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

VOL. III, ASSESSMENT OF LONG-RUN ECOLOGICAL BALANCES: AN ADDENDUM (CALIBRATION DATA)

PREPARED FOR THE NETHERLANDS RIJKSWATERSTAAT

J. H. BIGELOW, C. DZITZER, J. C. H. PEETERS

R-2121/3A-NETH
FEBRUARY 1978

Rand
SANTA MONICA, CA. 90406

This report was prepared with the support of The Netherlands Rijkswaterstaat under Contract No. DED-1683. Reports of The Rand Corporation do not necessarily reflect the opinions or policies of the sponsors of Rand research.

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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. In reaction to 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 rare ecology and its 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 alternative approaches for protecting the Oosterschelde from floods. Three approaches were proposed, either formally or informally: closing it off completely, as originally planned; leaving it open and building large new dikes; or constructing 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. 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.

Each organization concentrated 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). 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.

The three alternative cases that were analyzed in the POLANO project—the closed, the open, and the storm-surge barrier cases—are not fully described by what is done to the mouth of the Oosterschelde. There are 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 Krammer Volkerak, 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 Basin. In both compartment designs, the Western Basin remains saltwater whereas the Eastern Basin becomes freshwater.

On April 5, 1976, one year after POLANO began, Rand presented 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 those of several special Rijkswaterstaat studies. This work became the foundation of the Rijkswaterstaat's May 1976 report, *Analysis of Oosterschelde Alternatives*, that was presented first to the Cabinet and then to Parliament, along with the Cabinet's recommendation for a decision. Based on the Rijkswaterstaat report, the Cabinet recommended the storm-surge barrier case to Parliament, which accepted it in June 1976. (The Parliament also requested additional analysis by the Rijkswaterstaat to establish the best aperture size for the barrier.)

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 biological 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 explains in detail a mathematical model, called the general ecology model, that was developed using mathematical concepts new to ecology. The model predicts the effect of the different cases—open, closed, and storm-surge barrier—on the long-term average abundances of species (more accurately, ecological groups of species) found in the Oosterschelde. The report also presents the results of our attempt to calibrate the model and to validate it, 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 the Grevelingen's tide was reduced to zero by its 1971 transformation to a saltwater lake.

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 also produce bad odor. Because an upper bound on the risk of algae blooms is desired, the model uses linear programming techniques to predict the maximum algae biomass that could occur, subject to various constraints on growth (such as the availability of several nutrients).

Volume V, *Anaerobic Conditions and Related Ecological Disturbances* (R-2121/5), describes a mathematical model that was developed for estimating the potential for anaerobic conditions in an Eastern Basin and applied to the different cases. Oxygen-free (anaerobic) water 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 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 all-day briefing. The improvements in methodology and results have come not only from the leisure to experi-

ment 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 is an addendum to Vol. III of the POLANO series. The Addendum describes the biological data and methods used to estimate the initial abundances and average live weights of each ecological group of species for the different segments of the Oosterschelde and for the open and closed Grevelingen. These are major inputs for the calibration and validation of the general ecomodel described in Vol. III. The Addendum is not intended to stand alone. It is written with the assumption that the reader is acquainted with Vol. III.

ACKNOWLEDGMENTS

We greatly appreciate the generous cooperation and professional assistance provided by many individuals in the Netherlands, both in the Rijkswaterstaat and in other organizations, in collecting, organizing, and analyzing the raw data used as input to the general ecomodel.

At the Environmental Research Division of the Delta Service, T. Aldenberg, J.H.J. Terwindt, B. A. Bannink, H.L.F. Saeijs, J. P. Al, and J. Visser helped to construct the food web used in our model, and helped to make the overall model consistent with existing knowledge of sedimentation, water quality, morphology of basins, and types and characteristics of the various biological entities involved. Their efforts received overall guidance from A. C. deGaaij, head of the Environmental Research Division. We also appreciate the work of P. Eilers who helped update information on benthic and other organisms.

At the Delta Institute for Hydrobiological Research, Yerseke, K. F. Vaas, the Director of the Institute, gave permission to use unpublished data in general, and he and C. Bakker provided data on fish and zooplankton and helped with the construction of the food web. W. J. Wolff made available unpublished data on bottom animals in the Grevelingen. R. Peelen provided unpublished data on extinction coefficients and on phytoplankton. We are indebted to these people, as well as to P. H. Nienhuis, A. Sepers, and F. Vegter for their valuable comments during discussions at the Institute.

At the State Institute for Fishery Research, IJmuiden, we received useful comments from R. Boddeke, N. Daan, A. C. Drinkwaard, P. Korringa, K. H. Postuma, and J. F. de Veen. Also useful were the unpublished data these individuals provided on the demersal fish survey, on the distribution of flatfish, round fish, and shrimp, and on shellfish culture.

At the Directorate of Fisheries, J. D. Holstein and A. L. Abrahamse furnished important data relating to cockle and mussel fisheries.

At the Netherlands Institute for Sea Research, Texel, discussions with J. J. Zijlstra, F. Creutzberg, and W.W.C. Gieskes regarding the abundances of several species in the regions of interest and the factors affecting them provided valuable insights. W.W.C. Gieskes also furnished unpublished data on the chlorophyll concentrations at the mouth of the Oosterschelde.

We are also grateful to A.I.M. Meijering, R.S.P. Horjus, and J.C.M. van Kessel who collated data on the sizes of organisms, helped to calculate abundances of organisms, and aided in the special cockle survey organized to provide data for this model.

The following people worked very hard to make the special cockle survey a success:

A. A. Westdijk
L. M. Schat (Captain, *M. V. Ventjagen)*
C. Potter
J. Moerkerk
G. Lamers

J. Bayens
H. Korstanje
D. Lokerse
W. Venkerde
J. Meuldijk
Ch. Wessels,
and the crew of *M. V. Orisant* from Zierikzee.

We are also indebted to E. L. Birnbaum for his report on detritus in the region.

We appreciate the assistance of J. Aroesty and M. M. Lavin of Rand who reviewed this Addendum. We are also grateful to D. G. Stewart of Rand for her usual competent assistance as editor.

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Chapter 1

INTRODUCTION

1.1. THE ADDENDUM

This Addendum contains the calibration data for Vol. III, *Assessment of Long-Run Ecological Balances,* of the POLANO series, *Protecting an Estuary from Floods—A Policy Analysis of the Oosterschelde.* It describes the biological data and the methods we used to estimate the initial abundances and average live weights of each ecological group (ecogroup) of organisms for the different segments of the Oosterschelde and for the open and closed Grevelingen. These abundances and weights were major inputs for the calibration and validation of the general ecomodel described in Vol. III.

This Addendum assumes that the reader is acquainted with Vol. III and is not intended to stand alone. We will therefore only briefly describe the Oosterschelde issue and the general ecomodel here.

1.2. THE OOSTERSCHELDE PROBLEM AND ALTERNATIVE PLANS

To protect the lands surrounding the Oosterschelde estuary from floods, three alternative constructions have been analyzed: a closed case, an open case, and a reduced-tide (storm-surge-barrier) case. In the closed case, a dam would be constructed across the mouth of the Oosterschelde, thereby converting the estuary into a stagnant lake. In the open case, the mouth of the Oosterschelde would remain open, but its perimeter would be surrounded by large new dikes. In the storm-surge-barrier case, a "partial" dam with gates would be built across the mouth of the estuary. During calm weather, the gates would be open allowing the tide to flow through an area as large as 20000 sqm (about one-fourth the present unobstructed flow area). During storms, the gates would be closed and the barrier would act like a dam. Various-sized apertures in the barrier were analyzed in terms of their effect on the amount of tidal reduction. There are several other features of each case. The most important for the environmental ecology is the compartment design that describes the location of compartment dams and hence determines the size of the saltwater basin.

1.3. THE BIOLOGICAL ENVIRONMENT OF THE OOSTERSCHELDE

The Oosterschelde estuary provides food and habitats for a rich variety of flora and fauna. It is the northernmost living area for a number of species that enrich the diversity of the region. The Oosterschelde, in its present tidal form, serves as a way-station on an important north-south migratory route for birds, as well as a

breeding and overwintering area for them. The estuary is a breeding ground and nursery for commercially important sea fish and shrimps, in addition to being an attractive area for Dutch and Belgian sportfishermen. Shellfish, especially mussels and oysters, are an important commercial harvest.

1.4. THE GENERAL ECOMODEL

The alternative constructions will have different impacts on the environment of the Oosterschelde, i.e., on the tidal amplitude, the size of the saltwater basin, etc. These impacts will, in turn, affect the estuarine biota. To determine how the different constructions will affect the ecology of the Oosterschelde, a mathematical model, called the general ecomodel, was developed by The Rand Corporation and the Environmental Division of the Delta Service. The model can 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. Volume III describes in detail how we formulated, calibrated, and attempted to validate the model.

1.5. RAW DATA FOR THE GENERAL ECOMODEL

To calibrate the general ecomodel to the present Oosterschelde, we needed data on the abundances of the major groups of species living in different types of habitats (segments) in the estuary. By "abundance" we mean the amount of biomass of a particular group of species (ecogroup), as measured by ash-free dry weight. (We will explain our choice of ecogroups and segments in the separate sections of this Addendum.)

Since data for the Oosterschelde were too incomplete for this purpose, we used data from other locations (especially the open Grevelingen) to infer some of the abundances in the Oosterschelde. The Grevelingen is a saltwater 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, mostly before closure but to some extent after closure as well. Some of these data (e.g., densities of macrobenthos) were used to help us estimate abundances of ecogroups in the Oosterschelde. Also, one method we used to validate the model was to compare its predictions with data collected in the open and closed Grevelingen. 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 (see Chap. 11 of Vol. III).

Table 8.5 of Vol. III 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 the study.

In addition, data on the average live weight per individual organism for each ecogroup were required in order to compute the daily ration and metabolic fraction for the model (see Chap. 2).

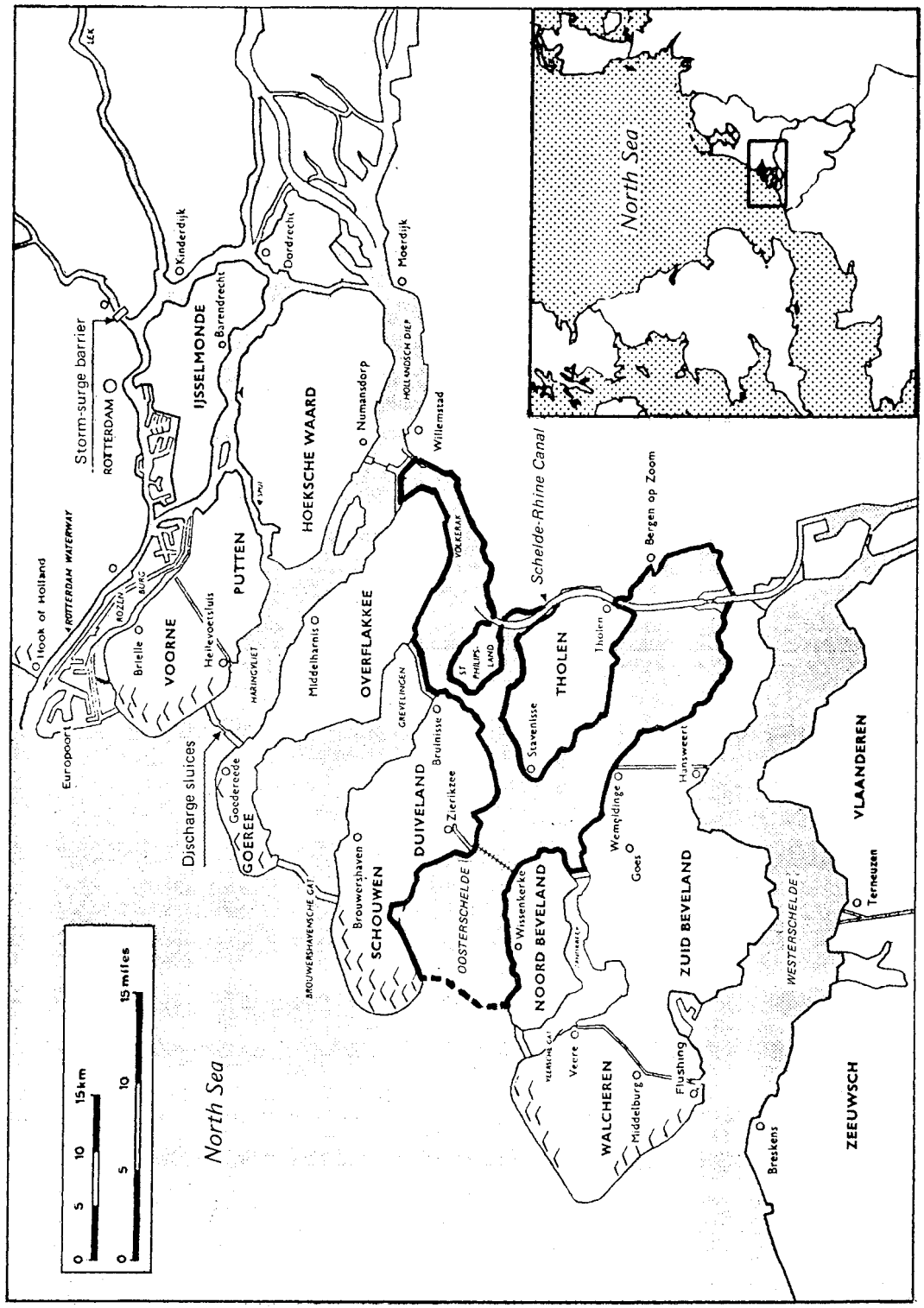

Fig. 1.1 — The Delta region in the southwest part of the Netherlands
(The heavy black line outlines the study area)

After the initial abundance estimates were originally published in Vol. III, we received some amendments to the original raw data and also new data and information. Consequently, we reworked the data, in some cases using different assumptions. Thus, many of the initial estimates have been revised here. However, the changes are relatively insignificant in terms of their effect upon the model calibration and have no influence on our conclusions. The initial estimates are presented in four tables in Vol. III: Table 8.4 (Oosterschelde), Table 11.4 (open Grevelingen), Table 11.5 (closed Grevelingen), and Table 6.6 (average live weight estimates and resulting parameters). The revised initial estimates are presented here in Tables 1.1, 1.2, 1.3, and 1.4, respectively.

Table 1.1

REVISED 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	1445.0	9930.0	--	--
Detritus/micro-benthos	24040.0	72790.0	58116.0	7250.0
Zooplankton/pelagic larvae	555.0	--	--	--
Mussels/oysters	--	--	--	1280.0
Cockles/limpets	--	7960.0	86.2	--
Selective deposit feeders with pelagic larvae	--	82.3	--	13.44
Crabs/shrimp	--	7.9	12.24	1.1
Sea stars	--	--	60.1	27.8
Deposit feeders with nonpelagic larvae	--	1553.7	0.762	253.8
Omnivores/predator worms	--	69.0	15.0	11.3
Benthic grazers	--	1081.8	1.20	176.7
Planktivorous fish	256.0	--	--	--
Benthos-eating fish	2200.0	--	--	--
Fish-eating fish	340.0	--	--	--
Plant-/detritus-eating fish	30.0	--	--	--
Fish-eating birds	0.0454	--	--	--
Plant-eating birds	--	0.416	--	--
Benthos-eating birds	--	9.0	--	--

Table 1.2

REVISED INITIAL ABUNDANCE ESTIMATES FOR THE OPEN GREVELINGEN

(In metric tons afdw)

Ecological Group	Segment			
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms	Shellfish Culture Plots
Photosynthetic organisms	275.0	2919.0	--	--
Detritus/micro-benthos	4573.0	22185.0	9686.0	5887.0
Zooplankton/pelagic larvae	105.0	--	--	--
Mussels/oysters	--	--	--	1000.0
Cockles/limpets	--	2072.3	367.2	--
Selective deposit feeders with pelagic larvae	--	142.6	3.33	6.72
Crabs/shrimp	--	2.4	2.1	0.9
Sea stars	--	--	10.0	14.0
Deposit feeders with nonpelagic larvae	--	473.8	0.127	126.9
Omnivores/predator worms	--	21.0	2.5	5.7
Benthic grazers	--	1019.2	0.63	88.4
Planktivorous fish	48.0	--	--	--
Benthos-eating fish	689.0	--	--	--
Fish-eating fish	64.7	--	--	--
Plant-/detritus-eating fish	51.1	--	--	--
Fish-eating birds	0.0124	--	--	--
Plant-eating birds	--	0.126	--	--
Benthos-eating birds	--	2.74	--	--

Table 1.3

REVISED INITIAL ABUNDANCE ESTIMATES
FOR THE CLOSED GREVELINGEN

(In metric tons afdw)

Ecological Group	Segment[a]		
	Pelagic	Shallow Bottoms and Tidal Flats	Deep Bottoms
Photosynthetic organisms	311.7	3314.0	--
Detritus/micro-benthos	(b)	(b)	(b)
Zooplankton/pelagic larvae	10.4	--	--
Mussels/oysters	--	(b)	--
Cockles/limpets	--	137.6	21.8
Selective deposit feeders with pelagic larvae	--	92.7	4.67
Crabs/shrimp	--	(b)	3.35
Sea stars	--	--	208.6
Deposit feeders with nonpelagic larvae	--	(b)	(b)
Omnivores/predator worms	--	(b)	3.6
Benthic grazers	--	13.6	41.3
Planktivorous fish	(b)	--	--
Benthos-eating fish	(b)	--	--
Fish-eating fish	(b)	--	--
Plant-/detritus-eating fish	(b)	--	--
Fish-eating birds	0.273	--	--
Plant-eating birds	--	2.83	--
Benthos-eating birds	--	0.717	--

[a]Note that in the closed Grevelingen there is no shell-fish culture segment.

[b]Unknown.

Table 1.4

REVISED AVERAGE MEAT WEIGHTS, DAILY RATIONS (r_j), AND METABOLIC FRACTIONS (m_j)

Ecological Group	Meat Weight	Daily Ration (r_j)	Metabolic Fraction (m_j)
Zooplankton/pelagic larvae	0.0000055	3.84×10^{-1}	9.02×10^{-1}
Mussels/oysters	1.25	3.89×10^{-2}	8.88×10^{-1}
Cockles/limpets	1.29	3.87×10^{-2}	8.88×10^{-1}
Selective deposit feeders with pelagic larvae	0.117	6.02×10^{-2}	8.93×10^{-1}
Crabs/shrimp	1.0	4.05×10^{-2}	8.88×10^{-1}
Sea stars	10.8	2.62×10^{-2}	8.80×10^{-1}
Deposit feeders with nonpelagic larvae	0.6355	4.12×10^{-2}	8.90×10^{-1}
Omnivores/predatory worms	0.0256	7.98×10^{-2}	8.98×10^{-1}
Benthic grazers	0.0083	9.83×10^{-2}	8.97×10^{-1}
Planktivorous fish	0.5	4.60×10^{-2}	8.90×10^{-1}
Benthos-eating fish	54.4	1.96×10^{-2}	8.70×10^{-1}
Fish-eating fish	225.3	1.52×10^{-2}	8.62×10^{-1}
Plant-/detritus-eating fish	162.0	1.61×10^{-2}	1.00[a]
Fish-eating birds	--	3.61×10^{-1}	1.00[a]
Plant-eating birds	--	3.23×10^{-1}	1.00[a]
Benthos-eating birds	--	4.27×10^{-1}	1.00[a]

[a]Set to 1.00 for technical reasons involving the fact that these ecogroups have no predators in the general ecomodel. See 7.2.8 of Vol. III.

1.6. DIFFICULTIES AND SHORTCOMINGS IN ESTIMATING ABUNDANCES

There are major shortcomings in the actual abundance data and in the methods of analysis. To analyze the data, we had to make some important but quite speculative assumptions (e.g., about gear efficiencies,[1] ratios of ash-free dry weight to live weight for various creatures, etc.). The abundance figures are thus uncertain. However, it is only the relative quantities that are important to the model calibration. Despite the shortcomings, which we will point out in this Addendum, the data still have value.

Data on biological abundances in natural ecosystems are generally difficult and costly to collect because the ecosystems are so large and varied. The Oosterschelde, for example, covers an area of approximately 476 sq km and contains thousands

[1] Fraction of fish caught in a net during a survey trawling operation. (See Sec. 9.2.2.)

of species. 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 from season to season. 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 daily. Still others have very short lifespans (e.g., phytoplankton) or undergo rapid changes in size and weight (e.g., young fish). The potential magnitude of monthly variations is suggested by graphs of the density of some macrobenthic creatures in Figs. 8.2, 8.3, and 8.4 of Chap. 8. 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 of Vol. III). (Recruitment figures for these species are equivalent to the abundances of 2-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).

Remember that our model deals with long-term average abundances, and not with the abundances of organisms at any particular instant in time. As we have pointed out, abundances will vary from season to season and from year to year; therefore, 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. However, the available measurement data are incomplete in these regards. In other words, the initial abundances described here, which 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.

Not only are abundance data incomplete; they are also very uncertain. Even direct measurements of abundances in the Oosterschelde have a high variance. For example, as previously mentioned, 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 such inference will be discussed in Sec. 9.

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. 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. 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.

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, the R.I.V.O. (State Institute for Fisheries Research) carried out a mussel-fishing experiment in the closed Grevelingen that recovered 10000 tons of mussels, about one-third the estimated abundance of cultured mussels in the Oosterschelde. Rather than change the model by adding a new "wild mussel" ecogroup, we reinterpreted the cockle and limpet ecogroup to include wild mussels, which are similar in the aspect considered by the model.[2]

The units of abundance were chosen to be in terms of ash-free dry weight (afdw) because this gives a better estimate of nutritional energy than does total live weight. (For further explanation, see Sec. 2.3 of Vol. III.) The ash-free dry weight percentage of the live weight varies from species to species; it also varies within a species, perhaps depending on the stage in the life cycle and the season of the year. Information on ash-free dry weight is difficult to obtain. Most of the ash-free dry weight ratios we used came from Vinogradov (1953), who compiled figures from numerous authors. The figures for a particular species vary with the informational source. This may be because of the traits of the particular organism analyzed and the methods of analysis (e.g., it is sometimes difficult to determine whether the shell of the creature is included). We chose to use what we considered to be the average ratio of ash-free dry weight to live body weight for each type of organism.

[2] 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.

Chapter 2

LIVE WEIGHTS, DAILY RATIONS, AND METABOLIC FRACTIONS

The biomass balance requirements in the general ecomodel 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. These parameters were needed to construct the mass-balance coefficient matrix (see Sec. 3.8 of Vol. III) for the ecomodel.

To estimate the average daily ration, r_j (the fraction of the body weight assimilated each day), and the metabolic fraction, m_j (the fraction of the daily ration, r_j, that is metabolized), for each ecogroup j (other than birds), we used a simple model that relates these quantities to the average and maximum live body weights of the individual organisms in each ecogroup. The model assumes that net assimilation, r, and metabolism, mr, are both proportional to body weight raised to a power. That is,

$$r = a \times W^{b-1}, \tag{1}$$

$$m \times r = c \times W^{d-1}, \tag{2}$$

where W is the live 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. (1) and (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. These calculations are described in detail in Chap. 6 of Vol. III.

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 maximum weight was chosen to be twice the average weight. The consequences of this choice are explored in Vol. III.

In this Addendum, we describe how we arrived at the live weight per individual for each ecogroup. The original live weight estimates have been somewhat revised here, and the daily rations and metabolic fractions have been recalculated from these revised weights. The most conspicuous revision is for crabs and shrimp because of additional information from Klein Bretler (1975) (see Sec. 8.6). However, as one can see from Table 1.4, the revised estimates make a relatively insignificant difference in the daily ration and metabolic parameters, even for the crab and shrimp group, for the following reason.

In Sec. 6.4 of Vol. III, we describe the consequences to the parameters r_j and m_j of perturbing the maximum weight and/or actual weight of an individual organism in an ecogroup. Note that the daily ration, r, is proportional to the actual body weight, W, raised to the minus one-third power (see Eq. (1)), and a factor of 2 results in only a 20 percent error in r. Similarly, dividing Eq. (2) by (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.

Chapter 3

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*. The types of organisms that we chose to represent each ecological group are the major species for which data were available, i.e., they are the most abundant. Species placed into the same ecological group eat similar things, have similar predators, and live in similar places.

The ecological groups 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. Consequently, our Oosterschelde model has 18 ecological groups:

1. Photosynthetic organisms (phytoplankton, benthic diatoms, seagrasses, 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.

Chapter 4

SEGMENTS

Segments are defined here as the places where ecological groups live and feed. We have tried to define segments to be 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; a pelagic segment and three benthic segments. The *pelagic segment* includes the bulk of water in the estuarine basin. The benthic segments are defined 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.*[1] The fraction of this area that 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.

The nominal areas for each segment of the Oosterschelde and the Grevelingen are shown in Table 4.1.

Table 4.1

NOMINAL SEGMENT AREAS FOR THE OOSTERSCHELDE AND THE GREVELINGEN

Segment Areas	Present Oosterschelde	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
Total areas (sq km)	476.4	130.2	106.7

As with the ecological groups, our classification of segments has flaws. 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 has also found that the amount of wave action in shallows and on tidal flats is a significant factor. However, our model requires the size of each segment as inputs, and data were so scanty that it proved impossible to estimate segment sizes if they were defined by 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).

[1] In Vols. I and III, this segment is defined as oyster banks and mussel beds.

Chapter 5

PHOTOSYNTHETIC ORGANISMS

5.1. PHOTOSYNTHETIC ORGANISMS IN THE OOSTERSCHELDE

5.1.1. Oosterschelde—Pelagic Segment

Photosynthetic organisms in the pelagic segment include mainly phytoplankton. Data on the biomass of phytoplankton in the Oosterschelde are difficult to obtain. We therefore used two different indirect methods to estimate the average yearly biomass of phytoplankton in the pelagic segment of the Oosterschelde.

The average chlorophyll-a concentration (milligrams per cubic meter) at the mouth of the Oosterschelde, according to unpublished data of Gieskes for 1973, 1974, and the first half of 1975, is 3.70 mg/cu m. By assuming an approximate conversion of 1 percent (Strickland, 1960), we find that this concentration is about 370 mg afdw/cu m of phytoplankton. Gieskes and Kraay (1975) present small isopleth maps of phytoplankton concentration, measured as algal volume at the surface of the Dutch coastal waters during the first half of the 1974 growing season. By interpolating and converting to ash-free dry weight, we estimated a concentration of phytoplankton at the mouth of the Oosterschelde of 377.4 mg afdw/cu m. According to Strickland's (1960) data, this value would be 421.8 mg afdw/cu m. We averaged these estimates and assumed that the phytoplankton concentration is 400 mg afdw/cu m. We then multiplied this concentration by the volume of water for the entire Oosterschelde (3156 million cm) to obtain an average biomass of 1262.4 $\times$ 10^6 g afdw.

Primary production per year is about 180 gC/sqm[1] (see Chap. 7 of Vol. III). We multiplied this by 1.9 afdw to carbon ratio (Winberg, 1971) to obtain 342 g afdw/yr of organic matter. If we assume that the P/B ratio is 100 per year (Parsons and Takahashi, 1973), the average biomass becomes 3.42 g/sqm. For the entire Oosterschelde, with a surface area at mean high tide of 476 sq km, this yields 1628 $\times$ 10^6 g.

We averaged the outcomes of the two approaches to obtain a phytoplankton abundance in the Oosterschelde of 1445 tons afdw.

5.1.2. Oosterschelde—Shallow Segment

Photosynthetic organisms in the shallow segment include benthic diatoms and seaweed plus seagrasses. Data on these organisms are also difficult to obtain.

To estimate the abundance of benthic diatoms in the shallow segment of the Oosterschelde, we used data on the Dutch Waddensea from Cadee and Hegeman (1974). They investigated the primary production of benthic microflora living on tidal flats in the Dutch Waddensea during the years 1968 to 1972. Since the biomass fluctuates with the time of the year, they calculated the biomass for the beginning

[1] Square meters are expressed as "sqm" throughout this Addendum.

of each month. They give the biomass (in milligrams of chlorophyll per square meter) of the top 1-cm layer of the bottom sediment in a 5-year graph for each month of the year (Cadee and Hegeman, 1974, Fig. 9). From this calculation, L. Vegter (in an unpublished paper, "Oostmeer") determined the average monthly biomass. Cadee and Hegeman (1974, Fig. 10) also graphed the depth distribution of functional chlorophyll-a in the bottom sediment during 2 years at a particular sampling station. From this, Vegter estimated that in order to obtain the biomass concentration of benthic microflora in an arbitrarily chosen top 5-cm layer, the average monthly biomass in the top 1-cm layer must be multiplied by a factor of 3.3. Therefore, the average for all months converted to ash-free dry weight (assuming that the chlorophyll-a content represents 1 percent of the afdw) was 38 g/sqm. We multiplied this concentration by the area of the shallow segment (251 sq km) to obtain a benthic diatom abundance of 9.538×10^9 g.

To estimate the abundance of seagrass and seaweed, we used production data from Nienhuis (1976). He presents limits for seagrass production in the Oosterschelde as .09 to .9 gC/sqm. We multiplied this range by a 1.9 C/afdw ratio (Winberg, 1971), which yielded .171 to 1.71 g afdw/sqm/yr. Table 4 from Nienhuis (1976) presents data on seaweed and seagrass production for 1973 and 1975 in the closed Grevelingen. From these data, we calculated a ratio of seaweed/seagrass production of .56. Then, assuming that the same ratio applies to the Oosterschelde, we divided the seagrass production range for the Oosterschelde by .56 to obtain a production of seaweeds and seagrasses of .266 to 2.66 g afdw/sqm/yr. Nienhuis (1976) states that the density in the Oosterschelde is lower than that in the Grevelingen, so an upper limit of 2.66 g afdw/sqm/yr seems reasonable.

To convert the production figure into biomass, we used a production/biomass ratio calculated from data on the closed Grevelingen as follows: The seaweed and seagrass production in the closed Grevelingen, 5.69×10^9 g afdw/yr, was derived by multiplying 28 gC/sqm/yr (production in 1973 from Table 4 of Nienhuis, 1976) by 107 sq km (the area of the closed Grevelingen) and by the 1.9 C/afdw conversion factor. The average yearly seaweed/seagrass biomass for the closed Grevelingen (calculated below) was estimated as 1.75×10^9 g afdw. Thus, the production/biomass ratio for the closed Grevelingen would be 3.2. Assuming that the same ratio exists for the Oosterschelde, we divided the assumed seaweed/seagrass production for the Oosterschelde, 2.66 g afdw, by 3.2, which resulted in an assumed seaweed/seagrass biomass of .83 g/sqm. We multiplied this biomass by the area of the Oosterschelde (476 sq km), which yielded 3.95×10^8 g afdw for seaweed and seagrasses.

We combined the abundances of benthic diatoms and seaweeds and seagrasses to obtain the total abundance of photosynthetic organisms in the shallow segment of the Oosterschelde, 9930 tons afdw.

5.2. PHOTOSYNTHETIC ORGANISMS IN THE GREVELINGEN

5.2.1. Open Grevelingen—Pelagic Segment

Assuming that the phytoplankton density in the open Grevelingen was similar to the density in the Oosterschelde, we multiplied 0.46 g/cu m by 601 million cm

(volume of the pelagic segment of the open Grevelingen) to obtain the abundance of phytoplankton, 275 tons afdw.

5.2.2. Open Grevelingen—Shallow Segment

To estimate the abundance of benthic diatoms in the open Grevelingen, we used the same diatom density (calculated from Cadee and Hegeman, 1974) as in the Oosterschelde. We multiplied 38 g afdw/sqm by 76.5 sq km (the area of the shallow segment of the open Grevelingen) and thus obtained a diatom abundance of 2.907 $\times$ 10^9 g afdw in the open Grevelingen.

Seagrass production in the open Grevelingen was determined by Nienhuis (1976) to be 3 gC/sqm. By assuming that the ratio of seaweed to seagrass in the open Grevelingen was the same as that calculated for the closed Grevelingen (.56), we estimated a seaweed production of 1.68 gC/sqm. Thus, the combined seaweed/seagrass production became 4.68 gC/sqm, or, using the 1.9 C/afdw conversion factor, 8.892 g afdw/sqm. For the entire open Grevelingen (130 sq km), the seagrass plus seaweed production would be 1.16 $\times$ 10^9 g afdw/yr. By using the 100/yr P/B ratio, we obtained an average yearly biomass of seagrass and seaweed of 1.16 $\times$ 10^7 g afdw.

We combined the abundances for benthic diatoms and for seaweed and seagrasses to obtain the total abundance of photosynthetic organisms for the open Grevelingen, 2919 tons afdw.

5.2.3. Closed Grevelingen—Pelagic Segment

The average chlorophyll concentration over 1972 and 1973 in the closed Grevelingen was 6.85 mg/cu m (de Bree et al., 1973). Therefore, the pelagic zone (579 million cm) contained 3.97 $\times$ 10^6 g of chlorophyll. We multiplied this value by 30 to obtain a carbon equivalent and by 2 to determine the ash-free dry weight of the organic matter (Strickland, 1960). This procedure yielded 2.382 $\times$ 10^8 g of organic matter.

The yearly phytoplankton production is approximately 180 gC/sqm/yr (see Sec. 7.1 of Vol. III). We multiplied this carbon value by 2 (Strickland, 1960) to obtain 360 g afdw of organic matter per square meter per year. Thus, for the entire area (107 sq km), we have 3.78 $\times$ 10^{10} g afdw/yr of phytoplankton. Assuming a P/B ratio of 100/yr (Parsons and Takahashi, 1973), we calculated an average biomass of phytoplankton of 3.852 $\times$ 10^8 g afdw. By averaging the outcomes of the two approaches, we determined the abundance of phytoplankton in the closed Grevelingen to be 311.7 tons afdw.

5.2.4. Closed Grevelingen—Shallow Segment

The area covered by seagrass and seaweed vegetation in the closed Grevelingen is 53.9 sq km. The vegetation cover is not, however, 100 percent, so part of this area will be used by diatoms. We assumed that the cover is 50 percent, i.e., that seaweed and seagrass cover an area of 26.85 sq km. Assuming that the area of diatoms is less than 5-m deep (68.0 sq km), we subtracted the area with seaweed and seagrass vegetation from the area of diatoms and obtained an area of 41.15 sq km for the diatoms. Then, by multiplying the diatom density calculated previously (38 g/sqm)

by the area of diatoms, we determined that the diatom abundance is 1.564×10^9 g afdw.

The Grevelingen Workshop of the Delta Institute for Hydrobiological Research, Yerseke, surveyed the macrophytobenthos in the closed Grevelingen during July-August, 1973 (de Bree et al., 1973). The maximum biomass of seagrasses and seaweeds was calculated as 2.92×10^9 g afdw. This represents the highest season of growth. Table 2 from Vegter ("Oostmeer") gives monthly macrophytobenthos biomasses for the Oostmeer, where the average yearly biomass equals 60 percent of the biomass in August. Thus, we adjusted the August biomass for the closed Grevelingen to 60 percent of its value to obtain the yearly average abundance. This yielded 1.75×10^9 g afdw in the closed Grevelingen.

By combining the figures for benthic diatoms and macrophytobenthos, we determined the benthic photosynthetic organisms in the closed Grevelingen to be 3314 tons afdw.

Chapter 6

DETRITUS AND MICROBENTHOS

6.1. DETRITUS

In our ecomodel, detritus is defined as dead organic matter that is suspended in the water with inorganic matter, e.g., clays and silt, and with the living matter, e.g., phytoplankton and fish. For convenience, two size categories are recognized: particulate (greater than 1 μ) and dissolved (less than 1 μ). Each type is measured differently.

6.1.1. Oosterschelde—Pelagic Segment

Manuels and Postma (1974) measured the ATP and organic carbon content in the Dutch Waddensea. The dead particulate organic matter was determined by means of total organic carbon content minus living carbon as estimated by the ATP method. Manuels and Postma (1974, Table III) found approximately 5 percent organic carbon content in the suspended matter, with a very small yearly fluctuation caused by plankton blooms. We used this percentage to estimate the particulate detritus content of the pelagic segment of the Oosterschelde.

The Environmental Division of the Delta Service, Rijkswaterstaat, conducted monthly measurements of the suspended matter at three depths for seventeen stations in the Oosterschelde between 1972 and 1975. The average suspended-matter concentration for the years 1972 and 1973 was much higher than for 1974 and 1975. This difference was probably due to a change in the measurement method. Having no other data source available, we weighted the suspended-matter concentration for each station by its location and averaged the concentrations for all 4 years. This yielded 27.5 g/cu m.

We multiplied this figure by 5 percent organic carbon content and an ash-free dry weight/carbon ratio of 1.9 (Winberg, 1971), which gave us 2.61 g/cu m of particulate organic matter. By multiplying this figure by the volume of water in the pelagic segment (3156 million cm), we obtained a total abundance of 8.24×10^9 g of particulate organic matter in the Oosterschelde.

There are no data on dissolved organic matter in the Oosterschelde. We do have some scanty unpublished data taken at five stations at six depths for the closed Grevelingen from Anton Seegers of the Delta Institute for Hydrobiological Research. From these data, it appeared that the concentration of dissolved organic matter is higher than the concentration of particulate organic matter. The average concentrations (in milligrams per liter) were

December	May	August
3.66	6.7	12.76

Seegers noted (personal communication) that the data for August were probably unusually high because of the dying off of an algae bloom.

Duursma (1961) listed the average dissolved organic matter concentrations (in milligrams per liter) in the Dutch Waddensea. They are

August	November
6.0	3.7

From the two sources above, we decided to use a concentration of dissolved organic matter of 5 g/cu m. Multiplying this value times the total volume of water gave us 1.58×10^{10} g of dissolved organic matter.

The total abundance of organic matter (particulate plus dissolved) in the pelagic segment is therefore 24040 tons afdw.

6.1.2. Oosterschelde—Benthic Segments

Wolff (1973a) measured the carbon content of organic matter in sediments from five areas, including the Oosterschelde, using a wet oxidation method. He found a statistically significant correlation between median sediment grain-size and the logarithm of the weight percentage of organic matter (Wolff, Table III). In the Oosterschelde, the size of most of the sediment is 200 to 300 phi-units (Wolff, 1973a, Fig. 4). The middle of this size range (250 phi-units) corresponds to about .145 percent organic matter. We do not know the average depth of the layer that contains organic material. Assuming an arbitrary .2-m layer, we then multiplied the volume of 1 sqm of bottom sediment (.2 cu m) by .145 percent organic matter content to get about 290 g/sqm organic matter. This is an arbitrary (but reasonable) figure, because we could just as well have assumed another percentage of organic content in the sediment and another organic layer depth. To estimate the abundance of detritus in the benthic segments, we multiplied this value by the areas of each benthic segment as follows:

$$\text{Shallow: } 251.0 \text{ sq km} \times 290 \text{ g/sqm} = 7.279 \times 10^{10} \text{ g}$$

$$\text{Deep Bottom: } 200.4 \text{ sq km} \times 290 \text{ g/sqm} = 5.8116 \times 10^{10} \text{ g}$$

$$\text{Shellfish Area: } 25 \text{ sq km} \times 290 \text{ g/sqm} = 7.25 \times 10^{9} \text{ g}$$

6.1.3. Grevelingen

The abundance of detritus in the open Grevelingen was estimated in the same manner as that in the Oosterschelde. Assuming the particulate organic matter to be 2.61 g/cu m, we multiplied this figure by 601 million cm (volume of water in the pelagic segment) to obtain 1.568×10^{9} g of particulate organic matter. Then, using 5 g/cu m as the amount of dissolved organic matter, we multiplied this figure by 601 million cm to obtain 3.005×10^{9} g of dissolved organic matter. Thus, we estimate that the organic matter (particulate plus dissolved) in the pelagic segment of the open Grevelingen was about 4573 tons afdw.

To calculate the abundance of detritus in the benthic segments, we multiplied 290 g/sqm organic matter by the areas of each segment as follows:

Shallow: 76.5 sq km $\times$ 290 g/sqm = 2.2185×10^{10} g

Deep Bottoms: 33.4 sq km $\times$ 290 g/sqm = 9.686×10^{9} g

Shellfish Area: 20.3 sq km $\times$ 290 g/sqm = 5.887×10^{9} g

6.2. 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 about 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 (mineralization) of detritus.

Chapter 7

ZOOPLANKTON AND PELAGIC LARVAE

7.1. OOSTERSCHELDE

We do have data on the zooplankton in the Oosterschelde and on the planktonic larvae of various organisms (usually macrobenthic) that inhabit the estuary. These data were provided by C. Bakker of the Delta Institute for Hydrobiological Research, Yerseke.

During 10 days of 1974, samples were taken at three different depths and during three periods of the incoming tide at two sampling stations: at Lodijkse Gat, in the eastern part of the Oosterschelde and at Colijnsplaat in the western part. The method for measuring the abundances of zooplankton was to count individual organisms in water samples under a microscope and then record the data in terms of numbers of individuals of a species per 100 liters of water.

The data needed to calculate the mean volume per species were collected at the Delta Institute by A.I.M. Meijering, who identified and measured the most important species through a microscope with the help of R. Peelen and his assistants at the Institute. Volumes of species that Meijering could not find were calculated on the basis of pictures and measurements given in the literature. The information was compiled in an unpublished report by R.S.P. Horjus, J.C.M. van Kessel, and A.I.M. Meijering.

Estimating the size (especially the ash-free dry weight) of zooplankton is difficult. Since Meijering had no experience with the identification of plankton, he was not able to see any difference between the "copepodiet"-stages and "adult"-stages. These two stages are combined in the adult stage. Lack of time made it impossible to measure many individuals of any species, and therefore the calculated volumes are rough approximations.

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 zooplanktonic organisms in the Oosterschelde is very incomplete.

Also, the abundance of zooplankton 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.

Table 7.1 lists the species, the number of individuals per 100 liters (N), the volume per individual (V), and the volume per 100 liters of water (NV). The total mean volume of zooplankton as averaged from Table 7.1 is 3×10^{-4} liters of zooplankton per 100 liters of water. This is .03 cu cm/100 liters. We assumed that 50 percent of this volume is empty space between the carapaces and that the density is the same as water. So the wet weight would be .15 g. Given that the average water content is 87 percent, and that the ash-free dry weight is about 90

Table 7.1

ZOOPLANKTON AND PELAGIC LARVAE IN THE OOSTERSCHELDE

N = number of individuals/100 liters
V = volume/individual
NV = liters of zooplankton/100 liters water

Species	N	V (cu μ)	NV
Lanice conchilega	194	2×10^{8}	4×10^{-5}
Euterpina acutifrons	854	3×10^{6}	3×10^{-6}
Temora	130	8×10^{7}	1×10^{-5}
Acartia	69	2×10^{7}	1×10^{-5}
Harpacticide	37	6×10^{6}	2×10^{-7}
Balanus cypris	98	6×10^{6}	6×10^{-7}
Gastropode	384	3×10^{6}	1×10^{-6}
Oikopleura	768	3×10^{8}	2×10^{-4}
Stenosemella ventricosa	17000	4×10^{5}	7×10^{-6}
Centropage species	209	2×10^{6}	4×10^{-7}
Longipedia	14	2×10^{6}	3×10^{-8}
Cyclops and *Oncea*	42	4×10^{6}	2×10^{-7}
Euterpina		3×10^{5}	
Centropage (diverse species)	152	5×10^{7}	8×10^{-6}
Polydora	313	1×10^{7}	3×10^{-6}
Alaurina composita	19	5×10^{6}	1×10^{-7}
Favella		7×10^{5}	
Pseudocalanus	39	4×10^{7}	2×10^{-6}
Echinoderme larvae	259	4×10^{6}	1×10^{-6}
Balanus balanoides	307	1×10^{7}	3×10^{-6}
Nematode	50	9×10^{5}	5×10^{-8}
Magelona	6	2×10^{7}	1×10^{-7}
Crab larvae	3	7×10^{7}	2×10^{-7}
Nereis diversicolor	46	3×10^{7}	1×10^{-6}
Lamellibranchia larvae	6230	7×10^{5}	4×10^{-6}

percent of the dry weight (Beers, 1966; Greze, 1970; Harris and Riley, 1956; Vinogradov, 1953), the ash-free dry weight of zooplankton would be 1.76×10^{-2} g/100 liters, or .176 g/cu m. We multiplied this zooplankton density by the volume of water in the Oosterschelde (3156 million cm), which yielded 5.55×10^{8} g of zooplankton in the Oosterschelde.

7.2. OPEN GREVELINGEN

We assumed that the density of zooplankton in the open Grevelingen was the same as that of the Oosterschelde. Multiplying that density (.176 g/cu m) by the volume of water in the Grevelingen (601 million cm), we obtained an abundance of zooplankton in the open Grevelingen of 1.04×10^{8} g afdw.

7.3. CLOSED GREVELINGEN

There are relatively low densities of zooplankton in the closed Grevelingen as compared with the Oosterschelde, and these organisms mainly consist of the larvae of spinoid worms (such as *Polydora)* and some rotifers. We took the density to be 10 percent of that of the Oosterschelde, or .018 g afdw/cu m. Multiplying this density by the mean volume of water in the Grevelingen (579 million cm), we obtained an abundance of zooplankton for the closed Grevelingen of 1.04×10^{7} g afdw.

7.4. AVERAGE WEIGHT PER INDIVIDUAL

The average wet weight per individual plankton specimen was calculated by dividing the total number of individual specimens per 100 liters of water (27223) into the total mean volume of species per 100 liters of water (0.3 cu cm). This yielded 1.1×10^{-5} g. Assuming that one-half of this is empty space between the carapaces, we calculate the wet weight per individual specimen to be 5.5×10^{-6} g.

Chapter 8

MACROBENTHIC DATA

Macrobenthic organisms are relatively large creatures that live on or in the bottom sediments of the aquatic habitat. We have categorized eight macrobenthic ecogroups for the general ecomodel. Data on the abundances of most of these ecological groups were collected in the open and closed Grevelingen by the Delta Institute for Hydrobiological Research, Yerseke. (Shrimp and shore crab are exceptions. The State Institute for Fisheries Research (R.I.V.O.), IJmuiden, obtained the data on these organisms while trawling for benthos-eating fish. Ecologically, however, shrimp and shore crab properly belong among the macrobenthos.)

8.1. SAMPLING PROGRAM

Sampling took place at several stations in the Grevelingen (Fig. 8.1) each month during the period from January 1970 to June 1975. The Grevelingen was closed in May 1971. At some stations, samples were taken both before and after closure. At others, they were taken only before or only after closure. Each station was taken to represent a certain area of the Grevelingen, as determined in Wolff (1977). The species density at each station was weighted by the area represented by that station so that the density of each species per segment could be calculated. Table 8.1 gives the sampling stations, their respective areas, and when the stations were sampled.

The method for collecting these data in shallow water and on intertidal flats was to vertically insert a hollow cylinder (core) into the bottom sand and clay to a depth of about 30 cm. The sampled areas were 0.005, 0.0155, and 0.0177 sqm. In deeper waters, a grab was used and the sampled areas were 0.05 and 0.1 sqm. The core and grab samples were sifted to find any macrobenthic organisms present, and then they were counted. If the number of species was too large, subsamples were taken and counted. The collected animals were split into age classes. Representatives were taken from each age class and were dried, weighed, and later ashed to determine ash-free dry weight. The major species found are listed in Table 8.2.

Except for shrimp and shore crab, macrobenthic 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 of them 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.

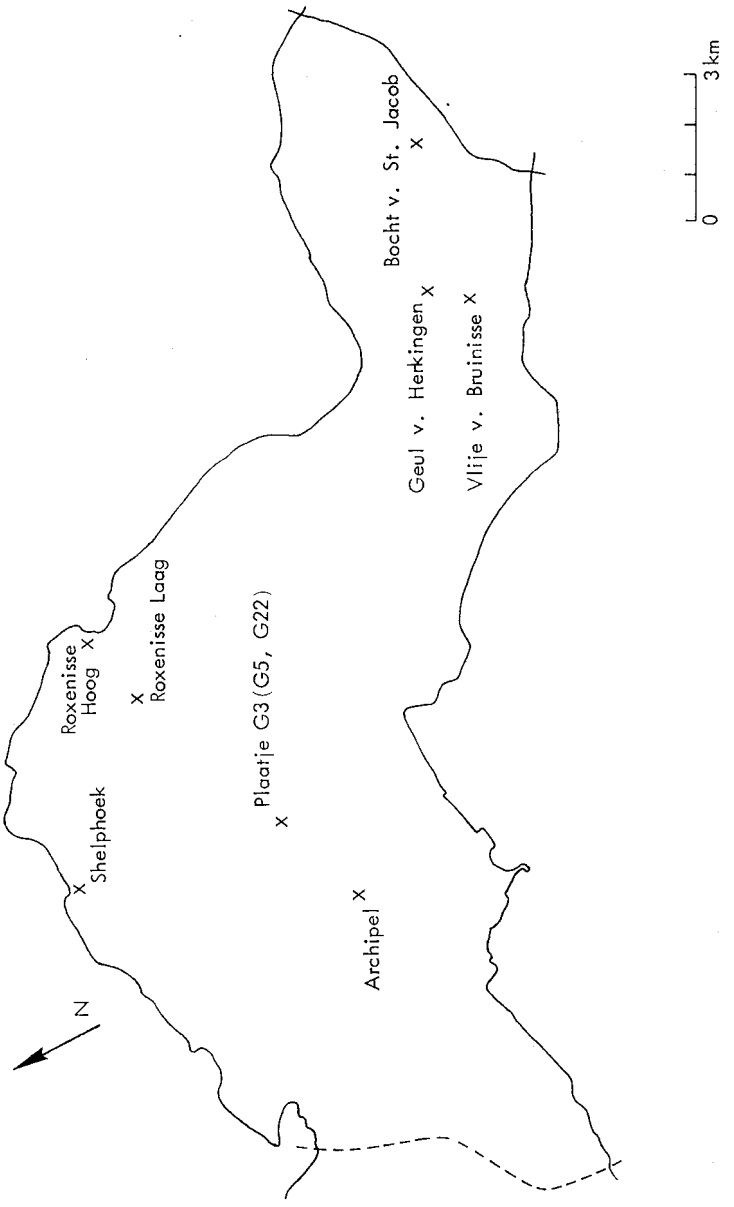

Fig. 8.1—Benthic sampling stations in the Grevelingen

Table 8.1

BENTHIC SAMPLING STATIONS AND THEIR AREAS IN THE GREVELINGEN

Stations	Area (sq km)	When the Station Was Sampled	
		Before Closure	After Closure
Deep Stations			
Archipel	31.4	X	X
Bocht v. St. Jacob	13.5		X
Geul van Herkingen	13.5	X	X
Total area of stations		44.9	58.4
Shallow Stations			
Plaatje G3	1.467	X[a]	X
Plaatje G5	1.467		X
Plaatje G22	1.467		X
Schelphoek	17.0	X	
Roxenisse Hoog	6.9	X	
Roxenisse Laag	19.0	X	
Vlije van Bruinisse	18.1		X
Total area of stations		7.3	22.5

NOTE: Since Plaatje G3, G5, and G22 have the same location, we used equal areas of 1.467 sq km for each station when samples were taken from all three (in the shallow segment after closure). However, we combined the areas, using 4.4 sq km when samples were collected only from Plaatje G3 (in the shallow segment before closure).

[a]Used 4.4 sq km instead of 1.467 sq km; see note above.

8.2. DATA ANALYSIS AND PROBLEMS

One of the problems encountered during the sampling 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.

The abundances of organisms other than mussels (i.e., deposit feeders, omnivores and worms, and benthic grazers) on the mussel plots had to be estimated by analogy with adjacent, uncultivated areas. We did this by means of a questionable procedure—namely, we assumed that the ratio of abundance of any ecogroup to mussels and oysters (oysters are relatively minor) in the shellfish area is the same as the ratio of the abundance of that ecogroup to cockles and limpets (limpets are relatively minor) in the shallow area. This assumption is based on the observation that cockles and mussels seemingly occupy a similar position in the food web and thus might be in the same numerical relationship to their predators. We believe this assumption to be reasonable though unproven.

Since the average annual mussel harvest in the open Grevelingen (15225 tons; Wolff, 1977) was about half the harvest in the Oosterschelde, the abundance estimates for the shellfish plots in the open Grevelingen are one-half of the estimates for the Oosterschelde shellfish plots.

Another 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

Table 8.2

SPECIES OF MACROBENTHOS SAMPLED IN THE OPEN GREVELINGEN

Ecological Group	Common Name	Species
Mussels/oysters	Mussels	*Mytilus edulis*
	Oysters	*Ostrea edulis*
Cockles/limpets	Cockles	*Cardium edule*
	Limpets	*Capitella*
Selective deposit feeders with pelagic larvae		*Macoma balthica*
		Scrobicularia plana
		Angulus tenuis
Crab/shrimp	Shore crab	*Carcinus maenas*
	Brown shrimp	*Crangon crangon*
Sea stars		*Asterias rubens*
Deposit feeders with nonpelagic larvae		*Scolopolos armiger*
		Tharix marioni
		Heteromastus filiformis
		Arenicola marina
		Corophium (diverse species)
Omnivores/predator worms		*Nereis diversicolor*
		Gammarus (diverse species)
		Harmothoes species
		Eteone longa
		Anaitides maculata
		Nephthys hombergi
Benthic grazers	Periwinkle	*Littorina littorea*
		Hydrobia ulvae

organisms that have been taken in the Oosterschelde suggest that they are not very dissimilar from those found in the Grevelingen.

A special cockle survey was conducted during February 1976 in the Oosterschelde by the Environmental Division of the Delta Service. From these data we have figures for cockles and limpets, benthic grazers, and selective deposit feeders. For these ecogroups, we could calculate the ratio of the February density to the yearly density from the data on the Grevelingen and use the same ratio to obtain a yearly estimate for the Oosterschelde.

The original benthic data were stored on tape. They were listed by sampling station, sampling date, and species size (year) class. The number of samples taken, the sample size, the mean ash-free dry weight per individual and its standard deviation, and the mean number of individuals per sample and its standard deviation were listed for each entry. From these data, we calculated the average density in grams per square meter and its standard deviation for each species, sampling date, and station. The data were separated into shallow and deep-sampling stations for before and after the closure date.

Each sampling station shown in Table 8.1 represents a certain area of the Grevelingen, as taken from Wolff (1977). To calculate the density of each species per segment, we multiplied the species density at each particular sampling station by the area represented by the sampling station from which it came; these figures were added, and then divided by the total area of the stations in the particular segment (see Table 8.1). The total abundance of an ecogroup in each segment was

calculated by combining the densities of the species within the ecogroup in the segment and then multiplying the density for the ecogroup by the areas of the respective segment (listed in Table 4.1).

We graphed the density (in grams of ash-free dry weight per square meter) and its standard deviation for each species at each station through the 5-year sampling period. Examples of these graphs are shown in Fig. 8.2 (*Cardium edule* at Plaatje G3), Fig. 8.3 (*Cardium edule* at Schelphoek), and Fig. 8.4 (*Littorina littorea* at Schelphoek). Not only do the abundances vary widely from month to month but also from year to year (see Chap. 1). The potential of these variations is suggested by the graphs. One can see that for cockles (*Cardium edule*) at a particular sampling station, Plaatje G3, the density varied from about 9 g/sqm in July 1970 to 185 g/sqm in September 1970, when the Grevelingen was open, to about 0.6 g/sqm in May 1973, when it was closed (Fig. 8.2). At another sampling station, Schelphoek, cockle densities ranged from about 83 g/sqm in September 1970 to 18 g/sqm in December 1970 in the open Grevelingen (Fig. 8.3). Similarly, *Littorina littorea* (benthic grazers) at Schelphoek ranged from about 37 g/sqm in May 1970 to 2 g/sqm in July 1970 (Fig. 8.4).

We can see from these graphs that data are missing for several months of some years. Sampling was too infrequent to account accurately for seasonal variations. Also, the sampling was not continued long enough to smooth out year-to-year fluctuations. However, the standard deviations are very large—in some cases, equal to or greater than the density itself. Thus, the monthly and yearly biomass fluctuations may be a reflection of errors in the measurement figures and not necessarily real. Because of the large standard deviations and the incompleteness of the data, we are skeptical of the density figures. We therefore chose the average values as representative of the biomass of each species at each station.

In many cases, the distribution of the locations at which a particular ecogroup was sampled is not broad enough to constitute a representative sampling from the highly nonuniform distribution of species. The sampling stations at which certain species were found when the Grevelingen was open were not necessarily sampled after closure. Some abundance estimates are based on samples taken at only three very close locations, i.e., cockles and selective deposit feeders at Plaatje G3, G5, and G22 in the shallow segment of the closed Grevelingen. The abundance estimates for benthic grazers and for deposit feeders with nonpelagic larvae in the deep segment of the open Grevelingen were based on samples taken at only one station. Thus, our estimates are indeed very uncertain.

8.3. MUSSELS AND OYSTERS

8.3.1. Oosterschelde

Since the shellfish growers did not permit sampling in the shellfish plots, we had to estimate the abundance of mussels and oysters indirectly from figures on commercial production. Drinkwaard (1975) reported an abundance for oysters of 4.1×10^6 kg in the Oosterschelde shellfish plots. We assumed that the meat weight is about 12 percent of the crude weight, including shell (Reay et al., 1943), and that the ash-free dry weight is approximately 18 percent of the meat weight (Vinogradov, 1953). This yielded an abundance of 0.89×10^8 g afdw.

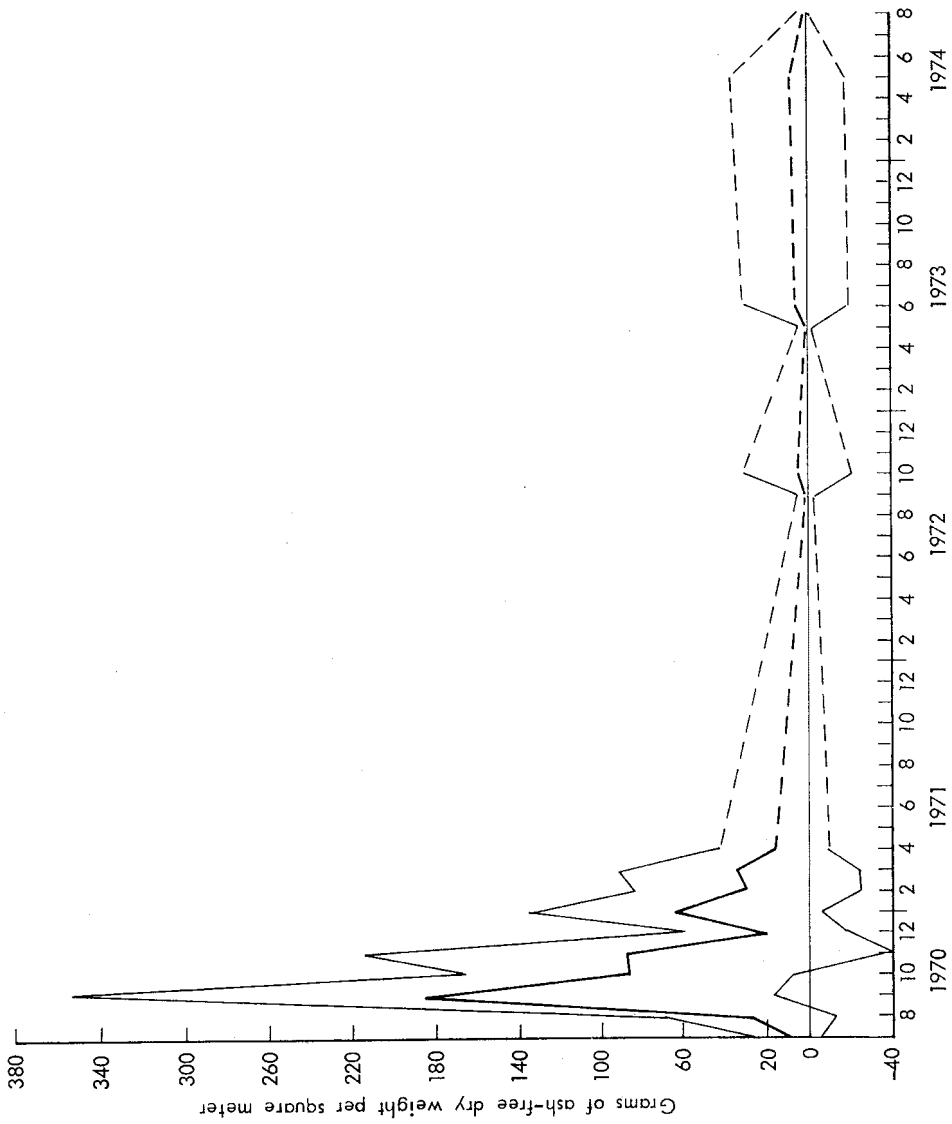

Fig. 8.2—Mean density—and mean density plus and minus one standard deviation—of Cardium at Plattje G3 in the Grevelingen

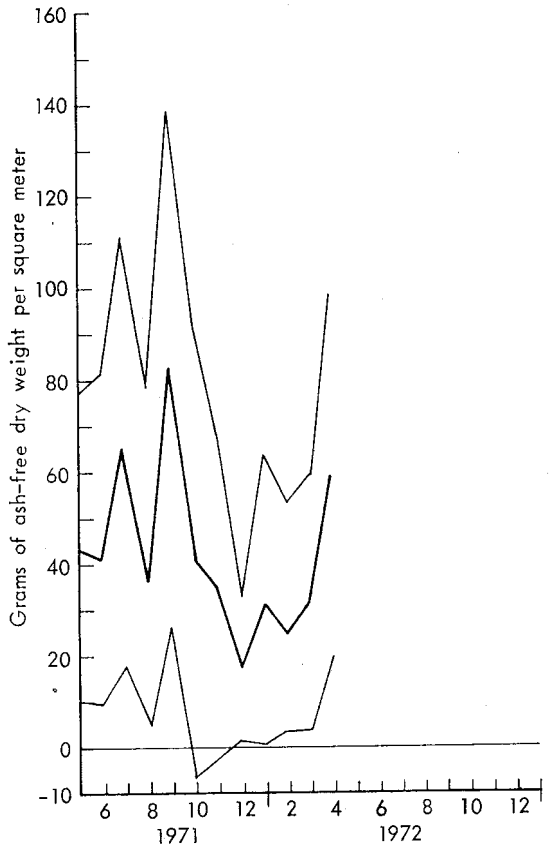

Fig. 8.3—Mean density—and mean density plus and minus one standard deviation—of Cardium at Schelphoek in the in the Grevelingen

The abundance of cultured mussels is a combination of the estimated abundance of the standing stock plus the rewatering stock. The harvest of mussels in the Oosterschelde has been reported as 3×10^7 kg crude weight per year (Ministry, Annual Report, 1971, Table II). Assuming a P/B ratio of 1.5 (calculated from Table 6.6 of Volume III, and also in accordance with W. J. Wolff, personal communication), the average biomass would be 20×10^6 kg. This is in accordance with A. C. Drinkwaard and J. D. Holstein (personal communication), who stated that the minimum and maximum biomass of mussels (not including those rewatered) are 10 and 30 million kg. Therefore, we chose the average standing stock (excluding Waddensea mussels in storage) to be 20×10^6 kg crude weight. We assumed that the meat weight of mussels is 28 percent of the crude weight (Reay et al., 1943) and that the ash-free dry weight is about 15 percent of the meat weight (Vinogradov, 1953). So the ash-free dry weight would be .042 times the crude weight. Multiplying the crude weight by .042, we obtained a standing stock of 8.4×10^8 g afdw.

Mussel rewatering takes place about 10 months per year, with an estimated mean biomass of 10×10^6 kg of mussels. On the average, this is ten-twelfths of 10

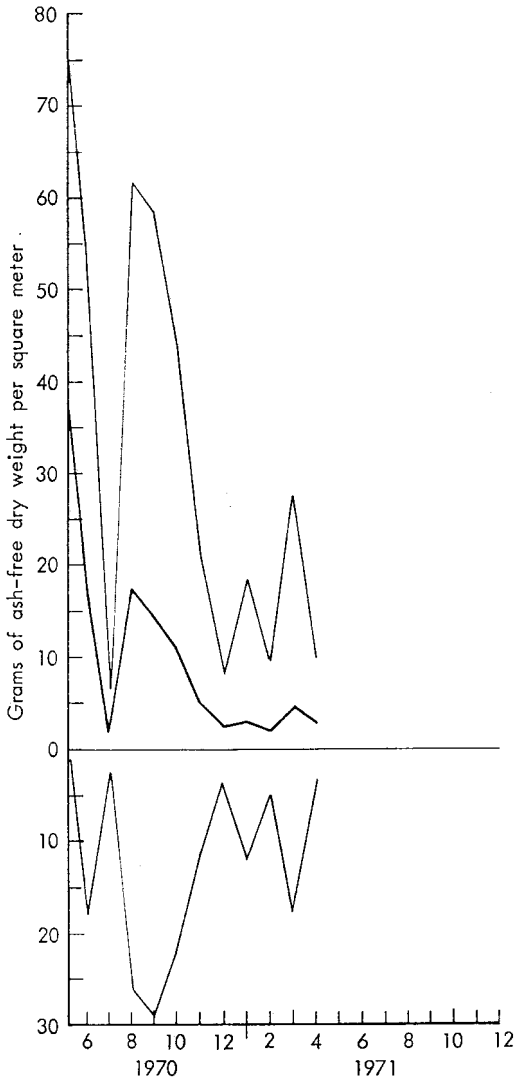

Fig. 8.4—Mean density—and mean density plus and minus one standard deviation—of Littorina at Schelphoek in the Grevelingen

$\times 10^9$ g times .042, or 3.5×10^8 g ash-free dry weight. Thus, by combining the standing stock and the rewatering stock, we obtained 11.9×10^8 g afdw of mussels in the Oosterschelde.

We therefore conclude that mussels and oysters in the Oosterschelde shellfish plots have a biomass of $(11.9 + .89) \times 10^8$ g, or 1.28×10^9 g afdw.

As we explained in Vol. III, this initial estimate assumed that man was the sole predator on mussels and oysters. This assumption is manifestly untenable, and we later increased our estimate to 2000 tons afdw.

8.3.2. Open Grevelingen

The average annual mussel harvest in the open Grevelingen (15225 tons) was about half the estimated harvest in the Oosterschelde (Wolff, 1977). We assume, therefore, that the open Grevelingen contained half the abundance found in the Oosterschelde, or 1000 metric tons afdw.

8.3.3. Closed Grevelingen

Using benthic data from the Delta Institute (see Sec. 8.4, below), we estimated that the closed Grevelingen contains only about 133 tons afdw of cockles. However, mussels and cockles are members of different ecogroups only because they live in different segments. Their diets and predators are essentially the same. So the ecogroup "cockles and limpets" must be interpreted as including mussels, oysters, and limpets in the shallow and the deep benthic segments. There are some data from the Delta Institute on uncultured mussels in the closed Grevelingen. Table 8.3 lists the average density per station for mussels in the shallow and deep segments of the closed Grevelingen. From these data, we calculated an abundance of 1893.9 tons afdw in the deep segment and 5815.8 tons afdw in the shallow segment. These figures seem too large. The R.I.V.O. recently conducted a mussel-fishing experiment in the closed Grevelingen, where they recovered about 420 tons afdw of mussels. Perhaps the actual abundance of mussels in the closed Grevelingen is somewhere in between these estimates.

Table 8.3

AVERAGE DENSITY OF MUSSELS IN THE CLOSED GREVELINGEN

(In gm afdw/sqm)

Stations	Average Density
Shallow Segments	*107.9*
Plaatje G3	12.5198
Plaatje G5	2.3658
Plaatje G22	0.5984
Vlije van Bruinisse	132.8831
Deep Segments	*35.87*
Archipel	60.6002
Bocht v. St. Jacob	1.6004
Geul van Herkingen	12.6358

8.3.4. Average Weight per Individual

Wolff (1977, Table IV) presents an average ash-free dry weight of .1875 g per individual mussel. This is .15 times the meat weight. We therefore chose 1.25 g as the average weight of the ecogroup. Although this is somewhat smaller than our original estimate, it does not markedly affect the daily ration or metabolic parameters used in the model (see Table 1.4).

8.4. COCKLES AND LIMPETS

8.4.1. Average Weight per Individual

We averaged Wolff's (1977, Table IV) 1964-1970 figures for the weight per individual cockle. This averaging yielded .2577 g afdw per cockle. Assuming that the ash-free dry weight is about 20 percent of the meat weight, we determined the average wet weight to be 1.29 g. Since the numbers of limpets are relatively minor compared with those of cockles, we use this average meat weight for the ecogroup.

8.4.2. Cockles in the Grevelingen

The average density (g afdw/sqm) of cockles for each station in the open and closed Grevelingen was calculated from the benthic data collected by the Delta Institute (Table 8.4). Multiplying the density per segment by the respective segment area (Table 4.1) yields the results (the value for the deep segment of the closed Grevelingen includes limpets) shown in Table 8.5.

Table 8.4

AVERAGE DENSITY OF COCKLES (*CARDIUM*) AND LIMPETS (*CAPITELLA*) IN THE OPEN AND CLOSED GREVELINGEN

(In g afdw/sqm)

Species	Stations	Average Density per Station	Average Density per Segment
	Open Grevelingen		
	Shallow Segment		
Cardium edule	Schelphoek	42.5219	25.9330
	Roxenisse-Hoog	0.0393	
	Roxenisse-Laag	15.2329	
	Plaatje G3	48.6505	
	Deep Segment		
Cardium edule	Archipel	6.7934	4.7675
	Geul van Herkingen	0.0553	
	Closed Grevelingen		
	Shallow Segment		
Cardium edule	Vlije van Bruinisse	1.2379	2.3044
	Plaatje G5	5.8893	
	Plaatje G22	9.5081	
	Plaatje G3	4.6314	
	Deep Segment		
Cardium edule	Geul van Herkingen	0.0879	0.4121
	Bocht v. St. Jacob	0.1206	
	Archipel	0.6769	
Capitella	Geul van Herkingen	0.0010	0.0006
	Archipel	0.0006	

Table 8.5

ABUNDANCE OF COCKLES IN THE OPEN AND CLOSED GREVELINGEN

Segment	Density (g afdw/sqm)	Abundance (tons afdw)
Open Grevelingen		
Shallow	25.9	1983.9
Deep	4.8	376.2
Closed Grevelingen		
Shallow	2.3	124.2
Deep	0.41	21.8

8.4.3. Cockles in the Oosterschelde

A cockle survey on the intertidal flats of the Oosterschelde was conducted in February 1976 by the Environmental Division of the Delta Service. The analysis included 92 samples of 0.25 sqm each. Cockles were found in 78 of the samples. The average ash-free dry weight (grams) for each year class per sample is shown in Table 8.6.

Table 8.6

AVERAGE WEIGHT OF COCKLES IN THE OOSTERSCHELDE

Year-class	*Average Weight (g afdw/sqm)*
1970 and earlier	0.35
1971	0.54
1972	1.19
1973	2.43
1974	0.30
1975	0.74
Sum over year-classes	5.64

Dividing by the area of a sample yields 22.56 g/sqm in the 78 samples, or 19.13 g/sqm in the 92 samples. From the data from the open Grevelingen, we calculated that the average yearly density in the flats of the open Grevelingen (16.33 g/sqm) was about 1.59 times its February average density. By applying the same ratio to the Oosterschelde, we obtained approximately 30.4 g afdw/sqm of cockles in the tidal flats.

In the same cockle survey, 38 samples from the deep segment of the Oosterschelde were analyzed, each having an area of about 0.2 sqm. Only 9 cockles were found having a total ash-free dry weight of 4.39 g, which gives us a density in the deep segment of about .58 g/sqm in February. The density in the deep segment of the open Grevelingen in February (6.52 g/sqm) was about 1.36 times its yearly average density. Applying this same ratio to the density in the Oosterschelde, we

obtained a yearly average of .43 g/sqm of cockles in the deep segment of the Oosterschelde. This is much less than the estimate for the open Grevelingen. The figures for the Oosterschelde are given in Table 8.7.

Table 8.7

ABUNDANCE OF COCKLES IN THE OOSTERSCHELDE

Segment	Density (g afdw/sqm)	Abundance (tons afdw)
Shallow	30.4	7630.4
Deep	0.43	86.2

8.4.4. Abundance of Cockles and Limpets

During the cockle survey in February 1976, a limpet density of .825 g adfw/sqm was found in the flats. Since we do not have data to estimate a seasonal correction, we assumed the same correction as for cockles and thus obtained an abundance of limpets of 329 tons and a total average abundance for the cockle/limpet group of 7960 tons afdw in the Oosterschelde. This limpet abundance is about .043 times the cockle abundance in the Oosterschelde tidal flats. If we assume the same ratio for the open Grevelingen flats, we get 88.4 tons of limpets in the open Grevelingen. Adding this figure to the abundance of cockles gives us about 2072.3 tons of cockles and limpets in the open Grevelingen tidal flats. Then, if we assume the same ratio for the shallow segment of the closed Grevelingen, we get 13.4 tons of limpets, or 137.6 tons of cockles and limpets.

We have data from the Delta Institute on limpet densities in the deep segment of the closed Grevelingen. These data show that there were .0006 g/sqm of limpets as compared with .4121 g/sqm of cockles. Since limpets are very minor, we ignore them in the deep segment.

8.5. SELECTIVE DEPOSIT FEEDERS WITH PELAGIC LARVAE

8.5.1. Grevelingen

This ecogroup includes three species: *Angulus tenuis, Macoma balthica,* and *Scrobicularia plana* (Table 8.2). We calculated the density of each species at each station in the open and closed Grevelingen from the benthic data from the Delta Institute (Table 8.8). Combining the species densities for each segment yielded the densities and abundances given in Table 8.9.

8.5.2. Oosterschelde

Selective deposit feeders were sampled on the Oosterschelde tidal flats during the cockle survey in February 1976. The densities are shown in Table 8.10.

Table 8.8

AVERAGE DENSITY OF SELECTIVE DEPOSIT FEEDERS WITH PELAGIC LARVAE IN THE OPEN AND CLOSED GREVELINGEN

(In g afdw/sqm)

Species	Stations	Average Density per Station	Average Density per Segment
	Open Grevelingen		
Macoma balthica	*Shallow Segment*		
	Roxenisse-Hoog	3.0919	1.8636
	Plaatje G3	0.2094	
	Schelphoek	2.9256	
	Roxenisse-Laag	0.8904	
	Deep Segment		
Macoma balthica	Geul van Herkingen	0.0163	0.0997
	Archipel	0.1355	0.0997
	Closed Grevelingen		
Macoma balthica	*Shallow Segment*		
	Plaatje G3	0.1873	0.0136
	Vlije van Bruinisse	0.0017	
Angulus tenuis	Plaatje G3	7.5938	1.7026
	Plaatje G5	18.3733	
	Vlije van Bruinisse	0.0076	
	Deep Segment		
Angulus tenuis	Archipel	0.1292	0.0706
	Geul van Herkingen	0.0048	
Macoma balthica	Geul van Herkingen	0.0076	0.0176
	Archipel	0.0295	
Scrobicularia plana	Archipel	0.0005	0.0003

Table 8.9

ABUNDANCE OF SELECTIVE DEPOSIT FEEDERS WITH PELAGIC LARVAE IN THE OPEN AND CLOSED GREVELINGEN

Segment	Density (g afdw/sqm)	Abundance (tons afdw)
Open Grevelingen		
Shallow	1.86	142.6
Deep	0.0997	3.33
Closed Grevelingen		
Shallow	1.72	92.1
Deep	0.0885	4.67

Table 8.10

DENSITY OF SELECTIVE DEPOSIT FEEDERS WITH PELAGIC LARVAE IN THE OOSTERSCHELDE DURING THE COCKLE SURVEY OF FEBRUARY 1976

Species	*Density (g afdw/sqm)*
Macoma balthica	0.154
Scrobicularia plana	0.038
Angulus tenius	0.001
Total density	0.193

The total density of the ecogroup is 0.193 g/sqm. From the open Grevelingen data for tidal flats, we find that the yearly density for the group is about 1.7 times the February density. We used this ratio for the Oosterschelde. Thus, the average yearly density in the tidal flats is .328 g afdw/sqm. This yields 82.33 tons afdw. None of these organisms were found in the deep segment.

Note how much smaller this estimate is than the estimate of Table 8.4 of Vol. III. That earlier estimate assumed that the density of selective deposit feeders was the same on the tidal flats of the Oosterschelde as on the tidal flats of the open Grevelingen. In fact, because the open Grevelingen was similar in so many ways to the Oosterschelde (including the similarity of cockle abundance), and because the estimate of density in the Grevelingen is based on so many more samples than were taken in the Oosterschelde, we are inclined to believe the new estimate of 82.33 tons afdw is a gross underestimate.

8.5.3. Average Weight per Individual

From Wolff (1977, Table IV), we obtain the average ash-free dry weight for *Angulus tenuis* (.0135), *Macoma balthica* (.0261), and *Scrobicularia plana* (.0166). Averaging these weights yielded .0187 g afdw/sqm for the group. Assuming the ash-free dry weight to be about 20 percent of the live weight, we find that the wet weight per individual is .1169 g.

8.6. CRABS AND SHRIMP

8.6.1. Abundance of Brown Shrimp

The brown shrimp (*Crangon crangon*) is a migratory resident of the estuary. Data on brown shrimp in the Oosterschelde were collected for the *Demersal Young Fish Survey* in terms of numbers of individuals per 1000 sqm during the spring and autumn of 1969 to 1975. (See explanation of flatfish data, Sec. 9.22.) Data for the open Grevelingen, also collected for the *Demersal Young Fish Survey*, were available only for the spring and autumn of 1969 and 1970.

The data are listed for three size (year) classes of brown shrimp (Table 8.11). To convert the length into weight per individual shrimp in grams (W), we use the equation $W = 0.007 \times L^3$, where L is the length in centimeters (Meijering, 1976).

The medium weights are calculated by using the average length of each size class. This procedure yields the minimum, medium, and maximum weights shown in Table 8.12.

The minimum weights constitute a gross underestimate, since they assign such a small weight to shrimp in the small size class. So we use the medium and maximum weight estimates to calculate the densities.

Table 8.11

AVERAGE DENSITY OF BROWN SHRIMP: NUMBER OF INDIVIDUALS PER 1000 SQM[a]

Sampling Date	Size Class (mm)		
	<54	54-67	>67
Oosterschelde			
April 1969	93.08	37.26	3.61
October 1969	507.84	75.75	8.26
May 1970	36.33	22.54	2.14
October 1970	476.94	125.96	10.73
August 1971	354.91	28.52	0.03
October 1971	536.73	77.75	2.06
April 1972	412.36	45.83	4.31
October 1972	293.18	76.32	6.55
April 1973	187.79	43.16	5.38
November 1973	1182.60	288.28	15.66
April 1974	204.80	46.92	3.83
October 1974	318.21	86.60	7.87
April 1975	166.21	36.66	2.38
October 1975	626.83	142.19	5.03
Open Grevelingen			
April 1969	28.22	18.54	0.74
October 1969	411.26	97.11	6.04
May 1970	62.53	30.96	1.78
October 1970	853.30	233.20	3.20

[a]These figures must be multiplied by ten-twelfths to account for shrimp being present in the estuary for only 10 months per year.

Table 8.12

WET WEIGHT PER INDIVIDUAL BROWN SHRIMP

Size Class (cm)	Weights (g)		
	Minimum	Medium	Maximum
3.0-5.4	0.19	0.52	1.10
5.4-6.7	1.10	1.50	2.11
6.7-8.0	2.11	2.78	3.58

The average density of shrimp in terms of numbers of individuals per 1000 sqm was calculated by taking the average of the spring and autumn values and then multiplying the result by ten-twelfths, because shrimp are present in the estuary for 10 months per year. We multiplied the numbers per 1000 sqm by the medium and maximum weight estimates to obtain the medium and maximum densities in terms of grams of wet weight per square meter and then averaged the medium and maximum densities. The results are shown in Table 8.13.

Table 8.13

MEDIUM AND MAXIMUM DENSITY ESTIMATES OF BROWN SHRIMP

Size Class (cm)	Density (individuals/ 1000 sqm)	Medium Weight (g)	Medium Density (g/sqm)	Maximum Weight (g)	Maximum Density (g/sqm)
Oosterschelde					
3.0-5.4	299.05	0.52	0.156	1.1	0.329
5.4-6.7	63.83	1.50	0.094	2.11	0.133
6.7-8.0	4.42	2.78	0.012	3.58	0.016
Open Grevelingen					
3.0-5.4	281.24	0.52	0.146	1.1	0.309
5.4-6.7	78.81	1.50	0.118	2.11	0.166
6.7-8.0	2.44	2.78	0.007	3.58	0.009

The average of the medium and maximum densities for both the Oosterschelde and the open Grevelingen is approximately 0.38 g/sqm. Ash-free dry weight is about 20 percent of the live weight (Vinogradov, 1953). In addition, a correction of 0.5 (Reay et al., 1943) is introduced for the shell of the shrimp. The ash-free dry weight then becomes 0.1 times the live weight. We thus have .04 g afdw/sqm of shrimp in the deep segment of the open Grevelingen and the Oosterschelde.

Fishing took place mainly at high tide, and the shrimp on the flats during high tide are very young. We therefore assumed their biomass to be 50 percent of the density in the deep segment, or .02 g afdw/sqm. Assuming a 0.66 correction for gear efficiency gives us densities of .06 in the deep segment and .03 in the shallow segment. Here we assumed the same density for the shellfish plots as in the shallow segment. Multiplying these densities by the respective segment areas, we obtained the abundances shown in Table 8.14.

Table 8.14

ABUNDANCE OF BROWN SHRIMP

Segment	Oosterschelde (tons afdw)	Open Grevelingen (tons afdw)
Deep	12.00	2.00
Shallow	7.53	2.30
Shellfish plots	0.75	0.61

8.6.2. Abundance of Shore Crab

Data on the shore crab (*Carcinus maenas*) in the deep segment of the Oosterschelde are from the *Demersal Young Fish Survey* and are shown in Table 8.15 in terms of numbers of individuals per 1000 sqm. By averaging the spring and autumn averages, we obtained a yearly density of about 5 individuals per 1000 sqm, or .005 individual per square meter.

Table 8.15

DENSITY OF SHORE CRAB IN THE OOSTERSCHELDE

(Individuals/1000 sqm)

Sampling Date	Spring (April/May)	Autumn (September/October)	
1971	--	16.26 [Aug.]	13.90 (avg. for autumn 1971)
1971	--	11.54 [Sept./Oct.]	
1972	4.07	1.64	
1973	2.07	12.98	
1974	1.75	0.94	
Average density	2.63	7.37	

Klein Bretler (1975) found the following relationship between the carapace width (mm) and ash-free dry weight (mg): $\log W = 2.82 \times \log L - 1.14$, where W is the ash-free dry weight and L is the carapace width. From Klein Bretler, we assumed that the average carapace width is about 10 mm. Thus, the average ash-free dry weight is about 0.048 g. The density in the deep segment is then .00024 g afdw/sqm. If we assume a gear efficiency of 0.2, it becomes 0.0012 g afdw/sqm.

Klein Bretler states that very young crabs are numerous on the flats but their biomass is very small. From his Table I (1976a), we infer that we may assume a similar density for the tidal flats.

We have no information on cultivated mussel plots, which differ from tidal mussel plots in that they are permanently covered with water. However, from Klein Bretler's Fig. 7 (1976b), we infer that the density of crabs on the tidal mussel beds is greater than that of the flats by a factor of about 10. So we estimate a density of .012 g/sqm on the shellfish plots. In Table 8.16, we assumed the same densities for both the open Grevelingen and the Oosterschelde.

Table 8.16

ABUNDANCE OF SHORE CRABS

Segment	Oosterschelde (tons afdw)	Open Grevelingen (tons afdw)
Deep	0.24	0.064
Shallow	0.32	0.064
Shellfish plots	0.32	0.24

8.6.3. Abundance of Crab and Shrimp

We combined the abundances for crab and shrimp to obtain the total abundances shown in Table 8.17. We obtained our data on crab and shrimp in the deep segment of the closed Grevelingen from the Delta Institute. From these data, we calculated .06 g/sqm, or 3.35 tons afdw, of crab and shrimp in the deep bottoms of the closed Grevelingen.

Table 8.17

ABUNDANCE OF CRAB AND SHRIMP

Segment	Oosterschelde (tons afdw)	Open Grevelingen (tons afdw)
Deep	12.24	2.064
Shallow	7.85	2.364
Shellfish plots	1.07	0.85

8.6.4. Average Weight per Individual

We use the data from the *Demersal Young Fish Survey* to determine the average weight per individual shrimp. The densities in the Oosterschelde and in the open Grevelingen are similar. The average number of individual shrimp per square meter is about .365, and the average number of grams of shrimp per square meter is about .38. This yields about 1.0 g per individual shrimp.

Reay et al. (1943) state that crab contain .4 edible part, which is assumed here to be the meat percentage of the total live weight. About 12 percent of the live weight is ash-free dry weight (Vinogradov, 1953). So the ash-free dry weight is .048 times the total weight. This yields a wet weight of about 1 g for crab, which is similar to that of shrimp. Although this is much larger than our original estimate, it makes relatively little difference in the ration and metabolic parameters.

8.7. SEA STARS

8.7.1. Average Weight per Individual

Van der Schort (1974) found a length ash-free dry weight (W) relationship of $W = 0.011\ L^3$. Here L is the distance from the tip of the arm to the point between the two opposite arms. He also found a length of approximately 5 to 6 cm at most sampling stations in the closed Grevelingen. The average individual would then have a weight of 1.38 to 2.38 g afdw, or about 2 g afdw. Assuming that the ash-free dry weight is about 18.5 percent of the live weight (Vinogradov, 1953), the wet weight is about 10.8 g per individual.

8.7.2. Shellfish Plots

We do not have data from the shellfish plots because the fishermen do not permit sampling there. According to A. C. Drinkwaard, A. L. Abrahamse, and J. D. Holstein (personal communication), crabs and sea stars in the Oosterschelde comprise about 1 percent of the biomass of mussels and oysters, which equals 1 percent of 3.0×10^7 kg live weight (Table 1.1), or 3.0×10^5 kg of crabs and sea stars. If we assume that sea stars have the same biomass as crabs, then sea stars have a biomass of about 1.5×10^5 kg wet weight, or 2.78×10^7 g afdw. The open Grevelingen is assumed to have contained one-half of this amount, or 1.4×10^7 g afdw.

Sea stars were collected from one station (Guel van Herkingen) in the deep segment of the closed Grevelingen by the Delta Institute. From the data, we calculated 3.95 g/sqm, or 208.6 tons afdw. However, this finding is probably misleading. We have been told that sea stars may reproduce less or not at all in the closed Grevelingen, and that since their life span is 5 to 6 years, we should now begin to notice a decrease in their numbers.

8.7.3. Deep Segment

The *Demersal Young Fish Survey* presents data on sea stars in the deep segment of the Oosterschelde (Table 8.18). From these data, we calculated 7.4 individuals per 1000 sqm, or 0.0074 individual per square meter. Unfortunately, the sampling method is likely to miss a high proportion of sea stars, because they will probably go under the chain at the mouth of the net. We therefore assumed that only 5 percent are caught, which makes their density 0.15 individual per square meter. If the average weight per individual is 2.0 g, then their biomass is .3 g/sqm. The total biomass thus becomes 6.01×10^7 g/afdw. We assumed the same density in the open Grevelingen, which gives us about 10 tons afdw.

Table 8.18

AVERAGE DENSITY OF THE SEA STAR IN THE DEEP SEGMENT OF THE OOSTERSCHELDE

Sampling Date	*Number of Individuals per 1000 sqm*
August 1971	16.40
October 1971	14.60
April 1972	3.19
October 1972	6.16
April 1973	2.83
November 1973	13.99
April 1974	1.86
October 1974	0.51

8.8. DEPOSIT FEEDERS WITH NONPELAGIC LARVAE

8.8.1. Abundance

This ecogroup includes the five species listed in Table 8.2. We calculated the densities for the open and closed Grevelingen from the benthic data from the Delta Institute. The average density of each species per station and per segment is listed in Table 8.19. Since we have no data for the Oosterschelde, we assumed that the densities were the same as those for the open Grevelingen. By combining the densities for the species, we derived, for each segment, the densities and abundances given in Table 8.20.

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 shallow segment of the Grevelingen after closure. However, since closure, sampling in the shallow segment 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 shallow segment of the closed Grevelingen.

Table 8.19

AVERAGE DENSITY OF DEPOSIT FEEDERS WITH NONPELAGIC LARVAE IN THE OPEN AND CLOSED GREVELINGEN

(In g afdw/sqm)

Species	Stations	Average Density per Station	Average Density per Segment
	Open Grevelingen		
	Shallow Segment		
Arenicola marina	Roxenisse-Laag	10.8980	6.1929
	Roxenisse-Hoog	3.2634	
	Schelphoek	3.7262	
	Deep Segment		
Arenicola marina	Geul van Herkingen	0.0127	0.0038
	Closed Grevelingen		
	Deep Segment		
Corophium	Geul van Herkingen	0.0268	0.0062
Heteromastus filiformis	Geul van Herkingen	0.0044	0.0010
Scoloplos armiger	Geul van Herkingen	0.0040	0.0306
	Archipel	0.0552	
Tharyx marioni	Archipel	0.0014	0.0032
	Geul van Herkingen	0.0105	

Table 8.20

ABUNDANCE OF DEPOSIT FEEDERS WITH NONPELAGIC LARVAE

Segment	Density (g afdw/sqm)	Abundance (tons afdw)
Open Grevelingen		
Shallow	6.19	473.8
Deep	0.0038	0.127
Oosterschelde		
Shallow	6.19	1553.7
Deep	0.0038	0.762
Closed Grevelingen		
Deep	0.0885	4.67

8.8.2. Average Weight per Individual

From Wolff (1977, Table IV), we find that *Arenicola marina* has an average ash-free dry weight per individual of 0.1271 g. We used this weight as a representative weight of the ecogroup, and, assuming that the ash-free dry weight is 20 percent of the live weight, established .6355 g as the wet weight per individual.

8.9. OMNIVORES AND PREDATOR WORMS

8.9.1. Average Weight per Individual

Our data on the weight per individual of each species in the deep segment of the closed Grevelingen were obtained from the Delta Institute. We average the values for each species as shown in Table 8.21. The average weight per individual for omnivores is .0078 g afdw and for predator worms, .0020 g afdw. Below we show that predator worms are about twice as abundant as omnivores. Thus, the total average ash-free dry weight is .00393 g/individual. Assuming that the ash-free dry weight is 16 percent of the live weight (Vinogradov, 1953), we obtain a wet weight of .0248 g.

Table 8.21

AVERAGE WEIGHT OF OMNIVORES AND PREDATOR WORMS

	Weight (g afdw/ individual)
Omnivores	
Gammarus (diverse species)	0.0092
Nereis diversicolor	0.0063
Average	0.0078
Predator Worms	
Anaitides maculata	0.00059
Nephthys hombergi	0.0034
Eteone longa	0.0012
Harmothoes species	0.0028
Average	0.0020

8.9.2. Abundance of Omnivores

There are two main organisms in this class: *Nereis diversicolor*, and *Gammarus* of various species. From Wolff (1977, Table I), we note that in the open Grevelingen, *Gammarus* was found at 5.7 percent of all sampling stations intertidally and at 2.7 percent subtidally. According to Wolff, each intertidal station was sampled with a device of 177 cm^2, and 35 to 50 samples were taken, for a total area sampled of .62 to .885 sqm (or approximately equal to 0.75 sqm). Each subtidal station was sampled 35 to 50 times with a 0.1 sqm device, which yielded 3.5 to 5.0 sqm (approximately equal to 4.25 sqm).

Assuming a Poisson distribution, we infer from these figures that if the expected number of *Gammarus* individuals is λ per intertidal station, then the chance of finding none at a station is $e^{-\lambda}$. Thus

Shallow Segment: $e^{-\lambda} = 1 - .057$ or $\lambda = .059$,
or .078 individual per square meter.

Deep Segment: $e^{-\lambda} = 1 - .027$ or $\lambda = .0274$,
or .0064 individual per square meter.

Assuming an average weight of .0092 g for *Gammarus* (Sec. 8.9.1), we get .0092 g/individual $\times$ .078 individual per square meter, or .000718 g/sqm in the shallow area of the open Grevelingen and .0092 g/individual $\times$ .0064 individual per square meter, or .0000589 g/sqm in the deep area. Of course, if *Gammarus* tends to cluster more, then these omnivores could be more numerous.

A similar procedure can work for *Nereis diversicolor*. Table I of Wolff (1977) shows that *Nereis* is found at 41.4 percent of the intertidal stations and at 0.9 percent of the subtidal stations. Using the method described for *Gammarus*, we derived the following:

Shallow Segment: $e^{-\lambda} = 1 - .414$ or $\lambda = .534$,
or .713 individual per square meter.

Deep Segment: $e^{-\lambda} = 1 - .009$ or $\lambda = .009$
or .002 individual per square meter.

We used an average weight for *Nereis* of .0063 g/individual. This yielded .713 individual per square meter $\times$ .0063 g/sqm, or .00449 g/sqm in the flats and .002 individual per square meter $\times$ .0063 g/sqm, or .0000126 g/sqm in the deep segment.

For *Nereis*, we can use another method to check the tendency of this species to cluster. We first obtain, from Fig. 27 of Wolff (1973a), a number of samples for each segment in the open Grevelingen that contain various numbers of *Nereis* individuals, as shown in Table 8.22. With these figures, we can calculate minimum, maximum, and "intermediate" average numbers of *Nereis* per sample. These numbers are based on the assumptions shown in Table 8.23. Our estimates then become those shown in Table 8.24.

Before we estimate biomass, we must estimate the proportion of samples that contain no individuals. Using the minimum estimates above, and assuming a Poisson distribution, we find that the chance of an empty sample is essentially zero. In

Table 8.22

NUMBER OF SAMPLES CONTAINING VARIOUS NUMBERS OF *NEREIS* INDIVIDUALS: OPEN GREVELINGEN

Number of Individuals per Sample	Number of Samples	
	Shallow Segments	Deep Segments
1-5/.1 sqm	3	27
6-25/.1 sqm	3	8
>25/.1 sqm	4	4

Table 8.23

ASSUMED AVERAGE NUMBER OF INDIVIDUAL *NEREIS* PER SAMPLE: OPEN GREVELINGEN

Range in Number of Individuals per Sample	Assumed Average Number of Individuals per Sample		
	Minimum Estimate	Intermediate Estimate	Maximum Estimate
1-5/.1 sqm	1	3	5
6-25/.1 sqm	6	10	25
>25/.1 sqm	26	35	50

Table 8.24

AVERAGE NUMBER OF *NEREIS* INDIVIDUALS PER SAMPLE IN SAMPLES CONTAINING ONE OR MORE INDIVIDUALS: OPEN GREVELINGEN

Segment	Average Number of Individuals per Sample		
	Minimum Estimate	Intermediate Estimate	Maximum Estimate
Shallow	12.5	17.9	29.0
Deep	4.6	7.7	13.7

the shallows, 58.6 percent of the stations have no individuals. Of the other stations, perhaps many samples fail to have individuals. Indeed, the parameters of Wolff's model (1973a) suggest that upwards of 90 percent of the individual samples (of size 0.1 sqm) will fail to have individuals. This is consistent if

$$P \text{ (no individuals in .75 sqm)} = [P \text{ (no individuals in .1 sqm)}]^{7.5};$$

then,

$$.586 = [P \text{ (no individuals in .1 sqm)}]^{7.5} = > P \text{ (no individuals in .1 sqm)} = .93.$$

On the other hand, in the shallow segment, we have an even larger probability of not finding individuals—namely, .991 (Wolff, 1977). This yields the densities shown in Table 8.25.

Table 8.25

DENSITY OF *NEREIS DIVERSICOLOR* IN THE OPEN GREVELINGEN

Segment	Number of Individuals per Square Meter in Samples with at Least One Individual	Fraction of Samples with Individuals	Density (g afdw/sqm)
Shallow[a]	179	0.07	0.790
Deep	77	0.009	0.0044

[a]Scale samples and probabilities to 0.1 sqm size.

Clearly, *Nereis diversicolor* has a considerable tendency to cluster. We will assume that *Gammarus* shares this tendency and scale up our previous estimates of its abundance by the ratios of abundances found by the two methods for *Nereis diversicolor*. That is, we will assume that the ratio of the new and previous density estimates for *Gammarus* is equal to the ratio of the new and previous density estimates for *Nereis*. The resulting densities for omnivores in the open Grevelingen are shown in Table 8.26.

Table 8.26

AVERAGE DENSITY OF OMNIVORES IN THE OPEN GREVELINGEN

Segment	Density (g afdw/sqm)		
	Nereis	*Gammarus*	Omnivores
Shallow	0.079	0.0126	0.0916
Deep	0.0044	0.0206	0.0250

8.9.3. Abundance of Omnivores and Predator Worms

Since Wolff found no predatory worms in the open Grevelingen, a direct estimate is not possible. We do have data for predatory worms from the Delta Institute for the deep segment of the closed Grevelingen only. From these data, we calculated the density of each species per station and per segment (Table 8.27). Adding the

Table 8.27

AVERAGE DENSITY OF OMNIVORES AND PREDATOR WORMS IN THE DEEP SEGMENT OF THE CLOSED GREVELINGEN

(In g afdw/sqm)

Species	Station	Average Density per Station	Average Density in Deep Segment
	Omnivores		
Gammarus species	Geul van Herkingen	0.0256	0.0059
Nereis diversicolor	Archipel	0.0020	0.0152
Nereis diversicolor	Geul van Herkingen	0.0609	
	Predator Worms		
Harmothoes species	Geul van Herkingen	0.0137	0.0032
Nephthys hombergi	Geul van Herkingen	0.0485	0.0386
Nephthys hombergi	Archipel	0.0510	
Eteone longa	Archipel	0.0024	0.0021
Eteone longa	Guel van Herkingen	0.0033	
Anaitides maculata	Archipel	0.0059	0.0032

density per segment of each species gave us a total density of omnivores (.0471 g afdw/sqm) and of predator worms (.0211 g afdw/sqm). It is apparent from these data that predatory worms have about double the density of omnivores in the deep segment of the closed Grevelingen. Assuming that this is also true for the Oosterschelde and the open Grevelingen, we triple the densities of omnivores to account for predatory worms in the final density estimates for the ecogroup. We assumed the same densities for the Oosterschelde as for the open Grevelingen and thus obtained the density and abundance estimates for the ecogroup shown in Table 8.28.

The estimates given in Table 8.28 are significantly higher than the earlier ones in Tables 8.4 and 11.4 of Vol. III. The reasons for the differences are (a) that we revised the average weights of *Gammarus* and *Nereis* and (b) that we found predator worms to be twice as abundant as omnivores, instead of merely equally abundant, based on new information. However, this ecogroup is not an abundant one, and changes in our estimates of its abundances in the different segments will not alter our conclusions.

Table 8.28

ABUNDANCE OF OMNIVORES AND PREDATOR WORMS

Segment	Density (g afdw/sqm)	Abundance (tons afdw)
Open Grevelingen		
Shallow	0.275	21.04
Deep	0.075	2.51
Oosterschelde		
Shallow	0.275	69.03
Deep	0.075	15.03
Closed Grevelingen		
Shallow	--	--
Deep	0.0682	3.60

8.10. BENTHIC GRAZERS

8.10.1. Grevelingen

This ecogroup includes *Hydrobia ulvae* and *Littorina littorea*. We calculated the average density per station and per segment for each segment in the open and closed Grevelingen from the data from the Delta Institute (Table 8.29). By combining the densities for the species in each segment, we obtained the densities and abundances shown in Table 8.30.

8.10.2. Oosterschelde

Littorina was collected during the cockle survey in February 1976, but *Hydrobia* was not. According to the data for the shallow segment of the open Grevelingen, *Hydrobia* was about 2.7 times as dense as *Littorina*. Applying the same ratio for the Oosterschelde yields about 2.1 g/sqm of *Hydrobia* and a total density of benthic grazers in February of 2.87 g/sqm. The average yearly density for benthic grazers in the open Grevelingen shallow segment was 1.5 times its February average. If we assume this ratio for the Oosterschelde, we find that the density of benthic grazers in the shallow segment of the Oosterschelde is 4.31 g afdw/sqm. The ratio between the densities in the shallow segment and the deep segment in the open Grevelingen is about .0014. Assuming the same ratio for the Oosterschelde, the density in the deep segment is .006 g/sqm. The densities and abundances of benthic grazers in the Oosterschelde are given in Table 8.31.

The new estimate of the abundance of benthic grazers in the shallow segment of the Oosterschelde is much smaller than our previous estimate from Table 8.4 of Vol. III (4620 tons afdw). Since raw data from the Oosterschelde had been unavailable, we based our initial estimate of the abundance of benthic grazers in the shallow segment of the Oosterschelde on the assumption that their density was the same as that found in the shallow segment of 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 were too great

Table 8.29

AVERAGE DENSITY OF BENTHIC GRAZERS IN THE OPEN AND CLOSED GREVELINGEN

(In g afdw/sqm)

Species	Station	Average Density per Station	Average Density per Segment
	Open Grevelingen		
	Shallow Segment		
Hydrobia ulvae	Plaatje G3	0.0036	
Hydrobia ulvae	Roxenisse-Laag	7.6418	
Hydrobia ulvae	Roxenisse-Hoog	4.5298	9.6834
Hydrobia ulvae	Schelphoek	16.5624	
Littorina littorea	Schelphoek	10.0784	
Littorina littorea	Roxenisse-Hoog	0.1171	3.6393
	Deep Segment		
Hydrobia ulvae	Geul van Herkingen	0.0003	0.0001
Littorina littorea	Geul van Herkingen	0.0627	0.0189
	Closed Grevelingen		
	Shallow Segment		
Hydrobia ulvae	Vlije van Bruinisse	0.3128	
Hydrobia ulvae	Plaatje G5	0.0111	0.2525
Hydrobia ulvae	Plaatje G3	0.0016	
	Deep Segment		
Hydrobia ulvae	Geul van Herkingen	2.6600	
Hydrobia ulvae	Bocht V St. Jacob	0.4476	0.7818
Hydrobia ulvae	Archipel	0.1179	

Table 8.30

ABUNDANCE OF BENTHIC GRAZERS IN THE GREVELINGEN

Segment	Density (g afdw/sqm)	Abundance (tons afdw)
Open Grevelingen		
Shallow	13.1	1019.2
Deep	0.019	0.63
Closed Grevelingen		
Shallow	0.2525	13.6
Deep	0.7818	41.28

Table 8.31

DENSITY AND ABUNDANCE OF BENTHIC GRAZERS
IN THE OOSTERSCHELDE

Segment	Density (g afdw/sqm)	Abundance (tons afdw)
Shallow	4.31	1081.8
Deep	0.006	1.2

for their predators to consume. Thus, we changed our assumption and reduced our estimate of their abundance to 1848 tons afdw (see Chap. 10 of Vol. III).

This estimate is still significantly different from the estimate of 1081.8 tons afdw that we have presented here. However, our current estimate is based on samples taken at only one time (February 1975). Based on estimates of the standard error of the mean estimates of densities in the Grevelingen (see Figs. 8.2, 8.3, and 8.4), the true long-term average abundance could well be twice as great as our current estimate of 1081.8 tons.

8.10.3. Average Weight per Individual

From Wolff (1977, Table IV), we find that the average ash-free dry weight for both *Littorina littorea* (.005 g/individual) and *Hydrobia ulvae* (.00043 g/individual) is about .00167 g/individual, where we have taken into account that *Hydrobia* is 2.7 times more abundant than *Littorina*. Assuming that the ash-free dry weight is 20 percent of the live weight, we establish a wet weight per individual of .0083 g.

CHAPTER 9

FISH DATA

Data on the densities of benthos-eating fish were available. 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 in Oosterschelde harbors. Some may have been caught elsewhere. Third, for various reasons (see Sec. 7.2 of Vol. III), the quantities reported are often inaccurate.

The most important species of fish found in the Oosterschelde are shown in Table 9.1.

Table 9.1

SPECIES OF FISH IN THE OOSTERSCHELDE

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

9.1. PLANKTIVOROUS FISH

9.1.1. Oosterschelde

Planktivorous fish include anchovy, herring, and sprat. The only data we have relating to these fish, either in the Oosterschelde or in the Grevelingen, are catch data (see Table 9.2), which are reported for anchovy and herring (but not for sprat) in the Ministry of Agriculture and Fisheries Annual Reports, *Visserij*. Most of these fish were probably caught in the Oosterschelde itself, rather than outside of it and then 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.

Table 9.2

CATCH DATA OF PLANKTIVOROUS FISH

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

The fluctuation in biomass seems to be a natural phenomenon, as there was no apparent change in fishing effort. Anchovy enter the Oosterschelde at the end of April. They require warm summer temperatures for good breeding, and the young fish are very dependent on temperature. The summer of 1968 was cold, and 1969 was the first warm summer in many years. This may explain the rise in catch.

These fish are 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. 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.

We assumed that the abundances were 10 times the catches.[1] Migration was accounted for by dividing the abundances by 2, because the fish were present only half the year. We obtained ash-free dry weight by multiplying by 0.2 (Vinogradov, 1953). Therefore, the ash-free dry weight would be equal to the catch number.

We have some data on herring and sprat from the *Demersal Young Fish Survey* in terms of numbers of individuals per 1000 sqm (see Table 9.3). From these data, we assumed that sprat are as numerous as herring. We chose the average catch of anchovy to be the average of the last three figures (31750 kg) and the average catch of herring to be the average of the last four figures (112000 kg) because the others appear to be anomalies. Then, assuming that sprat are as numerous as herring, the biomass in Oosterschelde would be 2.56×10^8 g afdw.

We estimated the abundance by using another method based on P/B ratios: Planktivorous fish live mainly on zooplankton, whose average biomass we have estimated to be about 5.6×10^8 g. We have calculated (Table 6.6 of Vol. III) that zooplankton produce eleven times their average biomass annually, and that planktivorous fish must eat 18.7 times their biomass annually, 80 percent of which is assimilated. If the abundance of zooplankton averages 560 metric tons, their annual production must equal 6160 tons, which is sufficient to feed an average biomass of 330 tons of planktivorous fish. Since not all the zooplankton production is consumed by planktivorous fish, this value provides an upper limit. We therefore chose 256 tons afdw as the abundance of planktivorous fish in the Oosterschelde.

[1] Catch is an index of production. Production to biomass ratios are typically between 5 and 20.

Table 9.3

DENSITY OF HERRING AND SPRAT

Length (cm)	Density (individuals/1000 sqm)	
	Herring	Sprat
71-10	0.6	1.8
74-4	1.3	--
73-11	6.4	1.6
74-4	1.8	5.6
74-10	--	0.8
Average density	2.53	2.45

9.1.2. Grevelingen

To estimate the abundance of planktivorous fish in the open Grevelingen, we assumed that the same density occurred there as in the Oosterschelde, or .08 g afdw/sqm. We thus established 4.8×10^7 as the abundance of planktivorous fish in the open Grevelingen.

9.1.3. Average Weight per Individual

No data are available to calculate actual average weight, but let us assume an average length of planktivorous fish of 5 cm. Herring and sprat have a length-weight relationship represented by the equation $W = 0.007 \times L^3$, where L is the length in centimeters and W is wet weight in grams (Meijering, 1976). This yields 0.875 g. De Silva's formula (1973) for autumn-spawned herring is $W = 0.0006 \times L^{3.5}$. This yields 0.17 g live weight. We chose an average of 0.5 g for herringlike fish.

9.2. BENTHOS-EATING FISH

Benthos-eating fish include eel (a resident fish), and migratory flatfish (plaice, dab, flounder, and sole).

9.2.1. Eel

Eel *(Anguilla)* is a nonmigratory resident of the estuaries. Official figures from *Visserij* (Ministry, Annual Reports, 1973) for eel catches in the Oosterschelde show that only 40000 kg of eel were caught in 1973. A. C. Drinkwaard, J. D. Holstein, and A. L. Abrahamse (personal communication) estimated the total yearly output to be 5 million guilders. The price per kilogram is approximately 8 guilders. So the yearly catch should be 625000 kg. We chose this figure. We assumed that the dry weight fraction is 33 percent and that the ash content of the dry weight is 20 percent (Vinogradov, 1953). We also assumed that the catch-yield/standing-stock ratio is 0.2/yr. This led to an average standing-stock estimate of 0.825×10^9 g afdw.

Assuming that eel was as dense in the open Grevelingen as it is in the Ooster-

schelde, we calculated its biomass as the area of the open Grevelingen (130 sq km) divided by the area of the Oosterschelde (476 sq km) (Table 1.4) multiplied by the estimated abundance of eel in the Oosterschelde. This procedure gave us $.225 \times 10^9$ g afdw of eel in the open Grevelingen.

9.2.2. Flatfish

Data on the abundance of flatfish in the Oosterschelde were collected by the State Institute for Fisheries Research (R.I.V.O.), IJmuiden (Tables 9.4 and 9.5). They were published in the semiannual *Demersal Young Fish Surveys* (1969-1975) in units of numbers of individuals per 1000 sqm for several size (year) classes for each species and for as many as 41 sampling stations. The R.I.V.O. measured twice yearly, in spring (April/May) and autumn (September/October), from 1969 to 1975, except for 1971, when they measured in August instead of April/May. Similar unpublished data are available for the open Grevelingen from the *Demersal Young Fish Survey* for 1969 and 1970 only (see Table 9.6).

The 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, are 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

Table 9.4

AVERAGE DENSITY OF FLATFISH IN THE OOSTERSCHELDE: PLAICE AND SOLE

	Average Density (individuals/1000 sqm)							
	Size Class (cm)				Size Class (cm)			
	<13	13-19	20-24	>24	<13	13-19	19-23	>23
Sampling Date	Plaice				Sole			
April 1969	11.81	5.03	0.84	0.0	0.84	0.0	0.0	0.43
October 1969	3.08	1.68	0.70	0.0	2.27	0.33	0.0	0.0
May 1970	0.88	0.98	0.99	0.23	0.54	0.0	0.0	0.0
October 1970	3.60	6.07	1.17	0.0	14.91	1.35	0.54	0.22
August 1971	10.57	1.05	0.32	0.04	7.26	0.48	0.95	0.48
October 1971	3.30	1.19	0.64	0.18	4.71	0.20	0.07	0.10
April 1972	8.56	2.28	0.48	0.12	1.15	0.15	0.03	0.06
October 1972	1.31	1.04	0.86	0.49	0.12	0.07	4.41	0.0
April 1973	0.73	0.41	0.70	0.11	0.11	0.14	0.06	0.17
November 1973	8.72	2.79	1.35	1.10	8.92	1.55	0.10	0.32
April 1974	1.42	0.67	0.17	0.22	0.20	5.37	3.66	0.32
October 1974	1.92	2.42	1.05	0.37	0.20	1.54	1.04	0.13
April 1975	1.14	2.33	0.87	0.22	0.22	0.0	0.0	0.0
October 1975	7.46	1.62	0.59	0.22	1.55	0.43	0.43	0.65

NOTE: These data do not account for gear efficiency.

Table 9.5

AVERAGE DENSITY OF FLATFISH IN THE OOSTERSCHELDE: DAB AND FLOUNDER

	Average Density (individuals/1000 sqm)					
	Size Class (cm)			Size Class (cm)		
	<11	11-14	>14	<13	13-20	>20
Sampling Date	Dab			Flounder		
April 1969	0.44	0.65	1.02	1.49	1.58	0.0
October 1969	0.0	0.0	0.0	0.0	0.0	0.0
May 1970	0.0	0.0	0.0	0.0	0.54	0.0
October 1970	9.73	0.41	0.0	0.0	0.33	0.22
August 1971	4.92	0.57	0.06	0.01	0.04	0.04
October 1971	2.17	0.41	0.10	0.0	0.19	0.11
April 1972	1.01	0.05	0.10	0.14	0.24	0.19
October 1972	3.82	0.64	0.36	0.0	0.02	0.08
April 1973	0.12	0.04	0.22	0.02	0.04	0.12
November 1973	3.55	0.09	0.26	0.0	0.01	0.15
April 1974	0.52	0.02	0.12	0.04	0.04	0.07
October 1974	27.24	2.56	2.05	0.0	0.09	0.20
April 1975	1.79	0.22	1.09	0.30	0.0	0.0
October 1975	3.06	0.77	0.0	0.0	0.0	0.0

NOTE: These data do not account for gear efficiency.

Table 9.6

AVERAGE DENSITY OF FLATFISH IN THE OPEN GREVELINGEN

	Average Density (individuals/1000 sqm)			
	Sampling Date			
Size Class (cm)	April 1969	October 1969	May 1970	October 1970
	Plaice			
<13	8.06	4.78	1.01	3.31
13-19	2.44	1.39	0.59	2.40
19-24	0.69	0.21	0.12	0.73
>24	0.04	0.0	0.02	0.55
	Sole			
<13	0.79	0.38	1.06	23.41
13-19	0.04	0.17	0.14	1.24
19-23	0.10	0.02	0.12	0.33
>23	0.0	0.0	0.02	0.15
	Dab			
<11	1.29	0.0	0.02	13.66
11-14	0.79	0.02	0.0	0.09
>14	1.94	0.06	0.02	0.15
	Flounder			
<13	3.71	0.02	0.0	0.88
13-20	4.17	0.06	0.19	1.37
>20	0.25	0.0	0.0	0.12

NOTE: These data do not account for gear efficiency.

younger and smaller individuals) feeding on the tidal flats. This creates a special problem for the ships used by the 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.

Data were recorded by size classes, which were chosen to correspond mainly to age classes. We converted the length limits for each size class of each species into weights using the formula $W = 0.012 \times L^3$, where W is wet weight in grams and L is length in centimeters (Meijering, 1976). The minimum (maximum) weights for each size class were calculated by using the lower (upper) length limits, and the medium weights were calculated by using the average of the lower and the upper length limits. The smallest length was assumed to be 7 cm in all cases. The upper limit of the largest size class was taken to be the average number between the lower limit of the largest size class and the maximum length reported for each species by Meijering, because the result seemed to correspond to the largest lengths that we had seen in the field. Of course, if the majority of fish occurred at the upper or the lower limits of each size class, the estimated weights would be different.

Table 9.7 gives the estimated minimum, medium, and maximum weights for each size class of each species of flatfish. We chose to use the medium-weight estimates in our calculations.

We assumed that plaice, dab, and flounder have similar success in avoiding the survey gear, i.e., nets. (The fraction caught is called *gear efficiency.)* According to suggestions from IJmuiden, the number of the smallest size fish must be multiplied by 6.7 to account for maximum gear efficiency, and by 10.0 to account for minimum gear efficiency. The numbers of the largest size classes must be multiplied by 11.0 and by 17.0, respectively. For our model, we wanted to assume medium gear efficiency; we calculated it as the average of maximum and minimum.

We calculated the numbers of plaice, dab, and flounder as follows: First we estimated the numbers of fish from the original data, supposing medium gear efficiency, i.e., that 12 percent of the smallest fish are captured and that 7 percent of the largest fish are captured. Next, we multiplied the number of fish per 1000 sqm by the medium-weight estimates and then added the values over all size classes and sampling dates for each species separately. Since we had six spring sampling dates and eight fall sampling dates for the Oosterschelde data, we averaged the numbers of fish per 1000 sqm separately for the spring and fall and then averaged the spring and fall values.

Because trawling occurred only in the deep segment, we assumed that the density in the shallow segment would be a multiple of the density in the deep segment for the different species (personal communication from IJmuiden).

9.2.2.1. Plaice in the Open Grevelingen. Since a large proportion of plaice stay through the winter, we simply averaged the biomass figures to obtain an estimate. The medium estimate of the density (grams per 1000 sqm) of plaice during the spring and autumn of 1969 and 1970 is the product of the numbers of individuals

Table 9.7

WEIGHT ESTIMATES FOR EACH SIZE CLASS
OF FLATFISH SPECIES

Length (cm)	Weight (g)		
	Minimum	Medium	Maximum
Plaice			
7-13	4.12	12.0	26.36
13-19	26.36	49.15	82.31
19-24	82.31	119.26	165.89
24-57	165.89	797.16	2222.32
Dab			
7-11	4.12	8.75	15.97
11-14	15.97	23.44	32.93
14-27	32.93	103.38	236.2
Flounder			
7-13	4.12	12.0	26.36
13-20	26.36	53.91	96.00
20-35	96.00	249.56	514.50
Sole			
7-13	4.12	12.0	26.36
13-19	26.36	49.15	82.31
19-20	82.31	111.13	146.00
23-50	146.00	324.00	583.53

per 1000 sqm (accounting for maximum gear efficiency) multiplied by the medium weight per individual. The results are shown in Table 9.8.

The average density of plaice in the deep segment is therefore 3177.93 g/1000 sqm, or 3.18 g/sqm. Inflating this value by 25 percent to account for uncertain gear efficiency yields 3.98 g/sqm in the deep segment. By assuming that the density is three times higher in the shallow segment, we obtained a density of 11.94 g/sqm of plaice in the shallow segment.

Table 9.8

MEDIUM ESTIMATES OF THE DENSITY OF
PLAICE IN THE OPEN GREVELINGEN

(Maximum gear efficiency)

Year	Spring	Autumn	Average
1969	3223.12	1411.35	2317.24
1970	733.02	7344.20	4038.61

9.2.2.2. Plaice in the Oosterschelde. To calculate the density of plaice in the Oosterschelde, we multiplied the average density of each size class of individual plaice (corrected for maximum gear efficiency) by the medium weight estimate. This yielded the densities shown in Table 9.9. We then added the densities for all the size classes, which gave us a total biomass of 4470.17 g/1000 sqm, or 4.47 g/sqm. Inflating this value by 25 percent to account for uncertain gear efficiency, we obtained 5.59 g/sqm of plaice in the deep segment. Here again we assume that the density is three times higher in the shallow segment, which gives us 16.77 g/sqm of plaice in the shallow segment.

It would appear that the abundance of plaice in the Oosterschelde, measured per square meter of bottom, is almost 50 percent higher than in the Grevelingen. In the face of a range of uncertainty that covers almost an order of magnitude, this difference is not very important.

Table 9.9

MEDIUM ESTIMATES OF THE DENSITY OF PLAICE IN THE OOSTERSCHELDE

(Maximum gear efficiency)

Size Class (cm)	Medium Weight (g)	Average Density	
		Number per 1000 sqm	Grams per 1000 sqm
7-13	12.0	30.52	366.24
13-19	49.15	22.99	1129.96
19-24	119.26	8.36	997.01
24-57	797.16	2.48	1976.96

9.2.2.3. Dab in the Open Grevelingen. We performed the same calculations (assuming maximum gear efficiency) with the data on dab. This yielded the densities shown in Table 9.10. We assumed that the low measurement in each year indicates that migration has already occurred (1969) or has yet to occur (1970). Thus, we did not need to introduce an additional factor to account for residence time. The average biomass is 894.32 g/1000 sqm, or .89 g/sqm. Inflating this value by 25 percent yielded 1.11 g/sqm of dab in the deep segment. Dab do not feed on the tidal flats.

9.2.2.4. Dab in the Oosterschelde. Calculations for dab yield the estimates shown in Table 9.11. To determine the total biomass, we added the densities for all the size classes, which gave us 770.54 g/1000 sqm, or .77 g/sqm. Inflating this value by 25 percent to account for uncertain gear efficiency yielded a biomass of .96 g/sqm of dab in the Oosterschelde.

It was difficult to interpret the biomass figures for the spring and autumn of each year, because in most years there is a very low number and a very high

Table 9.10

MEDIUM ESTIMATE OF THE DENSITY OF DAB
IN THE OPEN GREVELINGEN

(Maximum gear efficiency)

Year	Density (g/1000 sqm)		
	Spring	Autumn	Average
1969	2485.42	73.39	1279.41
1970	23.88	994.58	509.23

Table 9.11

MEDIUM ESTIMATE OF THE DENSITY OF DAB
IN THE OOSTERSCHELDE

(Maximum gear efficiency)

Size Class (cm)	Medium Weight (g)	Average Density	
		Number per 1000 sqm	Grams per 1000 sqm
7-11	8.75	25.0	218.75
11-14	23.44	4.62	108.29
14-27	103.38	4.29	443.50

number, indicating that one sample occurred while the fish were in the Oosterschelde, and the other when the fish had migrated out. But this was not true for 1975, and may not be true for 1972.

9.2.2.5. Flounder in the Open Grevelingen. The densities of flounder in the open Grevelingen are shown in Table 9.12. Flounders are present approximately 8 months a year. However, we assumed, as with dab, that the vastly different spring and autumn figures reflect the fact of migration and, therefore, we need not reduce the numbers to account for migration. The average for all size classes is thus 1292.41 g/1000 sqm, or 1.29 g/sqm. Inflating this figure by 25 percent yielded 1.61 g/sqm. The flounder population on the flats is much more abundant than that of plaice. We assumed its total abundance on the flats to be six times that of the deep segment, which gave us 9.66 g/sqm of flounder in the shallow segment.

9.2.2.6. Flounder in the Oosterschelde. The density of flounder in the Oosterschelde is given in Table 9.13. To determine the total biomass, we added the densities for all the size classes, which gave us 381.18 g/1000 sqm, or .38 g/sqm. Inflating this value by 25 percent for uncertain gear efficiency yielded a biomass of 48 g/sqm in the deep segment. Here again we assume its abundance on the flats to be six times that of the deep segment. This gave us 2.88 g/sqm of flounder in the shallow segment.

Table 9.12

MEDIUM ESTIMATE OF THE DENSITY OF FLOUNDER IN THE OPEN GREVELINGEN

(Maximum gear efficiency)

Year	Density (g/1000 sqm)		
	Spring	Autumn	Average
1969	3457.46	37.14	1747.30
1970	112.67	1562.36	837.52

Table 9.13

MEDIUM ESTIMATE OF THE DENSITY OF FLOUNDER IN THE OOSTERSCHELDE

(Maximum gear efficiency)

Size Class (cm)	Medium Weight (g)	Average Density	
		Number per 1000 sqm	Grams per 1000 sqm
7-13	12.0	1.11	13.32
13-20	53.91	2.75	148.25
20-35	249.56	0.88	219.61

9.2.2.7. Sole in the Open Grevelingen. Sole remain from April to October, a period of one-half a year (counting 6 months from the middle of each month). However, the factor for gear efficiency is 2 (advice from IJmuiden). Thus, these two factors cancel each other (see Table 9.14).

As Table 9.14 shows, the considerable difference between the value for autumn of 1970 and the other values introduces a large uncertainty in our estimate. By averaging the values, we calculated the total density of sole in the deep segment of the open Grevelingen as 125.02 g/1000 sqm, or 0.13 g/sqm. Sole do not occur on the flats.

Table 9.14

MEDIUM ESTIMATE OF THE DENSITY OF SOLE IN THE OPEN GREVELINGEN

(Maximum gear efficiency)

Year	Density (g/1000 sqm)		
	Spring	Autumn	Average
1969	22.56	10.95	16.76
1970	39.42	427.14	233.28

9.2.2.8. Sole in the Oosterschelde. The density of sole in the Oosterschelde is shown in Table 9.15. We added the densities for all the size classes, which yielded a total biomass of 226.88 g/1000 sqm, or .23 g/sqm of sole in the deep segment.

Table 9.15

MEDIUM ESTIMATE OF THE DENSITY OF SOLE IN THE OOSTERSCHELDE

(Maximum gear efficiency)

Size Class (cm)	Medium Weight (g)	Average Density	
		Number per 1000 sqm	Grams per 1000 sqm
7-13	12.0	2.75	33.00
13-19	49.15	0.84	41.29
19-23	111.13	0.79	87.79
23-36.5	324.0	0.20	64.80

9.2.2.9. Abundance of Benthos-Eating Fish in the Open Grevelingen. The combined densities of flatfish in the open Grevelingen are shown in Table 9.16. The sum of the product of the density of flatfish in the deep segment multiplied by the area of the deep segment (33.4 sq km), and the product of the density of the fish in the flats multiplied by the area of the flats (96.8 sq km), yields 2319 tons wet weight. Assuming that the ash-free dry weight is 20 percent of the wet weight, we calculated that there were 464 tons afdw of flatfish in the open Grevelingen. By adding this figure to the abundance of eel (225 tons afdw), we obtained a total abundance of benthos-eating fish in the open Grevelingen of 689 tons afdw.

Table 9.16

AVERAGE DENSITY OF FLATFISH IN THE OPEN GREVELINGEN

Species	Density (g/sqm)	
	Deep Segment	Shallow Segment
Plaice	3.98	11.94
Dab	1.11	--
Flounder	1.61	9.66
Sole	0.13	--
Total density	6.83	21.60

9.2.2.10. Abundance of Benthos-Eating Fish in the Oosterschelde. The combined densities of flatfish in the Oosterschelde are shown in Table 9.17. The sum of the biomass in the deep segment (200.4 sq km) and in the flats (276.4 sq km) is 6886 tons wet weight, or 1377 tons afdw. Adding this figure to the abundance of eel yielded about 2200 tons afdw of benthos-eating fish in the Oosterschelde.

Table 9.17

AVERAGE DENSITY OF FLATFISH IN THE OOSTERSCHELDE

Species	Density (g/sqm)	
	Deep Segment	Shallow Segment
Plaice	5.59	16.77
Dab	0.96	--
Flounder	0.48	2.88
Sole	0.23	--
Total density	7.26	19.65

9.2.2.11. Average Weight per Individual. To estimate the average weight of benthos-eating fish in the Oosterschelde, we divided the density in grams (5848.77 g/1000 sqm) by the density of individuals (107.58 individuals per 1000 sqm). This yielded 54.4 g wet weight per individual. Although this figure is almost twice the original wet weight figure (Table 6.6 of Vol. III), it makes a negligible difference in the daily ration and metabolic fraction used in the model.

9.3. FISH-EATING FISH

9.3.1. Oosterschelde

The data on fish-eating fish (cod, mackerel, garfish, whiting, and sea trout) are scanty. We had only some catch data and an estimate of cod abundance by N. Daan (personal communication) for the Oosterschelde. Daan estimated that during the winter the Oosterschelde probably contains 7×10^5 kg (wet weight) of cod. Sea perch is a summer visitor, perhaps as common as cod is in winter. Therefore, sea perch might replace cod in summer with the same mass.

We obtained the catch data shown in Table 9.18 from the Ministry of Agriculture and Fisheries, Annual Reports. Sea trout are clearly not important (at least commercially). The 1973 data indicate that mackerel plus garfish and whiting are 2.86 times as abundant as cod, and hence probably 1.43 times as abundant as cod plus sea perch. Therefore, the biomass of mackerel plus garfish and whiting would be 1.43 multiplied by 7×10^8 g, or 1001 tons. Thus, we estimated the biomass of all four species to be about 1700 tons. By multiplying by 0.2 to obtain the ash-free dry weight, we calculated that the abundance of fish-eating fish in the pelagic segment of the Oosterschelde is 3.4×10^8 g afdw.

Table 9.18

CATCH DATA OF FISH-EATING FISH
IN THE OOSTERSCHELDE

Species	Amount Caught (kg)	
	1971	1973
Mackerel	1800	1336
Cod	120	1761
Whiting	--	693
Garfish	3700	3008
Sea trout	5	--

9.3.2. Grevelingen

Using the same density of fish-eating fish as for the Oosterschelde (1.07×10^{-4} g/liter), we calculated that there were 6.47×10^{7} g afdw of fish-eating fish in the pelagic segment (601 million cm) of the open Grevelingen.

Since fish-eating fish are not able to reproduce in the closed Grevelingen, they have been disappearing very quickly. Given enough time, however, these fish will probably be replaced by other species. 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 in the closed Grevelingen as unknown.

9.3.3. Average Weight per Individual

We estimated the average weight per individual for benthos-eating fish (225.3 g) by using the length-volume relationship described by the equation $W = L^3 \times \alpha$, where W is the wet weight in grams, and L is the average length in centimeters. The equations and average weights shown in Table 9.19 are from Meijering (1976). Alpha for cod was taken from Daan (1974).

Table 9.19

AVERAGE WEIGHT OF FISH-EATING FISH SPECIES

Species	Length-Weight Equation	Average Length (cm)	Average Weight (g)
Cod	$W = 0.007\ L^3$	30	W = 189
Mackerel	$W = 0.012\ L^3$	30	W = 324
Garfish	$W = 0.0013\ L^3$	50	W = 163
Total average weight			225.3

9.4. PLANT-EATING AND DETRITUS-EATING FISH

9.4.1. Abundance

This group includes only the gray mullet (*Mugil* species). This quick fish is difficult to catch and is present during the summer. Nevertheless, some 15000 kg were landed in Zeeland (Oosterschelde and Westerschelde) in 1973 (Ministry of Agriculture and Fisheries, Annual Report). We assumed that half of these were caught in the Oosterschelde and that the abundance was 20 times the catch. By multiplying by 0.2 to obtain the ash-free dry weight, we calculated an abundance of 3.0×10^7 g in the Oosterschelde.

The abundance of gray mullet in the open Grevelingen was assumed to be in the same ratio to plant-eating and detritus-eating birds as in the Oosterschelde. This yielded 5.11×10^7 g afdw.

9.4.2. Average Weight per Individual

Full grown or nearly full grown mullets have an average length of 30 cm. Using the equation $W = 0.006\ L^3$ (Meijering, 1976), we calculated an average live weight of 162 g for mullets.

Chapter 10

BIRDS

10.1. GREVELINGEN DATA

Table 10.1 lists the species of birds in the Delta region by ecogroups. Data on birds in the Grevelingen were collected by the Delta Institute for Hydrobiological Research, Yerseke, and by H.L.F. Saeijs of the Environmental Division of the Delta Service. Since Wolff et al. (1975) have already condensed these data, we used their data instead of the raw data. Table II (open Grevelingen) and Table III (closed Grevelingen) from Wolff et al. (1975) give us data on bird-days per year, average wet weights in kilograms, and annual consumption in grams of ash-free dry weight per square meter for the most important bird species; Table IV lists the consumption in grams of ash-free dry weight per square meter per year for the three ecogroups in both the open and closed Grevelingen.

Birds were counted by means of visual observation, either from boats or from the shore, using various binoculars and telescopes. Small groups were actually counted; larger groups were estimated as well as possible. Wolff et al. (1975) believed that the maximum error in these estimates varies between 1 and 20 percent, depending on the species involved, the weather, and the state of the tide.

A complete census of all birds in the estuary was made seven different times between 1969 and 1971. From these seven censuses, the average number of individuals per census (A) was calculated for each species separately. In addition, a

Table 10.1

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	Dabbling ducks	
Dunlin		
Avocet		
Black-backed gull		
Herring gull		
Common gull		
Black-headed gull		
Common scooter		

5-year series (1964-1969) of fortnightly and monthly bird-counts from the Roggeplaat tidal flats in the Oosterschelde (Wolff, 1973b) were used. From this series, the median number of birds per month was determined for each species separately. From these median numbers, Wolff et al. (1975) took those that fell in the same months as the counts in the Grevelingen estuary, and in this way determined an average number of individuals for the Roggeplaat counts (B), which may be compared directly with the Grevelingen counts. The ratios A/B have been used to transform the median values of the Roggeplaat counts, available for all months of the year, to monthly population estimates for the Grevelingen estuary.

In the closed Grevelingen, bird numbers for the entire lake were estimated fortnightly or monthly by one or two observers in a boat. Additional observations were made from the shore to correct the estimates obtained from the boat. Birds not feeding in the area were not included. The number of bird-days per 2 weeks or per month was obtained by multiplication. The number of bird-days per year was determined by combining the numbers per month or per 2 weeks.

To determine consumption, the standard metabolism (M) in kilocalories per day was estimated as $\log M = \log 78.3 + 0.723 \log W$, where W is the body weight in kilograms. Body weights were taken from the literature. To obtain the consumption per bird, the standard metabolism was multiplied by 5. Kilocalories were converted to grams of ash-free dry weight by multiplying by 0.2. See Wolff et al. (1975) for further explanation of methods, assumptions, and possible sources of error.

There is an important problem in estimating abundances of birds. 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. A simultaneous count requires the concentrated effort of many persons for a short period. Also, finding enough people who can recognize different species of birds on sight, and who can accurately estimate their numbers, is difficult.

Wolff et al. (1975) indicated the possibility that some species—e.g., turnstone and knot—are likely to have been overlooked quite often during the Grevelingen counts because of their behavior. In the lake, this might have been the case for concentrations of waders. Thus, it can be assumed that their data represent minimum estimates. Wolff points out that a problem common to much ornithological work is the fact that information on the variance of bird counts is unavailable. Another problem was that the number of specimens of different species gradually increased during the observation period. This increase also caused the average estimates of consumption to be minimum values.

A complication occurs because birds may obtain some food in areas other than the area being considered. 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, say, the Oosterschelde itself, but in the entire Delta area.

What segment birds are placed in doesn't matter because their numbers are constrained. Thus, we placed fish-eating birds in the pelagic segment, and the others in the shallow and intertidal segment.

10.1.1. Abundance of Birds in the Grevelingen

Abundances were calculated from Table II (open Grevelingen) and Table III (closed Grevelingen) of Wolff et al. (1975). These tables give bird-days per year, and the average wet weights (in kilograms) of birds. We converted these data to average abundance in grams of birds for each ecogroup by (a) multiplying bird-days per year by the weight for each species, (b) averaging the species values for each ecogroup, and (c) dividing by 365 days per year. The dry-weight content of birds is about 30 to 50 percent (Clayton et al., 1974; Fisher, 1972; Vinogradov, 1953). Assuming a dry-weight content of 0.4 and an ash content of 0.25, we multiplied the live weight by 0.3 to obtain ash-free dry weight.

10.1.2. Daily Rations of Birds in the Grevelingen

Table IV of Wolff et al. (1975) gives consumption in ash-free dry weight per square meter per year, which we multiplied by the area of the open Grevelingen (130 sq km) or by the area of the closed Grevelingen (130 sq km) to obtain total consumption, and divided by 365 and by the average abundance to obtain the average daily rations.

We used the same average daily ration for both open and closed cases, and did not change it from one model run to the next, even though it changed the size distribution of birds.

The abundances and daily rations of birds in the open and closed Grevelingen are given in Table 10.2.

Table 10.2

ABUNDANCES AND DAILY RATIONS OF BIRDS IN THE OPEN AND CLOSED GREVELINGEN

Ecological Group	Abundance (g afdw)	Daily Ration (g afdw/g afdw consumed)
Open Grevelingen		
Fish-eating birds	1.24×10^4	0.344
Plant-eating birds	1.26×10^5	0.368
Benthos-eating birds	2.74×10^6	0.445
Closed Grevelingen		
Fish-eating birds	2.73×10^5	0.378
Plant-eating birds	2.83×10^6	0.281
Benthos-eating birds	7.17×10^5	0.408

10.2. OOSTERSCHELDE DATA

We have raw data (Table 10.3) on the number of each bird species that ate in the intertidal area of the Oosterschelde during 1972-1973 (Terwindt et al., 1975). An important group, gulls, is lacking in this table.

Table 10.3

DATA ON BIRDS IN THE OOSTERSCHELDE, 1972-1973

Bird	Type[a]	Number	Average Weight[b] (kg)	Average Ration[b] (g afdw/day)
Mallard	H	10,000	1.085	83
Teal	H	1,000	0.430	43
Wigeon	H	25,000	0.692	60
Pintail	H	5,000	0.880	71
Shoveler	H	1,300	0.586	53
Brent goose	H	3,000	1.382	99
Coot	H	2,500	0.687	60
Shelduck	B	5,800	1.237	91
Oystercatcher	B	49,400	0.496	47
Grey plover	B	3,400	0.223	26
Ringed plover	B	1,265	0.070	11.45
Kentish plover	B	240	0.042	7.9
Turnstone	B	1,075	0.106	15
Curlew	B	8,860	0.922	74
Bar-tailed godwit	B	3,330	0.248	29
Redshank	B	5,000	0.128	18
Knot	B	10,000	0.128	18
Dunlin	B	15,000	0.057	10
Avocet	B	355	0.340	35

[a]Herbivorous (H) or benthos-eater (B).

[b]From Wolff et al. (1975).

From these figures, we calculated the abundances by (a) multiplying the number of each species by its average weight, (b) averaging over the ecogroup, and (c) converting to ash-free dry weight. The daily rations were calculated by multiplying the mean number by the mean ration and then dividing by the abundance. This yielded the rations given in Table 10.4.

Clearly, daily rations in the two estuaries are consistent. However, since the data for the Grevelingen are much more complete than the data for the Oosterschelde, we used bird abundances calculated on the basis of the Grevelingen data.

Table 10.4

ABUNDANCES AND DAILY RATIONS OF BIRDS IN THE OOSTERSCHELDE

Ecological Group	Abundance (g afdw)	Daily Ration (g afdw/g afdw consumed)
Plant-eating birds	7.92×10^6	0.410
Benthos-eating birds	8.91×10^6	0.466

10.2.1. Plant-Eating Birds in the Oosterschelde

The abundance of plant-eating birds in the Oosterschelde, as shown in Table 10.4, is probably too high (about 60 times greater than their abundance in the open Grevelingen). The seagrass and seaweed vegetation in the Oosterschelde are much less dense than it was in the open Grevelingen. The area of tidal flats was 76.5 sq km in the open Grevelingen and 251 sq km in the Oosterschelde. So, at maximum, the biomass of plant-eating birds should be 251/76.5, or about 3.3 times higher in the Oosterschelde than in the open Grevelingen. Using this 3.3 ratio, we calculate that the abundance of plant-eating birds in the Oosterschelde is 4.16×10^5 g afdw, which is probably a more reasonable figure.

10.2.2. Benthos-Eating Birds in the Oosterschelde

We revised the abundance figure for benthos-eating birds in the same manner as for the plant-eating birds. In the open Grevelingen, the abundance was 2.74×10^6 g afdw. Based on the 3.3 ratio, the abundance in the Oosterschelde would be approximately 9.0×10^6 g. The figure calculated from the scanty Oosterschelde data listed above (8.91×10^6 g) was essentially the same number. Thus, our estimate is 9.0×10^6 g afdw.

10.2.3. Fish-Eating Birds in the Oosterschelde

No data are known for fish-eating birds because they are apparently rare in the Oosterschelde. This might be so because the closed Grevelingen is more attractive to them, or perhaps the tidal currents in the open Oosterschelde are too strong for fish-eating (diving) birds. There are, however, data from the open Grevelingen. Their biomass was 1.24×10^4 g afdw in the open Grevelingen. Dividing this biomass by 130.2 sq km (the mean area of the open Grevelingen) yielded 9.52×10^{-5} g of fish-eating birds per square mile in the open Grevelingen. If we assume that this same density applies to the Oosterschelde, we find that there are 4.54×10^4 g afdw of fish-eating birds in the Oosterschelde.

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