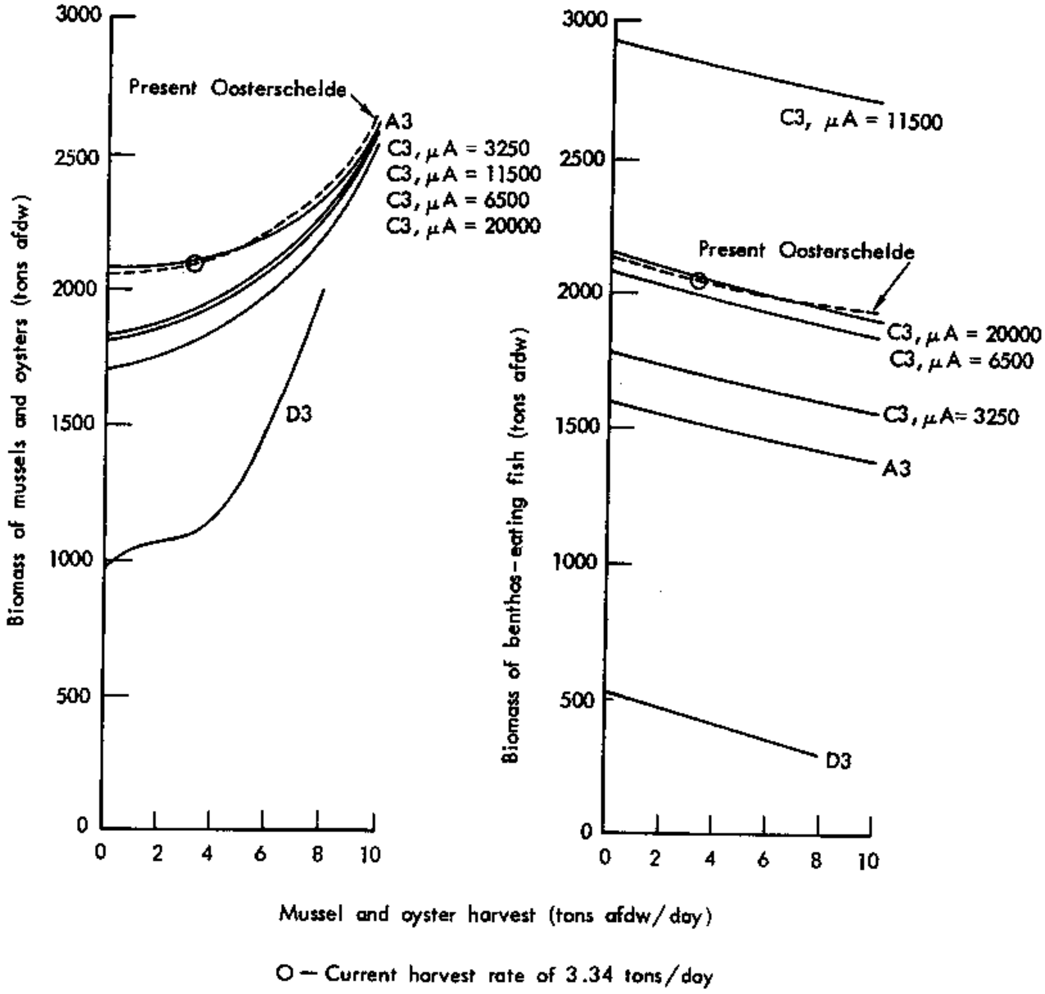

Fig. 13.9—The effect of variations in the mussel and oyster harvest in alternative cases with compartment design "3"

In Fig. 13.10, we present the results of the same experiment for all the alternative cases with compartment design "4." The reader will recall that a major difference between compartment designs "3" and "4" is that in design "3," the shellfish culture plots are the same size as those in the present Oosterschelde; whereas in design "4," the Wemeldingedam is placed so far to the west that almost 60 percent of the present shellfish culture plots lie in the freshwater lake to the east of this dam. This curtailment of the shellfish culture area causes the abundance of mussels and oysters to be much smaller in all the alternatives with compartment design "4," with or without a tide, than it is in the present Oosterschelde. We concluded that commercial culturing of mussels and oysters on the present scale would not be feasible in an Oosterschelde with compartment design "4."

In any alternative, some shellfish culture will be possible. Some oysters and mussels will survive even in alternative D4 (the alternative least favorable to them), and if a commercial fisherman wanted to harvest some of them, he could do

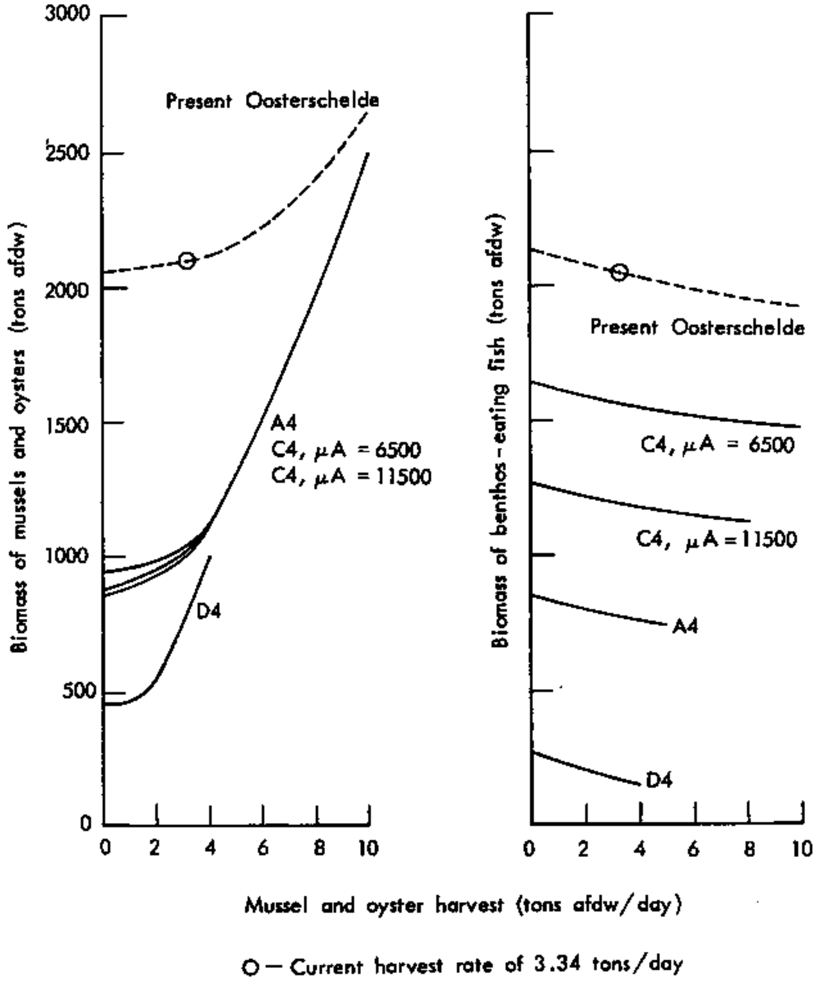

Fig. 13.10—The effect of variations in the mussel and oyster harvest in alternative cases with compartment design "4"

so. If there are fewer shellfish, they will be spread more sparsely on the shellfish culture plots, and therefore it may be economically less attractive to harvest them. But at least a small fraction of the men who now support themselves by culturing oysters or mussels could continue to do so even in alternative D4.

For each alternative, we can make a rough estimate of how much of the present shellfish culture could continue. The rule we have used to make these estimates is that the ratio of the abundance of oysters and mussels to the maximum feasible harvest rate should be the same in each alternative as is the ratio of the present-day abundance of mussels and oysters to the present-day harvest. At the harvest rates determined by this rule for each alternative, the abundances of mussels and oysters, and of benthos-eating fish, appear to be about as sensitive to variations in the harvest rate as is true for the present shellfish culture in the Oosterschelde. Of course, if the present-day harvest is much below the maximum harvest that could be sustained in the present Oosterschelde, then this procedure may underestimate the maximum feasible harvest in the various alternatives. And there is some evidence that what constrains the present harvest from becoming larger is not ecological conditions, but the absence of sufficient demand for even as many shellfish as are currently being produced (Heuer, 1976). These estimates appear in Table 13.4.

Table 13.4

ESTIMATES OF MAXIMUM COMMERCIALLY FEASIBLE MUSSEL AND OYSTER HARVEST FOR EACH ALTERNATIVE CASE

Case	Harvest Rate Estimates	
	Fraction of Present Rate	Amount (tons afdw/day)
Present Oosterschelde	1.0	3.34
A3	1.0	3.34
C3, μA = 20000	0.9	3.0
C3, μA = 11500	0.9	3.0
C3, μA = 6500	0.9	3.0
C3, μA = 3250	0.9	3.0
D3	0.5	1.67
A4[a]	0.5	1.67
C4, μA = 11500[a]	0.5	1.67
C4, μA = 6500[a]	0.5	1.67
D4[a]	0.13	0.43

[a] These potential harvests are of mussels alone. In compartment design "4," the oyster culture plots are in the freshwater lake east of the Wemeldingedam.

13.3.3. Increasing the Possibility of Shellfish Culture by Changing Cultivation Techniques

The estimates in Table 13.4 implicitly assume that shellfish culture in the Oosterschelde will continue to use the same techniques as today. However, other aquaculture techniques have been developed and successfully used elsewhere, and some of them show promise in the various alternatives we are considering. These other techniques are (a) culturing in artificial ponds and (b) off-bottom (hanging) cultures.

In Ostend, Belgium, mussel and oyster culture is carried on in a small (86 ha), shallow, stagnant, saltwater pond called "Bassin de Chasse." Both hanging and bottom culturing techniques are used. It is reported that oysters and mussels grow remarkably fast with both of these techniques (Polk and Burd, 1966; Daro and Soroa-Bofill, 1971). Another example of a culture pond is the French "claire." Claires are very shallow (0.25 m) small ponds (0.1 to 0.2 ha) where oysters are fattened and get a better flesh color. In 6 months, they are able to double their weight. Densities can be maintained at high levels, so that this method might be an interesting alternative to the present cultivation techniques in the Oosterschelde.

The major disadvantage to bottom cultivation of mussels and oysters in artificial ponds is that the ponds must be constructed. At Ostend, this was done by damming off a natural small bay. (A gate was retained in the dam so that tidal action can be used to flush the bay as needed.) Also, it is necessary that the ponds be very eutrophic, so that sufficient food will be available to support commercially attractive shellfish densities and production rates. In some operations, the ponds would have to be fertilized artificially, at considerable cost to the cultivator.

Oysters and mussels can also be grown commercially in hanging cultures. With this technique, the young shellfish are attached to ropes, which are then hung from a raft. In this way, the shellfish have access to primary production by phytoplankton in parts of the water column they could never exploit in a bottom culture. This technique results in very high production per unit area. For example, in Japan, the production per unit area of hanging cultures is about five times higher than the most intensive bottom culture in the United States. Another advantage of hanging cultures over bottom cultures is that some natural predators of shellfish, such as crabs and sea stars, cannot reach the oysters. Also, the quality of the culture is no longer dependent on the type of bottom available. A particular advantage is that mud will not enter the mussel shells when they are harvested, so that cleaning operations can be eliminated.

Hanging cultures do have disadvantages, of course. One is their relatively high labor costs. For example, in some bays in Galicia, Spain, mussels are produced in hanging cultures. There, one man can harvest about 60 tons of mussels per year, whereas the culture-plot production in the Netherlands is four times as great, or 250 tons/man-year. This difference is offset to some degree in Galicia because rewatering is not necessary. But even taking this into account, income per man-year in Galicia would be only 24000 Dutch florins (DFLs), whereas with the Dutch culture-plot method, the income per man-year in the Netherlands is DFL 50000. Production per unit area in Galicia is very high—among the highest recorded aquaculture yields (300000 kg/ha) (Bardach et al., 1972). The Netherlands, on the other hand, is at a higher latitude than Galicia, and hence receives less solar radiation. Thus, primary production, and as a consequence maximum aquaculture yields per unit area, should be somewhat lower there. This factor may reduce productivity per man-year even further.

It appears, therefore, that none of the alternative shellfish cultivation methods would enjoy an economic advantage over the methods now in use in the Oosterschelde. This is not surprising; if any method were considerably more attractive economically, one would expect it to have replaced the present methods long ago. Bottom cultures in artificial ponds are unattractive because of the large capital investment needed to construct the ponds, and because the ponds must be artificially fertilized for best results. Hanging cultures are unattractive because they require much more labor for each unit of production than the methods presently in use in the Oosterschelde. Furthermore, there appears to be no reason to believe that either of these alternative methods would gain in advantage under any compartmentation or tidal range that our alternative cases for the Oosterschelde envision. We concluded, therefore, that our estimates of potential shellfish culture given in Table 13.4 should not be changed because of the possibility that cultivation methods might change.

13.3.4. Possibilities for Rewatering in the Various Alternative Cases

The present mussel cultivation industry in the Netherlands, both in the Oosterschelde and in the Waddensea, depends on the rewatering plots in the Oosterschelde near Yerseke for cleaning and storing their mussels. In any alternative case in which these plots can no longer be used for this purpose, either an alternative cleaning and storage facility must be found or constructed, or commercial mussel growing must be abandoned. (As discussed in Sec. 13.3.3, growing mussels by the hanging culture technique, so that they need no cleaning, is probably uneconomical.)

At first sight, alternatives with compartmentation design "3" would appear to preserve the mussel rewatering capability of the plots near Yerseke, and this is almost surely true in alternative A3. However, in the alternatives in which a storm-surge barrier reduces the tide, the rewatering parcels might silt up because of the reduced current velocities. Furthermore, even if silting were not a problem, the slower currents would be less effective in cleaning the mussels. It is not clear, however, that a reduced effectiveness is economically significant, since a mussel now remains on the rewatering plots for an average of 6 weeks, only a few days of which are needed to clean it.

By contrast, in compartment design "4," the rewatering plots would lie to the east of the Wemeldingedam, in the proposed freshwater lake. In any alternative with this compartment design, cleaning and storing mussels on the plots near Yerseke would be impossible. This is also true of the closed alternative D3, in which the virtual absence of currents over the rewatering plots would render them useless for mussel cleaning. Thus, in these "closed" cases, the mussel industry of the Netherlands would collapse unless an alternative cleaning and storage facility were made available.

One solution might be to construct artificial cleaning plots to replace the plots near Yerseke. The two most likely locations for such artificial rewatering plots are in the Waddensea, or (in cases D3 and D4) just outside (i.e., on the sea side) the closure dam. Disadvantages of an artificial facility of this kind would be its high cost and its small size. It is unlikely that it would be built large enough for both cleaning the entire mussel production of the Waddensea and storing each mussel for an average of 6 weeks.

Another solution might be to rewater the mussels in the ships that transport them from the production plots in the Waddensea to markets in France and Belgium. Westbroek (1975) has reported on just such an experiment, and claims that the mussels are delivered in as good a condition as those rewatered on the plots near Yerseke. Furthermore, the loss by this method was only 18 percent, compared with a loss of about 28 percent with the traditional method. However, just as with the artificial rewatering facility, this method does not offer a substitute for the storage function of the plots near Yerseke.

Westbroek does suggest that marketable mussels could remain on the production plots themselves until needed for the market, but this might reduce the productivity of the plots. Another possible storage location for mussels would be the Oosterschelde itself. Even though it might be uneconomical to cultivate mussels in an Oosterschelde that was closed or had only a very small tide, or in an Oosterschelde with compartment design "4," it is still true that mussels and oysters can grow and reproduce in such conditions. This has been proved by the mussel-fishing experiment conducted recently by the R.I.V.O., in which they found 10000 tons (live weight) of mussels in the Grevelingen, many years after all cultivation had ceased. Thus, regardless of the potential of the Oosterschelde for shellfish cultivation, it may still serve well as a mussel storage facility.

We conclude that the cleaning and storage functions of the rewatering plots in the Oosterschelde can be satisfactorily replaced, if these functions are not maintained in their present state, in every alternative case we consider. In alternative A3, and in alternatives C3 with the larger apertures, it is likely that the rewatering of mussels can continue in the same manner, and in the same place, as it does at present. In the other alternatives, mussels will have to be cleaned either in ships or in a specially constructed mussel-cleaning facility. In any case, mussel storage would still be possible in the Oosterschelde, or it could be done on the production plots themselves.

Thus, the rewatering problem has not influenced us to change our opinion regarding the impact of each alternative on the potential for shellfish culture. Our opinion remains that there need not be any significant impact on mussel cultivation outside the Oosterschelde, and the impact within the Oosterschelde should be as we have estimated it in Table 13.4.

13.4. NURSERY FUNCTION

13.4.1. Definition and Importance of Nursery Function

Juvenile individuals of a number of species use the shallow areas near the open coast of the Netherlands, the Waddensea (both Dutch and Danish), and the Oosterschelde as nurseries. These species include several varieties of fish (plaice, sole, herring, whiting, and cod), as well as brown shrimp. Juveniles of these species spend parts of their first or second years in these shallow areas, where they are somewhat protected from larger predators, and where a rich food supply is available. Once an organism is mature (after 2 or 3 years, depending on the species), it will move permanently into the deeper areas of the North Sea, returning to the shallows only to spawn.

Many of these species are fished commercially in the North Sea. The stocks that are exploited in the North Sea have their origin in the shallow nursery areas.

Without nurseries, the present fishing rates could not be sustained, because the populations of fish and shrimp could never grow fast enough to replace fishing losses. Thus, for each alternative for the Oosterschelde, we ask to what degree that alternative would reduce or eliminate the Oosterschelde's function as a nursery, and whether that reduction or elimination would constitute a significant part of the entire nursery capacity serving the North Sea fishing stocks.

13.4.2. The Importance of the Oosterschelde as a Nursery

The importance of the Oosterschelde as a nursery is different for each species. Zijlstra (1972) has estimated the relative numbers of O-group and I-group sole and plaice in the Waddensea, along the open coast, and in Zeeland (which includes the Oosterschelde, Westerschelde, and, in the year of Zijlstra's study, the Grevelingen as well). These are the nursery areas for sole and plaice. Only 1 percent of the O-group sole and 15 percent of the I-group sole were found in Zeeland. Plaice in Zeeland consisted of 4 percent of the O-group and an average of 5 percent of the I-group (averaged over 2 years). A little more than half of these percentages can properly be associated with the Oosterschelde.

These percentages may be misleading. Fish are territorial creatures and tend to remain throughout their life cycles within a well-defined perimeter. Different nursery areas may therefore serve different parts of the North Sea fishing stocks. It could happen, then, that the destruction of the Oosterschelde as a nursery could virtually eliminate fishing for some species in the southern part of the southern North Sea.

Something of this nature occurred with shrimp when the Zuiderzee was closed in 1932, and again when the Grevelingen was closed in 1971. In both cases, landings of shrimp in adjacent areas of the North Sea declined considerably (Boddeke, 1975). From 1964, when the Grevelingendam at the eastern end of the Grevelingen was completed, until 1971, when the Brouwershavensedam at the western end was closed, landings of shrimp in Grevelingen harbors declined from 9 percent of the national landings to 3.6 percent. However, this evidence is clouded by two facts: total national landings were declining at the same time by a factor of more than 2; and the harbors of the Grevelingen, in 1972, accommodated 5.4 percent of the national landings, an increase from the 3.6 percent of the previous year. These facts suggest that natural variability in the stocks of shrimp, which Boddeke (1975) calculates have been declining rapidly in recent years, may be responsible for a large part of the decline in the relative and absolute landings of shrimp in Grevelingen harbors.

13.4.3. The Impact of the Alternative Cases on Nursery Function in the Oosterschelde

Whether the Oosterschelde can act as a nursery depends on two factors. First, it is necessary for the juvenile organisms to be able to migrate into and out of the Oosterschelde, and for the adults to spawn there. This will be true as long as migration is unrestricted, which we expect it to be in all the alternatives with a tide (A3, A4, and all cases with a storm-surge barrier). In these cases, the abundance of migratory species, and hence the nursery capacity of the Oosterschelde, will not be limited by a failure of large numbers of individual organisms to find a way in.

In the closed alternatives, we nominally assume that no migration can occur, and so the nursery function would be eliminated.

The second factor that determines nursery capacity is the suitability of the area for juveniles of the migratory species. In particular, there must be areas where the water is shallow, and food must be plentiful. Factors such as these are considered by our model. One of our segments includes the shallow bottoms and tidal flats, where these organisms are found most abundantly, both in nature and in the model. And food—the food web, the availability of sufficient food—is the basis for our balance constraints. In the alternatives in which migration can occur, therefore, we have used the model's predictions of the abundances of migratory ecogroups (shrimp and fish) as indices of the change in nursery capacity. In the closed alternatives D3 and D4, we have set the nursery capacity indices to zero, because no migration can take place.

In Table 13.5, we show our indices of the nursery capacity of the Oosterschelde in each alternative case. These indices are the abundances of four ecological groups: shrimp and shore crab, planktivorous fish, benthos-eating fish, and fish-eating fish. These abundances are expressed as fractions of the corresponding abundances in the present Oosterschelde. Note that one ecological group, plant- and detritus-eating fish, has not contributed a nursery capacity index, even though these fish are migratory. The reason is that these fish have no predators, as a glance at the food-preference matrix in Fig. 9.1 will show. As with birds, the balance equation for plant- and detritus-eating fish therefore prescribes the abundance of this ecogroup. Its abundance is an input, and not an output, and therefore cannot be used as an index of nursery capacity.

Migratory fish, and especially shrimp, will be harmed by the loss of the eastern tidal flats when the Oesterdam or Wemeldingedam is completed. These creatures feed mostly on flats, and flats are most prevalent in the eastern part of the Oosterschelde. Greater harm would be done if a closed alternative were chosen, since this would deprive these creatures of all the area of the Oosterschelde. But, depending

Table 13.5

NURSERY CAPACITY OF THE OOSTERSCHELDE (FRACTION OF PRESENT) FOR EACH ALTERNATIVE CASE

Case	Shrimp and Shore Crab	Planktivorous Fish	Benthos-eating Fish	Fish-eating Fish
Present Oosterschelde	1.0	1.0	1.0	1.0
A3	0.5	0.9	0.73	0.73
C3, $\mu A = 20000$	1.5	0.5	0.98	0.94
C3, $\mu A = 11500$	4.0	0.75	1.33	1.31
C3, $\mu A = 6500$	3.5	0.75	1.25	1.22
C3, $\mu A = 3250$	0.96	0.75	0.81	0.8
D3	0.0	0.0	0.0	0.0
A4	0.1	0.73	0.37	0.38
C4, $\mu A = 11500$	0.41	0.72	0.56	0.56
C4, $\mu A = 6500$	0.97	0.73	0.73	0.73
D4	0.0	0.0	0.0	0.0

on the actual amount of detritus that is brought in from the North Sea, reducing the tide may actually benefit migratory species. This effect is due to the increased lushness of the biota that the increased detritus import would cause.

Shrimp are also especially favored by increases in detritus import, and are especially harmed by changes in compartment design. The model predicts this effect because shrimp are the smallest of the migratory species, and therefore require the greatest amount of food per unit body weight. When food is scarce, these organisms will feel the pinch more severely than larger organisms, and, conversely, they will take greatest advantage of increases in the abundance of food. In addition, shrimp are both competitors and prey of benthos-eating fish, and hence are disadvantaged still further when food becomes less abundant.

13.5. TRANSIENTS

In each alternative case, the abundances of each ecogroup must adjust during some time period from the present abundances to the long-term average abundances characteristic of that alternative. Qualitatively, these adjustments will probably take place as follows. First, the eastern end of the Oosterschelde is to be dammed off and turned into a freshwater lake, the Zoommeer. For alternatives with compartment design "3," the eastern lake will be the smaller one bounded to the west by the Oesterdam. If the compartment design is "4," the lake will be larger, and bounded by the Wemeldingedam. At the same time, the northern Volkerak region is to be dammed off by the Philipsdam and turned into a freshwater lake. (See Fig. 12.1.) Any biomass trapped behind the compartment dams will surely die. If, in addition, the tidal range is reduced, some of the area to the west of the compartment dam that is presently submerged at high tide will be left dry. Any biomass that cannot move a few feet to the new high-water mark will also die. We define the "rapid kill" associated with an alternative to be the amount of biomass that dies from these two causes.

Next, the density of biomass in the remaining saltwater basin will adjust. This may take years if the required adjustment is large. Further, ecological disasters may occur during this adjustment period. For example, small, rapidly reproducing organisms might undergo population explosions in the early years before their larger predators can respond to the larger food supply. (People living near the IJsselmeer suffered from gnat plagues during an adjustment period of this kind immediately after that lake was made fresh.) As indices of the severity of this threat, we use the change in the density (g/sq m) of the benthic biomass, and the time it would take for the density to adjust to within 1 g/sq m of its final value, if the adjustment occurred exponentially with a half-time of 2 years. (We choose a half-time of 2 years because it approximates the doubling time for some of the most abundant benthic organisms in the Oosterschelde, such as cockles, mussels, and benthic grazers. Choice of another half-time will change all of our time estimates by the same factor.)

In calculating the rapid kill and the slow adjustment—our two measures of the transient impacts of each alternative—we considered only some of the ecological groups. We did not, for example, include changes in the abundances of fish or birds in these indices. We reason that birds cannot be trapped in the Zoommeer when it is separated from the western saltwater basin and turned fresh, and therefore birds should not contribute to the rapid kill. Similarly, most fish should escape from the Zoommeer before it is closed, and would likewise avoid the rapid kill. These ecogroups will participate in the slow adjustment, of course, but differently from less mobile creatures. Immobile organisms must adjust their numbers by changing their reproduction and growth rates—e.g., by starving slowly—whereas birds can fly to the Westerschelde or the Grevelingen, and fish can escape to the North Sea. Since these adjustments can take place on virtually any time scale at all, we estimate the time required for the slow adjustment by using only the change in biomass of relatively immobile organisms.

Not all immobile organisms contribute to the rapid kill and the slow adjustment. In particular, we excluded primary producers and zooplankton from these indices. Our reasoning is that these organisms have such rapid growth rates, and such short generation times, that they are continually transient. Neither the rapid kill nor the slow adjustment is unusual for these ecogroups. They experience these stresses every year.

What is left, then, are the benthic ecogroups. These ecogroups include mussels and oysters, cockles and limpets, selective deposit feeders with pelagic larvae, deposit feeders with nonpelagic larvae and suspension-feeding worms, omnivores and infaunal predators, benthic grazers, sea stars, and shrimp and shore crab. (We have included shrimp, which are mobile, in order to also include shore crab, which are relatively immobile. In any case, this group is not very abundant, and does not much affect our results.)

Table 13.6 lists the impacts we have discussed above, including (a) the rapid kill (both as a percentage of the present benthic biomass and as an absolute number), (b) the time required for slow adjustment, and (c) the densities of benthic biomass in each segment, separately and averaged over the entire benthic area.

Table 13.6

TRANSIENT IMPACTS OF THE VARIOUS ALTERNATIVE CASES ON THE OOSTERSCHELDE

Alternative	Rapid Kill (tons)	Rapid Kill (% present)	Years for Slow Adjustment	Densities of Benthic Biomass in Different Segments			
				Average	Inter-tidal	Deep	Shell-fish
Present Oosterschelde	--	—	--	35.2	54.3	1.3	115.4
A3	4220	25	0	34.4	55.4	1.3	116.4
C3, µA = 20000	4231	25	4	42.5	70.1	1.3	142.9
C3, µA = 11500	4491	27	6	57.1	99.7	1.8	202.0
C3, µA = 6500	5148	31	6	55.0	103.8	1.8	202.0
C3, µA = 3250	5930	35	2.5	38.6	78.6	1.4	154.3
D3	6218	37	6	13.0	36.1	0.8	--
A4	9972	59	2	32.1	58.6	1.3	131.9
C4, µA = 11500	10010	60	3.5	41.5	79.6	1.4	175.4
C4, µA = 6500	10195	61	5.5	51.1	103.3	1.7	223.2
D4	11492	68	6.5	10.2	31.5	0.5	—

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Chapter 14

DISCUSSION OF RESULTS

14.1. COMPARISON OF NOMINAL ALTERNATIVES

There are five nominal alternatives:

A3
C3, $\mu A = 20000$ sq m
C3, $\mu A = 11500$ sq m
C3, $\mu A = 6500$ sq m
D4

These were chosen as the nominal alternatives for the following reasons. The Dutch Government had specified that two possible methods for ensuring the safety of the land surrounding the Oosterschelde be investigated. The first method suggested was to close off the Oosterschelde permanently. For various reasons, compartment design "4" was felt by the Rijkswaterstaat to be preferable to design "3" for this method. Thus, we made Case D4 one of our nominal alternatives.

The second method for improving security around the Oosterschelde was to build a storm-surge barrier, with gates that could be left open most of the time but closed during storm conditions to exclude the storm surge from the Oosterschelde basin. The Rijkswaterstaat determined that compartment design "3" was preferred to design "4" for this method, but was not able to determine an optimal size for the aperture. Factors to be considered in determining the optimal aperture are the cost of the barrier, its reliability and contribution to the safety of the region, and its effect on the ecology. In view of this, we included three storm-surge barrier cases among our nominal alternatives, all with compartment design "3," and with apertures of 20000, 11500, and 6500 sq m. With these apertures, the tidal range may be as small as 43 percent ($\mu A = 6500$ sq m) or as large as 96 percent ($\mu A = 20000$ sq m) of its present value (see Table 13.1).

Finally, some opponents of the original closed plan, fearful of any meddling with the tidal amplitude, pressed for an open alternative. Thus, we have included case A3 among our nominal cases, in which compartment design "3" is built (in order to render the Rhine-Schelde canal tideless, as required by treaty with Belgium), and massive new dikes replace the existing ones (to meet the security requirements), but the mouth of the Oosterschelde is left completely open.

Table 14.1 shows the most important of the ecological impacts discussed in the previous chapters. Here, for each impact, we compare the cases and rank them according to how well they preserve the present ecology or increase its biomass. The rankings for each impact are shown by shading: white for the best ranking; black for the worst; and grey for intermediate. (Such a table is called a *scorecard;* see Vol. I for discussion.) In discussing and ranking the impacts, we have taken the viewpoint that it is better for an ecogroup to be more, rather than less, abundant—at least up to its biomass density in the present Oosterschelde. For brevity, we label

Table 14.1

ECOLOGICAL IMPACTS OF THE FIVE NOMINAL ALTERNATIVES

Item	Alternative A3	Nominal Reduced-tide Alternatives (C3)			Alternative D4
		μA = 20000 sq m	μA = 11500 sq m	μA = 6500 sq m	
Key inputs					
Salt basin area (sq km)	369.5	369.3	364.5	352.4	202.0
Tidal range at Zierikzee (m)	3.0	2.9	2.0	1.3	0.0
Primary production (tons/day)	352.9	352.7	348.1	346.1	193.8
Detritus import (tons/day)	546.0	640.0	990.0	916.0	0.0
Primary food availability (% of present)[a]	78	86	116	85	17
Total biomass					
Amount (tons afdw)	21300	24200	29700	27550	5160
Percent of present amount	75	85	104	96	18
Potential abundance of birds					
Benthos-eaters (tons afdw)	6.6-7.3	6.3-9.7	4.9-13.0	3.5-11.7	0.4-1.4
Fish-eaters (tons afdw)	0.0345	0.0445	0.063	0.0566	3.94
Plant-eaters (tons afdw)	Unch.	Unch.	Unch.	Unch.	Incr.
Potential shellfish culture					
Mussels (% of present)	100	90	90	90	13
Oysters (% of present)	100	90	90	90	0
Nursery function					
Shrimp (% of present)	50	150	400	350	0
Fish (% of present)	73	98	133	125	0
Transients					
Rapid kill of benthic biomass (tons afdw)	4220	4231	4491	5148	11492
Rapid kill (% of present benthic biomass)	25	25	27	31	68
Change in average density of benthic biomass from present (g/sq m)	-0.8	7.3	21.9	19.8	-25.0
Time for slow adjustment (yr)	0	4	6	6	6.5

[a] Primary food availability = primary production rate + detritus import rate.

Rankings: ☐ Best ▨ Intermediate ■ Worst

this viewpoint *ecological preservation;* we believe it to be the predominant viewpoint in the Netherlands.

Upon examining the impacts due to these nominal alternatives, one notes that D4 stands out in almost every category. Its total biomass is very low compared with that of the present Oosterschelde and with those of any of the other nominal alternatives. Its potential for both shellfish culture and nursery function is virtually nonexistent. It causes by far the largest rapid kill, and it is the only alternative that results in a significant decrease (during the slow adjustment) in the density of benthic biomass. Only fish-eating and plant-eating birds appear to benefit from this alternative. For the most part, the biota of the Oosterschelde suffer greatly from alternative D4.

It is less clear that these impacts differentiate among the remaining alternatives. True, the biomasses in alternative C3, $\mu A = 11500$, and C3, $\mu A = 6500$, are almost 40 percent larger than the biomass in alternative A3. But considering the great variation in biomass in the Oosterschelde from season to season and from year to year, a 40 percent change in its long-term average density would take several years of careful measurements to detect. This does not mean that such a difference is insignificant. Rather, it means that its significance is limited.

Similarly, the nursery-function impacts, and possibly the change in the density of benthic biomass from that of the present Oosterschelde, might single out the two alternatives, C3, $\mu A = 11500$ sq m, and C3, $\mu A = 6500$ sq m, in a meaningful way. However, considering the uncertainties in both the inputs and the assumptions concerning detritus import and sedimentation, we are not convinced that these alternatives are significantly different from either A3 or the other reduced-tide alternatives with compartment design "3." Therefore, before we draw conclusions about the relative merits of the nominal alternatives with compartment design "3," we shall examine the sensitivities of the impacts of these alternatives to changes in the various assumptions.

14.2. ARE THE REDUCED-TIDE ALTERNATIVES SIGNIFICANTLY DIFFERENT FROM ALTERNATIVE A3?

14.2.1. Questions Concerning the Nominal Impacts

The nominal impacts—those shown in Table 14.1—appear to demonstrate that the reduced-tide alternatives are preferable to the open alternative A3. (We are dealing here with alternatives C3, $\mu A = 11500$, and C3, $\mu A = 6500$. The alternative C3, $\mu A = 20000$, is so close to alternative A3 in its impacts on the ecology that we consider the two to be identical.) In the reduced-tide alternatives, the total biomass is greater, and the nursery function appears to be improved. However, these results necessarily depend on the many assumptions we have been forced to make. Consequently, we cannot accept them without determining how sensitive they are to the most important assumptions.

In this section we examine the sensitivity of the various impacts to changes in two crucial assumptions: the detritus import rate, and the degree to which benthic detritus eaters (as opposed to suspension feeders) benefit from an increase in the detritus import rate.

Because the two reduced-tide alternatives, C3, $\mu A = 11500$ sq m, and C3, $\mu A = 6500$ sq m, are so similar, we will examine the sensitivity of only one of them to these assumptions. The alternative we choose to examine is C3, $\mu A = 11500$ sq m, because it has a slightly higher biomass than the other candidate.

14.2.2. Sensitivity of Alternative C3, $\mu A = 11500$ sq m, to Changes in the Detritus Import Rate

Perhaps the most important assumption we have been forced to make is the assumption from which we have derived the detritus import rate for each of the alternative cases. This assumption, and the reasons for it, have been examined in Sec. 12.4.3. The importance of the detritus import rate, and by implication the assumption from which we estimate it, was amply demonstrated in Fig. 13.3. This figure, the reader will recall, shows that primary food availability, defined as the primary production rate plus the detritus import rate, is a very good predictor of total biomass.

We expected, therefore, that the impacts our model predicts for alternative C3, $\mu A = 11500$ sq m, would be very sensitive to changes in the assumed detritus import rate. To determine if this was true, we solved the model for a range of detritus import rates extending from 232.8 tons/day to 2000 tons/day. The former rate was obtained by assuming the detritus import rate to be proportional to the tidal volume, and the latter rate was taken arbitrarily to be approximately twice the nominal rate. Figure 14.1 shows the results.

As one can see from Fig. 14.1, our expectations were satisfied. Total biomass, as well as all of its components, increases as the detritus import rate is increased. For the lower values of the rate of detritus import, the dependence of total biomass

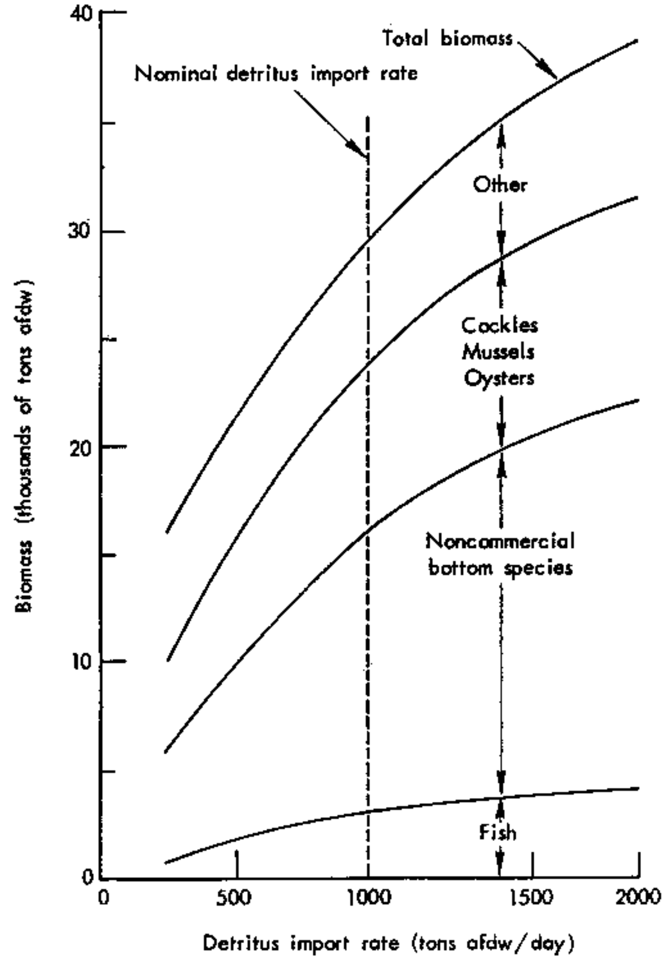

Fig. 14.1 — Biomass by component for a range of detritus import rates in alternative C3, $\mu A = 11500$ sq m

on detritus import rate is very close to what we would predict from Fig. 13.3, namely an increase of approximately 21000 tons afdw of biomass for each 1000 tons/day of detritus imported (or plant matter photosynthesized).

However, this relation no longer holds quantitatively at higher detritus import rates. Rather, each additional increment of detritus causes a smaller increase in total biomass than did the previous increment. This illustrates, as did the small, simple exemplary ecosystem we studied in Chap. 4, that our model exhibits a density limitation on biomass. When the density of biomass in a segment becomes high, further increases in the food supply favor the smaller creatures, which can consume the extra food without a large increase in biomass.

14.2.3. Sensitivity of Alternative C3, μA = 11500 sq m, to Changes in the Detritus Sedimentation Rate

Another crucial assumption centers on the question of how much of the detritus that is imported can be used by organisms that feed on suspended particles of organic matter, and how much sediments so fast that it only benefits organisms that eat benthic detritus. Our nominal assumption was that benthic detritus eaters would benefit from the nominal increases in detritus import, but that suspension feeders (particularly cockles) would neither benefit nor suffer. In this section, we will explore the consequences of changing this assumption.

The manner in which we implemented our assumption was described in Sec. 12.5. Briefly, we imposed new constraints that prescribed the abundances of the three most abundant consumers of benthic detritus: selective deposit feeders, deposit feeders with nonpelagic larvae, and benthic grazers. Nominally, each of these organisms was constrained to be 3.5 times as abundant in alternative C3, μA = 11500 sq m, as in the present Oosterschelde. In this section, we vary that factor (nominally 3.5), which we call the detritus sedimentation factor, between the values of 1.0 and 6.0. We chose a lower limit of 1.0 because we cannot believe benthic detritus eaters will decrease in abundance when detritus import increases. The balance equations impose an upper limit on the abundances of these organisms that is between 5.0 and 6.0 times the present abundances.

We show the results of this experiment in Fig. 14.2. Note that the larger the factor we use, the more cockles, mussels, and oysters suffer. This is expected, because these ecogroups are important consumers of detritus. When the detritus is consumed by benthic detritus eaters, it is unavailable to cockles, mussels, and oysters.

Another feature of Fig. 14.2 is extremely interesting. Note that total biomass reaches its maximum at about the nominal case. For both lower and higher values of the sedimentation factor, biomass is less than the nominal value. This suggests that sedimentation factors higher than approximately 4.0 are probably unreasonable. We say this because benthic detritus eaters can only achieve these large abundances if every barrier to their increase is removed. It is not enough to eliminate their competitors. It is also necessary to eliminate all other organisms except those that most efficiently convert matter that benthic detritus eaters do not consume into the detritus that they can consume. Cooperation to such a degree is never observed in nature.

When sedimentation factors are less than 3.5 to 4.0, it is clear from Fig. 14.2 that most of the biota are less well off the smaller the factor. Total biomass is less,

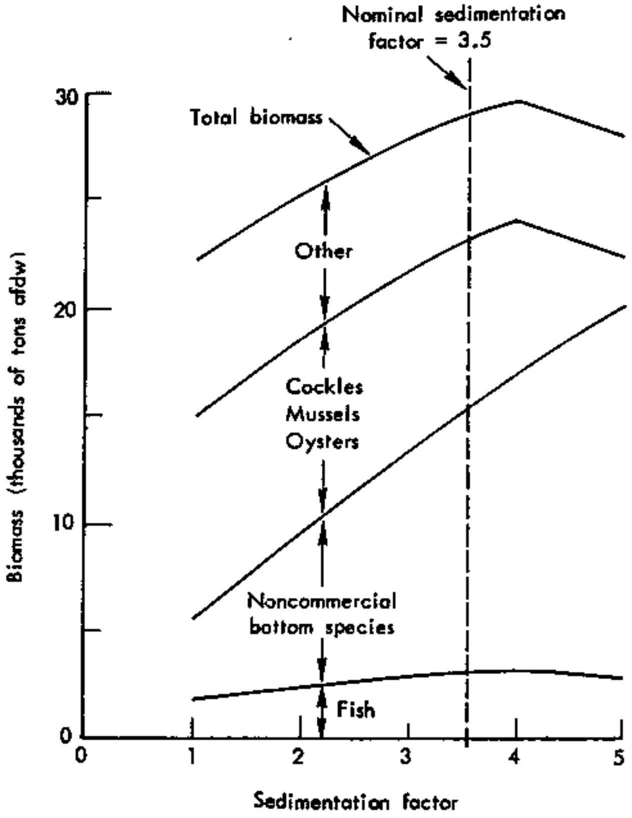

Fig. 14.2—Biomass by component for a range of detritus sedimentation factors in alternative C3, $\mu A = 11500$ sq m

as is the abundance of fish and shrimp. Only mussels, oysters, and cockles benefit from a reduction in this factor.

Even the increase in mussels, oysters, and cockles that accompanies a reduction in this factor may not be a benefit to humans. True, such an increase would suggest that commercial shellfish aquaculture could be expanded beyond the level that is possible under the nominal assumptions. However, under the nominal assumptions, it is possible to carry on a mussel-culturing industry at a level virtually equal to the level at which mussels are cultured in the present Oosterschelde. But there is evidence that even today the capacity of the Oosterschelde to support culturing operations exceeds the capacity of the market to absorb the additional mussels that would be produced. Thus, we cannot consider that an increase in mussel-culturing potential above the present level is a benefit.

It appears, therefore, that any change from the nominal in the assumption we have made concerning the detritus sedimentation factor must reduce the attractiveness of the reduced-tide alternatives.

14.2.4. Conclusions Concerning the Reduced-Tide Alternatives

Now we may suggest an answer to the question with which we began this section: Are the reduced-tide alternatives significantly different from alternative A3? We realize, of course, that the answer remains tentative, even after the sensitivity studies have been completed, because the assumptions we have made remain uncertain. However, we may note the following.

First, we see from Fig. 14.1 that if we have overestimated the detritus import in the nominal assumptions, then we will have overestimated total biomass and all of its components. We will also have overestimated the degree to which the mussel culture can be continued, and the degree to which the various nursery functions of the Oosterschelde will continue. In short, if the actual detritus import in these alternatives were less than we have nominally assumed, then these alternatives would look more like alternative A3.

Furthermore, if we are wrong about detritus import, it is likely that we have overestimated rather than underestimated it. We must thus expect that our nominal results have overemphasized the differences between the reduced-tide alternatives and alternative A3. We do not believe, however, that we have so greatly overestimated detritus import that there will be no difference between the reduced-tide alternatives and alternative A3. This would require that the detritus import rate in the reduced-tide alternatives be no larger than 500 tons/day, for this is the rate at which the two alternatives have essentially identical biomass, and hence essentially the same impacts. Based on our conversations with Terwindt, we think that the detritus import rate would certainly exceed 500 tons/day in these alternatives, and therefore that they would produce noticeably different impacts than alternative A3.

Next, we note that if we are mistaken about the nominal value of the detritus sedimentation factor, then the reduced-tide alternatives look less attractive than they do under the nominal assumptions. This is shown clearly in Fig. 14.2, and argued as well in Sec. 14.2.3.

Finally, one can question whether the increase in the density of biomass will occur uniformly throughout the saltwater basin. It is possible that the circulation of detritus-bearing North Sea water would be confined almost exclusively to the western end of the basin, leaving the eastern end much like a miniature D4 alternative. The western end would then become like alternative C3 with a greater-than-nominal detritus import rate (see Fig. 14.1). For reasons discussed above, this would reduce the attractiveness of both ends of the basin.

We must therefore conclude that our nominal assumptions tend in all respects to favor the reduced-tide alternatives. Any reasonable changes in these assumptions make the reduced-tide alternatives less attractive. Thus, from the point of view of ecological preservation, alternatives C3, $\mu A = 11500$, and C3, $\mu A = 6500$, are to be mildly, but only mildly, preferred to the open alternative A3.

However, we must add a caution. This preference on ecological grounds does not mean that one should endorse the reduced-tide alternatives. First, one must question whether the increased density of biomass is socially or aesthetically desirable. The organisms that increase in the reduced-tide cases may not be attractive. In fact, the organisms that benefit most from an increase in detritus import are worms and snails that live in the mud and that few people ever see. One can certainly question whether an increase in these organisms constitutes a benefit to mankind.

Second, there are categories of impacts other than the ecological ones. For example, one must consider the cost of each alternative, as well as its effect on the security of the region and the economy of the Netherlands. Viewed with these additional factors in mind, reduced-tide alternatives may not look so attractive.

14.3. IS ALTERNATIVE D4 REALLY SO BAD?

14.3.1. Questions Regarding the Nominal Impacts from Alternative D4

The nominal impacts, as given in Table 14.1, single out alternative D4 as being by far the worst alternative from an ecological point of view. To some degree, however, this is misleading. Alternative D4 has compartment design "4," whereas all other nominal alternatives have compartment design "3." This means that D4 has a smaller saltwater basin than the other alternatives, and will therefore necessarily have a lower total biomass, and lower abundances of every ecogroup individually. It also means that a larger freshwater basin is created in the eastern end of the present Oosterschelde, which accounts for the great difference in the rapid kill between this alternative and the others. In order to compare the quality of the ecology in a closed alternative with the quality in the open and reduced-tide alternatives, we ought to compare alternative D3 with the other alternatives having compartment design "3"; or the other alternatives having compartment design "4" should be compared with alternative D4.

(It should be remembered that our model deals only with the saltwater basin to the west of the compartment dam. It does not consider the freshwater basin to the east. In alternatives with the same compartment design, this is not important, because the freshwater basin will be the same in all such cases. However, when comparing alternatives with different compartment designs, it is important to remember that the alternative with the smaller saltwater basin will have the larger freshwater basin. Thus, the different impacts of the two alternatives on their saltwater basins may be counterbalanced by their different impacts on their freshwater basins. Our model only provides a fair comparison of alternatives with different compartment designs if in all cases the impacts on the freshwater eastern basin can be disregarded.)

One of the strongest objections to a closed Oosterschelde has been that mussels and oysters could not be commercially grown in such a closed basin. Our nominal results appear to bear this out. The reason most often given is that once the Oosterschelde is closed, the imported detritus on which mussel growth depends would cease. However, there is the possibility that sluices could be built in the closure dam which could be manipulated in such a way as to bring significant amounts of detritus into the basin from the North Sea. Conceivably, alternative D4 could thereby be made more attractive.

In addition, as we point out in the appendix, there is considerable question about the present rate of detritus import into the Oosterschelde. Specifically, our estimate is criticized as being too high. If our estimate is in fact too high, the closed alternatives would appear relatively more attractive. The reason is that the present detritus import rate would constitute a smaller fraction of the primary food supply (detritus import plus primary production). Eliminating this fraction is the major impact of closure, and so the closure will have less impact if this fraction is smaller.

14.3.2. Comparison of Alternatives A3 with D3, and A4 with D4

In Table 14.2, we show the impacts of alternatives A3, D3, A4, and D4 to illustrate the relative importance of closing the Oosterschelde, as compared with choosing compartment design "3" as opposed to "4." Clearly, both factors are important. Changing from compartment design "3" to "4" causes a reduction of approximately 45 percent in total biomass, and similar changes in other impacts, whether the change is from A3 to A4 or D3 to D4. (This result should perhaps have been expected, since the change from design "3" to design "4" causes similar reductions in both the basin size and the primary food availability.)

Similarly, closing the basin has a profound impact, whether the change is from A3 to D3, or from A4 to D4. If anything, the impact is greater than that which results from a change in compartment design. Instead of a 45 percent reduction, these changes result in more than a 55 percent reduction in total biomass. Under the nominal assumptions, therefore, alternative D4 suffers in comparison with the other alternatives, both because of its compartment design, and because it is closed and therefore has no detritus import.

Table 14.2

ECOLOGICAL IMPACTS OF ALTERNATIVES A3, D3, A4, AND D4

Item	A3	D3	A4	D4
Key inputs				
Salt basin area (sq km)	369.5	332.7	230.9	202.0
Tidal range at Zierikzee (m)	3.0	0.0	3.0	0.0
Primary production (tons/day)	352.9	317.8	220.5	193.8
Detritus import (tons/day)	546.0	0.0	341.2	0.0
Primary food availability (% of present)[a]	78	27	48	17
Total biomass				
Amount (tons afdw)	21300	9300	12400	5160
Percent of present amount	75	33	43	18
Potential abundance of birds				
Benthos-eaters (tons afdw)	6.6-7.3	0.7-2.5	3.8-4.1	0.4-1.4
Fish-eaters (tons afdw)	0.0345	6.85	0.0179	3.94
Plant-eaters (tons afdw)	Unch.	Incr.	Unch.	Incr.
Potential shellfish culture				
Mussels (% of present)	100	50	50	13
Oysters (% of present)	100	50	0	0
Nursery function				
Shrimp (% of present)	50	0	10	0
Fish (% of present)	73	0	37	0
Transients				
Rapid kill of benthic biomass (tons afdw)	4220	6218	9972	11492
Rapid kill (% of present benthic biomass)	25	37	59	68
Change in average density of benthic biomass from present (gm/sq m)	-0.8	-22.2	-3.1	-25.0
Time for slow adjustment (yr)	0	6	2	6.5

[a] Primary food availability = primary production rate + detritus import rate.

14.3.3. The Effect of Detritus Import on Alternative D4

As pointed out in Sec. 14.3.1, the influence of compartment design on the impacts of the alternatives should perhaps be discounted. But the effect of severing the basin from contact with the North Sea should not. Thus, our finding that alternative D4 is ecologically unattractive because it is closed, and not just because it uses compartment design "4," is important. In this section, we ask whether measures can be taken that would improve alternative D4. In particular, we ask how much detritus would have to be imported in order to make D4 appear as attractive as A4.

Figure 14.3 suggests an answer. In it, we see that the total biomass in alternative D4 achieves the value in A4 (12400 tons) when the detritus import rate reaches approximately 400 tons/day. Since the concentration of organic matter in the coastal waters of the North Sea is approximately 1.5 g/cu m, this could be achieved if all the organic matter in about 3000 cu m/sec of North Sea water were trapped in the Oosterschelde. Because water can be flowing in only when the tide outside the basin is above mean water level, and because entrapment will not be complete, to achieve this rate of detritus import would actually require sluices with greater than 10000 cu m/sec capacity. Such sluices are at least possible; but since they would be equivalent to a storm-surge barrier with an aperture of about 3000 sq m, they are not just ordinary sluices.

Furthermore, as shown in Fig. 14.4, even this rate of detritus import would not permit the mussel industry to operate in alternative D4 as it does in the present Oosterschelde. In fact, no rate of detritus import in D4 will permit mussels to be cultured at today's level. The reason is that the Wemeldingedam, which separates the freshwater and saltwater basins in compartment design "4," lies to the west of all of the oyster beds and 30 percent of the mussel plots now in use. These areas,

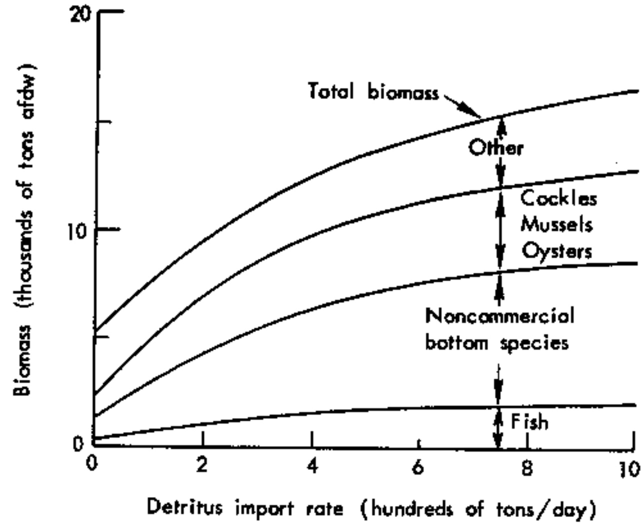

Fig. 14.3 — Biomass by component for a range of detritus import rates in alternative D4

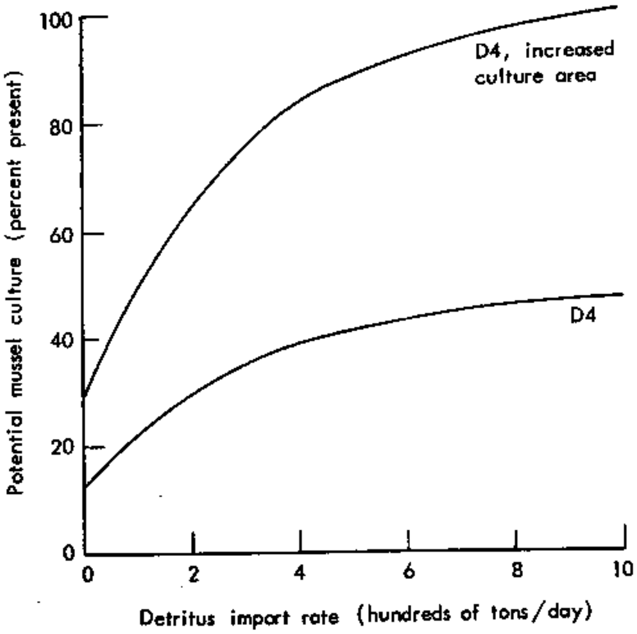

Fig. 14.4 — Potential for mussel culture in alternative D4 and in alternative D4 with an increased mussel-culture area for a range of detritus import rates

then, become part of the freshwater basin, and unsuitable for shellfish culture operations.

This suggests that part of the area left in the saltwater basin be converted from its present wild state into mussel plots. Potential locations for these plots are shown in Fig. 12.3. Under the assumption that this is possible—i.e., that there are areas that are not too muddy, or too exposed to waves, or too something else—we have calculated the second, higher curve in Fig. 14.4. We chose the area of the shellfish culture segment to be equal to its present size (2500 ha) and transferred this amount of the intertidal and shallow bottom area to this segment.

The consequence of this excursion is that mussel culture again becomes possible in alternative D4, if there is enough detritus import. The necessary amount of detritus import is again approximately 400 tons/day. (Thus, one might choose to call this a storm-surge barrier alternative, instead of an excursion from alternative D4.) However, this transfer of area from the intertidal segment to the shellfish culture segment has ecologically detrimental effects as well. The increase in the abundance of mussels is accompanied by a compensating decrease in the abundance of cockles.

14.3.4. Conclusions Concerning Alternative D4

At this point, we can offer an answer to the question addressed in this section: Is alternative D4 really so bad? The short answer appears to be "yes." However, this answer should be qualified.

First, even under the nominal assumptions, alternative D4 is not a wasteland. Nor should one expect it to be. Indeed, the nominal impacts of D4 approximate what has been observed in the Grevelingen since it was closed.

Second, alternative D4 appears to be worse in Table 14.1 than it actually is. Part of the reason why D4 has a low biomass is that it has a small saltwater basin. To some degree, the biomass that does not appear in the saltwater basin will be compensated for by other organisms that will live in the freshwater basin to the east of the Wemeldingedam.

However, alternative D4 is truly worse from the point of view of ecological preservation than any alternative we have considered with a connection to the North Sea, however much the tide may be reduced. Nor does it seem possible to arrange that D4 will have sufficient connection with the North Sea to bring in a significant amount of detritus, without also changing D4 into a reduced-tide alternative. Thus, unless other impacts (cost or security) are very much superior for D4 than for the other alternatives, it would probably be rejected on ecological grounds.

14.4. SUMMARY AND CONCLUSIONS

In this Part, we have used our model to help examine the ecological impacts to be expected from a variety of alternative plans for the Oosterschelde. The nominal alternatives, because the Rijkswaterstaat has selected them as candidates for serious consideration, are the open alternative A3, the closed alternative D4, and three intermediate alternatives with storm-surge barriers that reduce the tidal range by varying amounts. These reduced-tide alternatives are C3, $\mu A = 20000$ sq m, C3, $\mu A = 11500$ sq m, and C3, $\mu A = 6500$ sq m. In addition, we have examined the impacts from a number of other alternatives, chosen because they highlight various interesting features of the nominal alternatives, or because they help to determine the importance of some uncertain assumptions we were forced to make.

From the standpoint of ecological preservation, we have concluded that alternative D4 is the worst nominal alternative. Furthermore, the shortcomings it exhibits in comparison with the other nominal alternatives cannot be remedied either by increasing the size of the saltwater basin (changing to alternative D3) or by building sluices that will allow detritus to be imported from the North Sea. A combination of the two measures would make the closed alternative as attractive as the other nominal alternatives, but the sluices needed to import sufficient detritus would be so large as to constitute a storm-surge barrier. We conclude, therefore, that no alternative that justifies the name "closed" can compare favorably on ecological grounds with the open or reduced-tide alternatives.

This is not meant to imply that the closed alternative D4 is an ecologically disastrous alternative. Organisms would continue to inhabit the basin, just as they have continued to live in the Grevelingen since its closure in May 1971. In fact, a closed Oosterschelde would be very similar to the present Grevelingen. But closing the Oosterschelde would result in a major reduction in the density and the amount of biomass of all kinds, and in the elimination of commercial shellfish cultivation in the Oosterschelde.

The open case most closely preserves the ecology of the present Oosterschelde. In the part of the Oosterschelde that remains salt, we predict that the *density* of each ecogroup will remain as it is at present. Thus, the relative abundances of the ecogroups would be unchanged. However, the total biomass in the salt basin would be reduced from that in the present Oosterschelde; the reduction would be proportional to the reduction in the area of the saltwater basin caused by the compartmentation.

For the cases with a storm-surge barrier (the reduced-tide cases), the size of the aperture will largely determine the character of the ecology that results. Apertures of at least 20000 sq m would produce an ecology virtually indistinguishable from the open case (A3), both in terms of total biomass and relative species abundance.

Apertures between 6500 and 11500 sq m would tend to maximize the total biomass. However, there would be a shift in relative abundances of the present species in favor of noncommercial bottom species, such as snails and worms. Also, the transition period would be longer and would perhaps include some objectionable ecological transients.[1]

Apertures smaller than 6500 sq m would result in smaller total amounts of biomass, and larger shifts in relative abundances, than larger apertures.

We find, therefore, that one's preference among the alternatives depends on his ecological goal. If the goal is to minimize change from the present ecology, then the preference will be the open case or a reduced-tide case with a large aperture (20000 sq m). But if the goal is to maximize total biomass, one will probably prefer to build a storm-surge barrier with an aperture between 6500 and 11500 sq m.[2] However, the preference should not be firm, because of the uncertainties concerning detritus import and sedimentation in the reduced-tide cases. Thus, although ecological considerations may help one to reject alternative D4, they do not distinguish strongly enough between the open case A3 and the reduced-tide cases where the storm-surge barrier aperture exceeds 6500 sq m to much affect a choice between them. The choice among these alternatives will therefore depend strongly on other factors, such as cost and security.

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[1] Our best estimate is that biomass would be maximum for compartment design "3" with an 11500 sq m aperture. In addition, the shift in relative abundances ought to be less for this aperture than for smaller apertures, such as those of 6500 sq m.

[2] Neither ecological goal should influence one to choose the closed case or a reduced-tide case with a small storm-surge barrier aperture (under 6500 sq m).

Chapter 15

SUGGESTIONS FOR FURTHER RESEARCH

It should be clear from our earlier remarks that data limitations have detracted from this study. We are not charging anyone with having failed to collect data that should have been collected. After all, when the data needed for this study should have been collected, the study was not even being contemplated. Unfortunately, the data we did use had not been collected especially for our purposes, and therefore did not always suit them.

We also feel that the model itself could be greatly improved by further work. Some of this work would involve reexaminations of certain crucial decisions we made while formulating the model, such as the decision to minimize the Gibbs function rather than some other function. Other work would involve extending the model, so that we could predict impacts that the present model cannot.

15.1. THE RATE OF DETRITUS IMPORT

Because of its great importance, we propose that direct measurements be made of the rate of detritus import from the North Sea. This could be done by sampling the water at many points on a cross section near the mouth of the Oosterschelde. Water samples should be taken at all depths, and during several tidal cycles spread throughout the year. Sampling should be done during stormy weather as well as during calm weather. For each sample, the following information should be recorded:

1. Current speed and direction.
2. Concentration of dissolved organic matter.
3. Concentration of particulate organic matter.
4. Concentration of living biomass (phytoplankton, zooplankton, etc., perhaps estimated from ATP measurements).

With this information, we could use standard statistical techniques to estimate detritus import. To do this, we would have to estimate the integral of the mass transport rate of organic matter over all sampling points and over all tidal cycles of the year. Statistics would be required, because not all the samples needed to make this estimate directly would have been taken, and because unknown errors would be associated with each measurement.

15.2. OTHER QUESTIONS INVOLVING DETRITUS

Investigations should also be made of sedimentation and resuspension of detritus, with particular emphasis on how these processes interact with living organisms. Some questions of interest are: How much suspended detritus is actually consumed in the pelagic segment high above (e.g., more than 50 cm) the bottom?

How is the concentration of detritus in the water related to the height above the bottom, the current velocities experienced during the tidal cycle, and the composition of the bottom? In particular, is there ample detritus in suspension close to the bottom (e.g., less than 25 cm) for suspension feeders to subsist on even when the water higher up is quite free of detritus?

Mineralization rates are largely unknown, even though they are very important in ecosystems. After all, without mineralization, we could very well be knee deep in used brontosauri. We propose that mineralization rates be measured in a variety of situations in actual ecosystems. They should be measured in the water of the pelagic segment, on top of the bottom, and at several depths within the bottom sediments themselves. It should be determined how these rates depend on temperature, and on the concentration of detritus.

15.3. DATA FOR BETTER CALIBRATION AND VALIDATION

Lack of data on the detritus cycle was merely the most serious limitation. More generally, our data on abundances in the present Oosterschelde were scanty. We do not mean this as a criticism of those who collected it and so generously permitted us to use it. We recognize how difficult, time consuming, and expensive it has been to collect these data. Nevertheless, the study could have benefited greatly from more data on abundances, and on external mass transfers.

More data would have been extremely valuable both in calibrating the model and in validating it. For example, we were forced to assume that the abundance data we did use reflected a stable ecostate in the Oosterschelde, and in both the open and the closed Grevelingen. With more complete data, taken during more years, we might have been able to test this assumption, and perhaps to estimate the present rates and directions of ecological "drift" in today's Oosterschelde and closed Grevelingen.

To improve our validation of the model on the Grevelingen, we would require more extensive data than are now available on abundances in the (present) closed Grevelingen. However, there are plans to continue and extend the Grevelingen sampling program that produced the existing data, and this will provide more numbers with which to compare our validation. Of course, it is not possible to improve the data on the open Grevelingen to which we calibrated the model during the validation process.

We are therefore considering a number of other possibilities for validation. First, we hope to begin a study of freshwater ecosystems in the near future. This study will involve an elaborate sampling program on three small ecosystems. These ecosystems have been constructed to be as nearly identical as possible, except for deliberate differences in certain chemical inputs. We anticipate that an opportunity for validation will occur during this study.

We have also been searching for existing data that will permit validation. Our needs are for measurements on a small ecosystem, such as a lake or pond (we would prefer an aquatic system), with a relatively simple food web. There should be little exchange of living matter between the ecosystem and its surroundings (e.g., as a result of fishing and migration), and what exchange there is should be monitored. Any inflow or outflow of detritus should also be measured. The system must have been subjected to a continuing stress, such as an increase or decrease in primary production (e.g., because of an increase or decrease in nutrients in sewage discharge), or a change in segment sizes (e.g., perhaps as a result of dredging). All trophic levels should have been measured for several (at least 2) years both before and after the stress was initiated.

15.4. UNCERTAIN CIRCULATION PATTERNS

Finally, one of the uncertainties remaining for the storm-surge barrier alternatives is how the barrier will influence the circulation pattern within the Oosterschelde basin. With the reduced current velocities, will circulation of North Sea water only occur in the western part of the basin close to the mouth, or will it extend to the Oesterdam? How might the barrier be manipulated to produce a desired circulation pattern? For that matter, how much North Sea water circulates to the eastern end of the basin even now? We think an investigation of these questions could be carried out using existing computer and hydrologic models of the Oosterschelde.

15.5. IMPROVING AND EXTENDING THE MODEL

There are important theoretical questions concerning the model. For example, we chose to minimize the Gibbs function in order to select the stable ecostate. Although the Gibbs function is attractive for many reasons, is it the proper function to use? Even if it is, should we have used units other than biomass to express abundances, e.g., units of numbers of individuals? Perhaps no units of abundance are proper, and rates of mass or energy transfer should be used instead.

Another question concerns the possibility of reformulating the way our model deals with the influence of changes in segment sizes on the ecology. As we described in Sec. 4.2, our present model handles this influence with a variable Z_s for each segment s. We have interpreted Z_s as a measure of the amount of biologically inert "filler" substance in a segment, e.g., the sand and mud that are much of the substance of a benthic segment. An alternative formulation might be based on behavioral characteristics of organisms, such as the dependence of feeding rates on prey density. Would such an alternative formulation be essentially different from our present one? If so, which formulation is to be preferred, or should both be discarded?

Still another question concerns the role that reproduction may play in determining the long-term stable state of an ecosystem. In its present form, the model takes no account of reproduction or, more generally, of the relationship among the abundances of larvae, juveniles, and adults of the same species. We have assumed that these relationships are adequately captured in the values that we give to the parameters $c_{i,j,s}$ of the Gibbs function, and need not be modeled more explicitly. Alternatively, we might seek to model them by means of additional constraints, or changes in existing constraints.

We would like to extend our model, or build supplementary ones, so that we would be able to predict impacts that the present model cannot handle. One of these impacts is the magnitude of the fluctuations in biomass that one should expect both seasonally and from year to year. We need to have some conception of the extremes of biomass, of single species as well as of the total biomass. For this purpose, we distinguish between fluctuations in the biomass when the ecosystem is in a stable state, as opposed to transients observed while the system moves from one stable state to another.

We also want to estimate the effects of alternatives on rare species. Rare species are not included in the present model because they have little effect on the trophic relations. Because they are rare, they cannot eat much nor can they be a significant food source for other, more abundant organisms. However, they are often of great interest to ecologists, biologists, and the public generally. That our model does not currently deal with these species is a flaw that we would like to rectify.

Finally, we might extend the model to handle additional kinds of alternatives, such as toxic substances with species-specific effects, which percolate through the food web as the various organisms feed on each other. Pesticides, for example, have been known to accumulate in this way in critically high concentrations, high enough to prevent birds from producing live young, or to make shellfish unfit for human consumption.

Appendix

THE ROLE OF DETRITUS IMPORT FROM THE NORTH SEA

1. INTRODUCTION

To protect the lands surrounding the Oosterschelde from flooding, the Dutch are considering several alternative constructions that will alter or eliminate the flow of the tide between the Oosterschelde and the North Sea. One of the important effects of the tide on the ecology is that it brings with it organic material (detritus), which then serves as a basic food source for the estuarine biota. Thus, to understand the effect of the alternatives on the ecology, we must assess the present contribution of detritus import from the North Sea to the food base of the Oosterschelde.

The pelagic and benthic biota of the Oosterschelde are sustained by a food base of suspended and deposited organic matter. This food base represents the energy input into the ecosystem, including solar energy trapped in organic molecules by in situ photosynthesis, and energy contained in organic matter that is imported into the ecosystem from outside. Imported organic matter comes primarily from land runoff (including some inflow from the Rhine) and from the North Sea. The contribution of organic matter from each source is mixed, transported, and exchanged with the North Sea by tidal and current action. Land runoff probably contributes little to the food base (less than 10 tons/day based on measurements by the Environmental Division of the Delta Service, Rijkswaterstaat). However, we are uncertain of the relative importance of import from the North Sea as compared with in situ biological production.

Our focus will be on organic matter that is transported passively by tides and currents, such as dissolved and nonliving particulate matter (organic detritus) and microorganisms (phytoplankton, zooplankton, bacteria, yeasts, etc.). For convenience, we will refer to this organic import as "detritus import." We will not concern ourselves with actively migrating organic matter, such as migrating fish and shrimp. Organisms such as these represent only a small fraction of the particulate carbon present in the water column (Riley and Chester, 1971).

In our work we have referred to passively imported organic matter as "detritus." Not all of what we call detritus in our model is imported, of course. Some is produced in the Oosterschelde, e.g., animal feces and plants that have grown and died in the Oosterschelde. Nor is our designation of all imported organic matter as detritus entirely consistent. For example, living phytoplankton swept into the Oosterschelde with the tide is called "detritus." But the same species is called a "photosynthetic organism" if it grows within the Oosterschelde. In our model, this inconsistency is not critical because detritus and photosynthetic organisms are largely equivalent. Both are at the base of the food web, and every organism that eats one also eats the other. We have accepted this inconsistency so that we need not estimate two rates of organic matter import; one of living matter, one of dead matter. In more refined versions of the model, it might prove necessary to define "detritus import" more carefully and consistently.

We are aware that ours is not the classical definition of detritus. For example, according to one definition, detritus consists of coarse to microscopic organic and inorganic complexes that occur in suspension mainly in the form of a loosely aggregated, flaky, sometimes frothy mixture of organic molecules, including vitamins, organic colloids, and organic fragments. Detritus is intermixed with various proportions of clay, silt, fine sand, and living microorganisms (Carriker, 1967). This definition includes inorganic matter, which our use of the term excludes. Also, it excludes living organisms, about which our use is inconsistent.

The Dutch are considering several alternative methods to protect the land surrounding the Oosterschelde from flooding. One alternative would be to leave the mouth of the Oosterschelde untouched, and reinforce the dikes around the basin. This method should not affect detritus import significantly. Another alternative would be to close off the estuary from the North Sea and thereby convert the Oosterschelde into a saltwater lake. If, however, the present rate of organic matter import from the North Sea is significant, this alternative would deny the area an important food source.

Still another alternative would be to construct a storm-surge barrier across the mouth of the Oosterschelde. This barrier could be closed at times of dangerously high water in the southern North Sea. At other times, the gates would be open to permit water to flow between the Oosterschelde and the North Sea. The area through which water would flow, however, would be small enough to reduce the tide and thus possibly alter the circulation pattern within the Oosterschelde. This altered circulation might modify the exchange of organic matter with the North Sea, which might, in turn, affect the estuarine biota that depends on this exchange for food. (We have investigated this dependence, using the general ecomodel described in the main text.)

To estimate detritus import either at the present time or in the alternatives described above, we must understand the nature and transport of the food base in the present Oosterschelde. If there is either an equilibrium exchange of food between the Oosterschelde and the North Sea or a net export (i.e., less organic matter flowing into the estuary than out), then the estuarine fauna must depend primarily on food that originates from photosynthesis within the Oosterschelde. (We have calculated that other possible external sources of organic matter input—e.g., land drainage—are minor.) If a significant net import exists, then there will probably be a relatively large dependence on food originating from the North Sea. There is, of course, some chance that an amount of organic matter roughly equal to detritus import will not be used by secondary producers but, instead, will be deposited as peat. There is also a slight possibility that old peat, deposited years ago in the Oosterschelde, is now being eroded, thereby contributing to the present pool of detritus.

Estuarine transport of organic matter is at present poorly understood. Generally accepted principles or procedures (i.e., relating to topography, currents, depth, concentrations of organic and inorganic materials, etc.) by which we can estimate the importance of imported organic matter from available data are nonexistent. Furthermore, direct measurements of organic matter transport in the Oosterschelde are not yet available, although we have advised that such measurements be conducted. (Some preliminary direct measurements are now becoming available.) We must therefore estimate the net transport of organic matter indirectly. Our applications of the general ecomodel lead us to believe that there is a large net import of organic matter into the Oosterschelde, amounting to half or more of the food base. If this is true, then the Oosterschelde's present connection with the North Sea is crucial to its ecology.

2. IMPORTED ORGANIC MATTER

We are concerned with the passive import by water movements (tides and currents) of dead and living organic matter from the North Sea into the Oosterschelde. The living matter consists largely of unicellular organisms that are passively transported to and from the estuary. These organisms include small herbivores belonging to zooplankton (ciliates, larvae, etc.), nonfeeding microorganisms (phytoplankton, eggs, cysts, etc.), nonpigmented flagellates, and, in addition, some bacteria, yeasts, and fungi. The contributions from actively migrating organisms and of macroalgae to the imported food base are probably relatively minor in the Oosterschelde.

The dead organic matter includes all types of biogenic material in various stages of microbial decomposition and represents a potential energy source for consumer species. Such matter may enter the system either as large particles (carcasses, feces, shed exoskeletons, leaves), as small particles (fragments of organisms, regurgitations, smaller fecal particles), or as colloids (proteins, carbohydrates, lipids, etc.).

Methods for the measurement of total particulate material in seawater may be divided into three groups: optical methods, microscopic examination, and a combination of chemical and gravimetric determinations. Parsons (1963) reviews a number of methods, some of which when further developed may facilitate the study of suspended detritus. These methods involve photography, particle size analyzers, distinction of phytoplankton and other particles by means of red fluorescence of chlorophyll, and estimating the total living portion of particulate matter. Pure microscopic observations have the disadvantage of being too slow. Chemical methods have the advantage of permitting an analysis of a large number of samples per day with a comparatively small amount of equipment. These methods are still largely experimental, and no single one of them differentiates between living and dead particulate organic matter. Generally, they lack accuracy and are difficult and expensive to apply comprehensively enough to detect seasonal variations in levels of particulate organic matter.

Chemical methods are based on two different processes. In one, the dry weight of the total particulate matter collected on a filter is determined. From this particulate substance, the content of chlorophyll can be determined and the proportion of living matter can be calculated (assuming that the zooplankton and bacteria amount to only a small share). The quantity of nonliving detritus is obtained as the difference between the total dry weight and the dry live weight. In the other process, the amount of living matter can be determined by the biuret method (Krey et al., 1957) by means of variable conversion factors, ranging between 2.5 for pure dinoflagellates and zooplankton and 5.0 for pure diatomaceous plankton. One can also calculate the content of nonliving detritus by finding the difference. These two methods are uncertain because only average conversion factors are used. A third group of methods combines the microscopic and chemical processes.

There are various methods for determining particulate carbon, nitrogen, and phosphorus (Riley and Chester, 1971). It should be remembered that these methods determine total particulate organic material, not just that which can be assimilated by marine organisms. For this reason, there is some danger in using such data for ecological purposes, since even in productive surface waters there are appreciable proportions of nonassimilable material. It is often of greater value to ecologists to know the concentrations of each of the main classes of algal components. Simple spectrophotometric methods are available for the determination of carbohydrate, lipid, protein, and plant pigments (Strickland and Parsons, 1968).

There is at present no entirely satisfactory method for determining the proportion of living material in the particulate organic matter. Microscopic examination is of limited use for quantitative purposes. Since chlorophyll is rapidly degraded after the death of plant cells, it is commonly used as a chemical measure of the living plant material. This method suffers from three disadvantages: (1) the ratio of chlorophyll a to carbon in plant cells can vary as much as fivefold, depending on the species of algae and their nutritional state; (2) the degradation products of chlorophyll interfere with this method; (3) organisms that do not contain chlorophyll (i.e., bacteria and yeasts) are not determined. Recently, it has been suggested that determinations of ATP or DNA can be used to estimate total living matter in marine particulates (Holm-Hansen et al., 1968). However, before these substances can be adopted for this purpose, it is necessary to be sure that nonliving material does not contain them and, also, that they occur in a constant or predictable ratio to cell carbon or other measures of organic matter.

Smaller organic molecules may be dissolved in the seawater. These may include vitamins, amino acids, sugars, urea, nitrates, etc., or dissolved gases, such as methane, ammonia, hydrogen sulfide, etc. A major fraction of dissolved organic matter in the sea is a complex polymeric substance that is very resistant to bacterial attack. The minor fraction composed of more labile compounds is biologically more important.

There are various methods for measuring dissolved organic carbon, nitrogen, and phosphorus (Riley and Chester, 1971). The ratios of these elements for different samples are used to derive a gross estimate of the relative amounts of carbohydrates, proteins, amino acids, and other substances. Although simple calorimetric procedures exist for the estimation of one or two classes of dissolved organic compounds in seawater (e.g., the anthrone method for carbohydrates), the determination of individual, dissolved, organic compounds is a much more difficult task. The concentration of any individual compound rarely exceeds 10 μg/liter, and it is usually necessary to concentrate several liters of sample in order to obtain a sufficient quantity for analysis. The type of preconcentration technique to be used will be determined by the class of compound sought. Among those that may be employed are solvent extraction (e.g., for fatty acids and insecticides) and adsorption on carbon (e.g., for carbohydrates) and on polystyrene beads (e.g., for vitamin B12). Highly sensitive methods of determination must be used, and for this purpose thin-layer or gas-chromatographic procedures are frequently chosen. In a few instances, organic compounds can be determined directly in seawater by bioassay techniques.

The amount of dissolved organic matter in the sea usually exceeds the particulate organic fraction by a factor of 10 to 20; only one-fifth of the particulate matter, on the average, consists of living cells. The relative proportions of the various forms of particulate carbon found by McAllister et al. (1961) in the surface waters of the northeast Pacific are probably fairly characteristic of ocean surface waters as a whole. The concentrations of nonliving detritus, phytoplankton, zooplankton, and fish corresponded to about 125, 20, 2, and 0.02 micrograms of carbon per cubic meter. These values should be compared with a dissolved organic carbon content of approximately 1000 μg/cu m.

For a comprehensive review of the analysis, nature and origin, distribution, and ecological significance of both dissolved and particulate compounds in the sea, see Riley and Chester (1971).

3. THE ROLE OF DETRITUS IN ESTUARINE ECOLOGY

Detritus plays a vital role in marine ecology because it provides part of the energy, food, vitamin, and other requirements for bacteria, plants, and animals. Imported detritus is the same as organic matter produced internally except that it has been synthesized, ultimately, from solar energy located at another part of the earth. Thus, imported detritus is virtually imported sunlight.

All heterotrophic organisms ultimately depend on the floating and settled organic material for sustenance. Small heterotrophs (e.g., bacteria and zooplankton) and filter-feeding organisms (those that obtain food by filtration of organic matter from the water through gills or other retention structures) thrive solely on this organic material. They, in turn, are consumed by larger predators. Detritus is ingested in fairly high quantities by most estuarine consumers, whether they are vertebrate or invertebrate, large or small, suprabenthic or benthic. Even the most carnivorous species often take in a certain amount of detritus, and while they may derive little caloric value from the small amounts consumed, detritus may provide a source of vitamins (Darnell, 1967; Stephens, 1967).

Dissolved organic matter, in general, or specific classes of compounds within it, are believed to serve as nutrients, as activators or inhibitors of growth, and as chelating agents. For example, thiamin, biotin, vitamin B12, and other organic compounds are essential for the growth of many species of marine phytoplankton. In many cases, trace elements (essential mineral nutrients) may be tied up in chemical compounds so tightly that they are unavailable for biological nutrition. Dissolved organic chelating agents combine with these elements and make them available for nutrition. All soft-bodied marine animals are believed capable of taking up selected compounds of dissolved organic matter through their body surfaces, as well as through their gastrointestinal tracts when these exist. Aside from a utilization in metabolic pathways, these marine animals appear to store and use these substances to protect the interior medium of their bodies against the osmotic drying influence of the saline environment (DeHaven, 1976). In addition, dissolved organic matter can adsorb on the surfaces of particles and thereafter be used in the same manner as particulate organic matter.

MacGintie (1932) pointed out that detritus is more important to bottom-living animals than it is to free-swimming organisms. Mare (1942) estimated that 75 percent of the benthic fauna in the English Channel off Plymouth depend on detritus and the organisms associated with it as their main source of food.

The detritus cycle includes the creation, transport, deposition, recycling, utilization, and eventual loss of organic matter. Suspended organic matter is transported to and from the adjacent marine environment and within the estuary by water movements. The organic matter that settles to the bottom may serve as food for benthic deposit-feeders. It may also be entrapped for a period of time through sedimentation and then become resuspended by the tides and currents, by animals, or other dislodging processes so that it is again available for pelagic consumption. Detritus particles may grow in size or they may be reduced (mineralized) to an inorganic state whereby they may no longer be a direct food source for secondary consumers. Consumed organic matter that is not metabolized may be recycled in the form of excretions or carcasses and eventually reconsumed.

The sizes of detritus particles are important in determining their behavior in transport. For convenience, two states are recognized: the particulate (greater than 1 micron); and the subparticulate or dissolved state (less than 1 micron). Size analyses have shown that dead particulate organic matter is mainly concentrated in a size range of 1 to 55 microns. However, particles of dead organic matter are continually changing in size. Size reduction occurs through the process of biological decomposition (primarily by bacteria and fungi), which involves both mechanical and chemical simplification (brought about mainly through the processes of hydrolysis and oxidation). A number of factors (absorption, agglomeration, coacervation, etc.) cause an increase in particle size. Many aquatic consumers produce fecal pellets that are larger than the individual particles ingested.

The larger particles tend to precipitate rapidly, whereas the smaller ones usually precipitate more slowly (the relatively larger surface area of small particles results in sufficient friction with the surrounding water molecules to offset much of the gravitational force). Subparticulate organic detritus, which includes the colloids and the dissolved organic molecules, has less tendency to precipitate and is thus more readily transported by water currents over moderate to long distances than are the larger particles. Colloids may remain in suspension almost indefinitely.

The nonliving component of the food base may be particularly important as a source of stored energy and building materials. Some types persist longer than others, depending on their origin. The long-persisting structural elements may prove to be among the chief energy sources of productive areas during off-seasons. Organic detritus may thus act as a buffer to moderate the large, seasonal variations in available food.

The total dissolved and particulate carbon in the water column are usually an order of magnitude greater than the yearly primary production. The geographical and seasonal variation of detritus can be roughly correlated with productivity and is usually greater in coastal waters than in the open sea. The results given by Duursma (1961) for dissolved organic carbon at a station in the North Sea are typical of productive coastal waters. The highest values were found in spring and early summer, somewhat later than the period of maximum phytoplankton activity. The concentration decreased slowly during the summer and, with the exception of a minor maximum in the month after the autumn plankton bloom, remained relatively constant until the onset of the spring bloom. A similar trend was shown by dissolved organic nitrogen. Analogous seasonal variations correlating with phytoplankton activity have been found for individual organic nutrients and combined amino acids in coastal waters (Riley and Segar, 1970, and others).

It should be noted that pelagic detritus (mainly phytoplankton, and floating dead organic matter) and benthic detritus (chiefly plants, benthic diatoms, and settled phytoplankton) play similar ecological roles.

4. ESTIMATES OF DETRITUS IMPORT IN VARIOUS ESTUARIES

Quantitative data on the significance of the sources of the estuarine food base, one of which is detritus import, are scarce and nonuniform. What estimates we have seen indicate that the various sources differ in importance from one estuary to another because of differences in freshwater input, primary productivity, etc. Further, within a given estuary, the importance of each source may vary according to the season, to the position in the salinity gradient, and other factors. Preliminary studies on three Dutch estuaries, the Waddensea (Postma, 1954), the open Grevelingen (Wolff, in preparation), and the Oosterschelde (the present study), suggest reasons to expect a substantial net food import. By contrast, a net export of organic matter is believed to occur from estuaries along the American coasts. In addition to contrasts between estuaries, differing conclusions may be ascribed to differences in methods of investigation and schools of research.

4.1. Estimates Based on Measured Components

We have collected the following examples of the variability of different food sources among estuaries. Meade (1969) reports that in estuaries with low tidal ranges, such as those found at the mouth of the Mississippi River, river sources of suspended matter may dominate. In other estuaries, in situ primary production may prevail: Day et al. (1973) present data supporting the construction of a food budget for the aquatic part of the estuarine system of Barataria Bay, Louisiana. A comparable budget holds for Georgia estuaries, where Odum and de la Cruz (1967) and Pomeroy et al. (1972) indicate an important contribution of organic detritus from the salt marshes and a net export of particulate organic matter from the estuary to the shelf waters. Teal (1962) reports that 45 percent of the net production of a Georgia salt marsh is exported as detritus to the open water system of the estuary, whereas the remainder is consumed on the marsh. Nixon and Oviatt (1973) report that 23 percent of the net production of a New England marsh embayment is exported as detritus, and they propose an annual energy budget similar to those in Louisiana and Georgia. However, in most cases, the data are not adequate to estimate how much of the export is replaced by organic material imported by the tide.

Schelske and Odum (1961) reviewed general mechanisms maintaining high productivity in estuaries. They point out that in Georgia estuaries the primary production is maintained on a high level the year round because of the rapid turnover of nutrients and the release of dissolved nutrients by the sediment. They also state that the estuary acts as a nutrient trap because of the vertical mixing of waters of different salinities and the biological removal of nutrients by the benthic fauna. From their paper, it is not clear, however, what mechanism provides the nutrients to be trapped. They exclude a freshwater source of dissolved nutrients. A supply of particulate organic matter and/or sediment to the estuary from the ocean is not considered by these authors, although Odum (1971) points to a marine origin of nutrients.

Most studies are based on direct measurement of a component (e.g., carbon content) of one part of the food base (e.g., particulates). Emphasis is placed on a particular aspect of the food cycle, e.g., on the resuspension processes or the quantity of organic detritus derived from marsh grass. Estimates are based on qualitative assumptions that may relate only to the estuary being studied. This is understandable because direct measurements are difficult and the detritus cycle is complex.

Theoretically, if the relationships between geographical variables (e.g., topography, currents, depth, organic matter gradients, etc.) and the rate of food transport were understood, then the rate of food exchange in the Oosterschelde could be calculated without resort to direct and tedious measurements. However, because general quantitative principles or procedures are nonexistent, this is not possible.

Perhaps there are variations between the American and European estuaries that could account for the difference in detritus transport? The Oosterschelde more closely resembles a sea arm rather than a classical estuary because the freshwater input is almost nonexistent. Entrapment by salinity stratification does not occur, since the estuary is always well mixed. On American coasts, the marsh grasses occupy about two-thirds of the intertidal zone below high water mark. On European coasts, marsh plants hardly descend below high tide level. The contribution of detritus from sea grasses and marshes thus appears to be more significant in American estuaries (Wolff, in preparation).

4.2. Estimates Based on Chemical Replenishment

Postma (1954) concluded that there is a net import of organic matter into the Waddensea from the North Sea, even though the concentration of suspended organic matter in the Waddensea was two to three times higher than that in the North Sea. His estimate was based on the requirement that total phosphorus in the Waddensea be in balance. Postma therefore reasoned that the dissolved phosphorus that he believed was being exported to the North Sea (because its gradient favored movement in that direction) must be replaced by a net import from other sources. After accounting for replenishment from Den Helder harbor and from the IJsselmeer, he was left with a net loss of 1900 kg/tide. This, Postma believed, must be made up by the import of phosphorous-containing particulate matter from the North Sea, most of which is organic.

Postma's estimate of detritus import into the Waddensea in 1954 was about 80 gC/sqm/yr, an amount roughly equal to his estimate of in situ primary production. Phosphorous concentrations were remeasured over the entire Dutch Waddensea in 1970 and 1971. The phosphorous concentration, and therefore the import of organic particulate phosphorus, was found to have increased threefold since 1950, probably because of Rhine pollution (De Jonge and Postma, 1974).

Postma (1954) also measured particulate organic matter. He found that its concentration and distribution were similar to that of silt, which also showed an inwardly increasing gradient. According to Postma, this phenomenon is caused by the inward decrease in current velocity and water depth, the characteristics of the shapes of ebb- and flood-curves, and, locally, the differences in density between seawater and freshwater. These factors cause a net import of silt and organic matter from the North Sea until a certain balance is attained. In the case of particulate organic matter, this balance is influenced by consumption, mineralization, and sedimentation of detritus.

Wolff (in preparation) used the same method as Postma (1954) to quantify detritus import into the Grevelingen. He determined the average concentration of dissolved phosphorus at three sampling stations within the Grevelingen and at two entrance channels. He found an inwardly increasing gradient of dissolved phosphorus and calculated the amount of dissolved phosphorus that is exported to the North Sea per tidal cycle. This export is balanced by land runoff, which he estimated, and the remainder is assumed to come in from the North Sea. Wolff's estimate for organic matter import from the North Sea (200 to 285 gC/sqm/yr) was close to his value for in situ primary production.

In their 1970 article, Postma and Rommets criticized Postma's earlier method (1954), which was based on the assumption that the phosphorous balance of the area is in equilibrium. This may not be true. Also, a simplified method had been used to calculate the water exchange per tidal cycle between the North Sea and the Waddensea. There may be other questionable points in the aforementioned studies: The slight gradient of dissolved phosphorus could have been the result of an error in measurement methods. Postma and Wolff both assumed that the phosphorous percentage of organic matter is about 1 percent; however, this ratio varies. There may be other sources of in situ particulate organic phosphorus that were overlooked. A gradient of dissolved phosphorus is assumed to indicate a net exchange; however, the phosphorus may be consumed or entrapped within the estuary.

4.3. Estimates Based on Trophic Balance

Estimates based on the previous methods do not help us to determine detritus transport in the Oosterschelde. We have examined the existing phosphorous data for the Oosterschelde and found no consistent relation between concentrations at the mouth and those farther inward. Direct measurements of organic matter transport in the Oosterschelde are not yet available. Therefore, we have developed a method for estimating detritus transport which uses the general ecology model and is based on the trophic balance.

The model is based on the assumption that the estuarine ecosystem has a balanced energy budget and that each class of estuarine biota has the proper amount of food. That is, the inputs of energy into the estuarine system in the form of net organic matter import from the land and the adjacent sea, plus in situ primary production, must equal the energy lost through mineralization, migration and fishing, and metabolism of the biomass (excluding bacteria). This assumption gives rise to the following overall system balance equation, which we have discussed at length in Sec. 3.10:

$$\text{Net organic import} + \text{in situ primary production} = \text{mineralization} \\ + \text{migration and fishing} + \text{metabolism}.$$

The model estimates each term in the energy balance equation. The value of 180 gC/sqm/yr is the most accurate one possible for the rate of in situ primary production and is in rough agreement with numerous studies (see Sec. 7.1). Loss of energy from migration and fishing is assumed to be negligible. The rate of mineralization

(0.12 percent per day) is uncertain. As discussed in Sec. 10.8, this mineralization rate implies that 200 tons of organic matter are decomposed (mineralized) per day. A higher (lower) mineralization rate would imply that a larger (smaller) amount was mineralized daily, since what is added (subtracted) to one side of the energy balance equation must be added (subtracted) to the other side.

The major loss term in the overall system balance equation is the metabolism of the existing biota. We can calculate this as the sum of the metabolisms of all the ecological groups, where the metabolism of each group j is the product of its abundance W_j, its daily ration r_j, and its metabolic fraction m_j. Our estimates of r_j and m_j for each ecogroup can be found in Table 6.6.

Using the final consistent abundance estimates given in Table 10.5, we estimate that the metabolism of the biota in the Oosterschelde requires about 950 tons ash-free dry weight of organic matter per day. If we add to this amount the 200 tons/day that we assume is mineralized, and subtract 450 tons/day that we estimate is photosynthesized, we arrive at an estimated detritus import rate of 700 tons/day. Of course, this estimate depends on the abundance estimates we choose. For example, if we use the initial abundance estimates from Table 8.4, we obtain an estimated detritus import rate of over 900 tons/day. Clearly, then, if the data on present abundances of biota in the Oosterschelde are realistic, there is not enough food produced in situ to support the existing biomass. According to the available information, the organic matter input from land drainage, including rivers, agricultural runoff, and industrial and domestic sewage, is relatively insignificant. The bulk of this imported detritus must therefore come from the North Sea.

This conclusion may be criticized on a number of grounds. Each term of the energy balance equation is, in itself, complex and difficult to estimate from the available data. Furthermore, the estuary may not be a steady-state system, i.e., the overall balance equation given above may be unrealistic. The abundance data were incomplete, unreliable, and scattered. Direct measurements had a high variance. Indirect estimates relied on questionable assumptions. Estimates for the Oosterschelde were inconsistent and required adjustments. Certain data—e.g., those for mussels and cockles—were biased. Nevertheless, we find the conclusion inescapable that the ecosystem of the Oosterschelde receives substantial support from sources other than in situ photosynthesis—i.e., from imported organic matter.

There are a number of possible in situ and landward sources of this import. Sewage discharge and runoff from the agricultural lands adjacent to the Oosterschelde have been monitored by the Environmental Division of the Delta Service (Rijkswaterstaat). This potential source of organic matter accounts for only a few (≈ 10) tons per day. Water purification ponds in the Ruhr River are sluiced every so often (probably during high flow). During these times, the accumulated organic matter is released down the Ruhr and into the Rhine. However, because only a small fraction of the Rhine discharge is eventually delivered through the Volkerak sluices to the Oosterschelde, this source of detritus is probably not a significant one.

The Oosterschelde is considered to be an eroding estuary. It may be that old peat, deposited years ago, is now being eroded, thereby contributing to the present pool of detritus.

The major source for imported organic matter is undoubtedly the North Sea. The North Sea is a rich food source. Primary production of organic matter in the whole North Sea is roughly estimated at 250 g/sqm/yr. This is a minimum value, since the actual production per unit surface area for the Southern Bight is higher than that for the North Sea as a whole. (It is consistent with the production rate we have estimated at 180 gC/sqm/yr, which is equivalent to 342 g/sqm/yr of organic matter.) Potential productivity increases steeply toward the coast where the nutrient-rich waters of the Rhine, Meuse, and Scheldt enter the sea. In summer, this increase is more than twentyfold.

Increasing pollution from rivers and coastal areas may add to the nutrient and organic matter content of the North Sea. For example, in the early thirties, the Rhine contained only about one-tenth of the amount of the phosphate it contains at present. This increase is due to the increase in population and livestock, to improved sanitation, and to a greater use of fertilizers and detergents containing phosphorus. De Jonge and Postma (1974) estimated that organic particulate phosphorus import to the Waddensea from the North Sea has increased threefold since 1950, probably because of Rhine pollution. Although the North Sea currents generally flow northward, there is a possibility that, locally, currents flow toward the Oosterschelde, bringing nutrients and detritus from the polluted rivers. If dilution is minor, then organic input from rivers located farther north may help to support life within the estuary. Another man-made source of organic detritus may be the dredging of sediments along the North Sea coast during the past several years (e.g., at the mouth of the Rhine near Rotterdam).

Organic matter content in coastal and inland waters varies more with season than do concentrations in the sea, being related to plankton growth and decay and loading from the land. It is possible that the North Sea values may exceed the Oosterschelde values during seasonal transients and thereby recharge the estuary during some periods. Resuspension of organic material from bottom sediments may also be seasonal. For example, storms may enhance resuspension and import of organic material.

4.4. Collateral Musings

The rate of detritus import into the Oosterschelde appears to be comparable to the corresponding rate for the open Grevelingen. Wolff (in preparation) estimates that the rate of detritus import into the open Grevelingen is 135 to 200 tons afdw/day. Our estimate for the rate of detritus import into the Oosterschelde (700 tons afdw/day), modified to reflect the ratio of areas of the Grevelingen as compared with those of the Oosterschelde, is 190 tons afdw/day.

The net exchange of water between the North Sea and the Oosterschelde has been roughly approximated as 500 cu m/sec. Assuming that the organic matter content just outside the mouth is about 1.5 g/cu m, as we did in Sec. 12.4, then the net exchange of organic matter from the North Sea to the mouth of the Oosterschelde would be approximately 65 tons/day. This is an order of magnitude less than the 700 tons/day detritus import as estimated with the model. However, the exchange volume multiplied times the organic matter concentration gives a value for detritus transport only if the organic matter obeys Fick's law, and moves in proportion to its gradient. This may not be true.

The amount of suspended particulate and dissolved organic matter in the Oosterschelde can be roughly calculated. Manuels and Postma (1974) found approximately 5 percent organic carbon content in the suspended matter in the Waddensea with a very small yearly fluctuation caused by plankton blooms. Using a value for the average suspended matter concentration in the Oosterschelde calculated on the basis of 1972 measurements by the Environmental Division of the Delta Service (Rijkswaterstaat), the average abundance of particulate organic matter would be 9350 tons, and that of dissolved organic matter would be 15800 tons. Total organic matter in the pelagic zone would be 25150 tons.

The average concentration of suspended matter is higher at the mouth than further inward, 44.4 g/cu m at the mouth and 29.3 g/cu m within the Oosterschelde (1972 data base). If the organic proportion of the suspended matter is fairly constant, there would be an inwardly decreasing gradient of organic matter that might imply a net import.

5. DIRECT MEASUREMENTS

Because of the uncertainties involved with indirect estimates, we have recommended that the flow of both living and nonliving organic matter in and out of the Oosterschelde be directly measured so that the rate of net exchange of the food base can be calculated. Measurements should be conducted regularly throughout the year in order to reveal seasonal variations. Measurements should be taken during storms as well as during calm weather, in case storm-caused turbulence stirs up organic matter from the bottom and causes an unusually high import of organic matter. Measurements from different locations at the mouth may show that more organic material enters through particular channels because of the water circulation pattern.

Detritus transport was directly measured in August 1976 at the surface and half way to the bottom in the three channels at the mouth of the Oosterschelde: Hammen, Schaar, and Roompot. Several measurements of particulate carbon (ppm) were conducted during both the ebb and flow of a single tidal cycle and then averaged together. Comparison of the average amount of particulate carbon flowing in and out of the estuary at the mouth shows that a marginally larger quantity flows outward, both at the surface and below, indicating a detritus export. Although these findings relate to a very short time period—only one tidal cycle during one month of the year—they are the only direct measurements available so far and must be considered a contraindication to the indirect finding that there is a significant detritus import.

6. POSSIBLE EFFECTS OF THE VARIOUS ALTERNATIVES UPON DETRITUS TRANSPORT

The degree to which the tide is reduced and the manner in which the circulation of water is altered will depend on the method chosen to protect the land bordering the Oosterschelde from flooding. This may affect the quantity, transport, distribution, and perhaps even the composition of the food base in the Oosterschelde, which may, in turn, affect the numbers, distribution, and composition of biota.

Even if the Oosterschelde remains open, the planned internal compartment dams would change the size and shape of the basin. Nevertheless, the effect on detritus transport should be minor.

If the Oosterschelde is completely closed off from the North Sea, then detritus import will, of course, be eliminated. On the other hand, if there is presently a net export of detritus, then organic matter may increase in the closed basin.

Possible effects of the storm-surge barrier are more complex. The reduction in tidal volume may reduce, proportionally, the flow of detritus into and out of the Oosterschelde. However, the water velocities within the Oosterschelde should also be reduced by the barrier (although the local water velocities near the barrier gates may be increased). Consequently, a larger fraction of the suspended organic particles may settle to the bottom. The detritus import rate may therefore increase, depending on the balance between the reduction in tidal volume and the increase in the deposition rate.

An increase of deposited organic matter and a corresponding decrease in suspended organic matter could affect the composition of biota. Since benthic creatures would receive a larger share of food and pelagic creatures, a lesser share, the number or biomass of benthic species would increase.

The storm-surge barrier may alter the water circulation pattern within the Oosterschelde, thereby reducing (increasing) its velocity in certain localities and causing organic particles to be deposited in different places and in different concentrations than is now occurring. These changes could alter the distribution of benthic creatures and consequently of their predators. The largest possible effect of this kind would occur if circulation of North Sea water into the eastern end of the Oosterschelde effectively ceased when the tide was reduced. It seems likely, however, that the barrier could be manipulated during calm weather to produce almost any desired circulation pattern, and so the problem would not occur.

The proportions of the various components of detritus (e.g., dissolved organic material, organic particles, phytoplankton) seem to vary with season and also with depth. If the barrier dam somehow alters the seasonal proportions, it may also alter the composition of biota. Many creatures may be selective with regard to the components of detritus they consume (e.g., food is selected according to the size of the feeders and the construction of their filter mechanisms). However, the detritus preferences of various species are either unknown or uncertain.

Detritus may be imported only through certain portions of the channels, e.g., near the bottom. If this is true, it would suggest that the sills of the barrier's gates should be close to the sea floor. This requirement would seem to imply that the gates should be very tall, which would complicate the problem of raising and lowering them.

Perhaps the most disturbing possibility is that most detritus import may occur during storms. It could even be that import derived in this way serves to overbalance a net detritus export during calm weather, a conclusion consistent with the direct measurements reported earlier. If this reasoning is true, then closing the barrier during every storm to protect against flooding could only be done at grave cost to the ecology.

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