A Modelling Approach for Determining the Freshwater Requirements of Estuarine Macrophytes

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ABSTRACT

Increased abstraction of water in the catchment results in a reduced or altered pattern of river flow and this holds serious consequences for the downstream estuarine ecosystem. In South Africa this is a serious concern because freshwater is in limited supply and the demand for freshwater can be expected to increase in the future.

A large multi-disciplinary consortium of South African scientists are working on projects to determine the freshwater requirements of estuarine ecosystems. As part of this, this thesis reports on research undertaken to develop mathematical models to determine the freshwater requirements of estuarine macrophytes. Three key macrophytes are selected. The macrophytes are *Zostera capensis* Setchell, *Ruppia cirrhosa* Grande, and *Phragmites* australis. They are common macrophytes in South African estuaries. *Zostera* and *Ruppia* are submerged macrophytes and *Phragmites* is an emergent macrophyte. They have different freshwater environments and therefore respond differently to alterations in freshwater flow.

A first order differential equation model is used to determine the effect of different combinations of open and closed mouth conditions of the estuary on *Zostera* and *Ruppia.* The scenarios are selected to determine whether achieving a switch in states from a *Zostera*-dominated estuary to a *Ruppia*-dominated estuary is possible.

To predict encroachment rates and colonisation patterns, a cellular automaton of the vegetative spread of existing *Zostera* beds is developed. After analysing various scenarios accounting for both an increase and a decrease in freshwater supply, the cellular automaton is extended to include interactions between *Ruppia* and *Phragmites*. The multi-species model is applied to the Kromme estuary, South Africa and the Great Brak estuary, South Africa. Various freshwater scenarios are examined from the natural runoff condition to the situation of no freshwater inflow.

A sensitivity analysis of the spatial model with *Zostera*, *Ruppia* and *Phragmites* is conducted.

PREFACE

The research work described in this dissertation was carried out in the Department of Mathematics and Applied Mathematics, University of Natal, Pietermaritzburg, from January 1994 to July 1998 under the supervision of Prof J W Hearne of Department of Mathematics and Applied Mathematics.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it has been duly acknowledged in the text.

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CHAPTER 1

INTRODUCTION

1.1 Definition of an Estuary

An estuary is an intermediate habitat between the sea, the land and freshwater. On the one end of an estuary, the river ecosystems grade into the estuary itself, while on the opposite end, the most seaward sections of the estuary form a dynamic link with adjacent marine systems. Estuaries are therefore crucial transition zones between land and water and support an ecosystem of specialised plants and animals.

An estuary is defined as a partially enclosed coastal body of water that is either periodically or permanently open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water and freshwater derived from land drainage (Day 1980).

1.2 South African Estuaries

The nature of estuaries in South Africa reflects the semi-arid climate and the seasonal precipitation. Sixty five percent of the country, namely the central and western sector, receives less than 500 mm of rain annually, and twenty one percent receives less than 200 mm. Only a comparatively narrow region along the eastern and southern coastline is moderately well watered (between 600 mm and 1000 mm per year) (Department of Water Affairs 1986). The average annual rainfall for the whole of South Africa (497 mm) is considerably less than the world average of 860 mm (Department of Water Affairs 1986)

Five types of estuaries are recognised in South Africa, namely permanently open estuaries, temporarily open estuaries, estuarine lakes, estuarine bays and river mouths (Whitfield 1992). All are essentially water systems with emergent plants around the edges and varying degrees of development of submerged vegetation, and are extremely varied in shape, size and depth (table 1.1), (Wetlands of the World 1993, p. 79-110).

Table 1.1. The principal physical features of five South African coastal lakes (from Wetlands of the World 1993, p. 79-110).

System	Location	Length (km)	Width (km)	Area (km^2)	Depth (m) (mean/maximum)
Lake St Lucia	28°50'S32°30'E	60.0	6.0	350.0	1.0/2.0
Zeekoeivlei	34°06'S18°30'E	2.0	1.00	2.2	3.6/N/A
Lake Sibaya	27°25'S32°40'E	18.7	18.3	34.0	12.6/43.0
DeHoopvlei	34°31'S20°23'E	18.0	1.0	6.2	1.1/7.7
Verlorenvlei	32°19'S18°21'E	13.5	1.4	1.01	2.5/5.0

South Africa has 273 estuaries along approximately 2950 kilometres of coastline (Whitfield 1995). The results of the most recent assessment of South African estuaries, conducted by Whitfield (1995), are shown in table 1.2. (The assessment was conducted on 247 estuaries). Whitfield (1995) stated that an estuary is in:

Excellent condition: if the estuary is in a near pristine state, i.e. there is negligible human impact;

Good condition: if there are no major negative man-induced alterations on either the estuary or the catchment;

Fair condition: if there is a noticeable degree of ecological degradation in the catchment and/ or the estuary; and

Poor condition: if there is major ecological degradation arising from a combination of man-induced alterations.

Table 1.2. Recent assessment of South African estuaries (from Whitfield 1995). See text for the definition of excellent, good, fair and poor.

Condition	Excellent	Good	Fair	Poor	Total
Number of estuaries	74	76	59	38	247
Percentage of total estuaries	30%	31%	24%	15%	100%

Although Whitfield (1995) stated that 61% of South African estuaries are in excellent or good condition, it should be noted that this is due to the large number of estuaries in good or excellent condition that occurred in the former Transkei region. These estuaries have been relatively undisturbed by human populations. For comparative purposes, Whitfield's (1995) assessment of KwaZulu-Natal estuaries showed 48% in fair condition, 26% in poor condition, 25% in good condition and only one estuary out of a total of 73 in excellent condition.

1.3 The Importance of Freshwater Inflow for South African Estuaries

There is concern for the effects of freshwater impoundments on estuaries in South Africa. This concern is related to the growing demand for water (Department of Water Affairs 1986). Freshwater is a scarce commodity in South Africa. This may be attributed to the semi-arid climate and the increasing human population. The resultant growing demand for freshwater in South Africa has necessitated the construction of large storage dams and large inter-basin transfer schemes. Numerous small agricultural dams and barrages and weirs have been built to sustain stock-watering and irrigation requirements. Increased abstraction of water in the catchment results in a reduced or altered pattern of river flow. This has had severe consequences on the downstream estuaries, from physical changes, such as prolonged mouth closure (Wooldridge 1992), to hydrodynamic alterations, such as altered salinities and water motion (Adams 1994), to changes in the ecology of the estuary (Adams and Bate 1994c; Wooldridge 1994).

The condition of the estuary mouth, (open or closed), controls the tidal influence in the estuary and is itself influenced by both river flow and tidal exchange. Estuarine sediment is derived primarily from the near shore marine environment. When river flow velocity into the estuary is reduced, the sediment load is deposited in the mouth, resulting in an accumulation of sand on flood-tide deltas. Subsequent ebb tides scour the deposited sediment, transporting it into the marine environment. When the rate of scouring of the estuary mouth by tidal action is less than the rate of sediment deposition by wave action, sediment accumulates as a bar across the estuary mouth. Under flood events and high river flow conditions, or spring flood tides, the sand bar is scoured out.

River inflow is therefore critical in the maintenance of open mouth conditions and connection with the sea. Estuaries open to tidal flushing change with the tides. At high tides seawater transforms estuaries, submerging the plants and flooding the marshes. As the tides ebb, the water level is very low and mud flats are exposed. A decrease in freshwater flow results in flood peak attenuation that may increase the incidence of mouth closure and prolong closed mouth conditions owing to less effective scour of sediment near the mouth (Wooldridge 1992). When the estuary mouth is closed, water levels do not fluctuate with the incoming tides associated with open mouth conditions. Thus if water levels drop during mouth closure, then the survival of macrophytes that are normally submerged is threatened. In the Wilderness lagoon, South Africa, encroachment by emergent macrophytes into submerged macrophyte areas was associated with decreased water levels during periods of low freshwater input when the system was closed to the sea (Weisser and Howard-Williams 1982). On the other hand, high water levels during closed mouth conditions can cause extended flooding and water logging of macrophyte communities. Altered water level fluctuations also result in changes in the temperature and light availability of the estuary. During open mouth conditions, at high tides, water temperature is usually cool because light does not penetrate as far in deep water, so the lower layers remain relatively cool, whereas at low tides the water is heated all the way through. Changes in these patterns can affect the estuarine organisms adapted to survive these fluctuating conditions.

Estuaries play a vital role in the life history and development of many invertebrate and fish fauna (Day 1981; Wooldridge 1994). Because of their high nutrient level, and the relative shelter from wind and waves, estuaries are ideal environments for the growth of young. An increase in the incidence of mouth closure disrupts the migration of species between the sea and the estuary.

Estuaries are one of the most productive systems in the world, enriched relative to the sea in both organic matter and nutrients (Day 1981). Nutrients in estuaries are largely brought down by the river from the catchment area or, more rarely, are imported from the sea by tidal exchange (Kennesh 1986). A decrease in freshwater supply results in a reduction of land-derived nutrients and organic detritus that is a food source for a variety of estuarine organisms.

Reduced freshwater inflow prevents adequate dilution or flushing of wastes and makes it more difficult to maintain natural water quality. The resultant decline in water quality can result in blooms of nuisance algae (Adams 1994), and a decrease in water clarity (Chambers and Klaff 1985).

The productive nature of estuaries provides a suitable habitat and plentiful food supply for many plants and animals. The community of life found on the land and in the water includes mammals, birds, fish, reptiles and plants. The mixing of sea water and freshwater in estuaries creates a body of water that is brackish in nature. Some organisms have specifically adapted to these conditions, while others are from either fresh or salt water origins. Such distinct groups of different plant and animal assemblages (i.e. zonation patterns), each occupying particular stretches of the estuary, are well developed in South Africa's estuaries (Schlacher and Wooldridge 1996).

River inflow is the primary factor that causes the spatial variation in salinity from the mouth to the head of the estuary, and consequently the spatial zonation of species (Adams and Talbot 1992; Adams et al. 1992). A reduction in river inflow reduces the mouth to head salinity difference. This contributes to stress on organisms adapted to a specific estuarine environment, and marine communities extend into the upper reaches and the brackish communities are lost. Thus reduced river inflow results in a loss of macrophyte diversity (Adams and Talbot 1992; Adams et al. 1992).

The estuarine environment can therefore be stressed and severely damaged by changes in river inflow. Increased impoundment of water in South Africa's rivers has led to a decrease in the amount of freshwater available to the downstream estuaries. As discussed in the previous paragraphs, this may hold serious consequences for the estuarine ecology (Council for the Environment 1991; Baird and Heymans 1996).

1.4 Determining the Freshwater Requirements of Estuaries

The Commission of Enquiry into Water Matters in 1970 recognized for the first time in South Africa, that water was required for environmental management (Department of Water Affairs 1986). The Commission considered that Lake St. Lucia, a wetland of international

significance, and the Kruger National Park were the only two cases where water was required for management and it was estimated that 220 million cubic metres per year would be required. Since then, however, there has been growing acceptance that the utilization of water resources in South Africa should include the needs of conservation, and the water requirements for South Africa for environmental management have now been estimated to be more than 10 times the amount that was originally estimated by the Commission of Water Affairs in 1970 (see table 1.3).

Table 1.3. Estimated water requirements for environmental management in South Africa (total of estuaries, lakes and nature conservation). Values are in a million cubic metres per year (modified from Wetlands of the World 1993, p. 84, table 5).

Year	1980	1900	2000	2010
Volume of Water (10^6 m^3.$year^{-1}$)	2,946	2,949	2,954	2,958

The extent to which estuaries in South Africa have already become degraded because of diminished freshwater supply, and the likelihood that this trend will continue and extend to other estuaries as freshwater utilization pressures increase, suggests that the development of a management strategy for estuaries be a priority. The conservation of estuaries is important, not only because they provide habitats for distinct assemblages of birds, fish, invertebrates and floral communities, but because they are environments of high aesthetic value. They are scenic and provide a range of recreational activities (Quinn 1992). Recreation in estuaries includes activities such as bathing, windsurfing, water skiing, boating and canoeing

Although considerable effort has been directed towards documenting the effects of diminished freshwater supply to estuaries (Kriel 1966; Jezewski and Roberts 1986; Department of Water Affairs 1986), the development of techniques to reliably predict the effects of alterations in river inflow to an estuary is a critical management requirement. This focussed research on the development of a methodology for predicting the freshwater requirements of estuaries (Slinger 1994). This approach focussed on the numerous biotic-abiotic relationships within estuaries. A collaborative research project within the Consortium for Estuarine Research and Management (CERM) group, with a number of estuarine scientists, engineers and natural resource modellers was initiated in September 1992 (Slinger 1994, 1995, 1996). The aim of

the CERM project was to evaluate the freshwater requirements of estuaries by determining how the physical conditions and the associated biotic interrelationships respond as a consequence of a management action such as artificial breaching or a water release policy. The general aim of the project was to enhance the assessment of the freshwater requirements of estuaries and assist in the planning of regional and national water resource developments. The development of the models in this thesis was initiated during this project.

1.5 Determining the Freshwater Requirements of Estuarine Macrophytes

Estuarine macrophytes are plants which are generally rooted in the sediment. They are important components of estuaries for a number of reasons: they serve as a natural incubator for larvae and fry of many fishes and invertebrates; they act as a large source of detritus for eaters inhabiting macrophyte beds (Belyaev et al. 1977); they supply substrate to consumers and decomposers; they are important in nutrient cycling and sedimentation (Sculthorpe 1967); they absorb many natural wastes that are drained off the land (Adams 1994), thereby creating cleaner and clearer water.

Estuarine macrophytes have been relatively well studied throughout the world, (table of references in Adams 1994, table 1, p. 10; Short and McRoy 1984) and have been studied in South Africa since the early 1980's (Talbot and Bate 1987; Talbot et al. 1990; Adams et al. 1992; Adams and Bate 1994a, 1994b, 1994c; Reed 1994). In South Africa four groups of estuarine plants are recognised, namely floating macrophytes, emergent macrophytes, submerged macrophytes and macroalgae. Within each group different genera are typical of different zones in the estuary. These groups are:

Emergent macrophytes

Emergent macrophytes are plants rooted in soft intertidal or shallow subtidal substrata. They have aerial portions that are partially or periodically submerged. Salt marsh plants are emergent macrophytes that occur in distinct zones along an elevation and tidal inundation gradient. The marsh areas form an extensive habitat for typical estuarine faunal species, e.g. the marsh crab *Sesarma catenata* (Adams 1994). Salt marsh dominated estuaries provide natural buffers between the land and the ocean. *Spartina maritama* and *Sarcocornia perennis* are common salt marsh plants in South African estuaries (Adams, 1994).

Submerged Macrophytes

Submerged macrophytes are rooted in soft subtidal and low intertidal substrata. The plants' leaves and stems are completely submerged for most states of tides. Submerged macrophytes, through the provision of a diversity of habitats, increase invertebrate and fish faunal diversity (Balls et al. 1989) and provide a habitat for epiphytes. Submerged macrophytes help to anchor the sediment, and reduce phosphate and ammonia release (Adams 1994). Typical species include *Zostera capensis* Setchell and *Ruppia cirrhosa* Grande which are common in South African estuaries (Adams 1994).

Floating Macrophytes

Floating plants are not anchored in the sediment. These plants are generally restricted to the river end of estuaries where salinities are low and water conditions are calm. Typical species include *Eichhornia crassipes* (water hyacinth) which is exotic to South Africa and is regarded as a nuisance weed (Adams 1994).

Macroalgae

These seaweeds may be intermittently exposed or always submerged, and may be attached to hard or soft substrata, or they may be floating. It is generally believed that macroalgae form a minor part of the estuarine flora (Adams 1994).

Therefore by determining how much freshwater is needed for the survival of estuarine macrophytes, this will indirectly show the requirements for the spawning, hiding and feeding field for fishes, and the habitat requirements for epiphytes.

Differences in salinity, and the timing, duration, and frequency of tidal flooding within estuaries affect the vegetation. Estuaries become increasingly fresher upstream from the estuary mouth as salt water is diluted by the river's freshwater discharge. Plant composition markedly changes from the more saline portions of estuaries to the brackish areas. Even within areas of similar salinity, vegetation differs largely due to frequency and duration of tidal flooding. Thus, the plants selected for this study represent the different habitat types along the estuary. The plants selected are *Zostera capensis* Setchell, *Ruppia cirrhosa* Grande, and *Phragmites australis*. They are common macrophytes in South African estuaries. *Zostera*

capensis Setchell is a submerged macrophyte that forms dense and highly productive meadows in shallow estuarine waters of South Africa. *Zostera* survives near the mouth of permanently open estuaries because of its ability to survive marine conditions and periods of exposure during ebb tides. Moving upstream from the mouth, where seawater is diluted by freshwater, *Ruppia*, a brackish submerged macrophyte may be found. Unlike *Zostera*, *Ruppia* only survives if it is completely submerged. This is one reason *Ruppia* does not survive in the mouth of permanently open estuaries (Adams and Bate 1994a): When the mouth is open water levels may drop, especially during low tide, and *Ruppia* is exposed and dies back. Conversely, during periods of low freshwater flows the mouth closes and *Ruppia* encroaches into the mouth. The emergent reed, *Phragmites australis,* grows above the water level. *Phragmites* is a freshwater emergent macrophyte and occurs in the upper reaches of South African estuaries that have a gradient of decreasing salinity along the length of the estuary.

Zostera, *Ruppia* and *Phragmites* represent marine, brackish and freshwater habitats respectively. They are also representative of habitats that are periodically exposed (*Zostera*), always submerged (*Ruppia*), and emergent (*Phragmites*). They have been extensively studied in South Africa, being the subject of one PhD thesis (Adams 1994), and several papers (Adams and Talbot 1992; Adams and Bate 1994a, 1994b, 1994c).

1.6 An Outline of the Thesis

There is the need for the development of techniques for estimating the freshwater requirements of South African estuaries. Previous freshwater management techniques in South Africa have focussed on estimating the flooding and evaporative requirements of estuaries (Jezewski and Roberts, 1986, Department of Water Affairs, 1986). These estimates do not take into account the biotic-abiotic relationships within estuaries and are therefore not an assessment of the ecological requirements of estuaries. In addition, the estimates do not provide an indication of the seasonal or monthly distribution of this annual allocation (Whitfield and Wooldridge, 1994). Recent approaches (CSIR 1992) have been developed to take into account the ecological requirements of estuaries. However (Quinn, 1998) argues that these approaches are based on a collective and intuitive expert assessment and that there is no way of knowing in the long term whether these estimates are reliable. Furthermore, these estimates are usually annual totals and do not specify monthly flow regimes.

As discussed in section 1.4, the CERM project was initiated in 1994 in order to develop a scientific methodology for predicting both the physical and the ecological freshwater requirements of estuaries (Slinger 1994). The hydrological models of the CERM project predict, for various water releases, e.g. monthly releases, no freshwater inflow, the consequences on the physical dynamics of the estuary. The results from these models are then used in ecological models to predict the outcome on the fauna and flora of the estuary. The models in this thesis form part of the CERM project and focus on the freshwater requirements of estuarine macrophytes.

The first model appears in chapter 2 and describes the temporal dynamics of two submerged macrophytes in the mouth of the estuary. The aim of the model is to predict the consequences of different combinations of open and closed mouth conditions on the plants. The plants selected for the model are *Zostera* and *Ruppia* because *Zostera* and *Ruppia* survive in open and closed estuaries respectively. In South Africa increasing demand for freshwater resources has resulted in large impoundments from rivers with the consequence that freshwater inflow to estuaries has decreased. As most South African estuaries are maintained in an open state by freshwater outflow, a reduction in freshwater flow results in an increase in the frequency and duration of mouth closure periods (Wooldridge 1992), and consequently a change in the dynamics of the plants in the mouth of the estuary. Thus the model is used to answer questions such as how does prolonged mouth closure affect the long term survival of *Zostera* and *Ruppia*? And what would the effect be of mechanically opening the mouth of the estuary?

Spatial aspects are not considered in the above model of *Zostera* and *Ruppia* because the purpose is to predict the outcome in the mouth of the estuary. However, an additional factor to consider is that in South Africa a major effect of impoundments from rivers is the increase in salinity further up the estuary (Adams and Talbot 1992; Adams et al. 1992). Estuaries have a natural difference in salinity from the head of the estuary, where salinity is low, to the mouth of the estuary, where salinity is high. A reduction in river inflow reduces the mouth to head salinity difference. In some South African estuaries, e.g. the Kromme estuary (Adams and Talbot, 1992), impoundments have resulted in uniform high salinities throughout the estuary, with the result that marine macrophytes encroach into the upper reaches and displace brackish communities. The second model in chapter 3 therefore includes spatial dimensions so that we

can predict what happens to the location of marine species along the estuary if freshwater inflow is reduced. If estuarine flora is to be preserved in South Africa, freshwater managers will need to know what quantity of water that needs to be released to estuaries in order to prevent marine species from spreading further up the estuary. The marine plant selected for the model is *Zostera.*

In addition to answering questions on the encroachment of marine species along the length of the estuary, the spatial model in chapter 3 also answers questions on how the depth distribution of *Zostera* changes with freshwater inflow. In South Africa, a reduction in river inflow may cause water levels to drop. *Zostera* beds may be exposed and therefore start to die-back. On the other hand, if impoundments result in mouth closure then water levels may rise due to the damming effect caused by the closed mouth of the estuary. *Zostera* does not survive if submerged below 2.5 m. Thus the model is used to determine the extent to which impoundments affect the water level fluctuations in the estuary and consequently the survival of *Zostera* beds.

It is also important to be aware of the consequences of water releases on other types of macrophytes such as brackish or freshwater plants. For example, we may find that under certain impoundments *Zostera* is prevented from encroaching up the estuary because of the presence of a brackish plant further up the estuary. We therefore extend the spatial model of *Zostera* to include *Ruppia cirrhosa* Grande, a brackish submerged macrophyte, and *Phragmites australis*, a freshwater emergent plant. This model is presented in chapter 4.

The full model, with all three macrophytes, is applied to two estuaries in South Africa, namely the Kromme estuary and the Great Brak estuary. These estuaries represent two different types of estuaries found in South Africa. The Kromme estuary is a permanently open estuary, whereas the Great Brak estuary is a temporarily closed system. The physical effect of impoundments in the Kromme estuary is therefore different to the physical effects of impoundments in the Great Brak estuary. Therefore, the response of the plants to the impoundments may be different in the Kromme estuary and the Great Brak estuary.

Mathematical models are increasingly being used for environmental management (Prentice and Leemans 1990; Quinn 1992; Busing 1995; Chiarello and Barrat-Segretain 1997). The three models in this thesis are designed to enhance the assessment of the freshwater requirements of estuarine macrophytes in South Africa, and therefore assist in planning of regional and national water resource developments. This is a critical requirement in South Africa where freshwater impoundments have already threatened estuarine ecosystems (Adams et al. 1992; Adams and Talbot 1992) and can be expected to continue to pose a threat due to the increasing human population and therefore the increasing demand for freshwater.

1.7 Structure of Thesis

The nonspatial model of *Zostera* and *Ruppia* is derived in the following chapter. Three scenarios representing different mouth breach policies are analysed. The stability of the equilibrium states is determined. Stability means local stability. That is, an equilibrium state is said to be stable if a small perturbation from the equilibrium will result in the system returning to the equilibrium state. Phase plane analysis is used to determine the effect of initial conditions on the outcome.

Chapter 3 comprises the cellular automata model of *Zostera*. Results are obtained for scenarios with both freshwater impoundments and an increase in freshwater supply, and for scenarios with flood events and dry periods.

The application of the full multi-species cellular automata model, with *Zostera*, *Ruppia* and *Phragmites,* is presented in chapter 4. Results for runoff scenarios from natural runoff conditions to a situation of no freshwater input are obtained for the Kromme estuary and for the Great Brak estuary.

A technical analysis of the cellular automata model appears in chapter 5. The purpose of this chapter is to examine how the model assumptions change the outcomes to the runoff scenarios. The technical study determines effects of cell size, variations in model functions, variations in parameter values, and an alternative form of spread on the outcome to the runoff scenarios for the Kromme and Great Brak estuaries. The conclusion in chapter 6 provides suggestions for future research and improvements to the model.

CHAPTER 2

EVALUATING THE EFFECT OF MOUTH CONDITION ON THE SURVIVAL OF TWO SUBMERGED MACROPHYTES

2.1 Existing Models of Estuarine Macrophytes in South Africa

Predictive rule-based modelling of estuarine macrophytes was undertaken by Adams and Bate (1994c). This was one of the first models to be developed with the purpose of determining the plant response of the estuary to freshwater inflow in South Africa. The expert system includes rules for the following estuarine macrophytes:

Submerged macrophytes:	*Zostera capensis* Setchell and *Ruppia cirrhosa* Grande,
Emergent macrophyte:	*Phragmites australis*,
Salt marsh plants:	*Sarcocornia perennis* and *Spartina maritama*

The aim of the expert system is to predict whether macrophytes will die, show reduced growth or be unaffected by a manipulation of freshwater inflow. Thus given a set of physical parameters within an estuary, the expert system will diagnose the effect on the plants present. The knowledge the expert system uses comprises "if-then" rules and includes the tolerances of estuarine macrophytes to freshwater inflow.

The freshwater-related physical factors included in the expert system model of Adams and Bate (1994c) are salinity, water level fluctuations, water clarity and current velocity. These factors were selected for the following reasons:

(1) In estuaries where there is reduced freshwater input, high salinities have been observed to cause impoverishment of the estuarine flora (Adams et al. 1992).

(2) Impoundments have resulted in an increase in the frequency and duration of mouth closure (Adams 1994). During closed mouth conditions, water levels may drop due to reduced freshwater runoff. This results in the exposure of submerged macrophytes for extended periods. Therefore management decisions have to be made about the length

of time intertidal plants can survive under prolonged exposed conditions before the mouth of the estuary needs to be mechanically opened. On the other hand, water levels may rise during closed mouth conditions because there is no outlet for water to flow into the sea. This results in the inundation of intertidal plants for prolonged periods.

(3) Water clarity decreases with diminished freshwater supply. Water clarity is important because it determines the depth distribution of submerged macrophytes. In the expert system model water clarity depends on sediment load which is defined as high, medium or low.

(4) The freshwater inflow rate is incorporated in the model by using the rule that submerged macrophytes will not survive in estuaries where the current velocity exceeds 1 $m.s^{-1}$, which would represent flood conditions in South African estuaries.

The expert system is a useful predictive tool for different freshwater input scenarios. It can assess qualitative information and give logical conclusions. There is the need however to include a dynamic link between vegetation and the environmental factors that cause change, so that processes of growth and recovery of vegetation can be modelled. The expert system model predicts the outcome under constant environmental conditions. For example, if the expert system is predicting over one year then it would use the average salinity, freshwater inflow rate and water clarity for the year and make a prediction based on these average values. Thus the expert system model cannot predict the outcome based on daily changes in salinity and inflow rates. This is something that a differential equation model can do.

In addition, the expert system model cannot incorporate changes in the mouth condition. It is designed to make a prediction under a constant estuary mouth condition, namely open or closed. A differential equation model on the other hand can include dynamic changes in the mouth condition.

The results for the expert system model are based on growth adjustment with a score range of between -10 and +10. Growth adjustment score of zero means that plants will be unaffected and there is no change in the growth rate. A positive score means that the growth rate will

increase. A negative score means that the growth rate will decrease. A score of -10 means that the plants will die. A differential equation model on the other hand will give exact qualitative output.

Thus the model developed in this chapter is a differential equation model. The model is designed to predict the temporal response to various water release scenarios. In addition, the model will also be used to analyse how the run-off scenarios respond to sudden disturbances such as a drought or a flood. Although the expert system can predict what will happen as a result of a flood, it cannot predict how badly the system is affected by the flood, nor can it predict how long the system will take to recover after normal runoff conditions return. The differential equation model was not primarily designed to analyse the systems response to disturbances, but it may be used to analyse such responses.

2.2 A Model of *Zostera capensis* Setchell and *Ruppia cirrhosa* Grande

2.2.1 Purpose of the Model

In South African estuaries mouth closure is occurring more frequently due to diminished freshwater supply (Wooldridge 1992). Prolonged mouth closure influences the migration of species between marine and estuarine environments, and changes the hydrodynamics and consequently the fauna and flora of the estuary. Artificially breaching the estuary mouth costs money, so being aware of the implications of various breaching scenarios is important before a management decision is made. Decisions such as how often the mouth should be mechanically opened, and for how long dredging of sediment near the mouth should occur to maintain open mouth conditions, need to be made by examining both the cost implications and the ecological implications. That is, a policy needs to be chosen that is cost effective, but simultaneously results in a healthy estuarine ecosystem. A cost-effective policy would be one that requires least dredging of sediment or least frequency of mechanically opening the mouth.

To assist the above decisions, a mathematical model of two submerged macrophytes is developed. The purpose of the model is therefore to predict the consequences of different combinations of open and closed mouth conditions on estuarine macrophytes. The model will then be useful in determining how to maintain macrophyte communities in temporarily open

estuaries by breaching the mouth at various intervals. Thus management actions can be taken once the consequences of the actions on the submerged macrophyte communities are known.

2.2.2 Key Macrophytes Selected for the Problem

The model is used to determine the response of *Zostera capensis* Setchell and *Ruppia cirrhosa* Grande to various combinations of open and closed mouth conditions. *Zostera* and *Ruppia* are common submerged macrophytes in South African estuaries. They are also known as seagrasses. They are primary producers and provide habitat for fish for spawning, hiding and feeding. Seagrasses take up nutrients by their roots and excrete nutrients into the water as either dissolved or particulate organic matter through the leaves. They are therefore considered important in pumping nutrients from sediment to water (McRoy et al. 1972).

Zostera and *Ruppia* have differing tolerances to changes in the mouth condition. *Zostera* survives under open mouth conditions because of its ability to tolerate tidal currents and periods of exposure during low tides (Adams and Bate 1994a; Reed 1994). Unlike *Zostera*, *Ruppia* does not survive when exposed above the water level during low tides (Adams and Bate 1994a). *Ruppia* is also washed away by tidal currents during open mouth conditions (Reed 1994). Therefore *Ruppia* survives in closed estuaries where conditions are calm and water levels are steady. *Ruppia* is a brackish macrophyte which has a wide salinity tolerance range (*Ruppia* survives between zero and 75 ppt., although leaf production and rhizome elongation are much reduced at 75 ppt., Adams and Bate 1994b). *Zostera* is a marine plant that has narrow salinity tolerance range (between 15 ppt. and 35 ppt., Adams and Bate 1994b). Therefore *Zostera* is selected as the key macrophyte to represent a habitat that survives under open mouth conditions, and *Ruppia* is selected as the key macrophyte to represent a habitat that survives under closed mouth conditions.

2.2.3 Model Equations

Several authors (Verhagen and Nieunhuis 1983; Wright et al. 1986; Bach 1993; Scheffer et al. 1993; Zupo et al. 1997) have produced temporal models of submerged plants. These models explore the impact of environmental factors such as light, temperature, and wave action on the dynamics of the plant biomass. *Zostera* and *Ruppia* cannot be directly incorporated in these models because different physical factors are used for the model of *Zostera* and *Ruppia*. In addition, the models in the literature describe growth as a process of photosynthesis. The botanical information from which the physical multipliers for *Zostera* and *Ruppia* are obtained relates to the specific growth rate and the specific mortality rate, and not to respiration rates as in the models describing growth from photosynthesis. However, the general form of these model equations is adopted, namely:

$$\frac{dB}{dt} = B.[GR - MR] \tag{2.1}$$

where

B is the plant biomass ($g.m^{-2}$),

t is the time (days),

GR is the growth rate ($g.g^{-1}.day^{-1}$), and

MR is the sloughing or mortality rate ($g.g^{-1}.day^{-1}$).

The model of *Zostera* and *Ruppia,* which appears in the unpublished report of Busse and Hearne (1994), is therefore based on equation (2.1) and is given by:

$$\frac{dZ}{dt} = sgr_z * sgm_z * Z * (1 - \frac{Z+R}{K}) - \frac{sdr_z}{2} * Z * (sdm_z + scm_z) \tag{2.2a}$$

$$\frac{dR}{dt} = sgr_r * sgm_r * R * (1 - \frac{Z+R}{K}) - \frac{sdr_r}{2} * R * (sdm_r + scm_r) \tag{2.2b}$$

where

Z	is *Zostera* biomass per unit area (biomass density) at time t ($g.m^{-2}$),
t	is the time (days),
sgr_z	is the maximum specific growth rate of *Zostera* ($g.g^{-1}.day^{-1}$),
sdr_z	is the maximum specific mortality rate of *Zostera* ($g.g^{-1}.day^{-1}$),
sgm_z	is the salinity growth multiplier for *Zostera* (0-1),
sdm_z	is the salinity mortality multiplier for *Zostera* (0-1),
scm_z	is the scour multiplier for *Zostera* (0-1), and
K	is the maximum biomass per unit area ($g.m^{-2}$).

Similar definitions apply for *Ruppia*.

Equation (2.2) applies to a specific point in the estuary, which for this study is the mouth of the estuary.

Submerged macrophytes are normally coated with epiphytic algae that account for 28% of the total biomass of submerged macrophytes in summer (Penhale 1977). Epiphytes may, through excessive shading, lower the productivity rates of macrophytes to the point where the plants may die (Sand-Jensen 1977). However, following the models of aquatic macrophytes in the literature, epiphytic biomass and the effects of epiphytes on macrophyte dynamics are not included in the model.

In the submerged plant models in the literature (for example, Verhagen and Nieunhuis 1983; Wright et al. 1986; Bach 1993; Scheffer et al. 1993), the growth and mortality rates are related to plant density and the physical environment. The specific growth rate, (sgr), in (2.2a) is the maximum specific growth rate. That is, it is the growth rate under ideal physical conditions and low density. To include the effects of salinity on the specific growth rate, the specific growth rate is multiplied by a salinity growth multiplier. The salinity growth multiplier lies between zero and one. If salinity is favourable for growth, then the value of the salinity growth multiplier is one, so that growth occurs at the maximum specific growth rate, whereas if salinity is unfavourable for growth, then the salinity growth multiplier is less than one, so that the growth rate is less than the maximum specific growth rate. Similarly, in order to include

how biomass density affects the maximum specific growth rate, the maximum specific growth rate is also multiplied by a density-dependent growth multiplier. This multiplier lies between zero and one, so that when biomass density is low, the density-dependent growth multiplier is one, and the growth rate occurs at the maximum specific growth rate, whereas if density is high, then the density-dependent multiplier is close to zero and the growth rate is less than the maximum specific growth rate.

The salinity mortality multiplier and the scour multiplier have values between zero and one. If salinity is unfavourable for growth, then the salinity mortality multiplier is close to one, whereas if salinity is favourable for growth then the salinity mortality multiplier is close to zero. A similar definition holds for the scour multiplier, where the scour multiplier is close to one for high current velocities and close to zero for low current velocities.

The maximum specific mortality rate in (2.2b) is the mortality rate under the worst possible conditions for growth. Given that the mortality multipliers have values between zero and one, we use the sum of these multipliers to determine the effect of the combination of the multipliers on the maximum specific mortality rate. The use of the product of the mortality multipliers would mean that if there is no mortality due to one factor, for example if the salinity mortality multiplier is equal to zero, then there will be no mortality incorporated in the model because the product of the mortality multipliers would be equal to zero. In equation (2.2b) we divide the maximum specific mortality rate by 2 so that, under the worst possible scenario, when both the salinity mortality multiplier and the scour multiplier are equal to one, the mortality rate is equal to the maximum specific mortality rate.

2.2.4 Physical Multipliers

Following the expert system model developed by Adams (1994), the physical factors selected for the model are salinity and current velocity of the estuary. Adams (1994) argues that these are important factors that are directly related to freshwater inflow. There are no models in the literature that include these effects. In the macrophyte models of Park et al. (1975), Verhagen and Nieunhuis (1983), Wright et al. (1986), Collins and Wlonsinski (1989), Bach (1993) and Scheffer et al. (1993), the physical factors are light, temperature or nutrients function. Hence we could not use these models for the model of *Zostera* and *Ruppia*.

Effects of Salinity on the Growth and Mortality of Zostera and Ruppia

Zostera and *Ruppia* have an optimal/sub optimal salinity range of tolerance. Mouth closure will change the salinity in the estuary because the mixing of sea water with freshwater will be absent when the mouth is closed. Freshwater management decisions therefore have to consider the maximum time plants can be exposed to the resulting salinities before the mouth needs to be mechanically opened.

The salinity multipliers for the model are determined from Adams and Bate (1994c). Adams and Bate (1994c) showed that the wet mass, rhizome length and number of leaves (final - initial) of *Zostera* after three months growth in different salinity ranges were all maximal when grown at a salinity of 15 ppt. (see figure 2.1). Leaf length was greatest at 35 ppt. but was not significantly different from 15 ppt. *Zostera*, therefore, appears to survive best within the salinity range of 15 ppt. and 35 ppt. The change in wet mass of *Zostera*, the number of leaves, and the rhizome lengths were higher in freshwater than in hyper saline treatments (55 ppt. - 75 ppt.). It appears that *Zostera* could survive better under extended freshwater conditions than under extended hyper saline conditions. After only six weeks of incubation, the plants in freshwater (zero ppt.) began to show signs of stress, whereas after four weeks of incubation in 75 ppt., all *Zostera* plants had died. Plants in 55 ppt. initially survived, but as time progressed, they became increasingly stressed and had died after 12 weeks.

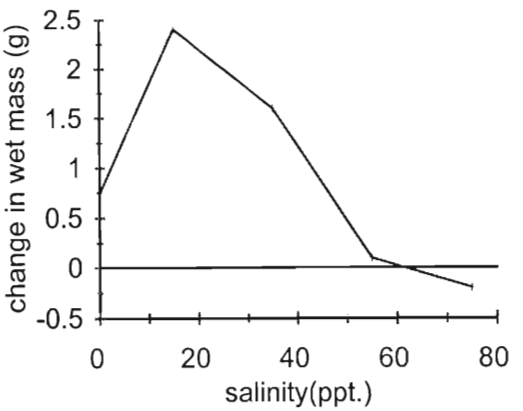

Figure 2.1. The effect of salinity on the change in *Zostera capensis* wet mass after three months in different salinity ranges. The change in rhizome length, number of leaves and average leaf length follow similar shape graphs. (Adams 1994, p.37).

The change in wet mass of *Ruppia*, rhizome length and number of leaves decreased as the treatment salinity increased from zero to 75 ppt. (figure 2.2). New growth was evident for all *Ruppia* plants but was greatest at the lower salinities. Leaf length peaked at 35 ppt., while there was a lack of vertical growth in *Ruppia* at low salinity (0-6 ppt.). In the field *Ruppia* is dominant in brackish estuaries (salinity < 30 ppt.), and survived and grew best in freshwater in the laboratory.

Under controlled laboratory conditions *Ruppia* had a wider range of salinity tolerance than *Zostera*, as new growth was initiated at 55 ppt. and 75 ppt. The wide salinity tolerance range of *Ruppia* makes it a more opportunistic species than *Zostera*. Growth of *Ruppia* is reduced at high salinity (55 ppt.), but it is not as sensitive as *Zostera capensis* that will die after one month at a salinity of 75 ppt. and three months at salinity 55 ppt. Under controlled laboratory conditions, with *Zostera* and *Ruppia* grown in the same tank, *Zostera capensis* died after nine weeks in the 55 ppt. treatment. Both species were of equivalent size and mass at the beginning of the growth period. In the absence of *Ruppia*, *Zostera* died after three months in 55 ppt. Adams (1994) argued that competition for nutrients and space by *Ruppia* may have affected the survival capacity of *Zostera* under high salinity conditions.

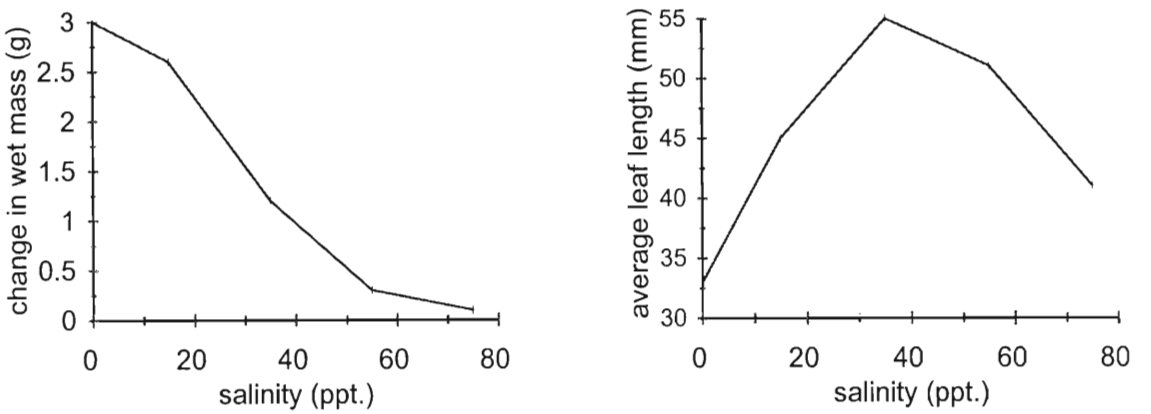

Figure 2.2. The effect of salinity on the change in *Ruppia cirrhosa* wet mass and average leaf length after three months in different salinity ranges. The change in rhizome length and number of leaves follow similar shape graphs to the change in wet mass graph. (Adams 1994, p.38).

Apart from the qualitative observations outlined above, no data exist which relate salinity to the growth rate of *Zostera* and *Ruppia*. Various authors (see Adams 1994, p. 10 for references), have obtained data to qualitatively describe the relationship between salinity and the growth rate of *Zostera* and *Ruppia*. Therefore based on the findings of Adams and Bate (1994b), the effect of salinity on the specific growth rate and the specific mortality rate as described by equations (2.2a) and (2.2b) was defined by the multipliers shown in figure 2.3. At a salinity of less than 20 ppt., *Ruppia* is a superior competitor to *Zostera* because of its ability to grow rapidly under these conditions (Adams 1994b). Therefore, the salinity growth multiplier of *Ruppia* is greater than that of *Zostera* for salinities less than 20 ppt. The salinity growth and mortality multipliers for *Zostera* have their maximum and minimum vales respectively between 15 and 35 ppt. because *Zostera* grows best under this salinity range (Adams and Bate 1994b). At high salinities, the salinity growth multiplier for *Ruppia* is above that for *Zostera* and the salinity mortality multiplier for *Ruppia* is below that for *Zostera*.

The salinity multipliers in figure 2.3 are functions of a smoothed value of salinity. This smoothing of the salinity values is achieved by means of a first order delay. Denoting the salinity at time t by s(t), and the smoothed salinity by ss(t), we have the relationship

$$\frac{dss(t)}{dt} = \frac{s(t) - ss(t)}{sst} \qquad (2.3)$$

where sst is the salinity smoothing time in days.

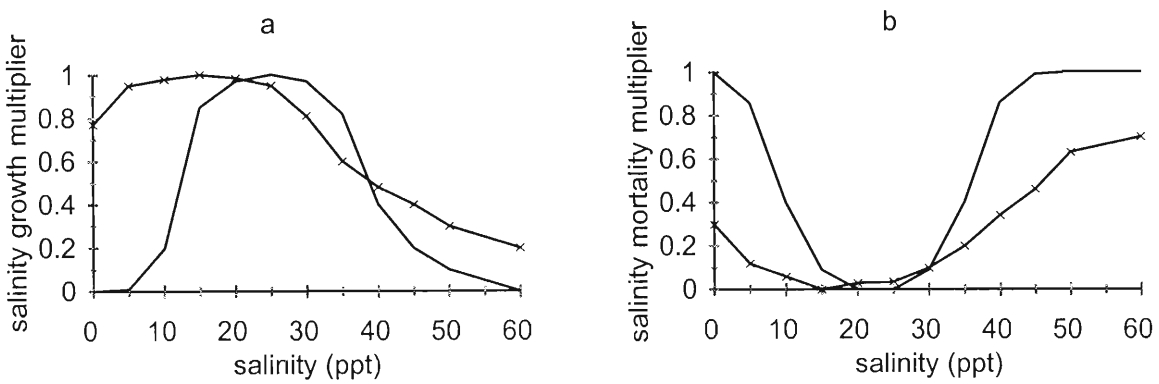

Figure 2.3. Graphs showing the salinity growth and mortality multipliers of the model for *Zostera* (_) and *Ruppia* (x) in equations (2.2a) and (2.2b). The salinity growth multipliers are shown in figure a and the salinity mortality multipliers in figure b. *Zostera* grows optimally for salinities between 15 ppt. and 30 ppt, whereas *Ruppia* has a wide range of salinity tolerance.

Effects of Water Current Speed on the Growth and Mortality of Zostera and Ruppia

A number of models of submerged macrophytes include biomass losses owing to wave damage (Park et al. 1975; Wright et al. 1986; Ewel and Fontaine 1982; Scheffer et al. 1993). Advective loss in Wright et al. (1986) is given by the scour function S = -a+bln(B) where a and b are positive constants and B is macrophyte biomass. Thus as plant biomass increases, the sloughing rate increases. In Scheffer et al. (1993), where a depth dimension is included in the model, losses owning to wave damage are maximal at the shoreline and decrease with rooting depth. This form of a scour multiplier is not used in the model of *Zostera* and *Ruppia* because it requires a depth dimension which is not included in the model.

A general rule for submerged macrophytes is that they will not survive in estuaries where the water current speed is greater than 1 $m.s^{-1}$ (which would represent high flow conditions in most South African estuaries, Howard-Williams and Liptrot 1980). Adequate South African literature (Branch and Day 1984; Bally et al. 1985) is available to support this. Research (Reed 1994) has shown that *Zostera* grows under higher current speeds than *Ruppia*. *Ruppia* is more productive in sheltered bays and lagoons where water currents and wave action is low (Congdon and McComb 1979). The experiments in Reed (1994) showed that *Zostera* can withstand higher current velocities than *Ruppia*. Therefore based on these results the effect of water current speed on the specific mortality rate as described by equations (2.2a) and (2.2b) was defined by the multipliers shown in figure 2.4.

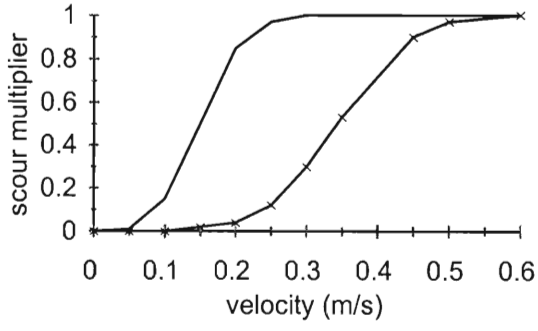

Figure 2.4. Graphs showing the scour multipliers of the model for *Zostera* (_) and *Ruppia* (x) in equations (2.2a) and (2.2b).

2.2.5 Parameter Values

The values assigned to the parameters are:

$sgr_z = 0.005\ g.g^{-1}.day^{-1}$, $sgr_r = 0.005\ g.g^{-1}.day^{-1}$,
$sdr_z = 0.005\ g.g^{-1}.day^{-1}$, $sdr_r = 0.005\ g.g^{-1}.day^{-1}$,
$K = 300\ g.m^{-2}$ (Adams and Talbot 1992), and
sst=30 days.

The parameter values were given by Adams (1994, pers. comm).A smoothing time of 30 days was selected as a reasonable delay time for the salinity in equation (2.3).

2.2.6 Physical Data for the Model

Physical data for the model consists of a time series of daily salinity and current velocity. This data is determined from the one dimensional hydrodynamic simulation programme called Mike 11 (Danish Hydraulic Institute 1992). This model simulates the physical characteristics of an estuary at the scale of days and months. Mike 11 requires information such as bathymetric cross-sections, water level recordings and river inflow as input data, and can provide time histories of water levels, flow velocities and salinity (Huizinga 1994). The physical data corresponds to data for the mouth of estuary.

Three scenarios are selected to determine the response of *Zostera* and *Ruppia* to different combinations of open and closed mouth conditions. These combinations consist of the situation where the mouth is closed for three months at a time, and then artificially opened and allowed to close naturally over one month; the situation where the mouth is closed for four months at a time, and then artificially opened and allowed to close over two months; and the situation where the mouth is alternately open and closed for one month at a time. The reason for choosing these scenarios is so that the effects of both long and short periods of mouth closure may be examined on the macrophyte communities.

The physical data for the above scenarios was modified from the Mike 11 simulations for the natural run-off scenario for the Great Brak estuary, a temporarily closed estuary (Slinger, 1996, pp. 74-80). Since Mike 11 cannot simulate mouth closure, the Mike 11 data was used for periods when the mouth is open. Although the estuarine systems model is able to simulate both open and closed mouth conditions, we could not use the data from this model because the estuarine systems model simulates physical conditions in the middle reaches of the estuary only. Hence for periods of mouth closure we assumed that current velocity was constant at 0.01 $m.s^{-1}$ and that salinity was constant at 10 ppt. (The estuarine systems model predicted that the mean salinity in the middle reaches of the Great Brak estuary under natural run-off is below 3 ppt. during closed mouth conditions. Hence in the lower reaches we assumed that

corresponding salinity would be slightly higher, namely 10 ppt.). The physical data for the scenarios for are given below in the discussion for each scenario.

2.2.7 Method of Solving the Model

The model was solved by using the discrete version of equation (2.2), namely

$$\Delta Z = [sgr_z * sgm_z * Z * (1 - \frac{Z+R}{K}) - \frac{sdr_z}{2} * Z * (sdm_z + scm_z)].\Delta t \qquad (2.4a)$$

$$\Delta R = [sgr_r * sgm_r * R * (1 - \frac{Z+R}{K}) - \frac{sdr_r}{2} * R * (sdm_r + scm_r)].\Delta t \qquad (2.4b)$$

where

ΔZ is the change in *Zostera* biomass density between successive time steps ($g.m^{-2}$);

ΔR is the change in *Ruppia* biomass density between successive time steps ($g.m^{-2}$); and

Δt is the timestep (days).

The timestep, Δt, is equal to one day.

2.2.8 Results

The following method is adopted in analysing the scenarios:

(1) The equilibrium states and their associated stability are determined. An equilibrium state is defined as the plant biomass density around which the system oscillates periodically. That is, the equilibrium state is defined as those values of *Zostera* and *Ruppia* biomass density for which

$$\frac{dZ}{dt} = 0, \frac{dR}{dt} = 0 \text{ for equation (2.2)}$$

The equilibrium state depends on the initial conditions, so all the equilibrium states are determined. An equilibrium state is said to be stable if, when the system is disturbed from the state, for example by increasing or decreasing plant biomass density to 299 $g.m^{-2}$ and 1 $g.m^{-2}$ respectively, the system returns to the state for every disturbance near the state. If a disturbance from the state results in the system moving away from the state, then the equilibrium state is unstable. The equilibrium points and their stability are shown in the phase-plane.

(2) The effect of perturbations is investigated by considering a disturbance scenario. A summer flood equivalent to the 1 in 50 year flood volume is superimposed on each of the runoff scenarios. Current velocity during the flood is 0.4 $m.s^{-1}$ and the estuary is completely flushed so that salinity is zero. Following the Mike 11 model salinities return to their characteristic state within 28 days.

A sensitivity analysis is not conducted for this model.

Scenario 1 *The timing of mouth breaches is every fourth month, and the duration of open conditions is one month*

This scenario was chosen to determine the implications of artificially opening the mouth after three months of closed mouth conditions, and then allowing the mouth to close naturally in one month, (i.e. there is no constant dredging of sediment once the mouth has been opened). The physical data for this scenario is shown in figure 2.5. Data is shown for one cycle of open and closed mouth conditions. For subsequent periods this cycle is repeated.

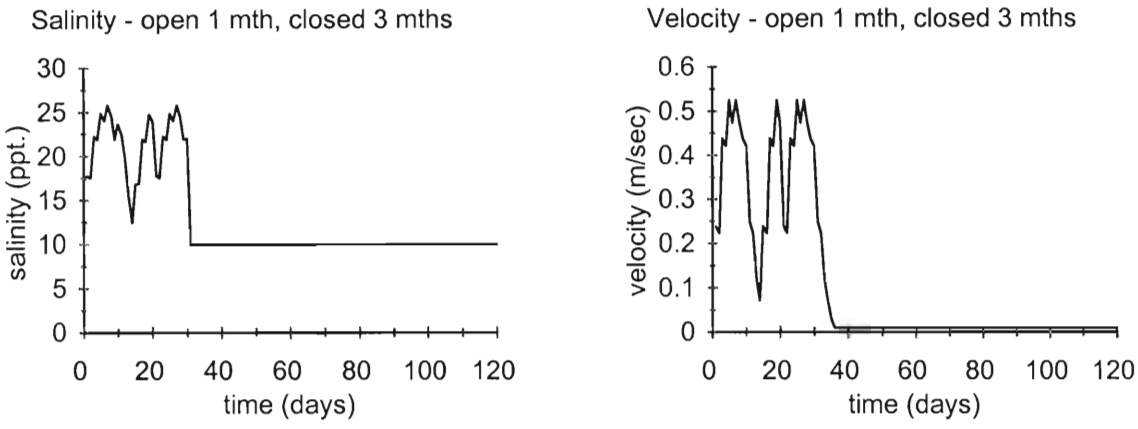

Figure 2.5. Physical data for scenario 1, for 1 month of open mouth conditions, followed by 3 months of closed mouth conditions.

Model results show that there are three equilibrium states, namely:

State 1: *Ruppia* fluctuates between 216 and 238 $g.m^{-2}$ and *Zostera* biomass density is zero, (initial condition *Ruppia* >0, *Zostera* >=0),

State 2: *Zostera* fluctuates between 201 and 212 $g.m^{-2}$ and *Ruppia* biomass density is zero, (initial condition *Zostera* >0), and

State 3: *Ruppia* and *Zostera* biomass density is zero (initial condition *Ruppia*=0=*Zostera*).

Figure 2.6 shows the biomass density dynamics for the non-trivial equilibrium states.

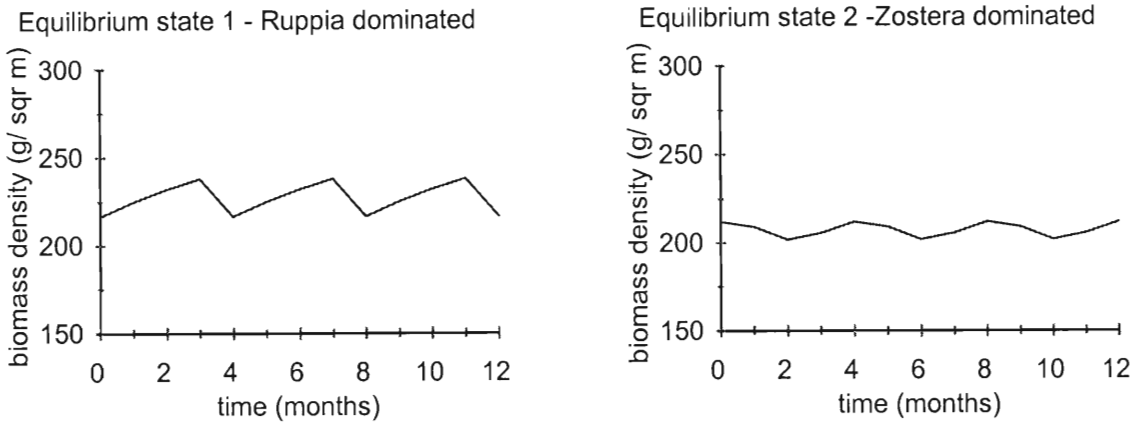

Figure 2.6. If the mouth is artificially opened after three months of closed mouth conditions, and is then allowed to close naturally in one month, then the model predicts that the estuary is either *Ruppia*-dominated or else *Zostera*-dominated, depending on the initial conditions.

The stability of the equilibrium states is (figure 2.6):

State 1: is stable,

State 2: is stable in the absence of *Ruppia*, otherwise unstable, and

State 3: is unstable.

The phase plane diagram (figure 2.7) shows that if the system is *Zostera*-dominated, i.e. in state 2, then a perturbation from this state in the form of the introduction of a small biomass of *Ruppia*, will switch the system to a *Ruppia*-dominated system, i.e. to state 1. State 1, on the other hand, is stable to small perturbations, i.e. if the estuary is *Ruppia*-dominated, then small biomass perturbations from this state will result in a return to the equilibrium state. The origin is unstable, which shows that if *Zostera* is introduced into the estuary, then the estuary will become *Zostera*-dominated, otherwise if either *Ruppia* or both *Zostera* and *Ruppia* are introduced, then the estuary will become *Ruppia*-dominated.

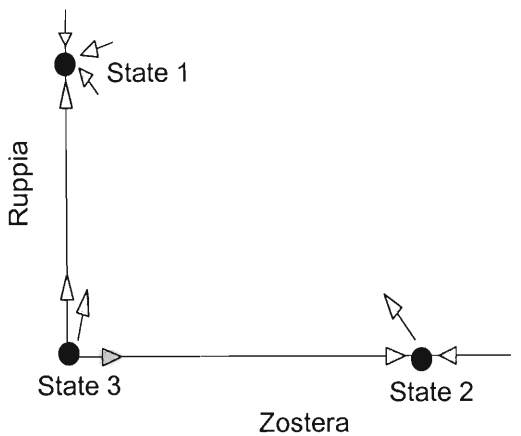

Figure 2.7. Phase plane analysis of the local stability of the equilibrium states for scenario 1. The origin is unstable, state 2 (*Zostera*-dominated) is unstable if *Ruppia* is present, and state 1 (*Ruppia*-dominated) is stable.

The effect of a flood on the equilibrium states is examined to determine whether obtaining a switch in states by disturbing the system is possible. The flood occurs after the 3 months of closed mouth conditions. Model results show that when the estuary is *Ruppia*-dominated, (state 1), *Ruppia* biomass density decreases to 93 $g.m^{-2}$ during the flood and takes 4 years to recover to its equilibrium state. For state 2, *Zostera* biomass density decreases to 97 $g.m^{-2}$ during the flood, with a recovery time of 6 years. Therefore, a flood will not change the state of the estuary from a *Ruppia*-dominated system to a *Zostera*-dominated system or vice versa.

Scenario 2 *The timing of mouth breaches is every fifth month, and the duration of open mouth conditions is two months*

In contrast to scenario 1, this scenario allows for the mouth to be closed for a longer period, namely four months instead of three months. Therefore over the long term the cost of mechanically opening the mouth will be less for scenario 2 than scenario 1. Under this scenario, the mouth is kept open for two months, instead of one month as in scenario 1, so dredging of sediment near the mouth may be required. This will increase the cost of scenario 2. The physical data for this scenario is shown in figure 2.8. Data is shown for one cycle of open and closed mouth conditions. For subsequent periods this cycle is repeated.

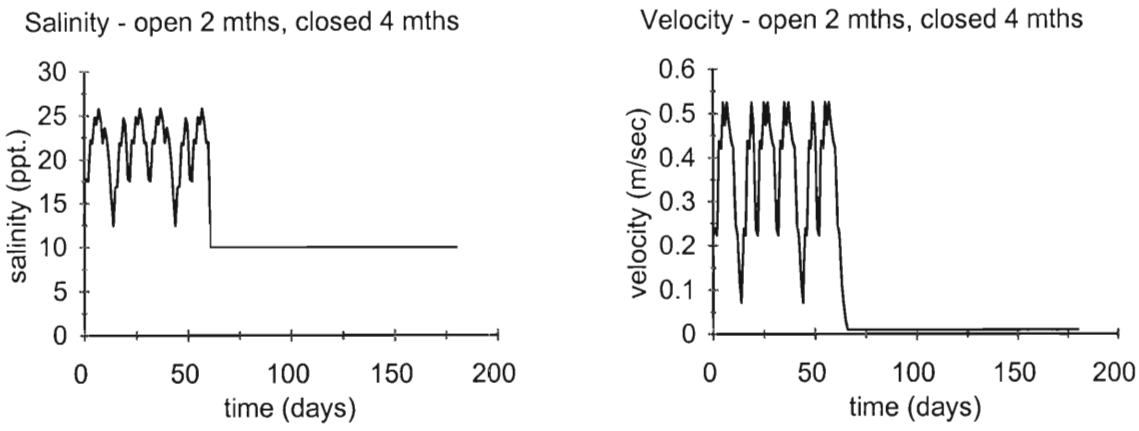

Figure 2.8. Physical data for scenario 1, for 1 month of open mouth conditions, followed by 3 months of closed mouth conditions.

Model results show that there are three equilibrium states, namely:

State 1: *Ruppia* fluctuates between 200 and 240 $g.m^{-2}$ and *Zostera* biomass density is zero, (initial condition *Ruppia*>0, *Zostera*=0),

State 2: *Zostera* fluctuates between 190 and 220 $g.m^{-2}$ and *Ruppia* biomass density is zero, (initial condition *Zostera* >0, *Ruppia* >=0)and

State 3: *Ruppia* and *Zostera* biomass density is zero (initial condition *Ruppia*=0=*Zostera*).

Figure 2.9 shows the equilibrium biomass density dynamics for the non-trivial equilibrium states.

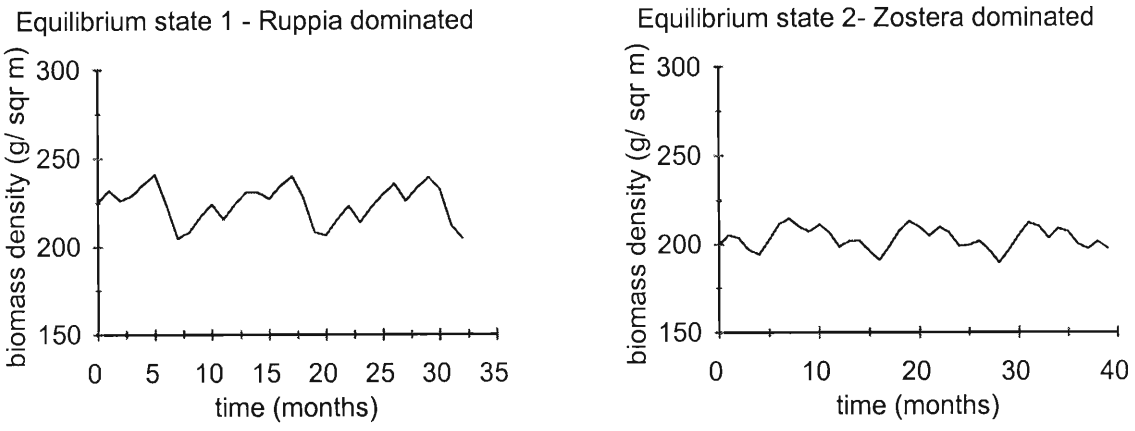

Figure 2.9. If the mouth is allowed to remain closed for four months, and kept open for two months, then the estuary is either *Ruppia*-dominated or *Zostera*-dominated, depending on the initial conditions.

The stability of the equilibrium states is the same as that for scenario 1, namely:

State 1: is stable,

State 2: is stable in the absence of *Ruppia*, unstable otherwise, and

State 3: is unstable.

The phase plane diagram is not shown because it is the same as in figure 2.7 (p.30). Therefore the results show that increasing the period of mouth closure from the previous scenario, and increasing the duration of open mouth conditions from the previous scenario, does not alter the resultant equilibrium states nor their stability to small perturbations. The effect of a flood is also the same, and the results show that switching the estuary from one equilibrium state to another by disturbing the estuary with a flood is not possible. The flood occurs after 4 months of closed mouth conditions. To examine the effect of short open and closure times, the next scenario has open or closed mouth conditions for one month at a time.

Scenario 3 *The timing of mouth breaches is every second month and the duration of open conditions is one month*

Under this scenario, the mouth is allowed to remain closed only for one month at a time, and is then mechanically opened and allowed to close naturally in one month. So this policy is more expensive than the previous two policies because the mouth is breached more frequently than under scenario 1 or scenario 2. The physical data for this scenario is shown in figure 2.10. Data is shown for one cycle of open and closed mouth conditions. For subsequent periods this cycle is repeated.

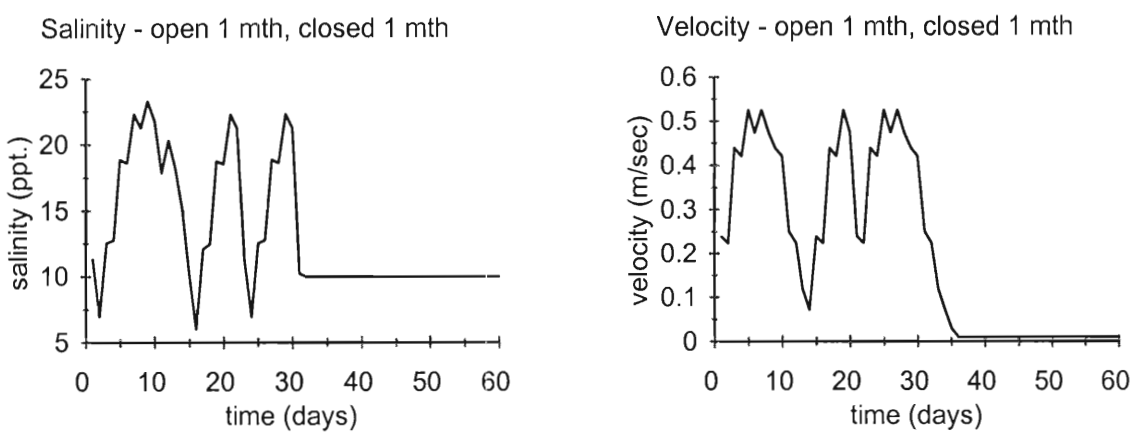

Figure 2.10. Physical data for scenario 1, for 1 month of open mouth conditions, followed by 3 months of closed mouth conditions.

Model results show that there are three equilibrium states, namely:

State 1: *Ruppia* fluctuates between 161 and 172 $g.m^{-2}$ and *Zostera* biomass density is zero, (initial condition *Ruppia*>0, *Zostera*=0),

State 2: *Zostera* fluctuates between 280 and 281 $g.m^{-2}$ and *Ruppia* biomass density is zero, (initial condition *Zostera*>0, *Ruppia*>=0), and

State 3: *Ruppia* and *Zostera* biomass density is zero (initial condition *Ruppia*=0=*Zostera*).

Figure 2.11 shows the equilibrium biomass density dynamics for the non-trivial equilibrium states.

The stability of the equilibrium states is (figure 2.12):

State 1: is stable in the absence of *Zostera*, unstable otherwise,

State 2: is stable, and

State 3: is unstable.

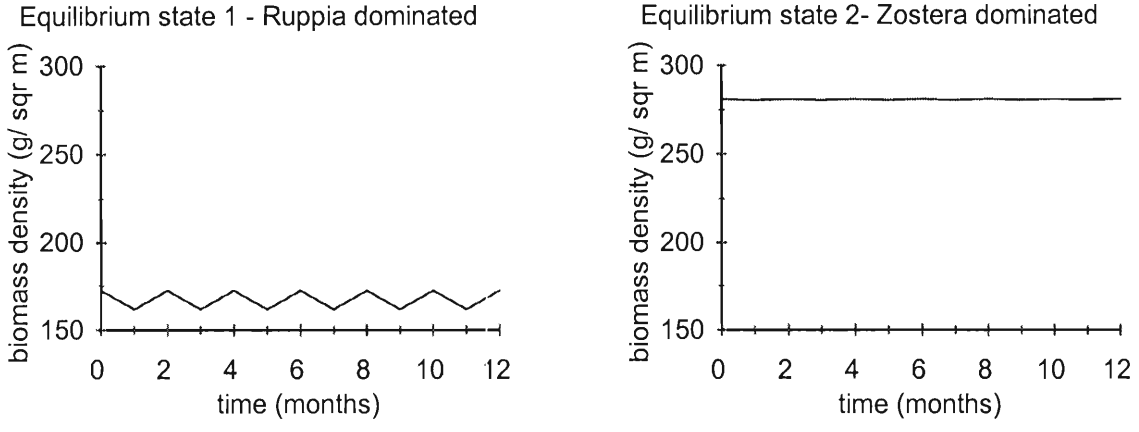

Figure 2.11. If the mouth is allowed to remain closed for one month, and is then mechanically opened and allowed to close naturally in one month, then the model predicts that the estuary is either *Ruppia*-dominated or *Zostera*-dominated, depending on the initial conditions.

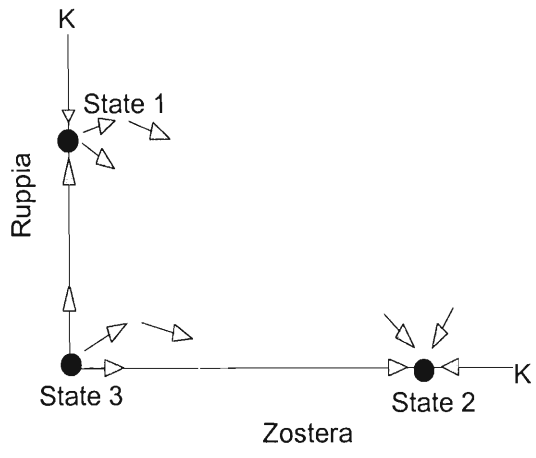

Figure 2.12. Phase plane analysis of the local stability of the equilibrium states for scenario 3. The origin is unstable, state 2 is stable, and state 1 is unstable if *Zostera* is present.

The stability of the *Ruppia*-dominated state and the *Zostera* dominated state is reversed from that of scenario 1 and scenario 2. Here, the *Zostera*-dominated state (state 2) is stable, so that small perturbations from this state will not result in a switch to a different equilibrium point. The *Ruppia*-dominated state (state 1) is unstable which means that the introduction of a small biomass of *Zostera* will switch the estuary to a *Zostera*-dominated system (figure 2.9).

The effect of a flood disturbance to the equilibrium states is examined. The flood occurs aftre one month of closed mouth conditions. Results show that for the *Zostera*-dominated state, (state 2), *Zostera* dies back to 7.93 $g.m^{-2}$ during the flood, and takes 6 years to recover to its equilibrium biomass density. So the *Zostera*-dominated state is stable with respect to flood disturbances equivalent to the 1 in 50 year flood. For a *Ruppia*-dominated estuary, *Ruppia* completely dies back during the 1 in 50 year flood. For this situation then, the estuary would be left with no submerged macrophyte community after the flood.

2.3 Discussion

Scenario 1 and scenario 2 were similar, with scenario 2 having longer (namely one month) open and closed mouth conditions. The model results were also similar, with the non-trivial equilibrium states being either a *Zostera*-dominated estuary or a *Ruppia*-dominated estuary,

depending on the initial conditions. We cannot say off hand which scenario would be cheaper to apply because although the mouth is opened less frequently under scenario 2 than under scenario 1, scenario 2 may require dredging of sediment when the mouth is open to maintain longer open mouth conditions than under scenario 1. Freshwater managers therefore need to calculate the costs carefully, and decide whether having a *Ruppia*-dominated submerged community or a *Zostera*-dominated submerged community is more important for a particular estuary. The phase plane diagram showed that the *Ruppia*-dominated state was stable for scenario 1 and scenario 2. Thus if the estuary contains mostly *Zostera* and a small biomass of *Ruppia*, then applying scenario 1 or scenario 2 will result in a *Ruppia*-dominated estuary. For example, if we assume that the estuary contains 200 $g.m^{-2}$ of *Zostera* and 10 $g.m^{-2}$ of *Ruppia*, then the transition to the *Ruppia*-dominated equilibrium state will take 61 years under scenario 1, and 53 years under scenario 2. The reason the transition to the *Ruppia*-dominated equilibrium state is shorter for scenario 2 than for scenario 1 is that under scenario 2, the mouth is closed for four months at a time, whereas under scenario 1 it is closed for 3 months at a time. Therefore the growing period for *Ruppia* is greater under scenario 2 than under scenario 1. So changing the state of an estuary to a *Ruppia*-dominated system by applying scenario 1 or scenario 2 is possible.

The difference between the equilibrium states for scenario 1 and scenario 2 was that the fluctuations in equilibrium biomass density for scenario 1 are less than those for scenario 2. The difference between maximum and minimum biomass density for *Zostera* is 11 $g.m^{-2}$ and 30 $g.m^{-2}$ for scenario 1 and scenario 2 respectively (figure 2.13). The corresponding difference for *Ruppia* is 22 $g.m^{-2}$ and 40 $g.m^{-2}$ for scenario 1 and scenario 2 respectively (figure 2.10). This may have implications on the habitat availability for fish and epiphytes.

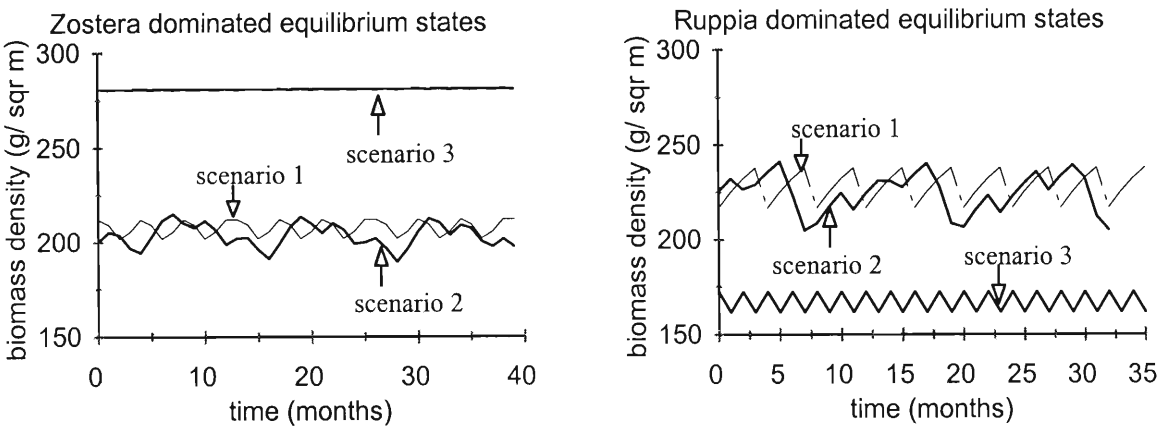

Figure 2.13. The biomass density for the stable states for scenarios 1, 2 and 3. The biomass density for scenario 1 and scenario 2 is similar, with scenario 2 having greater biomass oscillations than scenario 1.

The third scenario is more expensive than the first two scenarios because the mouth is breached every alternate month. The biomass density for the *Zostera*-dominated state is greater than that for scenarios 1 and 2 (figure 2.13), whereas the biomass density for the *Ruppia*-dominated state is less than that for scenarios 1 and 2 (figure 2.13). The results are different from those of the first two scenarios, where the *Zostera*-dominated state becomes the stable state. This means that if the estuary contains mostly *Ruppia* and a small biomass of *Zostera*, the applying scenario 3 will switch the estuary to being *Zostera*-dominated. For example, if the estuary contains 200 $g.m^{-2}$ of *Ruppia* and 10 $g.m^{-2}$ of *Zostera*, then applying scenario 3 results in a *Zostera*-dominated equilibrium state after 15 years. The switch in habitats from *Zostera* to *Ruppia* for scenarios 1 and 2 occurred over a much longer period, namely 53 years and 61 years respectively. This is due to the salinity growth multipliers: For scenarios 1 and 2, the salinity growth multiplier for *Ruppia* is on average 0.95 during the growing period for *Ruppia* (i.e. closed mouth conditions). For scenario 3, the salinity growth multiplier is on average 0.99 during the growing period for *Zostera* (i.e. during open mouth conditions). Therefore the higher salinity growth multiplier for scenario 3, with the duration of a short mortality period for scenario 3 (one month, as opposed to two months for *Ruppia* for scenario 2), result in the attainment of the *Zostera*-dominated state in a shorter period than the *Ruppia*-dominated state for scenario 1 and scenario 2. The results also showed that for scenario 3, the

Ruppia-dominated state was not stable to the 1 in 50 year flood, and that this disturbance could lead to state with no *Ruppia* present in the estuary.

Simulations were also conducted for estuaries which are open throughout the year except during the holiday season, when the mouth is artificially closed for either one month or three months. The results showed that for a mouth closure of one month or three months over the holiday season, the only non-trivial equilibrium state is *Zostera* biomass density equal to 287 $g.m^{-2}$ and 276 $g.m^{-2}$ respectively. This equilibrium state is stable, therefore after small perturbations from this state the system will return to equilibrium conditions. Although the biomass of *Zostera* decreases during floods, the zero equilibrium state (no *Zostera* and no *Ruppia*) is unstable, so the estuary will return to *Zostera*-dominated conditions after the flood for both scenarios. The major difference between having the mouth closed for one month or three months is that biomass density of *Zostera* is greater when the mouth is only closed for one month as opposed to three months.

2.4 Conclusion

The expert system model of Adams and Bate (1994) would have analysed the scenarios in section 2.2.6 as follows:

The expert system would use the average salinity over the periods of open and closed mouth conditions to predict the outcome when the mouth is open, and when the mouth is closed. Thus the results will show plant behaviour when the mouth is open, and plant behaviour when the mouth is closed. There are three disadvantages to using this approach.

(1) By using the average salinity it means that extreme salinities are not incorporated in the model.

(2) The expert system model does not predict overall behaviour. For example, for scenario 3, the expert system model predicts that *Zostera* and *Ruppia* grow and die back respectively when salinities are between 15 ppt. and 35 ppt. and the mouth is open for one month, and vice versa when salinities are less than 30 ppt. and the mouth is closed for one month. The mathematical model incorporates the dynamic changes in the

condition of the estuary mouth and predicts that *Ruppia* dies back completely under this runoff scenario if *Zostera* is present.

(3) The expert system model is also not able to incorporate dynamic changes to the system such as the 1 in 50 year flood. The mathematical model, on the other hand, measured the effect of the flood, calculated the recovery time, and determined whether achieving a switch in states by imposing a flood on the system was possible.

A major advantage of the expert system model is that it does not need as much input data as the time-dependent model, and is therefore useful in predicting the short term (months) response of plants in estuaries with poor data availability, a common situation for South African estuaries. (The information availability of 68% of South African estuaries could be considered poor or nil (Whitfield 1995). The time-dependent model is more data intensive than the expert system model, but it can give qualitative predictions and determine the stability of various equilibrium states.

Besides knowing how the biomass density of macrophytes responds to repeated variations in the condition of the mouth, it is also necessary to know how freshwater releases change the distribution of macrophytes along the length of the estuary, and how freshwater releases change the location of plants along the intertidal zone. It is known that impoundments cause the encroachment of marine macrophytes into the upper reaches (Adams et al. 1992; Adams and Talbot 1992). Therefore, being able to predict how fast this spread is occurring is important. It is also important to know whether brackish macrophytes further up the estuary can survive this invasion of marine species. Altered freshwater releases change the water level fluctuations in the estuary, particularly in the mouth of the estuary when the mouth is closed. A change in the water level fluctuations will affect the distribution of plants along the intertidal zone. The resultant shifts of plants up or down the intertidal zone therefore needs to be monitored so that freshwater management decisions can be made on the length of time plants are submerged or exposed. For these reasons, a new model is developed in the following chapter to provide answers to these additional freshwater management questions.

CHAPTER 3

EVALUATING THE EFFECT OF FRESHWATER RELEASE POLICIES ON A MARINE MACROPHYTE

3.1 Purpose of the Model

A certain amount of freshwater is allocated for the conservation of estuaries. Therefore freshwater managers need to know how this water should be released, for example, should it be released in one large release per year?, or should a policy of monthly releases of equal volume be used? Estuaries require freshwater to flush out high salinities, maintain a salinity difference between the mouth and the head of the estuary, improve water clarity, introduce land-derived nutrients to the estuary, and maintain connection with the sea. A policy of one large release per year will flush out high salinities that have accumulated in the estuary and scour sediment from the mouth, thereby opening the estuary to the sea. However, after the release, salinities in the estuary may rise slowly until they reach hyper saline conditions before the release the following year. This may threaten the survival of some plant communities. The mouth may also eventually close after the release for an extended period, causing a disruption in the migration of species between the sea and the estuary. On the other hand, monthly releases may maintain a constant mouth to head salinity difference, but they may not be sufficient to open the estuary mouth. Freshwater managers therefore need to know which release pattern will benefit the estuary ecologically.

The model in the previous chapter cannot provide a full answer to this question. It can only predict the consequences of various release patterns on *Zostera* and *Ruppia* in one location, which was the estuary mouth in the scenario analysis of chapter 2. However, an important consequence of freshwater releases is the change in the mouth to head salinity difference. These effects cannot be determined by the time-dependent model of *Zostera* and *Ruppia*. A change in the axial salinity or the salinity between the head (upper limits of tidal influence) and mouth of the estuary alters the pattern of distinct bands of different plant communities along the length of the estuary (Day 1981). In some South African estuaries, e.g. the Kromme estuary (Adams and Talbot, 1992), impoundments have resulted in uniform high salinities throughout the estuary, with the result that marine macrophytes encroach into the upper

reaches and displace brackish communities. Hence the model developed in this chapter includes spatial dimensions so that we can predict what happens to the location of marine species along the estuary if freshwater inflow is reduced.

In estuaries which have already become marine dominated due to diminished river runoff, freshwater managers need to be able to determine whether the present pattern of water releases is optimal. That is, we need to determine whether altering the current pattern of freshwater releases to reintroduce brackish components in the upper reaches is possible. If this is not possible, then the possibility of increasing the volume of freshwater released to the estuary could be examined. Thus the model in this chapter is used to determine a critical volume of freshwater such that releases with a volume less than the critical volume will not change the marine state of the estuary, while releases with a higher volume will cause the die back of marine macrophytes in the upper reaches. Freshwater managers can then weigh the value derived from using the water for agricultural, industrial and domestic needs as opposed to reserving that volume of water for conservation purposes.

The implications of water release policies on the intertidal plants is also an important factor to consider. Most South African estuaries are naturally closed to the sea for varying periods due to low seasonal runoff (Whitfield 1992). Freshwater impoundment in the catchment causes a further decrease in catchment runoff. This increases the period of mouth closure and, in temporarily closed estuaries, water levels may drop due to reduced river runoff, resulting in the prolonged exposure and die back of macrophytes that are normally submerged (Adams and Bate 1994a). Water levels may also rise during closed mouth conditions because the closed mouth dams the freshwater runoff causing an accumulation of water in the estuary, resulting in prolonged inundation of macrophytes that are normally exposed (Adams 1994). Thus the spatial model is also used to determine the extent to which impoundments affect the water level fluctuations in the estuary and consequently the survival of macrophytes.

The reason the model of *Zostera* and *Ruppia* developed in chapter 2 cannot be used for the above freshwater management problems is because it does not include spatial dimensions. Therefore it cannot predict encroachment and colonisation patterns, neither can it predict shifts in the intertidal zone as water level fluctuations change. Hence the model in this chapter is a

spatial model. The purpose of the spatial model is to assist freshwater management decisions by showing the consequences of water releases on the spatial distribution and encroachment rates of a marine macrophyte discussed in the following section.

3.2 Key Macrophyte Selected for the Problem

As discussed in chapter 2, *Zostera capensis* Setchell is a dominant and key submerged macrophyte in many South African estuaries. *Zostera* provides a substantial amount of primary productivity, nutrient storage and nursery habitats in shallow estuarine waters (Adams 1994). *Zostera* is selected for the current problem because it is a representative of both marine habitat and periodically submerged habitat.

Zostera is adapted to tidal habitats because it can withstand repeated cycles of drying during daily low tides (Adams and Bate 1994a). However, *Zostera* cannot survive prolonged periods of exposure. For example, a drop in water levels resulting from erratic freshwater input has resulted in the exposure and die back of *Zostera* communities in South African estuaries. Therefore, predicting the response of *Zostera* to altered water level fluctuations is important. Being a marine macrophyte, *Zostera* has been observed to encroach up estuaries in the Eastern Cape due to a reduction in freshwater inflow (Adams and Talbot 1992). Therefore, in selecting *Zostera*, we can provide answers on the consequences of impoundments on the spread rate and colonisation patterns of marine species in the estuary. Thus the model is a single species model. Additional macrohytes, namely *Ruppia* and *Phragmites* are included in the model in chapter 4. In this study we examine the effect of impoundments on *Zostera* only.

3.3 Mechanism of Spread Modelled

The main method of spread by *Zostera* is vegetative. Expansion through seed dispersal is rare because *Zostera* plants seldom produce flowers and seedlings are not readily established in new areas (Day 1981). In a survey of the Swartkops estuary, South Africa, Talbot and Bate (1987) found that *Zostera capensis* area expansion between summer and winter appeared to be via existing runners because no new beds were observed in the area. Most of the recovery of *Zostera* in the Kwelera estuary (Talbot et el 1990) after the flood in November 1985 came from regrowth and enlargement of existing beds. So the purpose of the mathematical model is to describe the spatial and temporal dynamics of existing *Zostera* beds.

3.4 Space Representation in Mathematical Models

Although there is widespread agreement that an understanding of spatial processes is important in ecological theory, it is not clear how best to proceed in terms of modelling the interplay of expansion and local interactions. A literature survey shows that there are two ways of incorporating spatial structure in models:

Using discrete spatial variables: The community inhabits a discrete series of separate sites (called patch models), see for example, Lewontin and Cohen (1969), Metz and Diekmann (1986), Perry and Gonzalez-Andujar (1993), Cipollini et al. (1994), or

Using continuous spatial variables: The community varies spatially in a continuous manner, e.g. Skellam (1951), Lonsdale (1993).

We choose to employ the discrete definition of space. However, before this method is outlined, we briefly discuss a continuous model in order to explain why continuous spatial variables were not used.

3.5 A Continuous Space Representation

Edelstein (1982) used a continuous space representation to describe the spread of a fungus. The spread of a fungus is similar to the vegetative spread of *Zostera*. The spread of the fungus is modelled by Edelstein (1982) by describing the movement of nodes (or root ends) through space. If we assume that the biomass density of *Zostera* is proportional to the number of nodes, then *Zostera* growth in a continuous space dimension may be described as follows:

Consider the strip of uniform height h in figure 3.1.

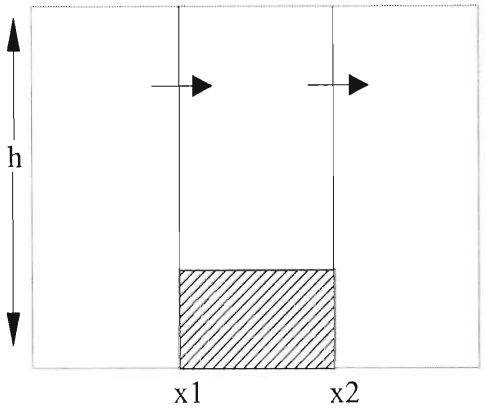

Figure 3.1. The number of nodes in the shaded region depends on (1) local growth, (2) the movement of nodes from adjacent sites into the shaded region, this is an increase in the number of nodes in the shaded region, and (3) the movement of nodes from the shaded region into adjacent regions, this is a decrease in the number of nodes in the shaded region.

Let

x be the horizontal distance along the strip, and

n(x,t) be the number of nodes per unit area at position x at time t.

Edelstein (1982) argued that the change in the number of nodes in the region between x_1 and x_2 (figure 3.1) is a result of two possible effects, the movement of nodes into or out of the interval (x_1, x_2), and local processes that result in growth or mortality of existing nodes. So the rate of change of the number of nodes between x_1 and x_2 is given by

$$\textit{rate of change} = \textit{entry rate into } (x_1,x_2) - \textit{departure rate out } (x_1,x_2) + \textit{source} \quad (3.1)$$

or

$$\frac{\partial}{\partial t}\int_{x_1}^{x_2} n(\xi,t).h.d\xi = J(x_1,t).h - J(x_2,t).h + \int_{x_1}^{x_2} S(\xi,t).h.d\xi, \quad \xi \in (x_1,x_2) \tag{3.2}$$

where

J(x,t) is the flux at (x,t), i.e. the rate at which nodes enter or leave per unit length per unit time, and

S(x, t) is the local source term at (x,t), i.e. the rate of growth per unit area at (x,t).

It can be shown (Edelstein, 1982) that (3.2) leads to the equation

$$\frac{\partial n(x,t)}{\partial t} = -\frac{\partial J(x,t)}{\partial x} + S(x,t) \tag{3.3}$$

where the negative sign in front of the partial derivative of J(x,t) in (3.3) indicates that the nodes move from regions of high node density (number of nodes per unit area) towards regions of low node density.

Typically one would append (mathematical) boundary conditions to this model, giving the behaviour of the nodes at the boundaries of the habitat considered.

If we base the spread of *Zostera* on (3.3) then the variable modelled would be the biomass density (biomass per unit area), instead of the number of nodes per unit area as in Edelstein (1982). Equation (3.3) would then be rewritten as

$$\frac{\partial b(x,t)}{\partial t} = -\frac{\partial J(x,t)}{\partial x} + S(x,t) \tag{3.4}$$

where

b(x,t) is the biomass density or the biomass per unit area of *Zostera* ($g.m^{-2}$).

Model (3.4) is called the diffusion model, and has its origins in the studies of Fischer (1937) on the spread of diseases and Skellam (1951) on dispersal in animal populations. In the model of Skellam (1951), the movement of animals occurred in the direction of decreasing biomass density. (Instead of modelling the number of nodes, Skellam modelled the biomass density of the population). In the model of Skellam (1951), the flux is proportional to the biomass density gradient, and is given by

$$J(x,t) = -D\frac{\partial b}{\partial x} \tag{3.5}$$

where D is the diffusivity of the population (area per unit time) and the minus sign shows that the animals move from a high to a low biomass density.

The flux term for *Zostera* would be based on (3.5), with the modification:

$$J(x,t) = -D\frac{\partial}{\partial x}\left[\frac{b(x,t)}{k(x,t)}\right] \tag{3.6}$$

where

D is the diffusion constant ($g.t^{-1}$),

k(x,t) is the carrying capacity (maximum biomass density) at (x,t) ($g.m^{-2}$), and is given by

$$k(x,t) = e(x,t)K_{max} \tag{3.7}$$

where

e(x,t) is a measure of the environmental conditions (e.g. nutrients, salinity, mouth condition) at position x at time t (-).

The function e(x,t) is defined to have a maximum value of one and a minimum value of zero. e(x,t) = 1 means optimal physical conditions for growth, and the carrying capacity is therefore equal to the maximum carrying capacity, e(x,t) = 0 means poor physical conditions for growth and the carrying capacity is therefore equal to zero. The function e(x,t) is called the

environmental gradient function. Environmental gradients may occur either in space or time. Spatial gradients in estuaries include environmental features such as salinity along the length of the estuary, light availability below the water surface, and water level fluctuations. As freshwater flow to an estuary decreases, the difference in mouth to head salinity decreases, water level fluctuations in the mouth change, and consequently the underwater irradiance environment changes. Predicting the response of *Zostera* to such changes in the environment from altered freshwater supply is important, and therefore including the spatial gradient of the estuary in model (3.4) is important. Environmental gradients in time include phenomena such as encroaching salinity up the estuary as freshwater supply decreases. Including the temporal changes in the estuarine environment in the model of *Zostera* is therefore also necessary so that the spread of *Zostera* up the estuary due to encroaching salinity may be modelled.

Equation (3.6) states that expansion growth is proportional to the gradient of [-b(x,t)/k(x,t)]. This means that spread of *Zostera* occurs towards the direction of decreasing biomass density, where the density depends on the physical conditions. Thus, for a uniform distribution of *Zostera*, expansion will occur towards favourable sites first.

Local growth of *Zostera* in (3.4) is given by

$$S(x,t) = r\,b(x,t)\left[1 - \left(\frac{b(x,t)}{k(x,t)}\right)\right] \tag{3.8}$$

where r is the maximum specific growth rate under reference conditions, i.e. under low density and optimal physical conditions for growth.

Substituting (3.6) and (3.8) in (3.4) we get the full equation for *Zostera*

$$\frac{\partial b(x,t)}{\partial t} = D\frac{\partial^2}{\partial x^2}\left[\frac{b(x,t)}{k(x,t)}\right] + r\,b(x,t)\left[1 - \left(\frac{b(x,t)}{k(x,t)}\right)\right] \tag{3.9}$$

The derivation of (3.9) was based on the derivation of the diffusion equation for the movement of nodes in Edelstein (1982), where the number of nodes could be considered proportional to the biomass density of *Zostera*. In the derivation of the node equation, if a node moved into a neighbour site, then the number of nodes in the source region decreased. This means that in the model for *Zostera*, if biomass grows into a neighbour site, then the biomass of the source region decreases. However, vegetative spread from a source region is not a loss to the source region. The runners lengthen and grow into the neighbouring site.

In addition, there are a number of criticisms on the simplifying assumptions that models based on the diffusion equation make. Van den Bosch et al. (1992) and Hengeveld (1994) criticised the diffusion model's inability to account for interactions between age, reproduction and movement. Since the mathematics of diffusion models are complicated, modifying the model is not simple. Allen et al. (1991) found that more than one mechanism of dispersal was required to account for the observed spread of Opuntia imbricata in a Texas, USA rangeland, and consequently suggested more than one diffusion coefficient may be required in diffusion-based models of plant spread. Work on animal spread suggests that diffusion models are more likely to be unsuitable at scales where the variability in the rate of movement of individuals is high (Goldwasser et al. 1994), where dispersal is directed and not random, and where environmental heterogeneity influences the pattern of organism movement (Johnson et al. 1992). So despite their successes in many case studies, the potential of diffusion models is clearly limited.

The diffusion equation was initially developed for modelling dispersal in animal populations. As such, they do not include specifically the following plant characteristics that arise due to their sessile or plastic nature: plants cannot move away from temporarily unfavourable habitats, and, interactions among plants are spatially local. In most partial differential equation models the physical environment is spatially and temporally homogeneous, whereas *Zostera* survival depends on resources such as light, mineral nutrients, salinity, water level fluctuations, factors that vary depending on the plants' location in the estuary. Many models from the seed to that of the whole population which include these aspects of plant growth have now been developed to understand and predict abundance and distribution of plants through time.

Therefore, based on the reasons above, the diffusion equation was not used to model the spatial dynamics of *Zostera capensis*.

3.6 Space Representation Using a Cellular Automaton

Cellular automata (CA) models represent space by a uniform grid, with each cell containing information such as the number of plants, vegetation density, or habitat type. The advantage of using the CA definition of space is that it is compatible with common sources of data such as satellite imagery and quadrant-based field observations. In a cellular automaton time advances in discrete steps. The behaviour of the system is expressed by a single recipe, called a set of rules, through which at each time step each cell computes its new state from that of its neighbours and its present state. Thus, the system's laws are local and uniform. "Local" means that the state of a cell is only determined from the state of nearby cells, i.e. there is no long distance interaction. "Uniform" means that the laws are the same everywhere. Thus cellular automata are 'bottom-up' models that generate global behaviour from local rules. Given a suitable recipe or set of rules, such a simple operating mechanism is sufficient to generate complex spatial and temporal patterns.

The most famous example of a simple CA rule with complex dynamics is the game of LIFE developed by the mathematician John Conway in 1970 (Gardner 1970). LIFE may be thought of as describing a population (each individual is represented by a cell) developing in time under the effect of counteracting propagation and extinction tendencies. LIFE is a two-state CA model (the states are alive or dead) where the transition rules depend on the state of the target cell and its eight surrounding cells (i.e. a two-dimensional model) according to the following:

Death: A live cell will remain alive if two or three of the neighbouring sites also contain individuals, otherwise it will die presumably from overcrowding (density dependence) or from lack of a suitable mate.

Birth: An individual is born (i.e. a dead cell will become a live cell) when surrounded by exactly three live neighbours. That is, birth is induced by the meeting of three parents.

After many iterations of the model three classes of patterns are produced.

a homogeneous fixed pattern develops, i.e. the population stabilises,

a periodic pattern develops, i.e. all activity subsides except a few isolated blinkers or cyclic patterns, and

a chaotic pattern develops, i.e. the population remains stable except a few places where there are sudden bursts of activity.

These classes of outcomes correspond to the equilibrium, limit cycle and chaotic behaviour observed in difference and differential equation models. These sorts of complicated dynamics are commonplace in simple CA models (Wolfram 1986).

Cellular automata have found a permanent and increasingly important role as models of spatially distributed dynamical systems, particularly in physical (e.g. Toffoli 1984; Vichniac 1984) and ecological systems (see Phipps 1991 for a review of applications of CA models in ecology). They are useful for understanding population dynamics because they can be structured in ways that mimic natural populations. The advantage of CA models is that they can generate complex behavioural patterns from simple rules (Wolfram 1986) and are compatible with environmental data sources because of their grid structure. The utility of cellular automata as models of plant populations has been recognised by many authors who have used them to achieve the greater realism that a spatial model provides. CA models have been used to examine the invasion of a weed species through seed dispersal (Auld and Coote 1990), the importance of spatial pattern on competitive outcome (van Tongeren and Prentice 1986; Silvertown et al. 1992; Colasanti and Grime 1993; Hendry et al. 1996), large-scale succession of wetland habitat (Sklar et al. 1985), forest stands (Jeltsch and Wissel 1994) and rangelands (Wiegand et al. 1995), and the effect of disturbance on community structure (Hobbs and Hobbs 1987; Green 1989).

3.7 Model Derivation

In constructing a cellular automaton, several decisions have to be made concerning which variables to include, the size of the time step and cell size, and the local rules. The decisions in these matters are not the only ones possible, but they are justified below in the light of the purposes of the model. The model derivation also appears in Wortmann et al. (1997).

3.7.1 The Geometry of the Model

Many authors have used cellular automata to describe plant spread: The grassland model of Hobbs and Hobbs (1987) is constructed on a grid of squares that each represents an area of grassland. Van Tongeren and Prentice (1986) use a rectangular grid-cell-based model to simulate the recovery and spatial spread of plants after fire damage. For the model of *Zostera*, a hexagonal, fixed grid of equally sized cells is chosen to represent space. This arrangement avoids the problems associated with exchanges across corners in square grids. As in the CA models in the literature the edges of the array are fixed and no flow of resources or plants can occur across them. The labelling technique for the hexagons is shown in figure 3.2. The left most corner of each hexagon is assigned Cartesian co-ordinates (x_i, y_j) where i=0,1,..,n and j=0,1,..m. H_{pq} denotes the (p,q) th cell with co-ordinates (x_p, y_q).

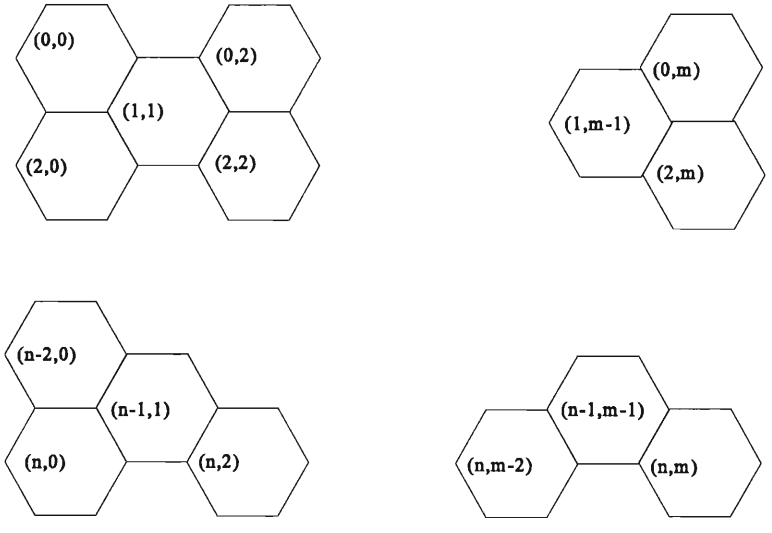

Figure 3.2. A hexagonal grid structure is used to describe space in the model. Each hexagon is assigned an x co-ordinate and a y co-ordinate, where x=0,1,..,n and y=0,1,..,m.

The length of a side of a hexagon is called W and the height of a hexagon is 2 H (figure 3.3). Note from the diagram that W > H (W is the hypotenuse of the triangle).

The grid represents the substrate along one side of the estuary floor, so that the water is deeper with increasing x. That is, we assume that the bank modelled lies vertically.

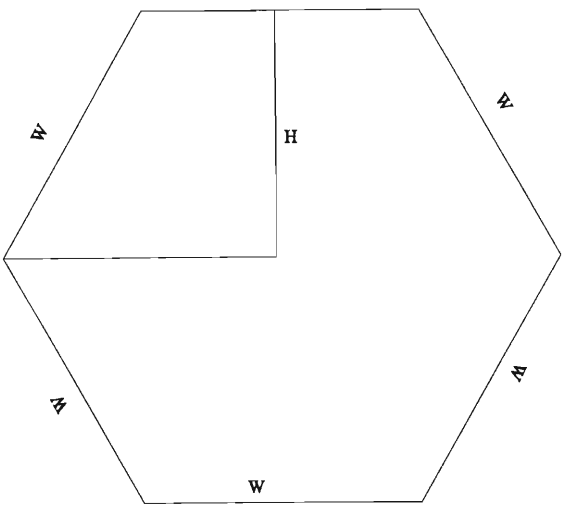

Figure 3.3. The graphical representation of the width (W) and height H of a hexagon. Note that W > H (Pythagorus).

From figure 3.3, we have that x_p and y_q in figure 3.2 may be written as;

$$x_p = pH \tag{3.10a}$$

$$y_q = qW + q\sqrt{W^2 - H^2} \tag{3.10b}$$

The square root in (3.10b) is defined because W >H.

3.7.2 The Cell States

In CA models each cell can have a number of variable characteristics or states associated with it: For example, the cell state may be the presence or absence of a given species (e.g. Sklar et al. 1985; Silvertown et al. 1992; Colasanti and Grime 1993; Molofsky 1994), the number of plants (e.g. Hobbs and Hobbs 1987; Aulde and Coote 1990), vegetation type and age or size (e.g. Green 1989), or plant height (van Tongeren and Prentice 1986), or biomass (Hendry et

al. 1996). For the macrophyte model assigning the cell state to be the presence or absence of a given species is not sufficient detail. We wish to see for example how much *Zostera* biomass there is in the zone between the high and low water level marks, and how this changes with altered water level fluctuations. In addition, most of the field data from estuaries on *Zostera* is in terms of biomass density (grams per square metre), area cover, and ratio of above to below ground biomass (Talbot and Bate 1987; Talbot et al. 1990; Adams Talbot 1992). There is some data on the height of the stem and length of leaves and number of leaves or stems (Adams and Bate 1994a, 1994b). We therefore choose the cell state to represent biomass density (biomass per unit area). So the cell state is a continuous variable, as in van Tongeren and Prentice (1986) and Hendry et al. (1996). The cells are chosen so that *Zostera* biomass density is distributed uniformly throughout the cell.

3.7.3 Neighbours and Neighbourhoods

Harper (1977), Antonovics and Levin (1980) and Pacala and Silander (1985) argued that a plant's survival may be affected by the presence and behaviour of neighbours. Experiments have shown that variation in patterns (e.g. different spacing) results in large-scale variation in population performance (Harper 1977). In a cellular automata model the state of a cell evolves synchronously in discrete time steps according to identical rules which consider the current state of a cell and of a neighbourhood of cells around it.

In models of individual plants, the neighbourhood of a plant is an area surrounding it, the size of which may be determined by its ability to acquire resources (Czaran and Bartha 1989), or it may be based on the size of its roots or crown (Harper 1985). All plants within the neighbourhood of a focal plant are termed its neighbours. The focal plant affects the growth, survival, and fecundity of its neighbours, so the term area or zone of influence is often used instead of the neighbourhood. The survival of all plants outside the neighbourhood of a focal plant is not affected by the focal plant. The shape of the neighbourhood is generally taken to be circular, with the focal plant at the centre of the circle (e.g. Pacala and Silander 1990), although there is evidence that this is not always the case: Roots of many plants are more developed away from the maximum competitive pressure of neighbours (Harper 1985), or towards areas of higher resource concentration (de Kroon and Hutchings 1995). Competitive pressure or crowding effects on a focal plant may be measured in terms of its number of

neighbours (e.g. Mack and Harper 1977; Schellner et al. 1982; Czaran and Bartha 1989; figure 3.4a) or else in terms of the degree of overlap of areas of influence (e.g. Weiner 1982; Ford and Diggle 1981; Firbank and Watkinson 1985; Bonan 1988, 1991; figure 3.4b). The basic assumption made in figure 3.4b (for degrees of overlap of areas of influence) regarding competition is that, as a plant grows its zone of exploitation of environmental resources is an expanding circle in the horizontal plane, centred at the plant. This circle continues to expand until meeting the expanding zones of exploitation of neighbouring plants, when competition for resources in the overlapping regions occurs.

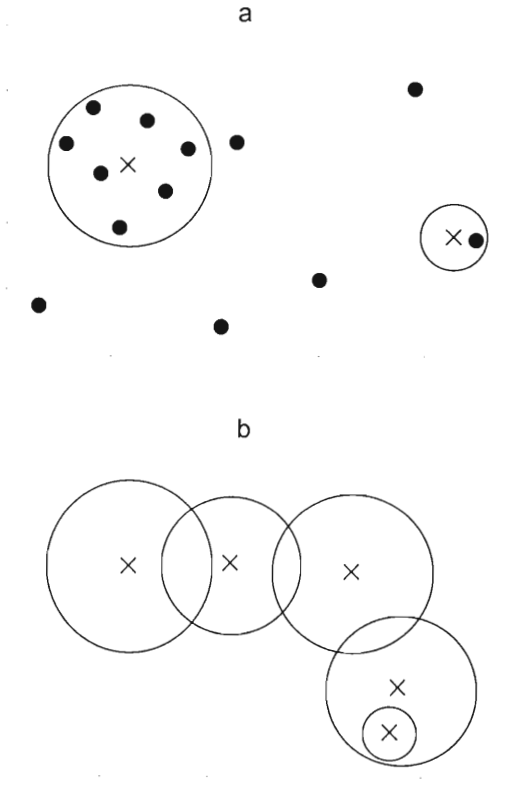

Figure 3.4. Graphical representation of neighbourhood models of plants. In figure (a) the neighbourhood of a focal plant, denoted by x, is the circular region. All plants inside the neighbourhood, denoted by ●, affect the growth and mortality of the focal plant, while all plants outside the circular region of the focal plant do not affect its growth and mortality. In (b), the neighbourhood of each plant, denoted by x, is given by the circular region surrounding it. The survival of the plants depends on the extent of overlap of the neighbourhoods.

In CA models of seed dispersal, the neighbourhood of a plant may extend to a number of cells away from the target cell: Seeds produced within each cell are dispersed to surrounding cells on the basis of distance-related dispersal functions (e.g. Hobbs and Hobbs 1987; Czaran and Bartha 1989; Green 1989; Auld and Coote 1990), and the neighbourhood therefore extends to a number of cells away from the target cell. Chiarello and Barrat-Segretain (1997) developed a stochastic cellular automaton of seed dispersal to describe the recolonisation of different species of macrophyte in the Rhone River. Their model is concerned with the probability that events will happen, and is based on spatial point processes and random mosaics. Section 2.4 in Chiarello and Barrat-Segretain (1997) describes this process.

When modelling vegetative spread, the neighbour cells consist of the cells adjacent to the target cell (e.g. Sklar et al. 1985; van Tongeren and Prentice 1986; Silvertown et al. 1992; Hendry et al. 1996). We choose to employ this definition of neighbourhood for the model of *Zostera*, i.e. the neighbourhood of a particular cell consists of its six adjacent cells (figure 3.5). Although it was mentioned previously that a neighbourhood may not always be circular, (Harper 1985;de Kroon and Hutchings 1995), Adams (1994, pers. comm) stated that the spread of *Zostera* occurs equally in all directions irrespective of the neigbouring cell conditions, i.e. that the neighbourhood is circular.

3.7.4 The Updating Rules

In the cellular automata model of Van Tongeren and Prentice (1986), stochastic equations are used to describe the growth and horizontal spread of individual shrubs. The growth component in this model is based on a relationship between the area occupied by the individual and the height of the individual, whereas the model for *Zostera* will be based on plant biomass equations. To avoid the situation where there is too much growth favouring one direction, Van Tongeren and Prentice (1986) assume that expansion is anisotropically distributed to adjacent cells up to a maximum rate. There is no evidence that expansion of *Zostera* favours low density areas or that it favours sites with optimal physical conditions for growth, so unlike Van Tongeren and Prentice (1986) we assume that expansion occurs radially. Sklar et al. (1985) adopt a different approach in determining when macrophytes expand to adjacent cells. They model the physical conditions of the cells, and when the physical conditions correspond to the conditions required for a particular habitat, the cell state is changed to reflect the new habitat.

The model of Sklar et al. (1985) does not describe the biomass dynamics of the plants and how neighbouring plant communities affect expansion and is therefore not applied to *Zostera*. Collins and Wlonsinski (1989) model the dyanmics of a submerged macrophyte in a reservoir. The model is spatial, but there are no horizontal interactions among neighbours. Vertical growth occurs when the biomass of a cell exceeds a certain value, after which growth occurs into the next higher cell. We will apply this approach in determining when vegetative growth occurs to neighbours. Other models of submerged macrpohytes in the literature are only spatial in the depth dimension (e.g. Verhagen and Nieunhuis 1983; Bach 1993; Scheffer et al. 1993). Therefore we develop a spatial model for *Zostera* that includes both depth below the water surface and length along the estuary. This model is developed in the following sections.

The updating rules for the model are deterministic, and are given by equation (3.11).

$$\frac{db_{ij}}{dt} = [g(b_{ij}, n_{ij}) - m(b_{ij})] \qquad i = 0,1,...,n, \qquad j = 0,1,...,m \tag{3.11}$$

where

b_{ij} is the biomass density of the (i,j) th cell at time t ($g.m^{-2}$),

n_{ij} is the biomass density of the six-cell neighbourhood of the (i,j) th cell at time t, defined below, and shown in figure 3.5,

g is a growth function (0-1),

m is a mortality function (0-1),

t is the time, (days) and

$$n_{ij} = [b_{i-1,j-1}, b_{i-1,j+1}, b_{i+1,j-1}, b_{i+1,j+1}, b_{i-2,j}, b_{i+2,j}] \quad i = 2,..,(n-2), \; j = 1,2,..,(m-1)$$

$$n_{00} = [b_{1,1}, b_{2,0}]$$

$$n_{0m} = [b_{1,m-1}, b_{2,m}]$$

$$n_{nm} = [b_{n-2,m}, b_{n-1,m-1}]$$

$$n_{n0} = [b_{n-2,0}, b_{n-1,1}]$$

$$n_{i0} = [b_{(i-2),0}, b_{(i-1),1}, b_{(i+1),1}, b_{(i+2),0}] \ , \ i = 2,...,n-2$$

$$n_{im} = [b_{(i-2),m}, b_{(i-1),(m-1)}, b_{(i+1),(m-1)}, b_{(i+2),m}] \ , \ i = 2,...,n-2$$

$$n_{0j} = [b_{2,j}, b_{1,(j-1)}, b_{1,(j+1)}] \ , \ j = 2,...,m-2$$

$$n_{nj} = [b_{(n-2),j}, b_{(n-1),(j-1)}, b_{(n-1),(j+1)}] \ , \ j = 2,...,m-2$$

$$n_{1j} = [b_{3,j}, b_{2,(j-1)}, b_{2,(j+1)}, b_{0,(j-1)}, b_{0,(j+1)}] \ , \ j = 1,...,m-1$$

$$n_{(n-1)j} = [b_{(n-3),j}, b_{(n-2),(j-1)}, b_{(n),(j-1)}, b_{(n),(j+1)}, b_{(n-2),(j+1)}] \ , \ j = 1,...,m-1$$

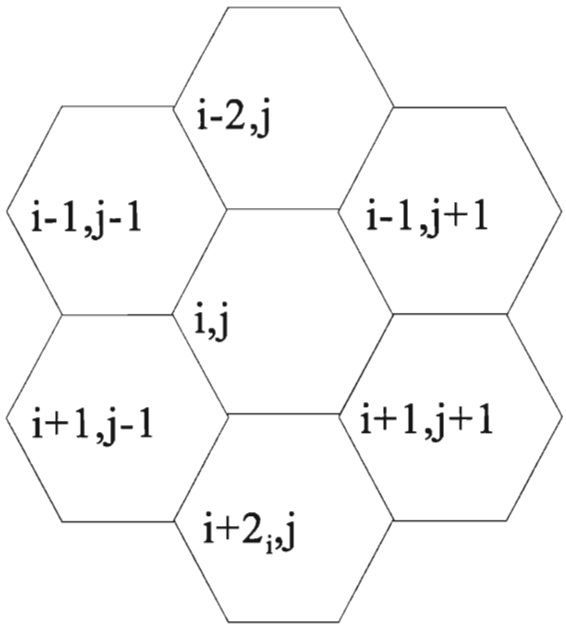

Figure 3.5. The neighborhood of the (i,j) th target cell.

In this model we do not distinguish between above- and below-ground biomass. That is, the biomass referred to comprises above- and below-ground biomass. In the model in the following chapter biomass is separated into above-and below-ground compartments.

The model is written in Turbo Pascal for Dos 7.0.

3.7.4.1 The Growth Rule

Unless otherwise stated, all functions defined in this section and following sections lie between zero and one.

The biomass growth from the (i,j) th cell is written as

$$growth = r.gm_{ij}b_{ij}g_1(b_{ij}) \qquad i = 0,1,...,n, \qquad j = 0,1,...,m \tag{3.12}$$

where

r is the maximum specific growth rate ($g.g^{-1}.day^{-1}$),

g_l is a nonlinear density-dependent function that shows how cell density modifies the maximum specific growth rate (0-1),

gm_{ij} is the growth multiplier of the (i,j) th cell (0-1), and is written as

$$gm_{ij} = sgm(sal_{ij}).wlgm(wl_{ij}).dgm(wl_{ij}) \quad (3.13)$$

where

sgm is the salinity growth multiplier (0-1),

wlgm is the water level growth multiplier (0-1),

dgm is the depth growth multiplier (0-1),

sal_{ij} is the salinity of the (i,j) th cell at time t (ppt.parts per thousand), and

wl_{ij} is the water level fluctuation (determined by the maximum and minimum water levels) of the (i,j) th cell at time t (metres).

Both the water level growth multiplier and the depth growth multiplier are functions of the water level fluctuation. The water level growth multiplier depends on the exposure of *Zostera* above the water level. *Zostera* is able to survive daily periods of exposure, but does not survive if constantly exposed (Adams, 1994). The depth growth multiplier depends on the depth below the water level surface. *Zostera* will not survive if submerged below 2.5 m (Adams, 1994).

The maximum specific growth rate is the growth rate under reference conditions. That is, it is the growth rate under ideal physical conditions for growth and under low density. The effect of the freshwater environmental factors and the density factor on the growth of *Zostera* is determined by multiplying the individual factors. This implies that *Zostera* grows from a combination of all the factors. This approach has been successful in modelling submerged macrophytes with combined light, temperature and nutrient effects (Bach 1993; Collins and Wlosinski 1989; Scheffer et al. 1993; Titus et al. 1975).

Density effects are least when cell density is low, i.e. the growth rate is close to its maximum specific growth rate, and thus g_l is close to one. As density increases, the value of g_l decreases so that the growth rate is less than the maximum specific growth rate (figure 3.6). For cell

densities less than 0.3, density effects would be small, so the value of g_1 is close to one for these densities. For densities greater than 0.3, we would expect density effects to come into play, so g_1 decreases approximately linearly until a density of 0.8, after which the function g_1 approaches the asymptote of one third. In a nonspatial model g_1 would be zero when density is one to show no further growth. However, to account for biomass overflowing into neighbouring sites, the minimum value of g_1 is not zero. The minimum value of g_1 is one third, i.e. when cell density is one, intraspecific competition results in an overflow of only one third of the growth to neighbouring sites. The function g_1 was not derived from literature or previous studies, but is a guess as to how growth is related to density. In chapter 5, section 5.1.5.1 the sensitivity of the model results to this function is analysed.

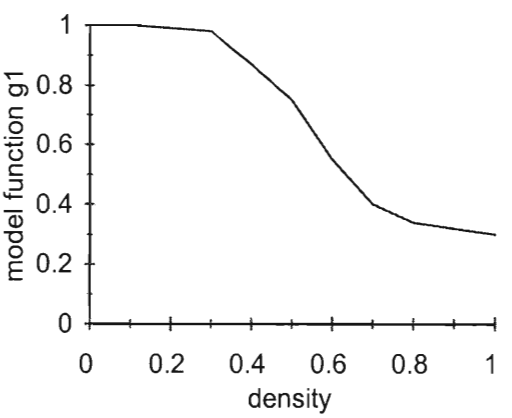

Figure 3.6. The model function g_1 in equation (3.12). This is a density-dependent growth function that determines internal and expansion growth for a target cell depending on the target cell density.

The physical growth multipliers modify the maximum specific growth rate as follows: If conditions are favourable for growth then the growth multipliers are close to one and the growth rate is close to the maximum specific growth rate. If conditions are unfavourable for growth then the growth multipliers are close to zero and the growth rate is less than the maximum specific growth rate. The multipliers are discussed in section 3.7.5.

As discussed in section 3.7.4 we assume that expansion occurs radially. The function g_2 (figure 3.7) determines how much total growth from a target cell is overflow or expansion to neighbour cells. The function g_2 was not derived from literature or previous studies, but is a guess as to how expansion is related to density. In chapter 5, section 5.1.5.1 the sensitivity of the model results to this function is analysed. As in Collins and Wlonsinski (1989), the rule for expansion to an adjacent cell is that when the biomass of the cell exceeds a certain value, the macrophyte grows into the neighbour cell. Therefore when the density in the (i, j) th cell is low, (below 0.1), there is no overflow or expansion to neighbouring sites ($g_2 = 0$). For cell densities between 0.1 and 0.3, most of the total growth in the cell is local growth, i.e. the proportion of expansion growth out of total growth is between 0.01 and 0.08 for densities between 0.1 and 0.3. For densities greater than 0.3 the proportion of expansion growth out of total growth increases rapidly. For cell densities greater than 0.7, we would expect most of the total growth in the cell to be expansion growth, therefore the value of g_2 for a density of 0.7 is 0.85, showing that 85% of total growth is expansion. When the target cell is full, there is only overflow or expansion growth and $g_2 = 1$.

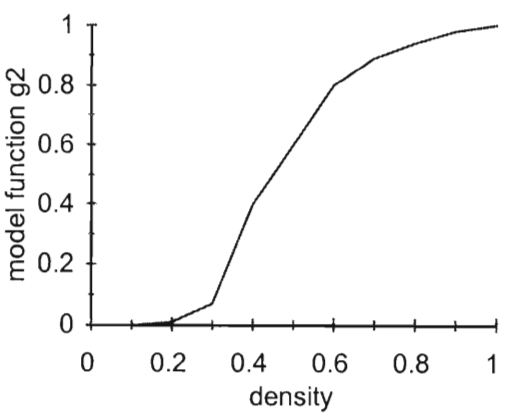

Figure 3.7. The model function g_2 in equation (3.14). This function determines how much total growth from a target cell is overflow or expansion to neighbour cells. The overflow depends on the target cell density: If target density is low, then there is no overlap or expansion, when target density is high most of the growth is overlap to neighbours.

Thus the change in biomass in the (i, j) th cell with no incoming encroachment from neighbours is

$$r.gm_{ij}b_{ij}g_1(b_{ij})[1 - g_2(b_{ij})] \qquad (3.14)$$

and the overflow o_{ij} to neighbouring sites is

$$o_{ij} = r.gm_{ij}b_{ij}g_1(b_{ij})g_2(b_{ij}) \qquad (3.15)$$

Combining (3.14) and (3.15) to give the growth of a cell from its own growth and that of neighbouring cells gives

$$g(b_{ij},n_{ij}) = r.gm_{ij}b_{ij}g_1(b_{ij})[1-g_2(b_{ij})] + \sum_{n_{ij}} \frac{1}{6} r.gm_{n_{ij}}n_{ij}g_1(n_{ij})g_2(n_{ij})g_3(b_{ij}) \qquad (3.16)$$

where

g_3 is a density-dependent growth function (0-1) (figure 3.8).

The term representing overflows from neighbouring sites to the (i,j) th cell, (the second term in (3.16)), is divided by 6 because expansion from these cells occurs radially to their six neighbours, one of which is the (i,j) th cell.

Including the function g_3 is necessary in (3.16) because when the (i, j) th cell is full, there is no increase in biomass in the (i,j) th cell, so g_3=0. For densities below 0.2, g_3 is close to one, to show that density effects on growth in the target cell are negligible. For densities between 0.2 and 0.8 the function decreases slowly as density effects of the cell start to affect the growth. For densities greater than 0.8, density effects would severely affect growth, therefore g_3 decreases to zero. As with functions g_1 and g_2 the function g_3 is not based on literature reviews or previous studies.

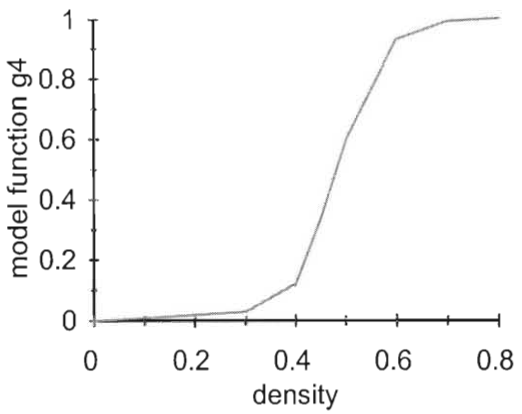

Figure 3.8. The model function g_3 in equation (3.16). This function is necessary because without it, having growth in a target cell is possible even if the target cell is full (see equation 3.16).

3.7.4.2 The Mortality Rule

Mortality in a cell is dependent on cell biomass density and the physical conditions, and is given by

$$m(b_{ij}) = \frac{q}{5} b_{ij}[g_4(b_{ij}) + sdm(sal_{ij}) + wldm(wl_{ij}) + ddm(wl_{ij}) + scm(velocity_{ij})] \quad (3.17)$$

where

q	is the maximum specific mortality rate ($g.g^{-1}.day^{-1}$),
g_4	is a density-dependent mortality function and is shown in figure 3.9 (0-1),
sdm	is the salinity mortality multiplier (0-1),
wldm	is the water level mortality multiplier (0-1),
ddm	is the depth mortality multiplier (0-1),
scm	is the scour multiplier (0-1),
sal_{ij}	is the salinity of the (i,j) th cell at time t (ppt.),
wl_{ij}	is the water level fluctuation (determined by the maximum and minimum water levels) of the (i,j) th cell at time t (m), and
$velocity_{ij}$	is the velocity of the (i,j) th cell at time t ($m.s^{-1}$).

The function g_4 in (3.17) is the density-dependent mortality function and was not derived from literature or previous studies. When cell density is below 0.3, g_4 is close to zero so that the mortality rate due to density effects is close to zero. The function increases linearly between densities of 0.4 and 0.8 so that mortality due to density effects approaches the maximum specific mortality rate linearly. For densities greater than 0.8 the function levels off to a value of one, so that mortality due to high density effects occurs at the maximum specific mortality rate.

Similarly, if physical conditions are favourable for growth, then the physical mortality multipliers are close to zero, and vice versa if the physical conditions are unfavourable for growth. The maximum specific mortality rate is the mortality rate under the worst possible physical conditions for growth and under high density. To show how a combination of density and physical conditions modify the maximum specific mortality rate, one fifth of the maximum specific mortality rate is multiplied by sum of the five mortality multipliers. The use of the product of the multipliers would mean that if there is no mortality due to one factor, for example if the salinity mortality multiplier is equal to zero, then no mortality will be incorporated in the model because the product of the mortality multipliers would be equal to zero. The reason why the maximum specific mortality rate in (3.17) is divided by five is so that under the worst case scenario, when all five mortality multipliers are one, mortality occurs at the maximum specific mortality rate.

The physical mortality multipliers are discussed in the following section.

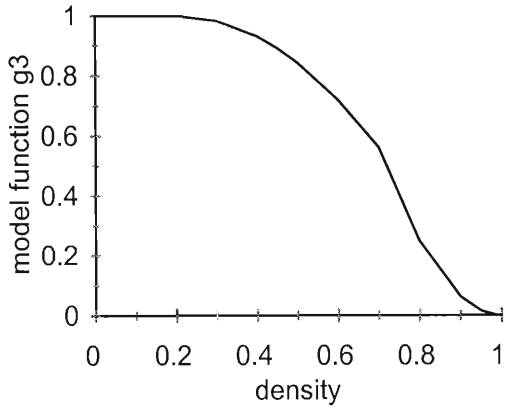

Figure 3.9. The density-dependent mortality function g_4 in equation (3.17).

3.7.5 The Physical Multipliers

Effects of salinity, water level fluctuations and current velocity are chosen to represent freshwater inflow in the model of *Zostera*. In the nonspatial model, the effects of water level fluctuations could not be included because these factors require the model to have a depth dimension.

Effects of Salinity on the Growth and Mortality of Zostera

The salinity growth and mortality multipliers for *Zostera* are discussed in chapter 2, section 2.2.4

Effects of Water Current Speed on Growth and Mortality of Zostera

The scour multiplier for *Zostera* is discussed in chapter 2, section 2.2.4.

Effects of Water Level Fluctuations on Growth and Mortality of Zostera

Zostera is adapted to survive periods of exposure (Adams and Bate 1994a). This is one reason *Zostera* is dominant in the middle and lower marine reaches of permanently open estuaries. Adams and Bate (1994a) found that a daily exposure time of five hours did not affect *Zostera*. The graph in figure 3.10 shows the average number of leaves left on *Zostera* plants exposed for five hours daily. Comparing this result with the control treatment, i.e. where *Zostera* is always submerged, Adams and Bate (1994a) showed that there was no significant difference

between average number of leaves on the control and the treatment plants. Based on this result, the water level growth and mortality multipliers are equal to one and zero respectively for a daily exposure time of five hours or less. If the daily exposure time is 12 hours then the water level growth and mortality multiplier is zero and one respectively. That is, *Zostera* does not survive if exposed for longer than 12 hours per day.

The underwater irradiance environment is determined by the water depth multiplier. According to Chambers and Klaff (1985) light, determined by depth, is one of the most important factors controlling seagrass distribution. The expert system rules of Adams and Bate (1994) state that if *Zostera* is below 2.5 m then it will die back. The depth growth and mortality multiplier is based on this rule, and depends linearly on the length of time *Zostera* is submerged below or up to a depth of 2.5 m.

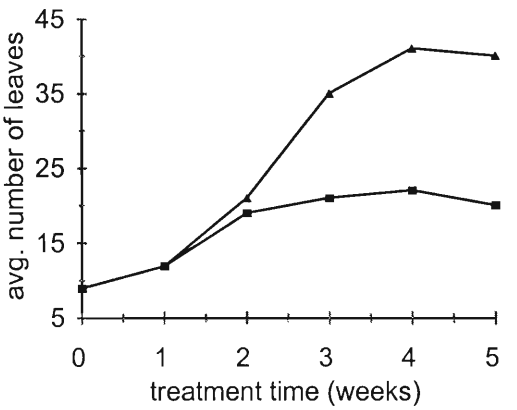

Figure 3.10. Change in the average number of leaves for *Zostera capensis* exposed for five hours daily over a period of various weeks. In the graph the series marked with a ▲ represents the change in average number of leaves when *Zostera* is always submerged. The series marked with a ■ represents the scenario where *Zostera* is exposed for five hours daily. (Adams and Bate 1994, p. 59).

The physical multipliers are shown in figures 3.11 and 3.12. The salinity multipliers and scour multipliers are the same as those used for *Zostera* in the model of *Zostera* and *Ruppia* from the previous chapter.

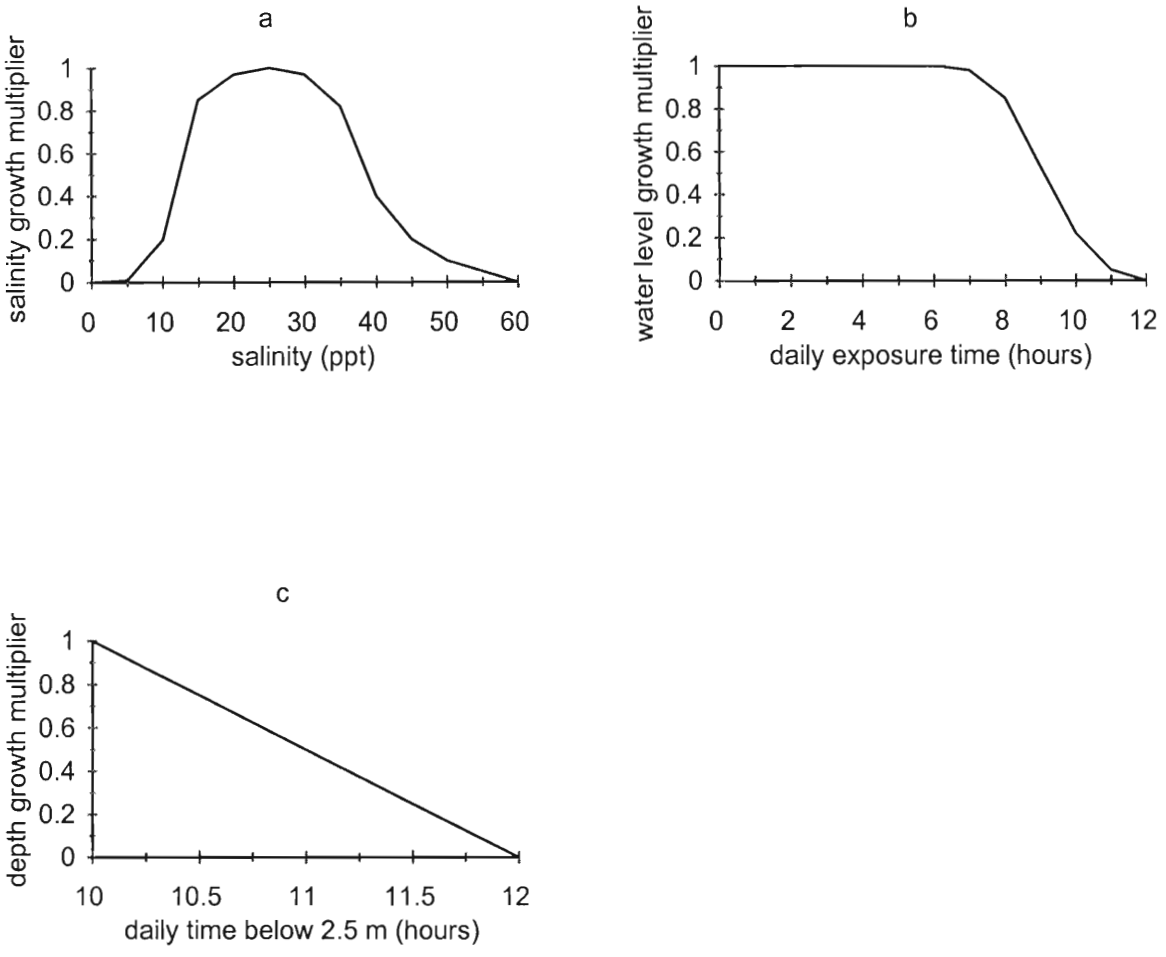

Figure 3.11. Graphs showing the physical growth multipliers of the model. *Zostera* grows optimally for salinities between 15 ppt. and 35 ppt. (figure a). The water level growth multiplier (figure b) shows that *Zostera* growth is reduced if exposed above the water level for more than five hours a day. The depth growth multiplier (figure c) depends linearly on the time submerged below 2.5 m.

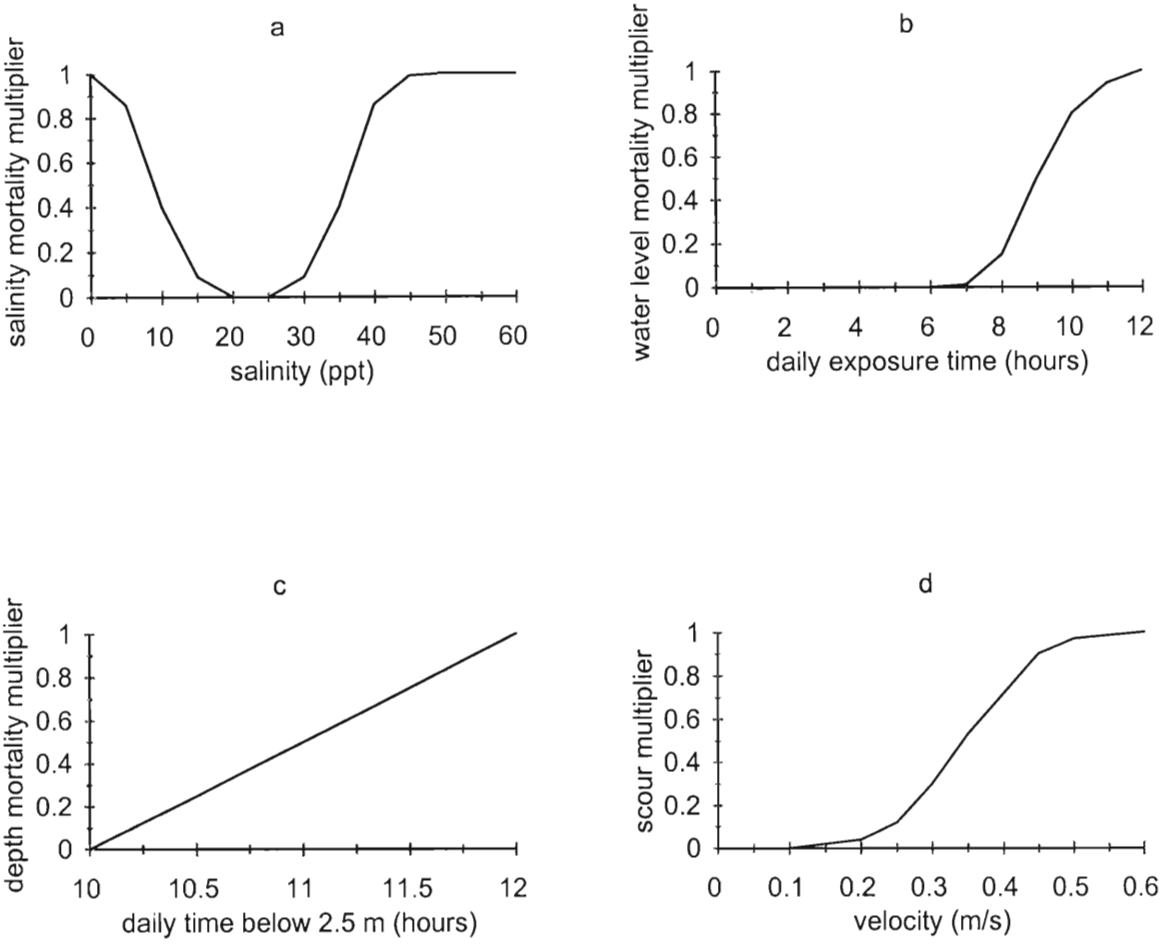

Figure 3.12. Graphs showing the physical mortality multipliers of the model. *Zostera* has a narrow salinity tolerance range (figure a), but is resistant to dessication (figure b). Mortality of *Zostera* increases when submerged below 2.5 m for long periods (figure c). Growth of *Zostera* is significantly reduced at 0.5 $m.s^{-1}$ (figure d) and *Zostera* will not persist in estuaries where the current velocity consistently exceeds 1 $m.s^{-1}$ (which would represent high flow conditions in most South African estuaries).

3.7.6 Parameter Values

The values assigned to the parameters are:

$r = 0.005\ g.g^{-1}.day^{-1}$ (specific growth rate, Adams, 1994, pers. comm.),
$q=0.005\ g.g^{-1}.day^{-1}$ (specific mortality rate, Adams, 1994, pers. comm),
time step = 1 day,
$K = 300\ g.m^{-2}$ (Adams and Talbot 1992),
cell dimension = $1.2\ m^2$ (see explanation below), and
time step = 1 day (see explanation below).

where K is the maximum biomass density that a cell can support and r and q are the maximum specific growth and mortality rates of *Zostera* respectively.

A report on the calibration technique for the full cellular automata model appears in chapter 5 section 5.1.3. For the present model, the calibration technique comprised determining a cell size and time step that resulted in bounded biomass values. A cell size of $1.2\ m^2$ and a time step of one day lead to bounded biomass values. As in the technique outlined in chapter 5, for the calibration an ideal environment for *Zostera* growth was assumed; i.e. the physical growth and mortality multipliers had values of one and zero respectively. This means that salinity was kept constant at 25 ppt., the current velocity was less than $0.1\ ms^{-1}$, and the area modelled was below the low tide mark so that *Zostera* was always submerged but not below a depth of 2.5 m. Results in the following section were obtained for a grid of 30 by 30 cells.

3.8 Predicting Estuary Hydrodynamics and Mouth Condition

Two hydrodynamic models were used to obtain information on the daily salinity, water level fluctuations and water current speed. The first physical model is the commercially available, one dimensional hydrodynamic simulation programme called Mike 11 (Danish Hydraulic Institute 1992). This model simulates the physical characteristics of an estuary at the scale of days and months. Mike 11 requires information such as bathymetric cross-sections, water level recordings and river inflow as input data, and can provide time histories of water levels, flow velocities and salinity (Huizinga 1994).

Consequently, simulation periods of days and months are manageable. However, plant processes are seldom modelled at the same time scale as hydrological processes. A water release policy, for example, may extend for a full year, the effects on the plants of which may only be evident in a few years time. For the purposes of estuary management, the model of *Zostera* needs to be run over a long period (years), requiring hydrodynamic information for a similar length of time. Slinger (1994) developed a generalised model of estuarine physical dynamics (Estuarine Systems Model). The purpose of the model is to predict the status of the estuary mouth given freshwater inflow and the near shore wave condition, and provides average salinity, water level and water current speed. As the Estuarine Systems Model only provides information in the middle reaches of an estuary, the Mike 11 model was used to obtain information at other locations.

The physical models provide the daily salinity, maximum and minimum water levels, and the freshwater inflow rate for various freshwater inflow scenarios. The daily exposure time (for the water level multipliers) is calculated from this data as follows: A sine wave with average position half way between the maximum and minimum water levels, and amplitude equal to half the difference between the maximum and minimum water levels, is derived. The period of the sine wave is equal to 12 hours (to account for approximately two low tides and two high tides per day). The daily exposure time at any position is then calculated based on the position relative to the sine wave. Similarly, the sine wave is used to calculate the time *Zostera* is submerged below 2.5 m (for the depth multipliers).

3.9 Results

The scenarios comprise either an increase or a decrease in freshwater flow to the estuary. Diminished freshwater supply reduces the mouth to head salinity difference, and may also lead to a drop in water levels. We examine these effects on the spatial distribution of *Zostera capensis*. An important consequence of diminished freshwater supply is a reduction in the amplitude of flood events. We therefore apply a flood disturbance to a system in the natural state and to a system where freshwater input has been reduced. The reason for selecting the scenario with an increase in freshwater supply is to examine how estuaries which have become *Zostera*-dominated due to diminished river runoff, can be restored by increasing the freshwater input and causing the die back of *Zostera* in the upper reaches.

Before results for the scenarios are discussed, we present results for scenarios for different mouth breach policies. Although answers to questions on when the mouth should be mechanically opened have been provided by the model in chapter 2, we choose to analyse more scenarios of this nature using the spatial model to compare results with those from the nonspatial model, and to illustrate what additional information the spatial model can provide. These results are discussed below.

Scenario 1: Effects of Breaching the Mouth - Comparison with Nonspatial Model

Figure 3.13 shows the initial biomass distribution of *Zostera* for the model simulations. Biomass distributions are shown at the high, average and low tide marks. Since *Zostera* can survive short periods of exposure (less than five hours per day, Adams and Bate 1994a), there is some biomass at the high and average tide marks.

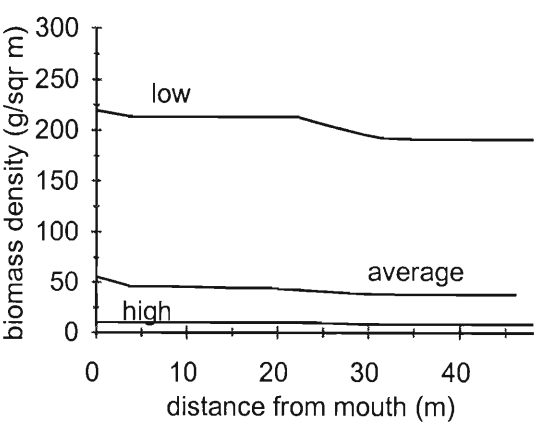

Figure 3.13. Graphs showing the initial biomass distribution of *Zostera* for the model simulations. Biomass distributions are shown at the high, average and low tide marks. Since *Zostera* can survive short periods of exposure, there is some biomass at the high and average tide marks. *Zostera* biomass decreases away from the estuary mouth due to the mouth to head salinity difference.

In the scenarios in chapter 2 (see section 2.2.6), the mouth open time was at most two months. The scenario in this section has a longer mouth open time, namely four months. Thus the cost of dredging sediment near the mouth to maintain open conditions for this long will be high. To reduce costs, the frequency with which the mouth is mechanically opened is decreased. Thus,

the mouth is allowed to remain closed for five months at a time. The physical data for this scenario is based on the Mike 11 data which was used for the non-spatial model in chapter 2.

The model results show that *Zostera* survives near the mouth and dies back with distance from the mouth. This is because of low salinities further away from the mouth (figure 3.14). This could not be predicted by the previous model. The model of *Zostera* and *Ruppia* from chapter 2 predicts that *Zostera* biomass density near the estuary mouth fluctuates between 210 and 228 $g.m^{-2}$ for this scenario. The spatial biomass density prediction is 225 $g.m^{-2}$ near the mouth. Therefore both sets of results indicate that *Zostera* survives near the mouth. However, the spatial model results also show that *Zostera* biomass density decreases with distance from the mouth under this policy. The spatial results are also able to predict *Zostera* dynamics at different water level marks, something which the nonspatial model could not predict.

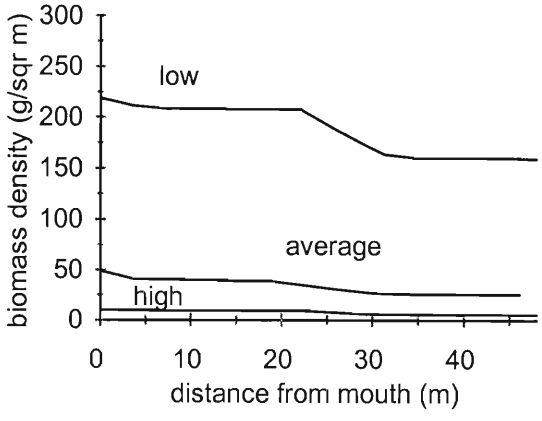

Figure 3.14. Graph showing how *Zostera* dies back from the estuary mouth when the mouth is allowed to remain closed for five months, and is then kept open for four months. Biomass density distributions are shown at the high, average and low tide marks.

Many model simulations for different mouth breaching scenarios were used to determine what combinations resulted in the survival of the *Zostera* community in the mouth. This relationship is shown in figure 3.15. In the graph, if the mouth open and closure times fall within the shaded or critical region, then *Zostera* will not survive. If the mouth open and closure times lie outside

the shaded region in figure 3.15, then *Zostera* will survive. The border between the critical and non-critical region is linear for closure times greater than or equal to 4.5 months.

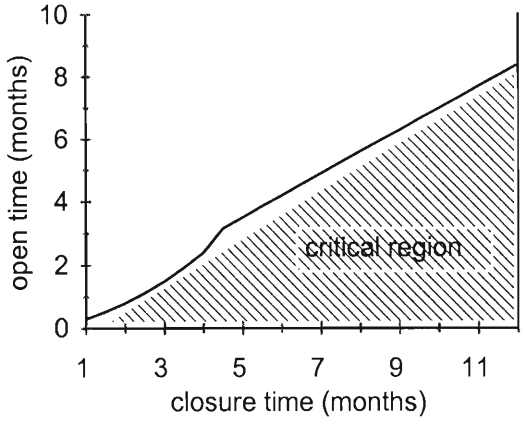

Figure 3.15. Graph showing the relationship between mouth open time and mouth closure time for the survival of *Zostera* in a temporarily closed estuary. The critical region is the shaded region where *Zostera* will not survive in the mouth.

Applying the above results to the scenarios from chapter 2 we find:

(a) Scenario 1: The open and closure time was 1 month and 3 months respectively. This lies in the critical region (figure 3.15), therefore *Zostera* does not survive. The nonspatial model predicted that *Zostera* did not survive.

(b) Scenario 2: The open and closure time was 2 months and 4 months respectively. This just lies within the critical region (figure 3.15), therefore *Zostera* does not survive. The nonspatial model predicted that *Zostera* survives in the absence of *Ruppia*.

(c) Scenario 3: Both the open time and the closure time was 1 month. This is above the critical region (figure 3.15), therefore *Zostera* survives. The nonspatial model predicted that *Zostera* survives.

Therefore the results from the nonspatial model agree with the results from the spatial model, except the second scenario, where the nonspatial model predicted that *Zostera* survives, whereas the spatial model predicted that *Zostera* does not survive. For this scenario, the mouth open and closure time was 2 months and four months respectively. For a closure time of four months, the critical region in figure 3.15 is below an open time of 2 months 12 days. Therefore if the mouth open time had been 2 months 12 days, then the spatial model would predict that *Zostera* survives. Out of scenarios 1, 2 and 3 above, scenario 2 has the longest period of closure time. This means that when the mouth is closed, water levels rise due to the damming effect created by the closed mouth. The longer the closure time, as in scenario 2, the higher the water levels rise. This means that the lower layers of *Zostera* may be submerged below the critical depth of 2.5 m and may start to die back. The nonspatial model does not consider this factor. This is why the nonspatial model predicts that *Zostera* can survive when the mouth is closed and open for four months and two months respectively, whereas the spatial model predicts that *Zostera* will survive if the open time is extended to 2 months 12 days.

Scenario 2: Effects of Freshwater Impoundment on Floods

Zostera fluctuates in response to episodic floods (Talbot and Bate 1987; Hanekom and Baird 1988). Decreasing or disappearing with the onset of major floods, these populations show rapid recovery after a lag of one to three years (Talbot et al. 1990). Freshwater managers therefore need to be able to determine how impoundments can be expected to alter the normal influence of floods on *Zostera* dynamics. Although the following result is not a spatial result and could have been obtained from the nonspatial model, we choose to use the spatial model in the derivation of the result because the spatial model has more physical multipliers than the nonspatial model so it is incorporating more factors related to freshwater inflow.

The spatial model results show that a pristine (i.e. no freshwater impoundment) estuary shows a 100% loss in *Zostera* biomass at the onset of a flood (figure 3.16), (high current velocities scour *Zostera* and high water levels reduce light available for photosynthesis). In contrast to this, there is a 50% difference between pre-flood and post-flood biomass values for estuaries with freshwater impoundment (figure 3.16). The physical data for the scenarios is taken from the Mike 11 simulations for the Great Brak estuary for the natural run-off scenario and the post-dam run-off scenario (see Slinger, 1996, pp. 74-80).

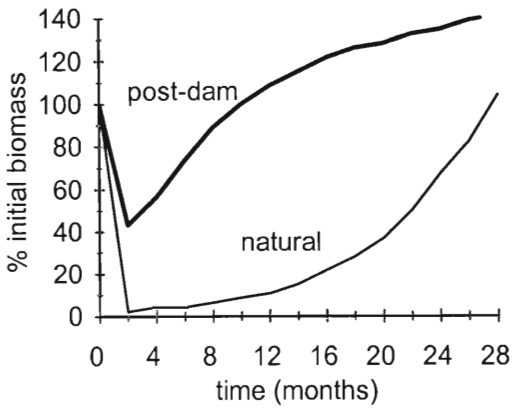

Figure 3.16. The overall response of *Zostera* to a flood in a permanently open estuary. The flood occurs at the beginning of the first year. The graph shows how impoundments attenuate floods and reduce the dynamic nature of the system.

Scenario 3: Effect of Freshwater Impoundment on Water Level Fluctuations

South Africa has a semiarid climate characterised by dry periods. The purpose of this scenario, therefore, is to determine the effect of a one year dry period on the depth distribution of *Zostera*. In many South African estuaries, during closed mouth conditions, dry conditions may result in low water levels and the subsequent exposure of *Zostera* beds. The physical data for this scenario was adapted from the results from the Estuarine Systems Model (Slinger, 1996, pp. 98) for the Great Brak estuary. The estuarine systems model predicted a drop in water level of 1 metre over four months of drought conditions for the natural run-off scenario. For the present scenario the drought is one year so water levels dropped by 2 metres after one year of dry conditions.

The graph in figure 3.17 compares the natural distribution of *Zostera* with the corresponding distribution after a one year dry period. The intertidal zone shifts down the bank and the maximum biomass density is reduced from 225 $g.m^{-2}$ to approximately 50 $g.m^{-2}$. If natural conditions return after one year of dry conditions, then results indicate that *Zostera* will take 2 years to recover (when calculating the recovery time we assumed that the mouth was permanently open. If the mouth is periodically closed, then the recovery time will be greater than 2 years).

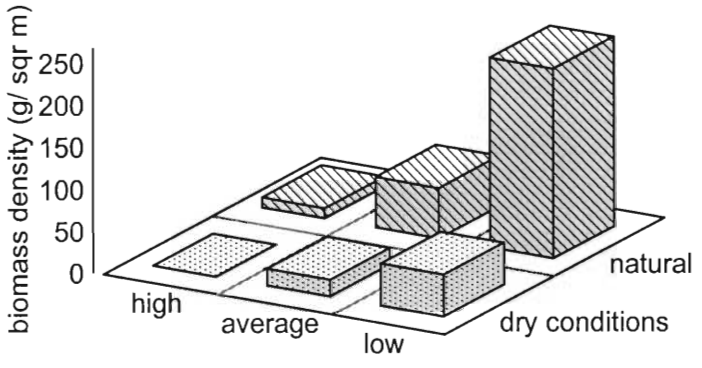

Figure 3.17. The response of *Zostera* to dry conditions of one year. Water levels drop and submerged macrophytes are exposed and die back. High, average and low are the high, average and low water marks under natural runoff conditions.

Scenario 4: Effect of Freshwater Impoundment on the Mouth to Head Salinity Difference

In these scenarios the freshwater supply to the estuary is reduced. The physical data corresponds to data from the Mike 11 model for the Kromme estuary in the lower reaches for the scenario with no freshwater releases (Slinger, 1996, pp.34).

Figures 3.18 (initial), 3.19 (after 1 year) and 3.20 (after 3 years) show the subsequent encroachment of *Zostera* upstream when freshwater inflow is reduced. The effect of impoundments is immediate, and the model predicts that after 1 year, *Zostera* has spread 20 m upstream. By knowing how fast *Zostera* encroaches, freshwater managers can assess whether the situation is critical and whether the policy will yield a marine dominated estuary in a short period. If this is the case, then they need to consider alternative release policies which prevent *Zostera* from colonising the upper reaches.

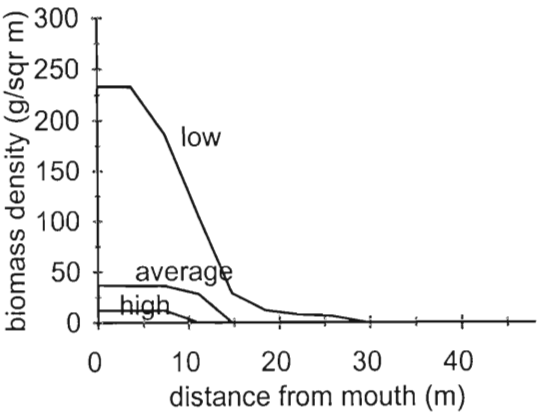

Figure 3.18. Graphs showing the initial distribution of *Zostera* for model simulation results in figures 3.19 and 3.20. Biomass distributions are shown at the high, average and low tide marks.

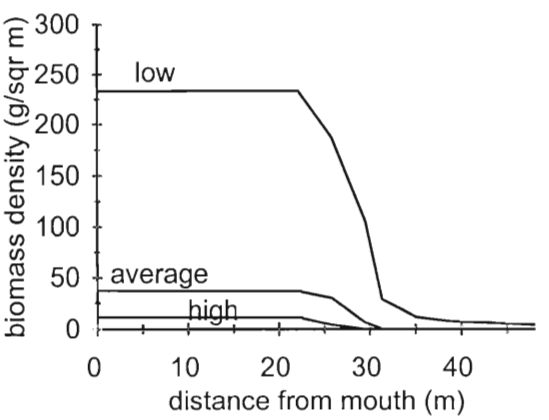

Figure 3.19. Graph showing the encroachment of *Zostera* upstream after a reduction in freshwater inflow for 1 year. Initial biomass distribution is given in figure 3.18. Biomass distributions are shown at the high, average and low tide marks.

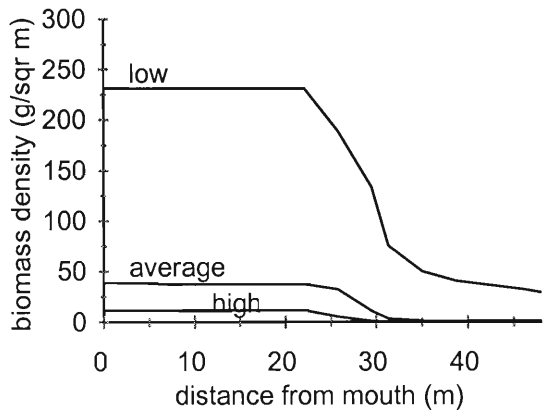

Figure 3.20. Graph showing the encroachment of *Zostera* upstream after a reduction in freshwater inflow for three years. Initial biomass distribution is given in figure 3.18 (p.75). Biomass distributions are shown at the high, average and low tide marks.

Scenario 5: Effect of Increasing Freshwater Supply to Estuaries

This scenario applies to estuaries where impoundment from rivers has resulted in a marine dominated system. We need to determine whether restoring brackish components in the upper reaches by changing the current pattern of releases from dams is possible. If this will not succeed, then we need to ask questions such as how much more freshwater needs to be released in order initiate the die back of marine species in the upper reaches?

Results showed that an increase in freshwater inflow by 5% is not enough to initiate the die back of *Zostera* (salinities did not decrease sufficiently), whereas an increase in freshwater inflow by 10% results in the die back of *Zostera* beds in the upper reaches (figures 3.21 (initial) and 3.22 (after 2 years)).

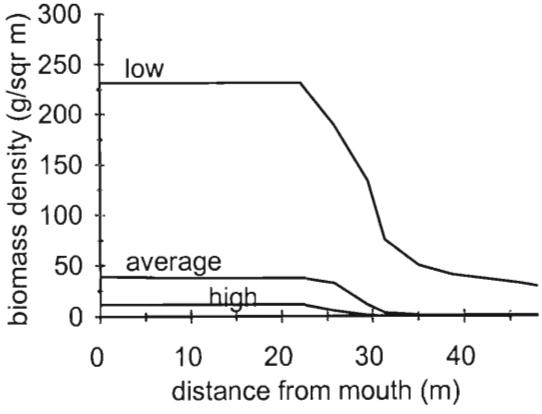

Figure 3.21. The initial distribution of *Zostera* for model simulation results in figure 3.22. Biomass distributions are shown at the high, average and low tide marks.

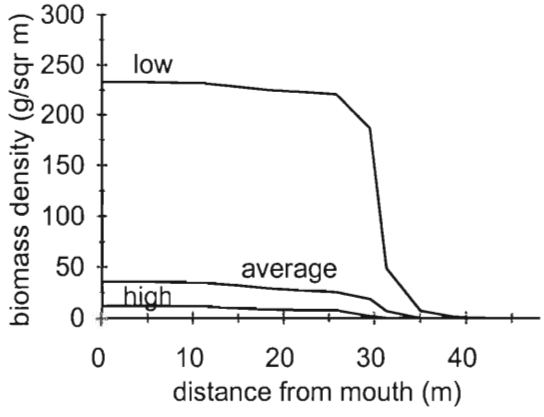

Figure 3.22. Graph showing the die back of *Zostera* (initial biomass distribution given in figure 3.21) after increasing the freshwater inflow for 2 years. Biomass distributions are shown at the high, average and low tide marks.

3.10 Discussion

It is only during the last decade that attention has been paid to seagrasses along the South African coastline (e.g. Hanekom 1982; Talbot and Bate 1987; Hanekom and Baird 1988; Talbot et al. 1990; Adams and Talbot 1992; Adams and Bate 1994a, 1994b). As a result, there is not much data available for model validation.

Talbot and Bate (1987) surveyed the distribution and biomass of *Zostera* in the Swartkops estuary, South Africa. Historical evidence, with their winter 1981 (following the flood) - summer 1981 surveys showed a short term variability in biomass within the estuary. Such changes were probably in response to flooding. (Hanekom (1982) showed *Zostera* biomass fluctuations were linked to episodic floods rather than to seasons). Talbot and Bate (1987) found that the average winter (post-flood) *Zostera* biomass was half that of the summer biomass. The post-dam scenario in figure 3.16 (p.73) closely resembles the situation in the Swartkops estuary during 1981. Salinities are high throughout the estuary. The model predicts that average biomass is halved after the flood (figure 3.16).

Talbot et al. (1990) recorded the variability in the distribution of *Zostera capensis* in the Kwelera estuary, South Africa. At the time of their study there were no dams on the Kwelera river. After a flood in November 1985, *Zostera* took three years to recover to 64% of the pre-flood *Zostera* biomass. The model in this study (figure 3.16, p.73) predicted that under natural runoff *Zostera* took approximately two years to recover to 64% of the pre-flood *Zostera* biomass. The flood in November 1985 in the Kwelera estuary was heavy, whereas the flood simulated in the model was moderate, which explains the longer recovery time in the Kwelera estuary. There is complete removal of beds in response to major floods. Moderate floods often lead to intensive deposition of fine muddy sediments which can result either in the smothering of beds or in the temporary impairment of growth. Nevertheless, some rhizomes remain rooted during moderate floods (Talbot et al. 1990).

Comparing the long-term behaviour of *Zostera* in Talbot and Bate (1987) and Talbot et al. (1990) with model output is difficult because of the lack of physical information on these estuaries. Validation of the encroachment rate predicted by the model should be tested experimentally.

The results from the nonspatial model, and the cellular automata model agree for the scenarios studied except the scenario with an open time and a closure time of 2 months and 4 months respectively. It was argued that the disagreement arises because the spatial model incorporates more freshwater related factors than the nonspatial model, these factors relating to depth.

The advantage of the nonspatial model is that it is not as data intensive as the spatial model, and its simulation time is much faster than that for the spatial model. For example, the nonspatial model simulates one year in less than one second, whereas the spatial model simulates one year in 3.5 minutes. These times were calculated from simulations run on a 166 MHz Pentium with MMX and 64 MB Ram.

The advantage of the spatial model is that it can answer questions which the nonspatial model cannot. Scenario 3, showed that it takes one year of dry conditions to completely change the intertidal zone from having *Zostera* vary from 225 to 50 $g.m^{-2}$ between the low and high water level marks, to having *Zostera* completely disappear at the high water level mark, and die back to approximately 50 $g.m^{-2}$ at the low water level mark.

Scenario 4 showed that *Zostera* spread rate was approximately 20 m after one year of reduced river inflow. After three years of these conditions, the leading biomass had increased in density from just more than zero to 50 $g.m^{-2}$.

Scenario 5 was useful in determining a critical volume of freshwater. The results showed that all that is needed to start the die back of *Zostera* in the upper reaches is an increase in the current volume of freshwater released by 10%. Freshwater managers therefore need to consider the ecological benefits derived from this increase in freshwater release (the ecological benefit would be macrophyte diversity), and the benefits this volume of water would provide if it were diverted, impounded or consumed.

3.11 Conclusion

The cellular automata model of *Zostera* was developed to answer questions which could not be answered by the nonspatial model. These questions were mainly related to colonisation patterns, encroachment rates, the distribution of *Zostera* along the length of the estuary, and the depth distribution of *Zostera*. That is, they are questions which require information on spatial dynamics.

The purpose of the cellular automata model was to assist management decisions related to freshwater. The model achieved this by predicting what happens as a result of impoundments. By using the model results, freshwater managers can learn how fast *Zostera* is likely to encroach up the estuary. This means that freshwater managers are able to analyse the consequences of their actions before they are applied, and this may avoid ecological disaster in the long term.

Many estuaries in South Africa are already in poor condition. Knowing how to restore certain estuaries to their natural state is therefore important. We showed how the model can determine an optimal freshwater release plan which allocated a maximum volume of water for consumptive purposes, and a minimum volume of water for estuarine purposes which ensured the absence of marine macrophytes in the upper reaches. This was called the critical volume of freshwater.

3.12 Summary of Macrophyte Models

There are now three models for the freshwater requirements of estuarine macrophytes in South Africa. The expert system model of Adams and Bate (1994) is the simplest model, and requires the least amount of physical data. It is therefore a useful initial predictive tool. However, to make informed decisions, more information on the consequences of freshwater release plans is necessary. This was why the nonspatial model was developed. This model is useful in helping managers decide when to breach the estuary mouth and for how long dredging should occur to maintain open mouth conditions. Mechanically opening the mouth is expensive, so managers need to know the implications before an action is taken. The model was useful in determining which mouth breach policy to adopt to obtain either a *Ruppia-dominated* estuary or a *Zostera*-dominated estuary. The spatial limitations of this model resulted in the

development of the cellular automata model. The cellular automata model fulfilled a role which the nonspatial model was unable to do. It can provide information on the consequences of freshwater releases on the distribution of *Zostera* along the length of the estuary, on colonisation patterns of *Zostera*, and on the depth distribution of *Zostera*. The complexity of the spatial model does not mean that it is superior to the other two models. All three models are important decision making tools. They answer different questions as they were designed to meet different management needs. So the state of predictive capability for estuarine macrophytes in South Africa has been extended to incorporate two additional mathematical models, one of which includes temporal dynamics and interactions among different species, and one of which includes spatial and temporal dynamics of a single macrophyte community.

One question that has not yet been answered is how macrophytes further up the estuary affect the encroachment of *Zostera*. This issue is examined in the following chapter where additional macrophytes are included in the cellular auotmata model.

CHAPTER 4

EVALUATING THE CONSEQUENCES OF FRESHWATER RELEASES IN TWO SOUTH AFRICAN ESTUARIES

4.1 Purpose of the Model

The cellular automata model answered questions on the effects of altered freshwater supply on a single macrophyte community, namely *Zostera*. However, to understand the full implications of a release pattern, freshwater managers need to know what happens to other communities. For example, the encroachment rate of *Zostera* up the estuary may not be as great as that predicted by the cellular automata model due to the presence of other plants. In addition, although the model can determine how much additional freshwater was needed to initiate the die-back of *Zostera* in the upper reaches of marine dominated estuaries, we do not know whether this volume is sufficient to start the regrowth of brackish and freshwater communities. The cellular automata model showed what happened to *Zostera* when water level fluctuations changed, but we also need to know how this affects the depth distribution of other intertidal plants: For example, if water levels drop then *Zostera* dies back, therefore we need to know whether there is enough time for another macrophyte to colonise the bare area before water levels rise again. We may even find that the presence of another plant would result in the complete displacement of *Zostera* as water levels drop. So to understand the full implications of a water release policy on the downstream estuary, we need to extend the cellular automata model of *Zostera* to include interactions among additional communities. Therefore, the purpose of this chapter is to predict the consequences of water releases on an estuarine environment with different macrophyte species.

4.2 Estuaries Selected

The two main types of estuaries in South Africa are temporarily closed estuaries and permanently open estuaries (Whitfield 1992). Therefore, estuaries representative of these environments are selected for the analysis of freshwater release policies. The estuaries selected are the Kromme estuary and the Great Brak estuary.

The Kromme estuary is in the eastern Cape, South Africa. It is a narrow sinuous water body that extends for 13.7 km from a permanently open mouth. The general topography and aspects of its ecology have been described by Hecht (1973), Hanekom (1982) and Hanekom and Baird (1988).

Figure 4.1 displays a map of the Kromme estuary. The upper reaches of the estuary are considered to extend from the head of the tidal influence (14 km upstream from the mouth) to the confluence with the Geelhoutboom River, the middle reaches to cross section 4, while the shallow, lower reaches lie downstream from this point.

Owing to impoundment in the catchment, the only guaranteed freshwater flow to the Kromme estuary is 2×10^6 m^3 per annum allocated for ecological purposes. This is less than 2% on average of the runoff it would have received under natural conditions. A discussion on the ecosystem changes in the Kromme estuary due to freshwater impoundment may be found in Baird and Heymans (1996).

The Great Brak estuary is a small (area of approximately 79 hectares) intermittently closed system located approximately half way between Mossel Bay and George on the southern Cape coast. It is 7.4 km in length. The major determinant of the physical dynamics of the Great Brak estuary is the state of the mouth, that is, whether the mouth is closed or open, and if open, to what extent and with what frequency. Currently 65% of the mean annual runoff to the Great Brak estuary is impounded (CSIR 1990). Figure 4.2 shows a map of the Great Brak estuary.

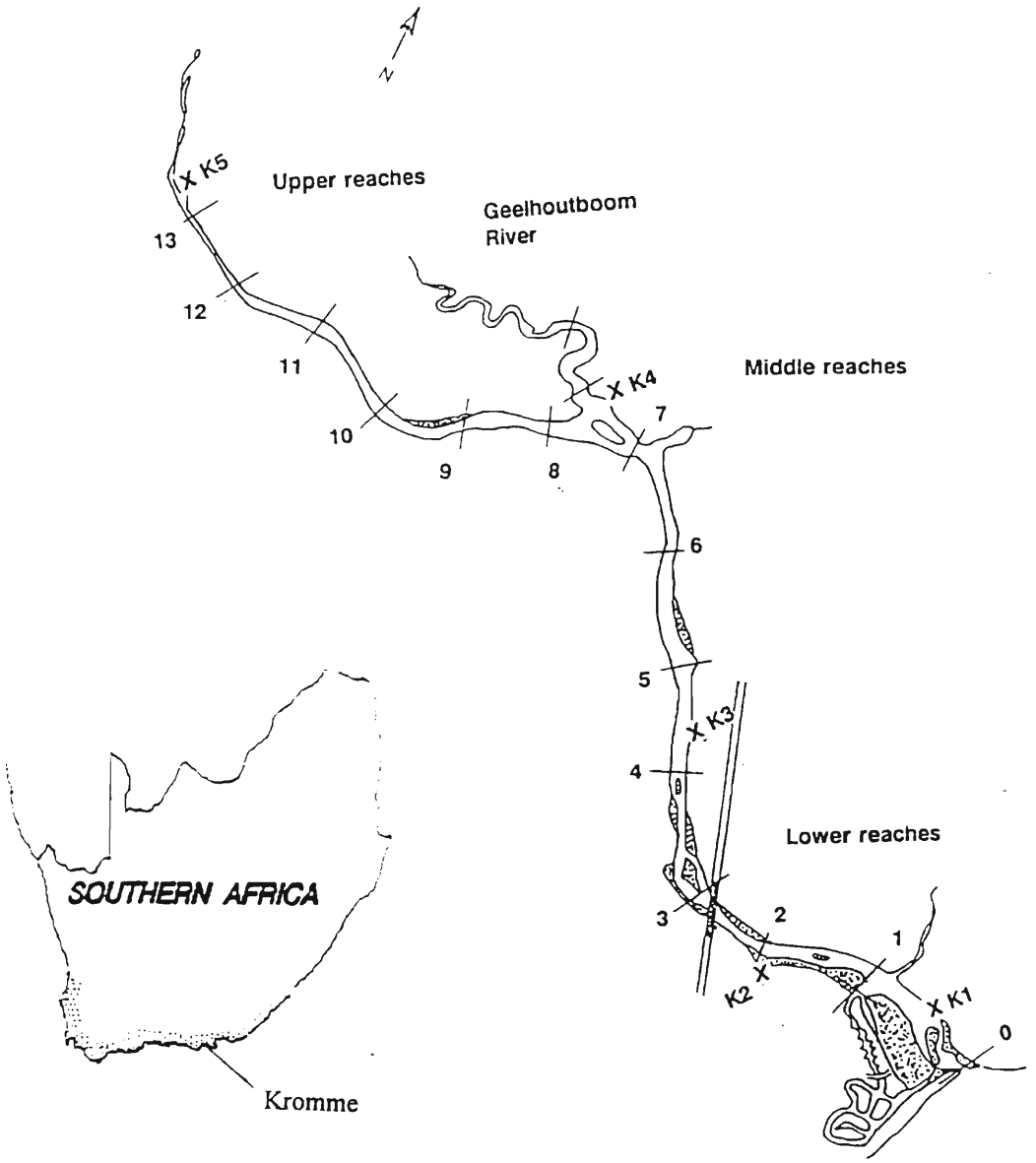

Figure 4.1. A map of the Kromme study area. Note the positions of the cross sections (K1, K2, K3, K4, K5) for which physical data is provided.

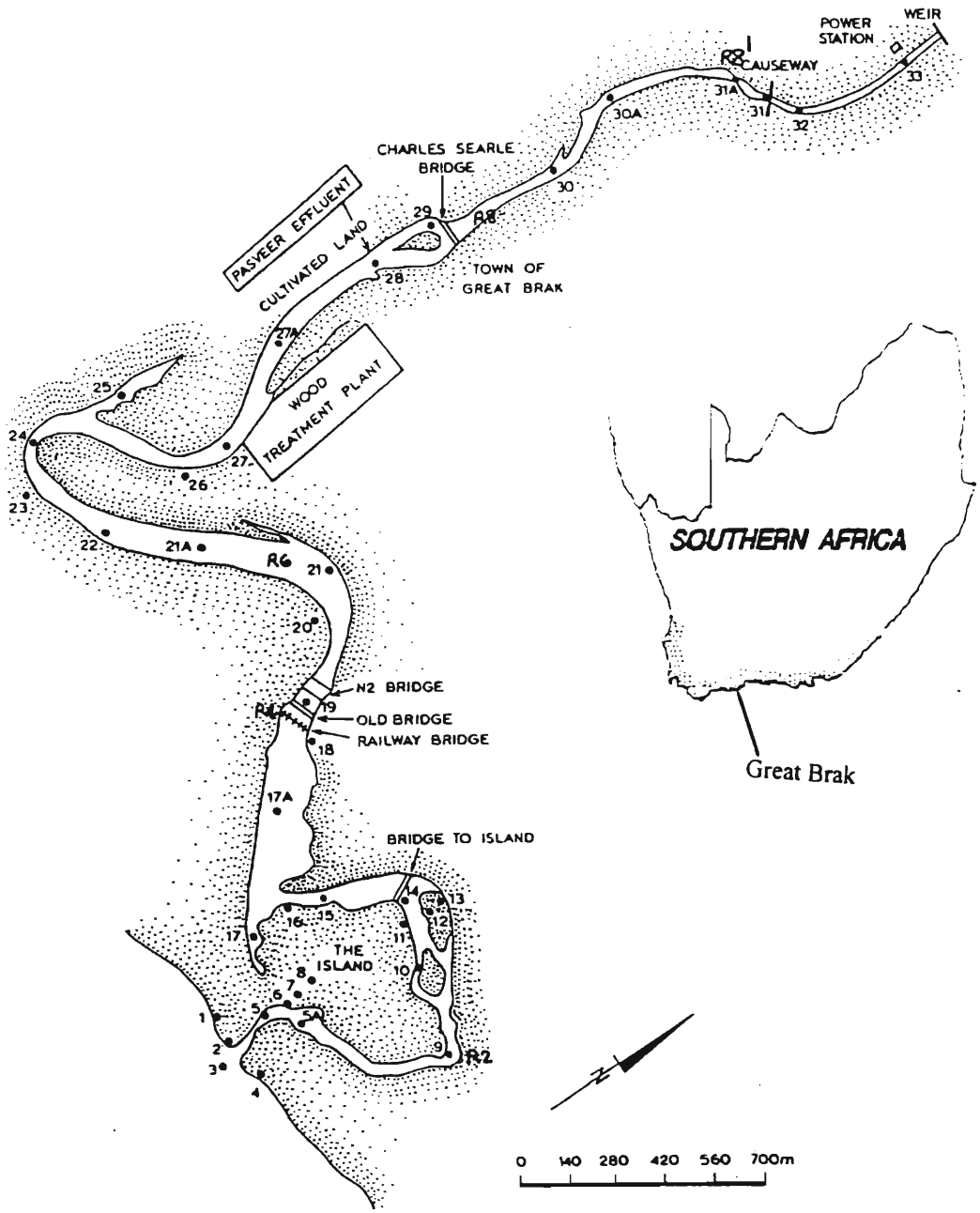

Figure 4.2. Map of the Great Brak estuary. Physical data is given for R2, R4, R6, R8 and R8.

4.2 Key Macrophytes

Key macrophytes included in the analysis are *Zostera capensis* Setchell, *Ruppia cirrhosa* Grande and *Phragmites australis*. These macrophytes have been extensively studied in South Africa (Talbot and Bate 1987; Talbot et al. 1990; Adams et al. 1992; Adams and Bate 1994a, 1994b, 1994c; Reed 1994), and in other parts of the world (table of references in Adams 1994, table 1, p. 10; McRoy 1972).

Phragmites is a rhizomatous grass species that grows in wet habitats (Hara et al. 1993). *Phragmites* reeds dominate freshwater wetlands in temperate regions throughout the world, including South Africa (Adams 1994). *Phragmites* forms dense beds in the upper reaches of South African estuaries that have a gradient of decreasing salinity up the length of the estuary (Adams et al. 1992).

Ruppia is a dominant and key submerged macrophyte in many South African estuaries. *Ruppia* is common in estuaries that are only seasonally open or in the upper, calm, brackish reaches of estuaries. Although *Ruppia* is not found in tidal environments in South Africa, it does occur intertidally in the sheltered gulfs and bays of South Australia and coastal bays and estuaries in North America (Verhoeven 1979; Shepherd and Robertson 1989).

Zostera is also a submerged macrophyte, but unlike *Ruppia*, it is adapted to tidal habitats and survives in permanently open estuaries in South Africa.

Zostera, *Ruppia* and *Phragmites* were selected because they survive under marine, brackish and freshwater conditions respectively. They are also representative of macrophytes that survive when completely submerged (*Ruppia*), periodically exposed, but mostly submerged (*Zostera*), and emergent (*Phragmites*). Therefore they respond differently to the consequences of reduced freshwater inflow, such as changes in water level fluctuations, and changes in the salinity gradient. For example, impoundments lead to an increase in *Zostera* aerial cover due to encroaching salinity up the estuary (Adams and Talbot 1992). This may lead to the displacement of the brackish and freshwater communities further up the estuary. On the other hand, an increase in freshwater supply, (for example, a flood), will favour *Phragmites* growth

and lead to the die back of submerged macrophyte communities such as *Zostera* and *Ruppia*. (*Zostera* and *Ruppia* do not have well-developed mechanisms of flood tolerance).

4.3 The Mechanism of Spread Modelled

The dominant means of reproduction by *Zostera*, *Ruppia* and *Phragmites* is vegetative. Flowers sometimes appear, but they are rare. As discussed in section 3.3 of chapter 3, area expansion of the macrophytes is mainly due to the extension of horizontal runners (Talbot and Bate 1987). So the purpose of the model is to describe the dynamics of existing macrophyte beds.

4.4 Formulation of the Model

4.4.1 Biomass Components

A number of models of aquatic macrophytes divide biomass into above- and below-ground compartments (Park et al. 1975; Titus et al. 1975; Verhagen and Nieunhuis 1983; Bach 1993). In this way, the different responses of roots and leaves may be modelled. For example, a flood may scour the leaves but the below-ground compartments may remain rooted. We choose to extend the cellular automata model of *Zostera* to include separate biomass components.

Zostera, *Ruppia* and *Phragmites* have two axes of growth, namely horizontal or vegetative growth, and vertical or leaf and root growth. The extensive rhizome system consists of a network of more or less horizontal branches or runners, from which vertical rhizomes or roots grow. The roots give rise to aerial shoots (in the case of *Phragmites*) or stems (in the case of *Zostera* and *Ruppia*). In the case of *Phragmites* the above-ground biomass consists of groups of closely connected shoots connected to other groups via runners. In the case of *Zostera* and *Ruppia* above-ground biomass consists of stems bearing long, flexible leaves. Therefore the model consists of three biomass compartments, namely runner density, and above- and below-ground biomass density.

4.4.2 Model Equations

The model is derived for a single macrophyte. Interactions among plants are then incorporated.

Let

L(i, j, t) represent above-ground biomass density (biomass per unit area) in the (i, j) th cell at time t ($g.m^{-2}$),

R(i, j, t) represent below-ground biomass in the (i, j) th cell at time t ($g.m^{-2}$), and

U(i, j, t) represent the calibrated runner or horizontal rhizome density on a scale between zero and one in the (i, j) th cell at time t (-).

The calibration technique for runner density is discussed in section 4.4.4. The model is derived in Wortmann et al. (1998). As in chapter 3, the model is written in Turbo Pascal for Dos version 7.

Runner Equations

The model for runner growth is based on the CA model of *Zostera.* The rate of change in runner density in the (i, j) th cell is therefore given by

$$rate\ of\ change\ of\ U(i,j,t) = \frac{dU(i,j,t)}{dt} = growth\ rate - mortality\ rate \qquad (4.1)$$

$$growth\ rate = growth\ within\ cell + \sum_{n_{ij}} \frac{1}{6}.expansion_{n_{ij}}.g_3[U(i,j,t)] \qquad (4.2)$$

$$growth\ within\ cell = a.gm_{i,j}.U(i,j,t).g_1[U(i,j,t)][1 - g_2(U(i,j,t))] \qquad (4.3)$$

$$expansion_{k,l} = a.gm_{k,l}.U(k,l,t).g_1[U(k,l,t)].g_2[U(k,l,t)] \qquad (4.4)$$

$$mortality\ rate\ = \frac{b}{4}.U(i,j,t).[g_4(U[i,j,t]) + sdm(sal_{ij}) + wldm(wl_{ij}) + ddm(depth_{ij})] \quad (4.5)$$

where

n_{ij} is the neighbour set of the (i,j) th cell and is given by the cells {(i-1,j-1), (i-1,j+1), (i+1, j-1), (i+1, j+1), (i-2,j), (i+2, j)},

a is the maximum specific growth rate ($g.g^{-1}.day^{-1}$),

b is the maximum specific mortality rate ($g.g^{-1}.day^{-1}$),

sdm is the salinity mortality multiplier (0-1),

wldm is the water level mortality multiplier (0-1),

ddm is the depth mortality multiplier (0-1),

sal_{ij} is the salinity of the (i,j) th cell at time t (ppt.),

wl_{ij} is the water level fluctuation of the (i,j) th cell at time t (metres),

$depth_{ij}$ is the depth fluctuation below the water surface of the (i,j) th cell at time t (metres),

g_1, g_2, g_3, g_4 are density-dependent functions defined in chapter 3 section 3.7.4 (0-1), and

gm_{ij} is the growth multiplier for the (i, j) th cell that depends on the physical conditions in the given cell (0-1), and is given by

$$gm_{ij} = sgm(sal_{ij}).wlgm(wl_{ij}).dgm(depth_{ij}) \quad (4.6)$$

where

sgm is the salinity growth multiplier (0-1),

wlgm is the water level growth multiplier (0-1), and

dgm is the depth growth multiplier (0-1).

As in the cellular automata model of *Zostera* in chapter 3, the maximum specific mortality rate in (4.5) is the mortality rate under the worst possible physical conditions for growth and under

high density. To show how a combination of density and physical conditions modify the maximum specific growth rate, one fourth of the maximum specific growth rate is multiplied by sum of the four mortality multipliers. The use of the product of the multipliers would mean that if there is no mortality due to one factor, for example if the salinity mortality multiplier is equal to zero, then no mortality will be incorporated in the model because the product of the mortality multipliers would be equal to zero. The reason the maximum specific mortality rate in (4.5) is divided by four is so that under the worst case scenario, when all four mortality multipliers are one, mortality occurs at the maximum specific mortality rate.

Model Equations for root growth

The rate of change in root biomass is written as

$$\frac{dR(i,j,t)}{dt} = growth\ rate - mortality\ rate \tag{4.7}$$

The growth rate of the roots depends not only on the root biomass density, but also on the horizontal rhizome density. This is because new roots grow from the rhizome system. Thus in the equations for root growth, the biomass that is responsible for root growth is given by the sum of the root biomass density and the runner biomass density. Recall that the runner system was modelled using a calibrated runner density on a scale between zero and one. Therefore in order to convert the calibrated runner density into biomass density, we multiply the calibrated runner density by K_{max}, which is the root carrying capacity. Thus if the calibrated runner density is zero, then there will be no root growth from the rhizome system, and if the calibrated runner density is one, then the equivalent biomass density responsible for root growth from the rhizome system is equal to the root carrying capacity. Thus, total biomass responsible for root growth is written as:

$$biomass = \min[\, R(i,j,t) + U(i,j,t).K_{max},\ K_{max}] \tag{4.8}$$

where K_{max} is the root carrying capacity and U(i, j, t) is the calibrated runner density. We choose the minimum of the total biomass responsible for root growth and the root carrying capacity to avoid the situation where the total biomass responsible for growth is greater than the root carrying capacity. Therefore, the root growth may be written as

$$growth\ rate = sgr.gm_{i,j}.g_3\left(\frac{R(i,j,t)}{K_{max}}\right).biomass \tag{4.9}$$

where

sgr is the maximum specific growth rate ($g.g^{-1}.day^{-1}$),

K_{max} is the root carrying capacity ($g.m^{-2}$), and

biomass is the total biomass responsible for root growth ($g.m^{-2}$) and is defined by equation (4.8).

Mortality of roots depends on a combination of density effects and environmental conditions. That is,

$$mortality\ rate = \tag{4.10}$$

$$\frac{sdr}{4}.R(i,j,t).\left[g_4\left(\frac{R(i,j,t)}{K_{max}}\right) + sdm(sal_{ij}) + wldm(wl_{ij}) + ddm(depth_{ij})\right]$$

where

sdr is the maximum specific mortality rate ($g.g^{-1}.day^{-1}$).

Model Equations for above-ground biomass growth

Vertical growth is partitioned into two components, root growth and above-ground growth, so that if there are strong current velocities, e.g. during a flood, the rhizome system remains rooted, the above-ground portion is scoured, and the subsequent regrowth of the shoots or

stems after the flood may be monitored. The root biomass determines the above-ground biomass. If there are no roots, then the growth of stems or shoots is impossible. An extensive root system can support a large above-ground portion. We assume that the percentage above-ground to total (root+above-ground) mass is 50%. For example, in the Kromme estuary, South Africa, field recordings for the average percentage above-ground to total plant mass of *Zostera* biomass for 1989 was 49.9% in the lower reaches, 51.7% in the middle reaches, and 40.7% in the upper reaches. The percentage of above-ground to total plant mass of *Zostera* biomass in the Swartkops estuary varied from 49.5% in winter (1981) to 56.14% in summer (1981), Talbot and Bate (1987). Talbot and Bate (1987) argue that this comparatively low leaf mass in winter could have been a result of extensive leaf loss during the floods of March 1981. Alternatively, they argue that it could show an increased transfer of mass to the rhizomes during winter. This winter-summer difference is low in comparison with the excessive losses reported in more temperate latitudes due to exfoliation and winter leaf necrosis (Iverson and Bittaker 1986). So the growth rate of above-ground biomass is given by

$$growth\ rate = sgr.gm_{i,j}.L(i,j,t).g_3[\frac{L(i,j,t)}{R(i,j,t)}] \tag{4.11}$$

The above-ground carrying capacity in the (i, j) th cell is equal to the root biomass density in the (i, j) th cell.

Mortality of above-ground biomass is written as

$$mortality\ rate = \tag{4.12}$$

$$\frac{sdr}{5}.L(i,j,t).[g_4(\frac{L(i,j,t)}{R(i,j,t)}) + sdm(sal_{ij}) + wldm(wl_{ij}) + ddm(depth_{ij}) + scm(velocity_{ij})]$$

where

scm is the scour mortality multiplier in the (i, j) th cell that is a function of the freshwater inflow rate (0-1), and

$velocity_{ij}$ is the velocity of the (i, j) th cell at time t ($m.s^{-1}$).

Note that the equations for mortality of runners (4.5), roots (4.10) and above-ground biomass (4.12) are the same, but the carrying capacity for above-ground biomass is different and the scour multiplier is included in the equations for above-ground biomass.

The carrying capacity for root biomass represents some limiting factor for growth (e.g. nutrients, soil substrate, space, turbidity). We assume that nothing is limiting growth apart from the physical factors in the model related to freshwater inflow. Thus the carrying capacity is assigned its maximum value, approximately 300 $g.m^{-2}$. The inclusion of additional species is modelled by assuming that the limiting factor for growth affects species according to the total biomass of all species present. The model equations are therefore modified as follows:

(a) runner equations: the functions g_1 and g_2 in (4.3) and (4.4) and the function g_3 in (4.2) and g_4 in (4.5) depend on total runner density in the (i, j) th cell (total runner density = *Zostera* + *Ruppia* + *Phragmites* runner density);

(b) root equations: the function g_3 in (4.9) and the function g_4 in (4.10) depend on total root biomass in the (i, j) th cell (total root biomass = *Zostera* + *Ruppia* + *Phragmites* root biomass), and

(c) above-ground equations: the function g_3 in (4.11) and the function g_4 in (4.12) depend on total above-ground biomass in the (i, j) th cell (total above-ground biomass = *Zostera* + *Ruppia* + *Phragmites* above-ground biomass).

Seagrasses are often described as temporally highly unstable. Most of the reports are from temperate areas where cold winters cause partial to complete disappearance of these plants (Nienhuis and de Bree 1980; Orth and Moore 1984, 1986). In warmer latitudes seasonality is less readily observed (Hanekom 1982). It is debated whether the reported increase in standing stock of estuarine macrophytes (Talbot and Bate 1987) during summer months infers

seasonality or is simply a recovery after flood damage. Support for the latter comes from Hanekom (1982) who, working in the Kromme estuary, showed large biomass fluctuations in *Zostera* linked to episodic floods rather than to seasons. So no seasonality is included in the model equations for *Zostera* and *Ruppia*.

During the winter months (May to July), *Phragmites* shoots die back. Most of the food reserves are transferred to the rhizomes, the shoots disintegrate and add to drifting organic detritus (Hara et al. 1993). This is incorporated by setting growth of above-ground *Phragmites* biomass during the winter months equal to zero.

4.4.3 Physical Multipliers

The derivation of the multipliers for *Zostera* and the graphs of these multipliers appear in chapter 3, section 3.7.5.

Effects of Salinity on the Growth and Mortality of Ruppia and Phragmites

The salinity growth and mortality multiplier for *Ruppia* is discussed in chapter 2, section 2.2.4.

Surveys of several Cape estuaries have shown that *Phragmites australis* is dominant in the upper reaches of estuaries where salinity is less than 30 ppt. These plants generally form dense beds in the upper lower salinity reaches of estuaries. Benfield (1984) reported 100% mortality of *Phragmites* after three months at 30 ppt. Laboratory studies have shown that the optimal salinity range for *Phragmites* is less than 15 ppt. Adams (1994) showed that the weekly stem elongation was significantly reduced under a treatment of 20 ppt. compared with a treatment of zero ppt. (figure 4.3a). After four weeks of the saline treatment, there was almost no weekly stem elongation, whereas the corresponding weekly elongation for the fresh treatment was 3.8 cm per week. In addition the percentage dead leaves of the total leaves of the plants was 72% for the 20 ppt. treatment after four weeks, and 30% after four weeks of the zero ppt. treatment (figure 4.3b).

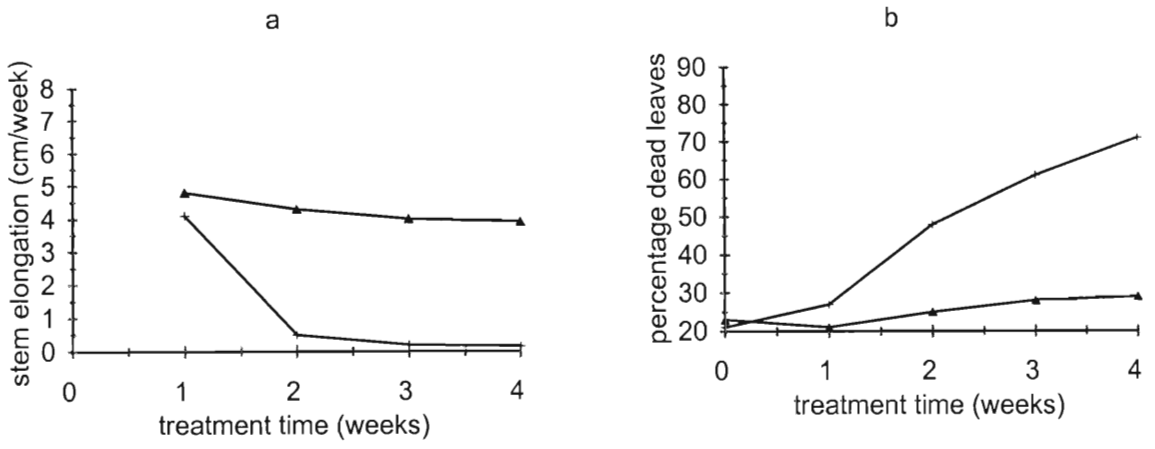

Figure 4.3. The effect of a fresh (▲) and saline (+), (20 ppt.) treatment for various treatment times on (a) *Phragmites australis* weekly stem elongation and (b) the percentage dead leaves compared with the total number of leaves times. (Adams 1994, pp. 106).

The graph in figure 4.3a shows that if *Phragmites* is exposed to a salinity of 20 ppt. for two or more weeks, then there is very little stem elongation. So the salinity growth multiplier is close to zero for a salinity of 20 ppt. (figure 4.4). Similarly the salinity mortality multiplier for a salinity of 20 ppt. is greater than 0.5 to show that mortality is high when *Phragmites* is exposed to salinities of 20 ppt. (figure 4.4). Figure 4.3b shows that if *Phragmites* is exposed to 20 ppt. for three or more weeks then the percentage dead leaves out of total leaves is more than 50%. *Phragmites* grows best under freshwater conditions. Therefore, the salinity growth multiplier is equal to or close to one for salinities less than 10 ppt., and the salinity mortality multiplier is equal to or close to zero for salinities less than 10 ppt.

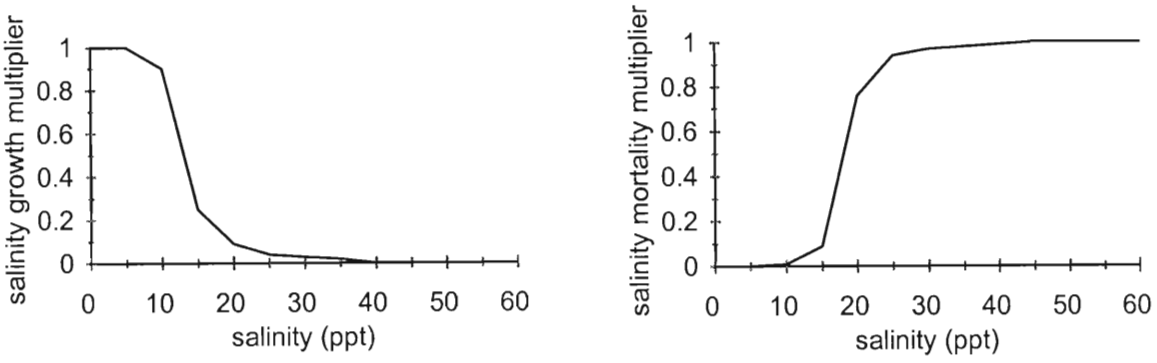

Figure 4.4. The salinity growth and mortality multipliers for *Phragmites*.

Effects of Water Current Speed on Growth and Mortality of Ruppia and Phragmites

The scour multiplier for *Ruppia* is discussed in chapter 2, section 2.2.4.

A scour multiplier for *Phragmites* is excluded. This is justified by evidence reported by Armstrong and Armstrong (1990, 1991) that *Phragmites australis* has well-developed mechanisms of flood tolerance.

Effects of Water Level Fluctuations on Growth and Mortality of Ruppia and Phragmites

Ruppia cannot survive periods of exposure (Adams and Bate 1994a). This is one reason *Ruppia* does not survive in the mouth of permanently open estuaries. Adams and Bate (1994a) found that a daily exposure time of five hours was lethal for *Ruppia*. The average number of leaves left on *Ruppia* plants exposed for five hours daily were lower than on control plants (the control plants are always submerged, figure 4.5). By the fourth week Adams and Bate (1994a) reported that all the leaves were brown. Based on this result, the water level growth multiplier is equal to one for a daily exposure time of two hours or less, after which it decreases exponentially. Similarly the water level mortality multiplier is equal to zero for a daily exposure time of two hours or less, after which it increases exponentially. After five hours of exposure, the water level growth multiplier is close to zero and the water level mortality multiplier is close to one. Figure 4.6 shows the water level multipliers for *Ruppia*.

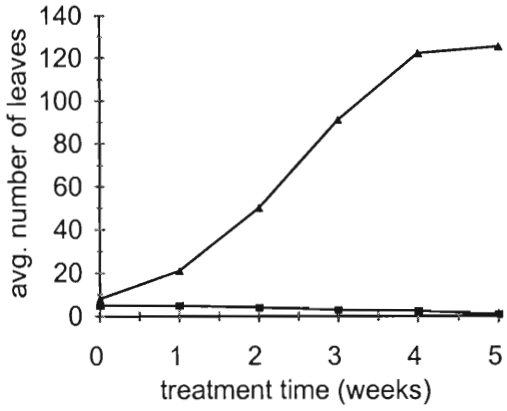

Figure 4.5. Change in the average number of leaves for *Ruppia cirrhosa* exposed for five hours daily for various treatment times. In the graph the series marked with a ▲ represents the change in average number of leaves when *Ruppia* is always submerged. The series marked with a ■ represents the scenario where *Ruppia* is exposed for five hours daily.

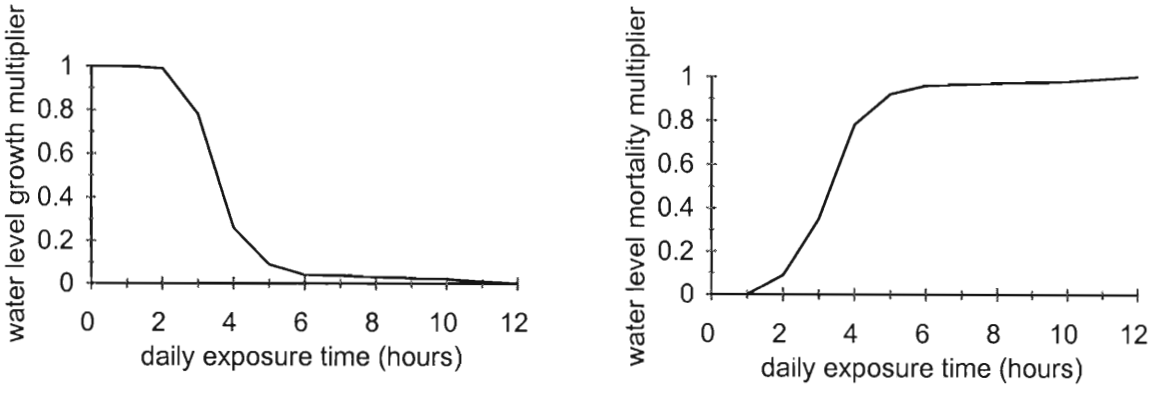

Figure 4.6. The water level growth and mortality multipliers for *Ruppia cirrhosa*.

Following the depth multiplier of *Zostera*, the depth growth and mortality multiplier for *Ruppia* depends linearly on the length of time *Ruppia* is submerged below or up to a depth of 2 m (figure 4.7). The critical depth for *Zostera* is 2.5 m. *Ruppia* is reported to survive in shallower water than *Zostera*.

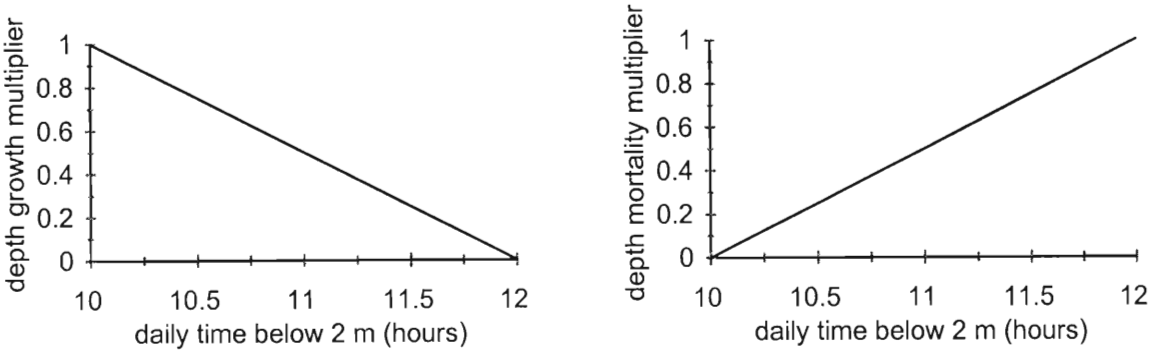

Figure 4.7. The depth growth and mortality multipliers for *Ruppia cirrhosa*.

In the model simulations water levels are on average less than 2 m. Therefore the water level growth multiplier and depth growth multiplier for *Phragmites* are set to their maximum values, namely one, and the water level mortality multiplier and depth mortality multiplier for *Phragmites* are set to their minimum values, namely zero.

4.4.4 Model Calibration and Parameter Values

Observations show that the macrophytes can achieve a spread rate of up to 12 m per year. That is, the maximum spread rate of the macrophytes is 12 m per year. So the purpose of the calibration is to vary the relevant model parameters under ideal conditions until a spread rate of 12 m per year is achieved. In the model the outward spread rate is determined by runner dynamics, so the parameters calibrated are a and b in the runner equations (4.3), (4.4) and (4.5). (The specific growth and mortality rates of above- and below ground biomass are known). The calibration technique is outlined in chapter 5, section 5.1.3.1. When the growth and mortality multipliers equal one and zero respectively, a value of a= 0.14 day^{-1} yields a maximum spread rate of 12 m per year. Under conditions that are not optimal for growth, (i.e. the growth multiplier is less than one, the mortality multiplier is greater than zero), then assigning b=a will yield a spread rate of less than 12 m per year. For this calibration the length of a cell side is 0.4 m and the width of a cell is approximately 0.73 m.

Following is a list of the model parameters: (z, r, p denotes *Zostera*, *Ruppia* and *Phragmites* respectively), unless otherwise stated, parameters taken from Adams, 1994, pers. comm.

$sgr_z = 0.005\ g.g^{-1}.day^{-1}$, $sgr_r = 0.005\ g.g^{-1}.day^{-1}$, $sgr_p = 0.05\ g.g^{-1}.day^{-1}$,
$sdr_z = 0.005\ g.g^{-1}.day^{-1}$, $sdr_r = 0.005\ g.g^{-1}.day^{-1}$, $sdr_p = 0.05\ g.g^{-1}.day^{-1}$,
$a = 0.14\ day^{-1}$ (from section 5.1.3.1), $b = 0.14\ day^{-1}$ (from section 5.1.3.1),
length of cell side = 0.4 m (from calibration in ssection 5.1.3.1) and
$K_{max} = 300\ g.m^{-2}$, although this will vary for different systems (Adams and Talbot 1992).

A grid of 160 (length along the estuary) x 6 (depth) cells is used. This grid comprises a length of approximately 90 m, a length that is large enough to adequately show the competitive dynamics between the macrophytes along the estuary. These dimensions and grid sizes were used for both case studies.

4.5 Predicting Estuary Hydrodynamics

As discussed in chapter 3, section 3.8, physical data for freshwater inflow scenarios is provided by two models, the Mike 11 model and the Estuarine Systems Model (Slinger 1994). The output data supplied to the macrophyte model comprises daily minimum and maximum water levels, average salinity and maximum current velocity.

For the Kromme estuary, the Estuarine Systems Model only provides information for the middle reaches. The Mike 11 model can be used to obtain physical data at other locations, namely stations (K1, K2, K3, and K5). We assume that the physical data varies linearly between the various stations.

For the Great Brak estuary, the Estuarine Systems Model only provides information for the middle reaches. The Mike 11 model can be used to obtain physical data at other locations, namely stations (R2, R4, R6, R8, and R8). In figure 4.1 there are two points labelled R8. We assume that the physical data varies linearly between the various stations.

For both case studies we assume that there is no feedback between the hydrodynamics and the macrophyte density. Scoured plants will therefore not in turn reduce the hydraulic resistance

and consequently reduce the flow rates. The Kromme estuary is a permanently open estuary and therefore the scoured biomass will be washed to sea and not affect flow rates. The Great Brak estuary is periodically closed, with the longest period of closure being 50% to 70% of the year, and thus scoured biomass will always be transported towards the mouth and washed out to sea when the mouth is open.

4.6 Validation of the Mixed Community Spatial Model

Aerial photographs of the Kromme estuary were used to validate model predictions. Aerial photographs are useful in establishing the presence / absence of macrophyte beds in the estuary. However, estimation of bed size or biomass calculated from aerial photographs will have a large standard error due to temporal variability of cover in response to flooding and sedimentation (Talbot et al. 1990).

Adams and Talbot (1992) used aerial photographs of the Kromme estuary dating back to 1942 to determine the long-term changes in the distribution and area of *Zostera*. The photographs showed that in 1992 there was a linear increase in *Zostera* biomass from the mouth (155.1 $g.m^{-2}$ ± 72.8 SD) to the middle reaches (233.1 $g.m^{-2}$ ± 30.4 SD) and from the middle reaches to the upper reaches (302.8 $g.m^{-2}$ ± 53.1 SD) of the estuary (SD means standard deviation). The strong tidal currents near the mouth scour *Zostera* stems, hence the increase in biomass away from the mouth. The model predicts that under present runoff conditions *Zostera* attains a biomass of 220 $g.m^{-2}$ (lower reaches) and 260 $g.m^{-2}$ (middle and upper reaches), (see section 4.7.6). These results are within the field range recorded by Adams and Talbot (1992).

The aerial photographs show that since the construction of two major dams in the catchment of the Kromme estuary the *Zostera* population has increased and encroached into the upper reaches. The aerial photographs show that brackish submerged macrophyte species were absent in the Kromme estuary in 1992. Model results showed that *Ruppia* was absent under present runoff conditions and that the estuary was dominated by *Zostera* (see section 4.7.6). Aerial photographs showed that *Phragmites* occurs at the confluence of small streams and seeps in the Kromme estuary (Adams et al. 1992). Such outcrops of *Phragmites* are characteristic of freshwater seepage into marine lagoons (Christie 1981). Adams (1994) stated that *Phragmites* grows either in the upper reaches of estuaries that have a salinity gradient or

at the confluence of streams where salinities are low. Physical data on runoff below impoundments and groundwater seepage is not provided by the hydrodynamic models. Therefore the macrophyte model showed that *Phragmites* did not survive in the Kromme estuary under present runoff conditions (see section 4.7.6).

Adams et al. (1992) showed that a continual flow of freshwater into estuaries created a salinity gradient along which different macrophyte communities were distributed. In estuaries with a salinity gradient, e.g. the Kromme estuary or the Great Brak estuary under natural runoff conditions, Adams and Talbot (1992) stated that *Zostera* is associated with the marine end of estuaries, and *Phragmites* survives in the upper reaches. The models predicted that this zonation was maintained under natural runoff conditions in the Kromme estuary and the Great Brak estuary, with *Ruppia* occurring between *Zostera* and *Phragmites*. A study of the Swartkops estuary also shows that *Zostera* survives near the mouth of estuaries with a salinity gradient. Aerial photographs from 1949-1978 of the Swartkops estuary, South Africa, showed that *Zostera* beds were restricted largely to the lower reaches in 1981 (Talbot and Bate 1987). The mouth of the Swartkops estuary is perennial and strongly influenced by the sea, with salinity close to that of sea water (34 ppt. to 36 ppt., Hilmer 1984). This influence diminishes up the estuary until the salinity range in the upper reaches becomes 14 ppt. to 22 ppt. The macrophyte model predicted that when there is a salinity gradient in either the Kromme or the Great Brak estuary, then *Zostera* survives in the lower reaches only. The model also predicts that the switch between *Zostera* and *Ruppia* along the length of the estuary is sudden in most cases (within 50 m). Aerial photographs also show this switch in habitat availability occurs suddenly in most cases (Adams and Talbot 1992; Adams et al. 1992).

4.7 Results for the Kromme Estuary

4.7.1 Introduction to the Freshwater Runoff Scenarios

The inflow scenarios selected for the Kromme estuary range from the natural situation to the present regime of 2% mean annual runoff. Under the natural regime there is unimpeded flow into the estuary. This means that there is perennial river flow with periodic river flooding and natural scouring of the mouth (Whitfield and Wooldridge 1994). The natural runoff scenario is therefore selected to determine the effect of natural freshwater supply on the emergent and

submerged plants selected for the study. Slinger (1996, pp. 20-36, pp. 48-57) gives the physical data for the scenarios.

The intermediate runoff scenarios range from a runoff of 40% mean annual runoff, to the present situation of 2% mean annual runoff. The reason for choosing these scenarios is so that the effects of damming and extraction of freshwater from the catchment may be examined on the macrophyte communities. As impoundments increase, river flow becomes intermittent with less frequent river flooding and reduced scouring efficiency (Whitfield and Wooldridge 1994). However, the mouth of the estuary remains permanently open under these scenarios: The volume of water entering and leaving the estuary on ebb and flood tides is of sufficient magnitude to maintain the mouth in a permanently open state, provided the volumes of sediment and the rates of delivery to the estuary are comparable with present day quantities. The intermediate runoff scenarios are therefore selected to determine the macrophyte response to different volumes of impoundments in the catchment of the Kromme estuary. Apart from the natural run-off scenario, all releases are assumed to occur at the maximum release rate, which is between 20 and 22 $m^3.s^{-1}$ (Slinger, 1996).

The following method is adopted in analysing the runoff scenarios:

(1) The equilibrium states and their associated stability are determined. As in chapter 2, an equilibrium state is defined as the plant biomass around which the system oscillates periodically. An equilibrium state is said to be stable if, when the system is disturbed from the state, for example by increasing or decreasing plant biomass density to 299 $g.m^{-2}$ and 1 $g.m^{-2}$ respectively, the system returns to the state for every disturbance in the vicinity of the state. If a disturbance from the state results in the system moving away from the state, then the equilibrium state is unstable. Phase plane diagrams are used to give a picture of the overall behaviour from some initial state. (See Doucet and Sloep 1992, p. 104-111 for a discussion on phase portraits and trajectories).

(2) If there is a switch along the estuary from a marine dominated habitat to a brackish dominated habit, then the spatial distribution of the associated macrophytes at this boundary is determined.

(3) The effect of perturbations is investigated by considering disturbance scenarios. Since the most likely perturbation to an annual water allocation policy in the Eastern Cape region is the occurrence of a drought, the effects of perturbation scenarios of one and three year periods of no freshwater inflow to the Kromme estuary are evaluated. The purpose of this analysis is to determine whether the imposition of a drought can switch the estuary from one equilibrium state to another equilibrium state, and to determine how the spatial distribution of the macrophytes changes under drought conditions.

Equilibrium states are determined for the upper, middle and lower reaches of the Kromme estuary. The upper reaches of the Kromme estuary are considered to extend from the head of the tidal influence (14 km upstream from the mouth) to the confluence with the Geelhoutboom River, the middle reaches to cross section 4, while the shallow, lower reaches lie downstream from this point (figure 4.1, p. 84).

In the tables in the following sections, Z, R and P represent *Zostera*, *Ruppia* and *Phragmites* respectively.

4.7.2 Natural Runoff Scenario: MAR = 120 x 10^6 $m^3.yr^{-1}$

The natural runoff scenario refers to runoff before any modification through the construction of dams or abstraction for irrigation, with a mean annual runoff of 120 x 10^6 $m^3.yr^{-1}$. The hydrodynamic models show that under natural runoff conditions the minimum difference between the head to mouth salinity is 20 ppt. (Slinger 1995). Thus all three types of macrophyte (i.e. marine, brackish and freshwater) are likely to be present in the Kromme estuary under natural runoff conditions.

4.7.2.1 Equilibrium States

The equilibrium states in the Kromme estuary under the natural runoff scenario are shown in table 4.1. These states correspond to equilibrium conditions in the absence of the other plants. The states are stable in the absence of the other plants. In the table the maximum and minimum periodic biomass density is shown (the equilibrium biomass density fluctuates periodically over a period of one year).

Table 4.1. The equilibrium states in the Kromme estuary for natural runoff conditions for the single plant communities. The maximum and minimum periodic biomass density is shown. All the states are stable in the absence of the other plants.

Location in estuary	State	Macrophyte biomass density ($g.m^{-2}$)
Lower reaches	*Zostera*	$Z \in (245, 279)$
Middle reaches	*Zostera*	$Z \in (60, 63)$
	Ruppia	$R \in (88, 102)$
	Phragmites	$P \in (153, 247)$
Upper reaches	*Ruppia*	$R \in (104, 108)$
	Phragmites	$P \in (154, 258)$

Zostera is the only macrophyte that survives in the lower reaches. This state is stable which means that *Zostera* survives for any initial *Zostera* biomass density in the lower reaches.

To analyse the effect of initial conditions on the outcome in the middle reaches, the phase plane diagram of the equilibrium states is given in figure 4.8. Figure 4.8a shows the outcome for *Zostera* and *Ruppia*: *Zostera* will only survive in the middle reaches if there is no *Ruppia*, otherwise *Ruppia* will be the dominant submerged macrophyte in the middle reaches and *Zostera* will die back. Figure 4.8b shows the outcome between *Ruppia* and *Phragmites* in the middle reaches. Both *Ruppia* and *Phragmites* can survive in the middle reaches at their equilibrium biomass densities. Any initial condition with both *Ruppia* and *Phragmites* present will result in both *Ruppia* and *Phragmites* surviving.

The effect of initial conditions on the behaviour of *Ruppia* and *Phragmites* in the upper reaches is the same as that for the middle reaches and is therefore not shown in a phase plane diagram.

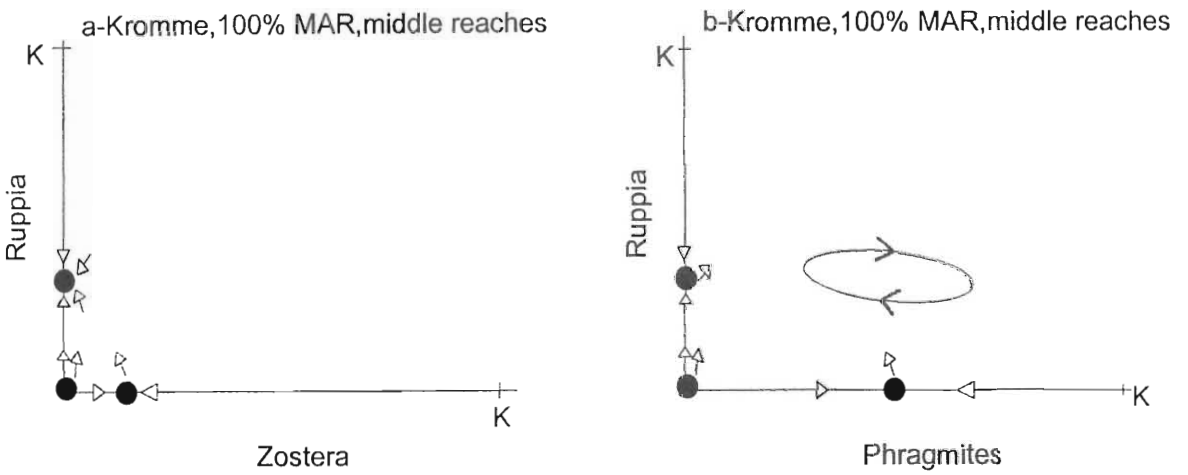

Figure 4.8. Stability of the equilibrium states in the middle reaches of the Kromme estuary under natural runoff conditions. (a) shows the outcome between *Zostera* and *Ruppia*: *Zostera* will only survive if *Ruppia* biomass density is zero, (b) shows the outcome between *Ruppia* and *Phragmites*: For any initial condition, provided *Phragmites* and *Ruppia* are both present, both macrophytes will survive. In both figures the origin is unstable. K is the maximum carrying capacity which is 300 $g.m^{-2}$.

4.7.2.2 Spatial Distribution

If the initial conditions are that *Zostera*, *Ruppia* and *Phragmites* are present throughout the estuary, then model results indicate that imposing the natural runoff scenario on the system will result in the middle and upper reaches being dominated by *Ruppia* and *Phragmites* (figure 4.8), and the lower reaches being dominated by *Zostera*. Results indicate that the switch in submerged habitats from *Zostera* to *Ruppia* then occurs approximately 6 km up from the mouth of the estuary. The graph in figure 4.9 shows the biomass distribution of *Zostera* and *Ruppia* along this boundary. The reason *Ruppia* does not survive lower down the estuary is because of high water current speeds near the mouth. A comparison of the salinity and scour multipliers for *Zostera* and *Ruppia* along the natural boundary (table 4.2) shows that *Ruppia*

has a higher salinity growth multiplier than *Zostera*. So based on the salinity, it could survive lower down the estuary. However, *Ruppia* has a higher scour multiplier than *Zostera* and therefore does not survive near the mouth of the Kromme estuary.

Table 4.2 Average salinity growth and mortality multipliers and scour multipliers of *Zostera* and *Ruppia* at the end points of their natural boundary in figure 4.9.

Macrophyte	Salinity		Velocity
	growth multiplier	mortality multiplier	scour multiplier
Zostera	0.4459 to 0.4238	0.3979 to 0.41803	0.2057 to 0.1845
Ruppia	0.9614 to 0.9603	0.06868 to 0.07343	0.8824 and 0.8647

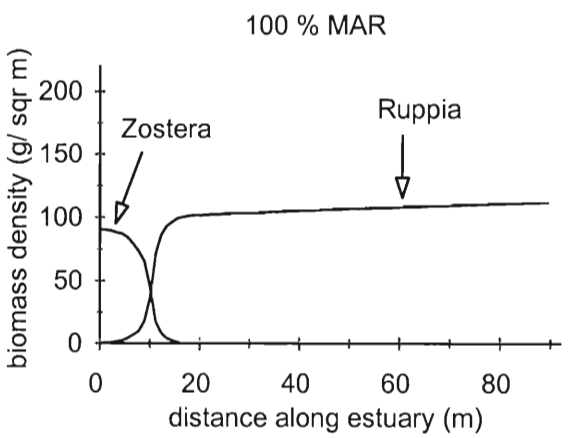

Figure 4.9. The switch in submerged habitats from *Zostera* to *Ruppia* in the Kromme estuary under natural runoff conditions occurs approximately 6 km up from the mouth. The graph shows the distribution of *Zostera* and *Ruppia* along this boundary.

4.7.2.3 The Effect of One and Three Year Periods of No freshwater Inflow on the Equilibrium States

The disturbance scenarios were applied to the equilibrium states. The results, with the phase-plane analysis, were then used to show whether a change in states can occur by imposing a drought on the system (table 4.3 and table 4.4). In table 4.3 for the middle reaches for the state R only or R &P, the initial and final *Phragmites* biomass density is the same as that in the line

below, which corresponds to the state P only or R & P. A similar definition holds for the upper reaches in table 4.3, and for similar situations in table 4.4 and similar tables that follow.

Table 4.3. The response of the equilibrium states of the Kromme estuary under natural runoff conditions to a one year period of no freshwater inflow. The biomass density after the disturbance is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state.

Location	State	Initial ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
Lower	Z only	$Z \in (245,279)$	Z=216	60 days	No
Middle	Z only	$Z \in (60,63)$	Z=230	200 days	No
	R only or R & P	$R \in (88,102)$	R=75	300 days	No
	P only or R & P	$P \in (153,247)$	P=64	1 year	No
Upper	P only or R & P	$P \in (154,258)$	P=65	1 year	No
	R only or R & P	$R \in (104,108)$	R=111	60 days	No

Table 4.4. The response of the equilibrium states of the Kromme estuary under natural runoff conditions to a three year period of no freshwater inflow. The biomass density after the disturbance is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state. If a state is omitted, it is because the three year drought has no further effect than the one year drought.

Location	State	Initial ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
Middle	R only or R & P	$R \in (88,102)$	R=66	330 days	No
	P only or R & P	$P \in (153,247)$	P=56	1 year	No
Upper	P only or R & P	$P \in (154,258)$	P=58	1 year 1 month	No

Tables 4.3 and 4.4 show that one and three year periods of no freshwater inflow do not cause a shift in any of the equilibrium states. That is, after the disturbance recovery to the previous state is possible. In addition, the results show that a three year drought is not worse than a one year drought for: *Zostera* in the lower and middle reaches, and *Ruppia* in the upper reaches. That is, if a drought occurs, during the first year of the drought, *Zostera* in the lower and middle reaches, and *Ruppia* in the upper reaches are affected, but thereafter, there is no further change in *Zostera* and *Ruppia*. Of all the macrophytes, *Phragmites* is affected by the drought the most, with a 68% and 72% reduction in biomass density after one and three year periods of no freshwater inflow respectively in the middle reaches. The corresponding reduction in the upper reaches is 50% and 55%. So the critical duration for drought for *Phragmites* is one year, after which *Phragmites* biomass density does not decrease as rapidly as during the first drought year.

4.7.2.4 The Effect of One and Three Year Periods of No freshwater Inflow on *Zostera* Encroachment

The cellular automata model of *Zostera* developed in chapter 3 indicated that reduced freshwater inflow resulted in a *Zostera* encroachment rate of 20 m per year up the estuary. For the Kromme estuary, we do not know that *Zostera* encroachment will necessarily occur during a drought (no freshwater inflow) if *Ruppia* is present further up the estuary. Results from the previous section show that *Ruppia* is able to survive drought periods of three years. Therefore *Ruppia* may act as a barrier and prevent *Zostera* from colonising the upper reaches under drought conditions. On the other hand, *Zostera* may displace *Ruppia* during drought conditions.

Model results show that *Zostera* displaces *Ruppia* and encroaches up the estuary during drought conditions. So *Zostera* will become the dominant macrophyte in the Kromme estuary when a drought occurs for prolonged periods during natural runoff conditions. The graphs in figure 4.10 show the effect of one and three year periods of no freshwater inflow on the natural boundary between *Zostera* and *Ruppia* in figure 4.9 (p. 106). Table 4.5 presents an analysis of the effect of these disturbances on biomass density values and distance encroached along this border. In the first year *Zostera* only encroaches 5 m up the estuary. In the following two years it encroaches a further 24 m. This is because in the first drought year competition with

Ruppia is high, whereas in the following two years *Zostera* has displaced a large portion of *Ruppia* and is therefore able to colonise these areas rapidly.

Table 4.5. Analysis of disturbances of one and three year periods of no freshwater inflow to the Kromme estuary for the natural runoff scenario for a section of the estuary approximately 6 km from the mouth. The relative boundary position is the distance the boundary between *Zostera* and *Ruppia* has moved further up the estuary from their natural boundary.

Condition	Initial	one year drought	three year drought
maximum biomass *Zostera* ($g.m^{-2}$)	90	200	210
maximum biomass *Ruppia* ($g.m^{-2)}$	102	70	30
relative boundary position (m)	0	+5	29

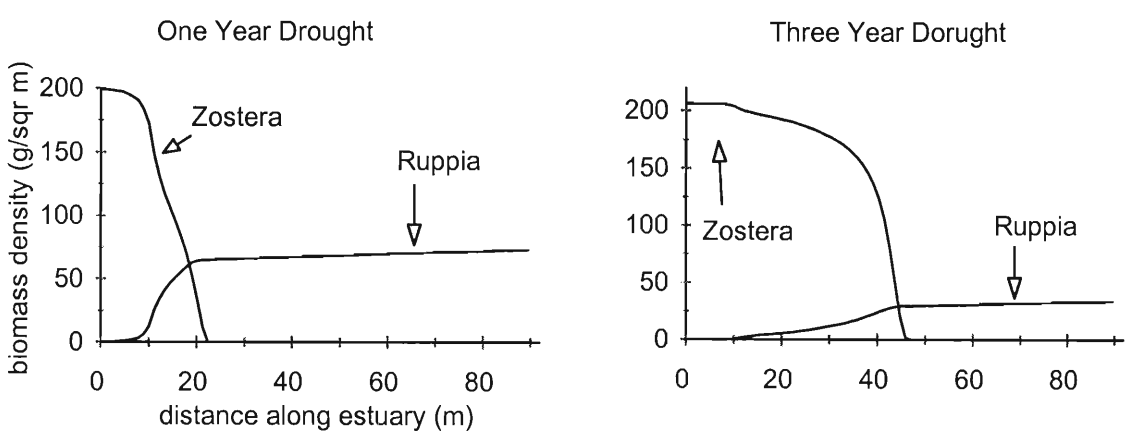

Figure 4.10. Graphs showing the effect of one and three year periods of no freshwater inflow on the natural boundary between *Zostera* and *Ruppia*. *Zostera* encroaches up the estuary and displaces *Ruppia*.

4.7.3 Intermediate Runoff Scenario: 40% of annual MAR

This scenario represents runoff due to small impoundments in the catchment of the Kromme estuary. The timing of releases is an annual flood equivalent to the 1 in 2 year flood (8.610×10^6 $m^3.year^{-1}$) in early summer (October/November), and a late summer flood volume of 2×10^6 $m^3.year^{-1}$ four months after the first flood. The remainder of the annual allocation of 48×10^6 $m^3.year^{-1}$ is assumed to enter the estuary as continuous base flow, i.e. 37.39×10^6 $m^3.year^{-1}$ .This scenario was selected to determine whether small impoundments cause a large change in the natural ecology of the estuary. If the effect is small, then freshwater managers know that minor abstractions will leave the Kromme estuary in a close to natural state.

4.7.3.1 Equilibrium States

The equilibrium states and their associated stability are shown in table 4.6. These states correspond to equilibrium conditions in the absence of other plants. All the states are stable in the absence of the other plants.

Table 4.6. The equilibrium states in the Kromme estuary for the intermediate runoff scenario with 40% of MAR. The maximum and minimum periodic biomass density is shown. All the states are stable in the absence of the other plants.

Location in estuary	State	Macrophyte biomass density ($g.m^{-2}$)
Lower reaches	*Zostera*	$Z \in (262,279)$
Middle reaches	*Zostera*	$Z \in (120,124)$
	Phragmites	$P \in (137,243)$
	Ruppia	$R \in (109,114)$
Upper reaches	*Zostera*	$Z \in (63,66)$
	Ruppia	$R \in (118.5, 118.7)$
	Phragmites	$P \in (145,235)$

As in the natural runoff scenario, *Zostera* is the only macrophyte which survives in the lower reaches. The phase plane diagrams in figure 4.11 shows the effect of initial conditions on the

outcome in the middle reaches. Figure 4.11a shows that *Ruppia* will die back if *Zostera* is present in the middle reaches. This is different from the result for the natural runoff scenario where *Ruppia* was the superior macrophyte out of *Zostera* and *Ruppia* in the middle reaches. Figure 4.11b shows the effect of initial conditions on the behaviour of *Zostera* and *Phragmites* in the middle reaches. The graph shows that any initial condition with both *Zostera* and *Phragmites* present will result in both macrophytes surviving at their equilibrium biomass densities.

The effect of initial conditions in the upper reaches is the same as that in the middle reaches for the natural runoff scenario: If all three macrophytes are initially present, then *Ruppia* and *Phragmites* survive, if *Ruppia* is absent, then *Zostera* and *Phragmites* will survive.

Therefore, there are two major differences between the equilibrium states for the intermediate runoff scenario and the natural runoff scenario:

(1) If both *Zostera* and *Ruppia* are present in the middle reaches, then applying the natural runoff scenario will result in *Ruppia* dominating the middle reaches, whereas applying the intermediate runoff scenario (40% MAR) will result in *Zostera* dominating the middle reaches, and

(2) *Zostera* can survive in the upper reaches under 40% MAR whereas it cannot survive in the upper reaches under natural runoff. *Zostera* is only able to survive in the upper reaches under 40% MAR if *Ruppia* is absent.

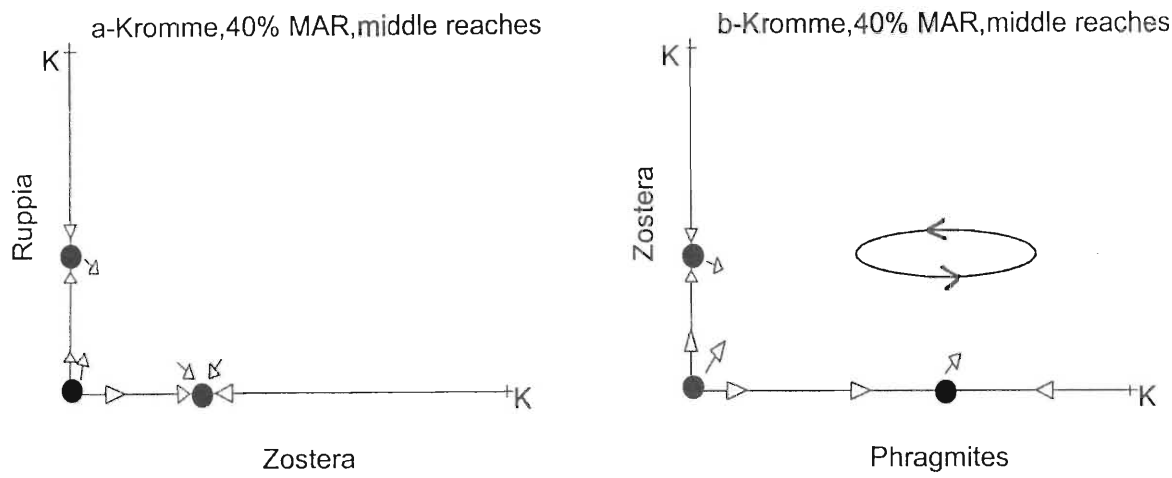

Figure 4.11. Stability of the equilibrium states in the middle reaches of the Kromme estuary under 40% MAR. (a) shows the outcome between *Zostera* and *Ruppia*: *Ruppia* will only survive if *Zostera* biomass density is zero, (b) shows the outcome between *Zostera* and *Phragmites*: For any initial condition, provided *Phragmites* and *Zostera* are both present, both macrophytes will survive. In both figures the origin is unstable. In the graphs K is the maximum carrying capacity which is 300 $g.m^{-2}$.

4.7.3.2 Spatial Distribution

If we assume that initially all three macrophytes are present throughout the Kromme estuary, then applying the intermediate runoff scenario will result in the boundary between *Zostera* and *Ruppia* occurring 1.2 km up from the boundary under natural runoff. The biomass distribution of the seagrasses along this boundary is shown in figure 4.12.

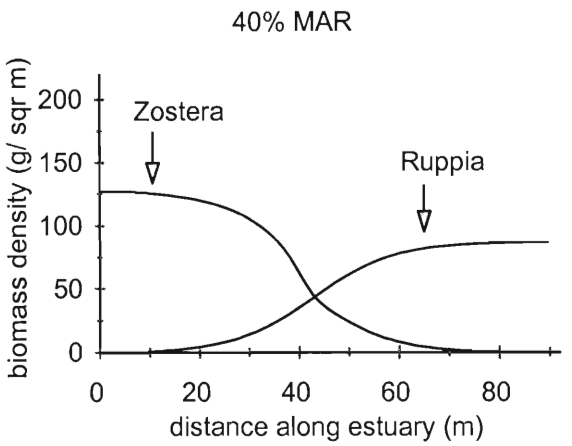

Figure 4.12. The distribution of *Zostera* and *Ruppia* in a section of the Kromme estuary, approximately 7.2 km up from the mouth, under the intermediate runoff scenario (40% MAR). The initial conditions for this simulation are that *Zostera*, *Ruppia* and *Phragmites* are present throughout the estuary.

4.7.3.3 The Effect of One and Three Year Periods of No Freshwater Inflow on the Equilibrium States

The disturbance scenarios were applied to the equilibrium states. The results, with the phase plane analysis, were then used to show whether a change in states can occur by imposing a drought on the system (tables 4.7 and 4.8)

Table 4.7. The response of the equilibrium states of the Kromme estuary under 40% MAR runoff to a one year period of no freshwater inflow. The biomass density after the disturbance is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state.

Location	State	Initial ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
Lower	Z only	$Z \in (262,279)$	Z=216	60 days	No
Middle	Z only, or Z&P	$Z \in (120,124)$	Z=231	120 days	No
	P only, or P&Z, or P&R	$P \in (137,243)$	P=65	150 days	No
	R only, or R&P	$R \in (109,114)$	R=111	0 days	No
Upper	P only, or P&R, or P&Z	$P \in (145,235)$	P=60	180 days	No
	R only, or R&P	$R \in (118.5,118.7)$	R=78	60 days	No
	Z only, or Z&P	$Z \in (63,66)$	Z=237	270 days	No

Table 4.8. The response of the equilibrium states of the Kromme estuary under 40% MAR to a three year period of no freshwater inflow. The biomass density after the disturbance is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state. If a state is omitted, it is because the three year drought has no further effect than the one year drought.

Location	State	Initial ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
Middle	P only, or P&Z, or P&R	$P \in (137,243)$	P=59	180 days	No
Upper	R only, or R&P	$R \in (118.5,118.7)$	R=68	300 days	No
	P only, or P&R	$P \in (145,235)$	P=46	210 days	No

Tables 4.7 and 4.8 show that one and three year periods of no freshwater inflow do not cause a shift in any of the equilibrium states. That is, after the disturbance recovery is possible. As

in the natural runoff scenario, the results show that a three year drought is not much worse than a one year drought. *Zostera*, in the upper reaches is affected by the drought the most, and biomass density more than doubles after one year of no freshwater inflow. There is no further change in *Zostera* in the upper reaches for subsequent drought periods. *Phragmites* biomass density decreases on average by 67% after a one year drought, and a further 5% for the subsequent drought years. Therefore, the critical drought year for *Phragmites* is the first year.

4.7.3.4 The Effect of One and Three Year Periods of No freshwater Inflow on *Zostera* Encroachment

The effect of a drought on the encroachment of *Zostera* from the boundary in figure 4.12 (p 113) shows that *Zostera* encroaches up the estuary every drought year and displaces *Ruppia* beds. In the first drought year *Zostera* encroaches 6 m up the estuary (figure 4.13).

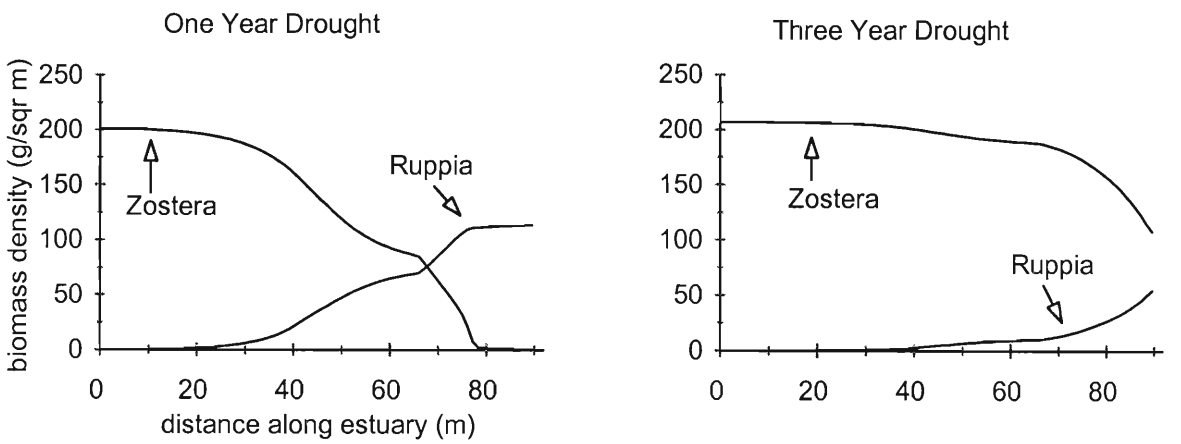

Figure 4.13. The response of *Zostera* and *Ruppia* in the Kromme estuary when a drought is imposed on the intermediate runoff scenario (40% MAR). This figure shows how the boundary between *Zostera* and *Ruppia* changes after one and three year periods of no freshwater inflow. Although *Ruppia* can survive drought in the absence of *Zostera*, *Zostera* displaces *Ruppia* and encroaches up the estuary.

4.7.4 Intermediate Runoff Scenario: 20% of annual MAR

For this runoff scenario the freshwater input to the Kromme estuary is half that of the previous intermediate runoff scenario. The timing of releases is an annual flood equivalent to the 1 in 2 year flood (8.610×10^6 $m^3.year^{-1}$) in early summer (October/November), and a late summer flood volume of 2×10^6 $m^3.year^{-1}$ four months after the first flood. The remainder of the annual allocation of 24×10^6 $m^3.year^{-1}$ is assumed to enter the estuary as continuous base flow, i.e. 13.39×10^6 $m^3.year^{-1}$. This scenario therefore represents major impoundments in the catchment of the Kromme estuary. Under the intermediate runoff scenario (20% MAR) the physical models predict that salinities average 12 ppt. in the upper reaches, 23 ppt. in the middle reaches, and 27 ppt. in the lower reaches. Therefore we would expect *Zostera* or *Ruppia* to survive, although we cannot say off hand how competitive interactions affect the outcome. Further examination of the physical data shows that freshwater conditions persist at the head of the estuary for about 45 days in November, salinities then increase to 8 ppt. by March, following which a late summer release decreases salinities at the head to zero, but after four months the upper reaches have salinities varying between 7 ppt. and 20 ppt. Therefore we cannot conclude whether or not the duration of freshwater conditions in the upper reaches is long enough for the survival of *Phragmites*.

4.7.4.1 Equilibrium States

The equilibrium states for the single macrophyte communities are shown in table 4.9. Unlike the previous two runoff scenarios, *Phragmites* is unable to survive in the middle reaches. All the states are stable in the absence of the other plants.

Table 4.9. The equilibrium states in the Kromme estuary for the intermediate runoff scenario with 20% MAR for the single macrophyte communities. The maximum and minimum periodic biomass density is shown. All the states are stable in the absence of the other plants.

Location in estuary	State	Macrophyte biomass density ($g.m^{-2}$)
Lower reaches	*Zostera*	$Z \in (254.5,255)$
Middle reaches	*Zostera*	$Z \in (274.7,278)$
	Ruppia	$R \in (125.9,126.3)$
Upper reaches	*Zostera*	$Z \in (142,145)$
	Ruppia	$R \in (159.8,160.9)$
	Phragmites	$P \in (142,191)$

Zostera is the only macrophyte which can survive in the lower reaches.

Figure 4.14a shows the effect of initial conditions in the middle reaches: If *Zostera* and *Ruppia* are initially present, then *Zostera* will grow and *Ruppia* will die back. Thus *Ruppia* is only able to survive of there is no *Zostera*. Figures 4.14b and 4.14c show the outcome in the upper reaches. Out of the submerged macrophytes, *Ruppia* is the dominant macrophyte in the upper reaches, and *Ruppia* can coexist with *Phragmites* (figure 4.14c). The only way *Zostera* will survive in the upper reaches under 20% MAR is if *Ruppia* is absent from the upper reaches (figure 4.14b). This is in contrast to the lower and middle reaches where *Zostera* is the dominant macrophyte.

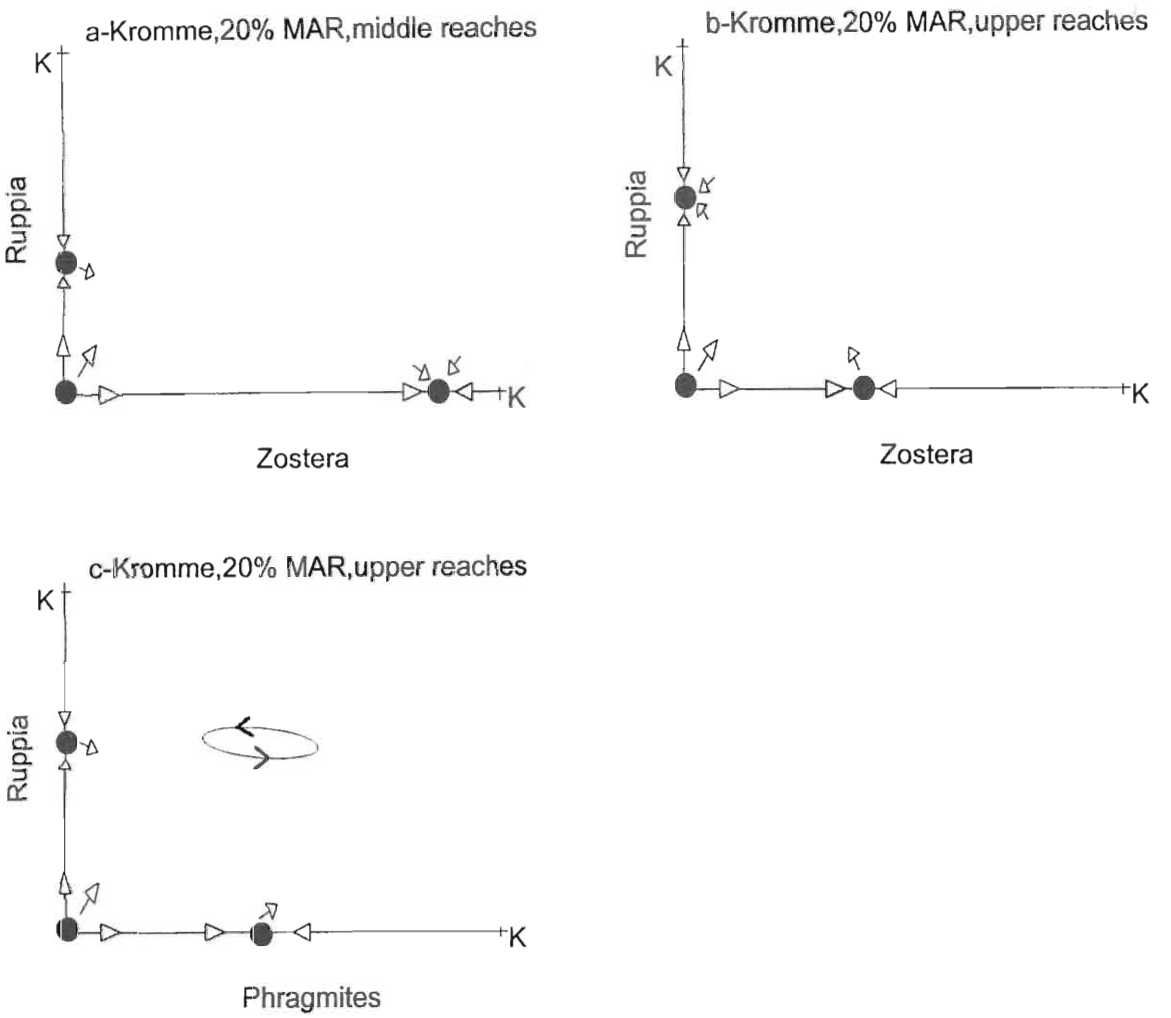

Figure 4.14. The effect of initial conditions in the middle and upper reaches of the Kromme estuary under 20% MAR. In (a), *Zostera* is the dominant macrophyte in the middle reaches, in (b) *Zostera* will only survive in the upper reaches provided there is no *Ruppia*, and in (c) *Ruppia* and *Phragmites* coexist. In the graphs K is the maximum carrying capacity which is 300 $g.m^{-2}$.

4.7.4.2 Spatial Distribution

The location of the boundary between *Zostera* and *Ruppia* occurs 8.5 km up from the mouth. (This was determined for initial conditions being that all three macrophytes are present throughout the estuary). The biomass distribution of *Zostera* and *Ruppia* along this boundary is shown in figure 4.15

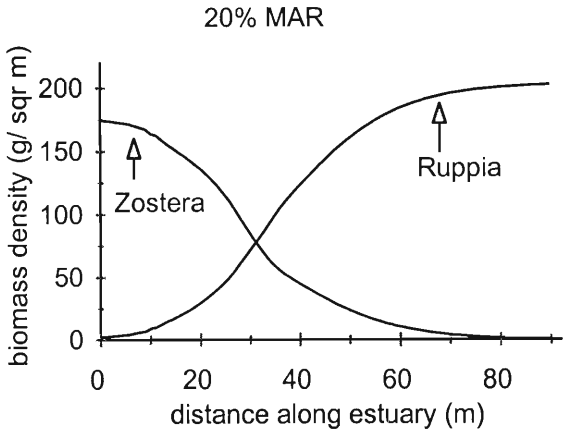

Figure 4.15. The distribution of *Zostera* and *Ruppia* along the Kromme estuary, 8.5 km up from the mouth, under 20% MAR conditions. This distribution was determined with the initial conditions being that *Zostera*, *Ruppia* and *Phragmites* were initially present.

4.7.4.3 The Effect of One and Three Year Periods of No Freshwater Inflow on the Equilibrium States

The disturbance scenarios were applied to all the equilibrium states. The results, with the phase plane analysis, were then used to show whether a change in states can occur by imposing a drought on the system (table 4.10 and 4.11). The results show that although *Ruppia* and *Phragmites* biomass density decreases during the drought, they can recover and there is no shift in the equilibrium states of the estuary. *Phragmites* and *Ruppia* biomass density in the upper reaches decreases on average by 64% and 51% respectively during the first drought year, after which the decrease during subsequent drought years is an additional 9% for *Phragmites*. *Zostera* biomass density almost doubles in the upper reaches after one year of no freshwater inflow.

Table 4.10. The response of the equilibrium states of the Kromme estuary under 20% MAR runoff to a one year period of no freshwater inflow. The biomass density after the disturbance is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state.

Location	State	Initial ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
Lower	Z only	Z∈ (254.5,255)	Z=219	30 days	No
Middle	Z only	Z∈ (274.7,278)	Z=231	330 days	No
	R only	R∈ (125.9,126.3)	R=79	330 days	No
Upper	Z only, or Z&P	Z ∈ (142,145)	Z=237	330 days	No
	P only or P&Z, or P&R	P ∈ (142,191)	P=60	120 days	No
	R only, or R&P	R ∈ (158.8,160.9)	R=78	240 days	No

Table 4.11. The response of the equilibrium states of the Kromme estuary under 20% MAR runoff conditions to a three year period of no freshwater inflow. The biomass density after the disturbance is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state. If a state is omitted it is because the three year drought has no further effect than the one year drought.

Location	State	Initial ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
Upper	P only, or P&Z, or P&R	P ∈ (142,191)	P=46	150 days	No

4.7.4.4 The Effect of One and Three Year Periods of No freshwater Inflow on *Zostera* Encroachment

The effect of a drought on the encroachment of *Zostera* from the boundary between *Zostera* and *Ruppia* is shown in figure 4.16. In the first year *Zostera* has encroached approximately 10 m, whereas under a drought for the natural runoff scenario, *Zostera* only encroaches 5 m

during the first year. This is because under the intermediate runoff scenario, *Ruppia* biomass decreases by 37% in the middle reaches after one drought year, whereas under the natural runoff scenario, the corresponding decrease in *Ruppia* biomass density is 21%. This means that for the intermediate runoff scenario there is less competition with *Ruppia*, and so *Zostera* can encroach further up the estuary in one year than under a drought in the natural runoff scenario.

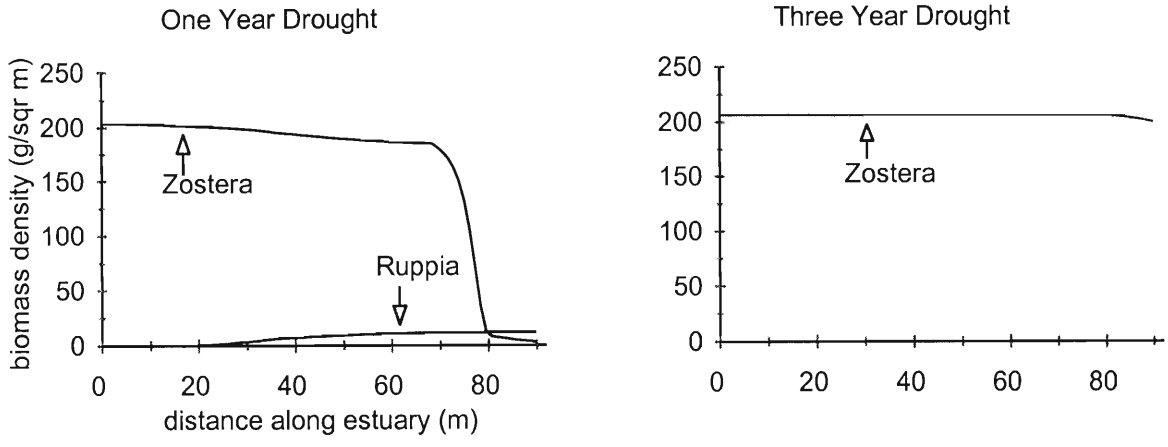

Figure 4.16. The response of *Zostera* and *Ruppia* in the Kromme estuary when a drought is imposed on the intermediate runoff scenario (20% MAR). This figure shows how the boundary between *Zostera* and *Ruppia* changes after one and three year periods of no freshwater inflow.

4.7.5 Intermediate Runoff Scenario: 10% of annual MAR

4.7.5.1 Equilibrium States

This scenario represents major impoundments in the catchment of the Kromme estuary. It is very close to the situation of no river runoff to the Kromme estuary. The timing of releases is an annual flood equivalent to the 1 in 2 year flood (8.610 x 10^6 $m^3.year^{-1}$) in early summer (October/November), and a late freshette of 1 x 10^6 $m^3.year^{-1}$ four months after the first flood. The remainder of the annual allocation of 2.372 x 10^6 $m^3.year^{-1}$ is assumed to enter the estuary as continuous base flow. The difference between this runoff scenario and the 20% MAR scenario is that low salinities in the upper reaches persist for less time than under 20% MAR, and that salinities of the estuary are generally higher under 10% MAR than 20% MAR.

The model predicts that *Phragmites* does not survive anywhere along the estuary. *Zostera* survives in the lower reaches, while either *Zostera* or *Ruppia* can survive in the middle and upper reaches, depending on the initial conditions. The equilibrium states for the single macrophyte communities are shown in table 4.12.

Table 4.12. The equilibrium states in the Kromme estuary for the intermediate runoff scenario with 10% MAR for the single macrophyte communities. The maximum and minimum periodic biomass density is shown. In the absence of other macrophytes, all the states are stable.

Location in estuary	State	Macrophyte biomass density ($g.m^{-2}$)
Lower reaches	*Zostera*	$Z \in (227.6,227.8)$
Middle reaches	*Zostera*	$Z \in (272,273.2)$
	Ruppia	$R = 99.8$
Upper reaches	*Zostera*	$Z \in (277,279)$
	Ruppia	$R \in (150.5,151.5)$

The lower, middle and upper reaches are dominated by *Zostera* under 10% MAR. That is, if both *Zostera* and *Ruppia* are present, then *Zostera* will survive and *Ruppia* will die back under 10% MAR. *Ruppia* is only able to survive in the absence of *Zostera*.

4.7.5.2 The Effect of One and Three Year Periods of No Freshwater Inflow on the Equilibrium States

The impact of a one year drought period on the equilibrium states is shown in table 4.13. There is no switch in states under the disturbance scenarios. The effect of a three year drought is not shown, the only difference from the one year drought being that *Ruppia* decreases a further 9% in the middle reaches during the last two years of drought conditions and then takes 240 days to recover.

Table 4.13. The response of the equilibrium states of the Kromme estuary under 10% MAR runoff to a one year period of no freshwater inflow. The biomass density after the disturbance is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state. There is no change for three years of drought conditions, except *Ruppia* in the middle reaches, which decreases to 67.8 $g.m^{-2}$ after three drought years and takes 240 days to recover.

Location	State	Initial ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
Lower	Z only	$Z \in$ (227.6,227.8)	Z=220.2	30 days	No
Middle	Z only	$Z \in$ (272,273.2)	Z=231.5	210 days	No
	R only	R = 99.8	R=77	120 days	No
Upper	Z only	$Z \in$ (277,279)	Z=236	one year	No
	R only	$R \in$ (150.5,151.5)	R=113	210 days	No

4.7.6 Present Runoff Scenario: monthly releases of total annual volume of 2 x 10^6 $m^3.yr^{-1}$, i.e. 2% MAR

The present runoff scenario comprises monthly releases over one day of one twelfth the total annual volume of 2 x 10^6 $m^3.year^{-1}$. Model results show that *Zostera* can survive in the lower, middle and upper reaches, and that *Ruppia* can survive in the middle and upper reaches. However, all the equilibrium states of *Zostera* are stable, which means that if there is a small biomass of *Zostera* in the middle or upper reaches, then *Ruppia* will disappear and the estuary will become marine dominated. The equilibrium biomass density for *Zostera* is 260 $g.m^{-2}$ (upper reaches), 260 $g.m^{-2}$ (middle reaches) and 220 $g.m^{-2}$ (lower reaches). Field data collected by Adams and Talbot (1992) also shows an increase in *Zostera* biomass density in the Kromme from the mouth to the head of the estuary. Biomass is smaller at the mouth because of strong tidal currents that cause a reduction in growth. The average scour multiplier for *Zostera* is 0.2582 (lower reaches), 0.01117 (middle reaches) and 0.0018 (upper reaches). The equilibrium biomass density for *Ruppia* is 86 $g.m^{-2}$ and 142 $g.m^{-2}$ in the middle and upper reaches respectively. The response of the system to a three year drought is that *Zostera* biomass density decreases on average by 4% in the lower, middle and upper reaches, and that *Ruppia* decreases by 10% and 18% in the middle and upper reaches respectively.

4.7.7 Alternative releases totalling an annual volume of 2 x 10^6 $m^3.yr^{-1}$

The present runoff release policy comprises monthly freshwater releases. The effect of these releases is confined to the head of the estuary, with salinities at the head decreasing from about 34 ppt. to between 16 ppt. and 20 ppt. immediately after a release. Using the present annual allocation of freshwater, the timing and duration of freshwater releases were varied. The aim of these scenarios was to optimise the duration of salinity gradients created by freshwater inflow, and to determine whether reintroducing fresh or brackish components in the upper reaches was possible. The model results show that under scenarios a, b and c below, *Zostera* attains a biomass of approximately 260 $g.m^{-2}$ in the upper reaches. Therefore, *Ruppia* does not survive in the estuary. *Phragmites* survives in the upper reaches. That is, under policies of

(a) One large release per year in early summer, which is the growing season for *Phragmites*,

(b) Two releases of equal volume per year (early summer and six months later), and

(c) Two releases of equal volume per year (early summer and four months later),

Phragmites maintains a biomass of 60 g. m^{-2} in the upper reaches. A policy of three releases per year (larger release in summer, two smaller releases later, but not in winter) leads to the die back of *Phragmites*. Current velocity and water level fluctuations did not change much for the different scenarios. Therefore, the survival of *Phragmites* is due to the salinity multiplier. Under the release policies (a), (b) and (c) the percentage increase in the average salinity growth multiplier of *Phragmites* in the upper reaches, from the present runoff scenario, is 193%, 138% and 114% respectively. This is a sufficient increase for a *Phragmites* to survive. Under a policy of three releases per year, the corresponding increase is 99%, which is insufficient for *Phragmites* to establish itself. The change in the average salinity mortality multiplier is not as large. Under the release policies (a), (b) and (c), the percentage decrease in the average salinity mortality multiplier of *Phragmites* in the upper reaches, from the present runoff scenario, is 9.59%, 9.71% and 8.22% respectively. For three releases per year, the corresponding decrease is 6.41%. So the reason *Phragmites* survives under policies (a), (b) and (c) is because of the large increase in the salinity growth multiplier compared with the present runoff scenario.

Model results show that a three year drought will not eliminate *Phragmites* from the upper reaches under release policies (a) to (c). The biomass density will decrease to 46 $g.m^{-2}$ after a three year drought and the recovery time will be 3 years.

4.7.8 Implications for Management

The results show that release policies of 20% MAR or more will lead to the survival of all three macrophytes (provided all macrophytes are initially present in the estuary). In contrast, a release policy of 10% MAR or less than 10% MAR will result in a marine (*Zostera*) dominated estuary (table 4.14).

Table 4.14. A summary of the runoff scenarios for the Kromme estuary. The initial condition is that all three macrophytes are present. The stable states that result from the various runoff policies are shown for the lower, middle, and upper reaches.

Scenario	Lower reaches	Middle reaches	Upper reaches
Natural	Z	R, P	R, P
Intermediate 40% MAR	Z	Z, P	R, P
Intermediate 20% MAR	Z	Z	R, P
Intermediate 10% MAR	Z	Z	Z
Present	Z	Z	Z

The graph in figure 4.17 shows how the location of the boundary between *Zostera* and *Ruppia* varies with freshwater inflow. As freshwater input decreases, this boundary moves further up the estuary. The shape of the graph suggests an exponential increase in the position of the boundary from the mouth as freshwater inflow decreases.

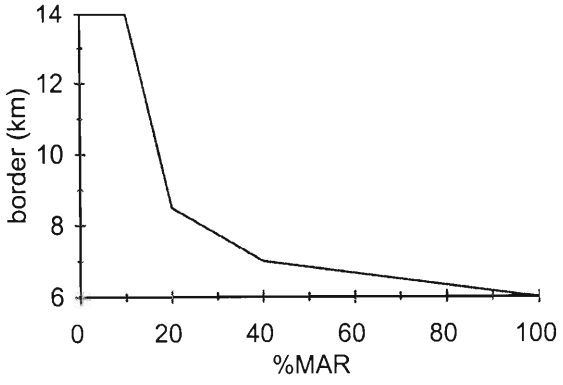

Figure 4.17. The relationship between freshwater input and the location of the boundary between *Zostera* and *Ruppia* for the Kromme runoff scenarios.

The graph in figure 4.17 shows that the critical region is between 10% MAR and 20% MAR. For 20% MAR the boundary between the marine component and the brackish component occurs just over 8 km from the mouth, whereas under a policy of 10% MAR the estuary is marine dominated. In addition, the graph is almost horizontal between 40% MAR and 100% MAR, showing those release policies between this range have similar effects on the distribution patterns of estuarine macrophytes. Freshwater managers therefore know that restricting the consumptive use of water to only 10% MAR, (so that 90% MAR is available for estuarine purposes), as opposed to 30% MAR, (so that 70% MAR is available for estuarine purposes), achieves little difference in terms of the distribution of the estuarine plants.

The graphs in figures 4.18 show why there is an exponential increase in the position of the boundary between marine and brackish macrophytes as freshwater inflow to the Kromme estuary decreases. The graph in figure 4.18a shows the relationship between the average salinity growth multiplier of *Zostera* in the upper reaches and freshwater inflow. As freshwater inflow decreases, the salinity growth multiplier of marine species such as *Zostera* increases exponentially in the upper reaches. Similarly, the graph in figure 4.18b shows the relationship between the average salinity mortality multiplier of *Zostera* in the upper reaches and freshwater inflow. There is an exponential decrease in this multiplier in the upper reaches as freshwater input decreases. So there is encroachment of marine macrophytes into the upper reaches as freshwater inflow decreases.

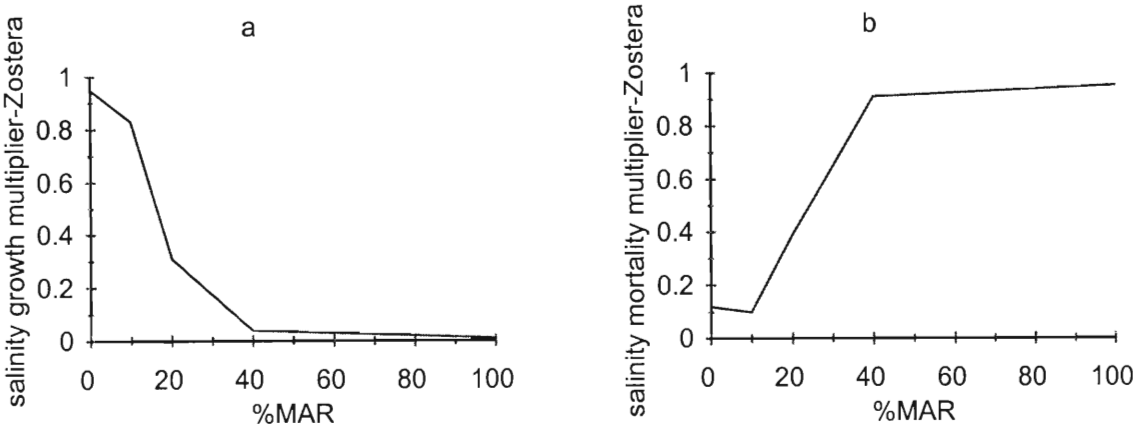

Figure 4.18. The relationship between the average salinity growth (a) and mortality (b) multiplier of *Zostera* in the upper reaches for the Kromme runoff scenarios.

We know therefore that impoundments will result in *Zostera* encroachment up from the estuary mouth. In the following analysis we compare how fast *Zostera* encroaches up the Kromme estuary under minor impoundments, as opposed to major impoundments. The scenario selected to represent minor impoundments is the intermediate runoff scenario with 40% MAR, and the scenario selected to represent major impoundments is the scenario where there is no freshwater inflow to the Kromme estuary (0% MAR). For 40% MAR, we know that the border between *Zostera* is approximately 1.2 km up from the boundary under natural runoff conditions. What still needs to be investigated is how quickly this boundary would be reached if the natural system was subjected to 40% MAR. When there is no freshwater inflow the results show that *Zostera* survives in all reaches of the estuary. What now needs to be investigated is how fast *Zostera* colonisation occurs under this runoff scenario.

Given the natural boundary of *Zostera* and *Ruppia* at 6 km up from the mouth, the effects of the 40% MAR and 0% MAR (no freshwater inflow) scenarios on the distribution of *Zostera* and *Ruppia* were determined. The results are shown in table 4.15. The response rate of the natural system to 40% MAR is slower than the response rate to 0% MAR: After 3 years *Zostera* has encroached 9 m, in contrast to 29 m for 0% MAR. The rate of change in biomass is also slower for 40% MAR than for 0% MAR. There are no significant changes in water levels and current speeds for the 40% and 0% MAR scenarios, so the difference in spread rate may be due to differences in salinity between the two scenarios. A comparison of the average

salinity growth multiplier of *Zostera* for the 40% MAR and 0% MAR scenarios shows that this is not so (table 4.16). There is only a 2% increase in the average salinity growth multiplier of *Zostera* from 40% MAR to 0% MAR. This does not account for the 220% increase in encroachment rates from 40% MAR to 0% MAR after three years.

To explain this difference we consider *Ruppia*. After one year, the encroachment rates of *Zostera* are similar for 0% MAR and 40% MAR. The reason for the difference after 3 years is due to the effects of interactions between *Zostera* and *Ruppia* beds. For both scenarios, competition with *Ruppia* is approximately the same during the first year because the biomass of *Ruppia* is approximately the same after one year of each scenario. During the next two years however, for 40% MAR, *Ruppia* does not die back, whereas for 0% MAR, *Ruppia* dies back to 30 $g.m^{-3}$. There is therefore less competition for *Zostera* for 0% MAR than for 40% MAR and *Zostera* is therefore able to spread further for 0% MAR than for 40% MAR.

Table 4.15. The response of the natural system in the Kromme estuary to one and three year periods of 40% MAR and 0% MAR.

Condition	natural	40% MAR		0% MAR	
		1 yr	3 yrs	1 yr	3 yrs
max biomass Z ($g.m^{-2}$)	90	150	150	200	200
max biomass R ($g.m^{-2)}$	110	100	100	70	30
relative boundary position (m)	0	+3	+9	+5	+29

Table 4.16. The average salinity growth multiplier for *Zostera* for 40% MAR and 0% MAR along a length of 90 m approximately 6 km up from the mouth.

Scenario	Average salinity growth multiplier
40% MAR	0.9421 to 0.9384
0% MAR	0.9695 to 0.9692

The total biomass of *Zostera* and *Ruppia* along the Kromme estuary was calculated for the stable equilibrium states (listed in table 4.14, p.125). This is presented in figure 4.19 below where the biomass is reflected as a percentage of the biomass under natural runoff conditions. The intermediate runoff scenario with 40% MAR has a total *Zostera* and *Ruppia* biomass 10% greater than that under natural runoff conditions. For the intermediate runoff scenarios with 20% MAR, 10% MAR and present MAR, the corresponding difference in total *Zostera* and *Ruppia* biomass is at least 40% greater than that under natural runoff conditions. Therefore, in terms of total *Zostera* and *Ruppia* biomass, the scenarios with large impoundments are better than the natural runoff scenario. However, the greater the impoundment, the further up the estuary *Zostera* survives. Therefore the natural runoff scenario is better than the scenarios with impoundments in that it maintains macrophyte diversity, and results in *Zostera* being restricted to the lower reaches of the estuary. Both the 10% MAR scenario and the present runoff scenario result in *Zostera* occurring from the mouth to the head of the estuary, but the 10% MAR scenario results in greater total *Zostera* biomass than the present runoff scenario. This is because the present runoff scenario has higher salinities (greater than 35 ppt.) than the 10% MAR scenario, resulting in a higher salinity mortality multiplier under present runoff than under 10% MAR.

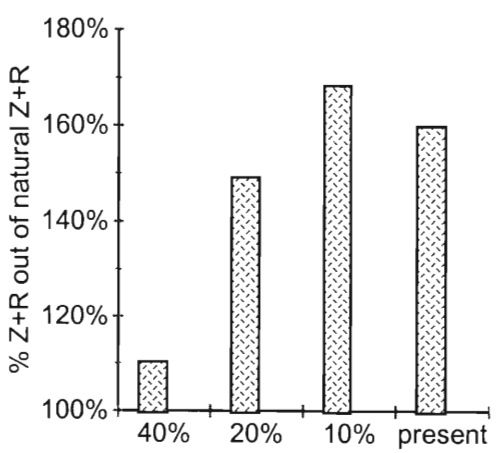

Figure 4.19. The ratio of total *Zostera* and *Ruppia* biomass in the Kromme estuary for the equilibrium states listed in table 4.14 (p. 125) as a percentage of the corresponding biomass under natural runoff conditions.

4.7.9 Comparison of Results with Expert System Results

Selected results for the scenarios from the expert system model are presented. The results for the expert system model are based on growth adjustment with a score range of between -10 and +10. Growth adjustment score of zero means that plants will be unaffected and there is no change in the growth rate. A positive score means that the growth rate will increase. A negative score means that the growth rate will decrease. A score of -10 means that the plants will die. The expert system model calculates the response of the macrophytes to the mean salinity, water level and current velocity for each runoff scenario. This means that extreme salinities are not taken into account.

Expert system model predictions were made for three representative sites in the Kromme estuary, namely at the mouth, the middle reaches and the upper reaches. The growth rate adjustment scores for *Zostera* were negative for the middle and upper reaches for the natural runoff scenario, and for the upper reaches for the intermediate runoff scenario (40% MAR), (Table 4.17). The mathematical model on the other hand predicted that in the absence of *Ruppia* a small biomass of *Zostera* can survive in the upper reaches under the intermediate runoff scenario (40% MAR). This is because the expert system model predictions are based on the average salinity, whereas the mathematical model predictions are based on the daily salinity values. For all release policies with less than 40% MAR, *Zostera* has a high growth rate adjustment score. This agrees with the mathematical model results.

Table 4.17. Growth rate adjustment scores for the submerged macrophyte *Zostera capensis* in the lower, middle and upper reaches of the Kromme estuary for the runoff scenarios.

Runoff scenario	lower reaches	middle reaches	upper reaches
Natural runoff	3.6	-9.6	-9.4
Intermediate,40%MAR	8.4	10	-4.3
Intermediate,20%MAR	8.4	10	10
Intermediate,10%MAR	8.4	10	10
No freshwater release	8.4	10	10

The growth rate adjustment scores for *Phragmites* indicated optimal growth in the middle and upper reaches under the natural runoff scenario and the intermediate runoff scenario (40% MAR), (table 4.18). The mathematical model also predicted that *Phragmites* can survive in the middle and upper reaches for these runoff scenarios. Both models also predicted that *Phragmites* survives in the upper reaches under 20% MAR, and that it disappears from the estuary for release policies with less than 20% MAR.

Table 4.18. Growth rate adjustment scores for the emergent reed *Phragmites australis* in the lower, middle and upper reaches of the Kromme estuary for the runoff scenarios.

Runoff scenario	lower reaches	middle reaches	upper reaches
Natural runoff	0	10	10
Intermediate,40%MAR	0	10	10
Intermediate,20%MAR	0	0	10
Intermediate,10%MAR	0	0	0
No freshwater release	0	0	0

There were no expert system model predictions for *Ruppia*.

4.7.10 Discussion on Kromme Estuary Results

Ruppia can survive for all release policies provided there is no *Zostera* in the estuary. If *Zostera* is present, then *Ruppia* can survive for release policies with a mean annual runoff greater than or equal to 20% MAR. The greater the impoundment, the further up the estuary the boundary between *Zostera* and *Ruppia* occurs.

Phragmites does not survive under release policies of 10% MAR and less than 10% MAR. However, reintroducing *Phragmites* into the upper reaches by changing the present water release pattern is possible. Thus restoring freshwater macrophytes in the upper reaches with the present volume of water which is released to the Kromme estuary is possible.

The encroachment rate of *Zostera* up the estuary due to impoundments increases with less freshwater inflow. A comparison of two scenarios, namely 40% MAR and 0% MAR, showed that *Zostera* spread rate is greater under higher impoundments because of higher salinity growth multipliers for *Zostera*. In addition, *Ruppia* also dies back fast under greater impoundments, thereby reducing the interactions between *Zostera* and *Ruppia* and thus allowing for a faster *Zostera* spread rate.

If *Ruppia* is absent from the Kromme estuary, then achieving a marine (*Zostera*) dominated estuary with freshwater releases less then or equal to 40% MAR is possible. Otherwise, if *Ruppia* is present in the estuary, then a marine dominated state will only occur from release policies of 10% MAR and less than 10% MAR.

For all the runoff scenarios, if the Kromme estuary is in an equilibrium state, then if a drought occurs, the critical year for *Phragmites* is the first drought year. That is, all major changes in biomass density occur during the first year of drought conditions, after which the rate of change under further drought conditions is slower than that during the first year.

If all three macrophytes are present initially, then the critical volume for freshwater inflow is 20% MAR. For releases above or equal to this volume, *Zostera*, *Ruppia* and *Phragmites* survive, whereas below the critical volume only *Zostera* survives. Moreover, it was shown that for releases above the critical volume, the difference in the location of the boundary between marine and brackish macrophytes is: For natural runoff the boundary is 6 km up from the mouth, (approximately 46% of the total length of the estuary), whereas for 20% MAR, the boundary is 8.5 km up from the mouth (approximately 69% of the total length of the estuary).

For all the scenarios, the recovery time after a one year drought for *Zostera* and *Ruppia* varied between 30 days and one year. *Phragmites* recovery times varied between four months and three years.

4.8 Results for the Great Brak Estuary

4.8.1 Introduction to Freshwater Runoff Scenarios

The freshwater scenarios for the Great Brak estuary address a variety of flow conditions, ranging from estimated pristine natural runoff to the long term mean runoff expected as a result of the construction of the Wolwedans dam. The natural runoff scenario refers to the situation when there are no impoundments in the catchment of the Great Brak estuary. This scenario was selected to examine the macrophyte dynamics of the estuary under ideal runoff conditions. The second scenario, namely the pre-dam runoff scenario represents runoff due to minor impoundments due to, for example, the damming of small tributaries for irrigation. Under this scenario, freshwater runoff to the estuary is reduced, so that the estuary mouth will close more frequently and be closed for longer periods (CSIR 1990). Under this release pattern, the effect of floods will be normal. The post-dam scenario represents extreme impoundments in the catchment. This freshwater release will result in frequent mouth closures, a deterioration in water quality, attenuation of normal floods and a change in water levels during closed mouth conditions (CSIR 1990). Slinger (1996, pp. 74-80, 83-90) gives the physical data for the scenarios.

By selecting a range of inflow scenarios from the natural to the post-dam situation we can monitor which impoundments cause the die back of certain macrophytes, and which impoundments disrupt the natural distribution of the macrophytes along the estuary.

The method used for analysing the runoff scenarios is as follows:

(1) The equilibrium states and their associated stability are determined. The definition of an equilibrium state is the same as that for the Kromme Estuary Case Study (defined in section 4.7.1 under point 1).

(2) If there is a switch along the estuary from a marine dominated habitat to brackish dominated habit, then the spatial distribution of the associated macrophytes at this boundary is determined,

(3) The effect of perturbations is investigated by considering two disturbance scenarios: A summer flood equivalent to the 1 in 50 year flood volume is superimposed on each of the runoff scenarios, and a 50% decrease in freshwater inflow to the estuary over the period March to June is superimposed on each of the runoff scenarios.

In the tables that follow, Z, R and P represent *Zostera*, *Ruppia* and *Phragmites* respectively.

4.8.2 Natural Runoff Scenario

The natural runoff scenario refers to runoff before any modification through the construction of dams or abstraction for irrigation, with a mean annual runoff of approximately 37 x 10^6 $m^3.yr^{-1}$ (CSIR 1990). Under natural runoff conditions the estuary mouth would be predominantly open. A closed mouth would occur on average between one and two months per year, but would rarely remain closed for more than one month at a time (Slinger 1995).

4.8.2.1 Equilibrium States

The equilibrium states for the single macrophyte communities are shown in table 4.19. All the states are stable in the absence of the other macrophytes.

Table 4.19. The equilibrium states for *Zostera*, *Ruppia* and *Phragmites* in the Great Brak estuary for natural runoff conditions in the absence of the other plants. For the equilibrium states biomass density fluctuates periodically over a period of one year. The maximum and minimum periodic biomass density is shown. In the absence of the other plants, all the states are stable.

Location in estuary	State	Macrophyte biomass density ($g.m^{-2}$)
R2	*Zostera*	$Z \in (184,200)$
R6	*Zostera*	$Z \in (124,140)$
	Ruppia	$R \in (171.7,172.16)$
R8	*Ruppia*	$R \in (129.21,131.29)$
	Phragmites	$P \in (155,240)$

Results show that *Zostera* survives in the lower reaches for any set of initial conditions, provided initial *Zostera* biomass density is not zero.

Zostera can survive in the middle reaches, provided *Ruppia* is absent from the middle reaches. If both *Zostera* and *Ruppia* are present in the middle reaches, then *Ruppia* will survive and *Zostera* will die back (figure 4.20 a). In the upper reaches, both *Phragmites* and *Ruppia* can survive for any set of initial conditions. The phase plane diagram in figure 4.20b shows the effect of initial conditions on the behaviour of *Phragmites* and *Ruppia* in the upper reaches. If both *Phragmites* and *Ruppia* are present, then any initial condition will result in the survival of both macrophytes.

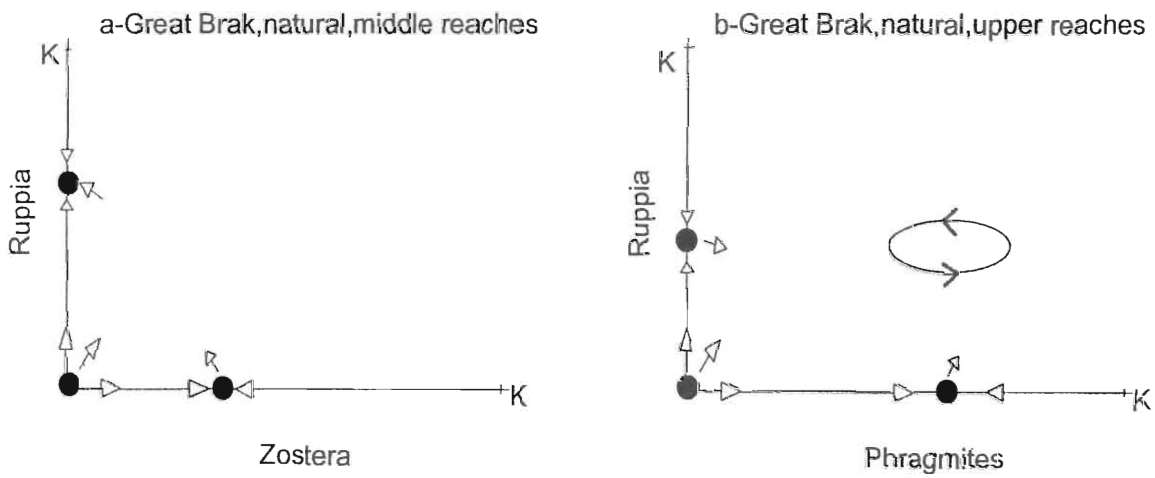

Figure 4.20. Stability of the equilibrium states for the Great Brak estuary for natural runoff conditions in the middle (a) and upper reaches (b). *Zostera* does not survive in the upper reaches under natural runoff conditions. *Zostera* is only able to survive in the middle reaches if *Ruppia* is absent. *Ruppia* and *Phragmites* can coexist in the upper reaches. In the graphs K is the maximum carrying capacity, namely 300 $g.m^{-2}$.

4.8.2.2 Spatial Distribution

The spatial distribution of *Zostera* and *Ruppia* was determined with initial conditions in the estuary being that all three macrophytes are present. So the middle reaches become *Ruppia*-dominated (figure 4.20), and therefore the boundary between *Zostera* and *Ruppia* will occur below the middle reaches. Results show that the boundary between *Zostera* and *Ruppia* occurs approximately 1 km up from the mouth (figure 4.21). A comparison of the salinity growth and mortality multipliers and scour multipliers for *Zostera* and *Ruppia* along this boundary (table 4.20) shows that although *Ruppia* has a higher salinity growth multiplier than *Zostera*, it has a higher scour multiplier than *Zostera*. This is why *Ruppia* does not survive lower down the estuary.

Table 4.20 Average salinity growth and mortality multipliers and scour multipliers of *Zostera* and *Ruppia* at the end points of their natural boundary in figure 4.21.

Macrophyte	Salinity		Velocity
	growth multiplier	mortality multiplier	scour multiplier
Zostera	0.4467 to 0.3758	0.3534 to 0.4087	0.0130 to 0.1316
Ruppia	0.9823 to 0.9807	0.0468 to 0.0569	0.3242 and 0.13164

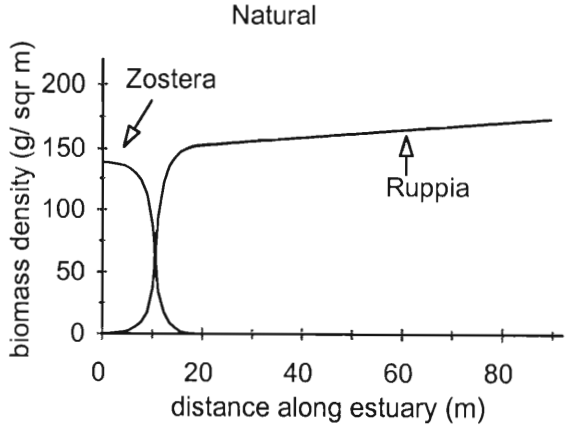

Figure 4.21. The distribution of *Zostera* and *Ruppia* in the Great Brak estuary under natural runoff conditions. This boundary occurs 1 km up from the mouth.

4.8.2.3 The Effect of a Flood or Drought on the Equilibrium States

The results for the disturbance scenarios are shown in table 4.21 and 4.22. The results show that if *Phragmites* is absent in the Great Brak estuary, then there is no switch in the equilibrium states for *Zostera* and *Ruppia* after a flood or a drought. That is, the estuary returns to the equilibrium state after a flood or a drought. However, if *Phragmites* is present, then the imposition of a flood or drought will result in a change in macrophyte composition in the upper reaches: *Phragmites* will encroach into the *Ruppia*-dominated areas and displace the *Ruppia* beds.

Table 4.21. The response of the equilibrium states of the Great Brak estuary under natural runoff conditions to a flood. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state. The response of *Ruppia* in the upper reaches to a flood depends on whether *Phragmites* is present. If *Phragmites* is present, then *Ruppia* does not recover after the flood. If *Phragmites* is not present, then *Ruppia* is able to recover after the flood.

Location	State	Before ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
R2	Z only	$Z \in (184, 200)$	Z=21.7	2 years	No
R4	Z only	$Z \in (124, 140)$	Z=20	1 year	No
	R only	$R \in (171.7, 172.16)$	R=20	3 years	No
R8	R only	$R \in (129.21, 131.29)$	R=32	2 years	No
	P only	$P \in (155, 240)$	P=253	210 days	No
	R&P	$R \in (129.21,131.29)$ $P \in (155, 240)$	P=253, R=0	210 days to P only	Yes, P only

Table 4.22. The response of the equilibrium states of the Great Brak estuary under natural runoff conditions to a drought. The biomass density after the drought is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state. If *Phragmites* is present, then *Ruppia* does not recover after the drought. If *Phragmites* is not present, then *Ruppia* is able to recover after the drought.

Location	State	Before ($g.m^{-2}$)	Biomass density	Recovery time	New State?
R2	Z only	$Z \in (184,200)$	Z=64.4	1 year	No
R4	Z only	$Z \in (124,140)$	Z=56	1 year	No
	R only	$R \in (171.7,172.16)$	R=62	1 year	No
R8	R only	$R \in (129.21,131.29)$	R=60	1 year	No
	P only	$P \in (155,240)$	P=270	< 1 month	No
	R&P	$R \in (129.21,131.29)$ $P \in (155,240)$	P=270, R=0	< 1 month	Yes, P only

If both *Phragmites* and *Ruppia* are present in the upper reaches, then their equilibrium depth distribution is given by the graph in figure 4.22. The resultant depth distribution of *Phragmites* and *Ruppia* in the upper reaches after a flood or a dry period is shown in figures 4.22 b and c respectively. During a drought or a flood *Ruppia* completely dies back. Results show that *Ruppia* can survive these disturbances in the absence of *Phragmites* (table 4.21 and table 4.22), so the complete die back of *Ruppia* when *Phragmites* is present is due to the displacement of *Ruppia* beds by *Phragmites*. A flood equivalent to the 1 in 50 year flood volume is favourable for *Phragmites* growth (figure 4.22b) because salinities are low and water levels are high (they are as high as 3 m above mean sea level). *Ruppia* has a high scour multiplier (average scour multiplier of 0.6532 during the flood) and a depth mortality multiplier of one (*Ruppia* does not survive in water more than 2 m deep). During a drought water levels drop so *Ruppia* dies back and *Phragmites* can colonise these areas (figure 4.22c).

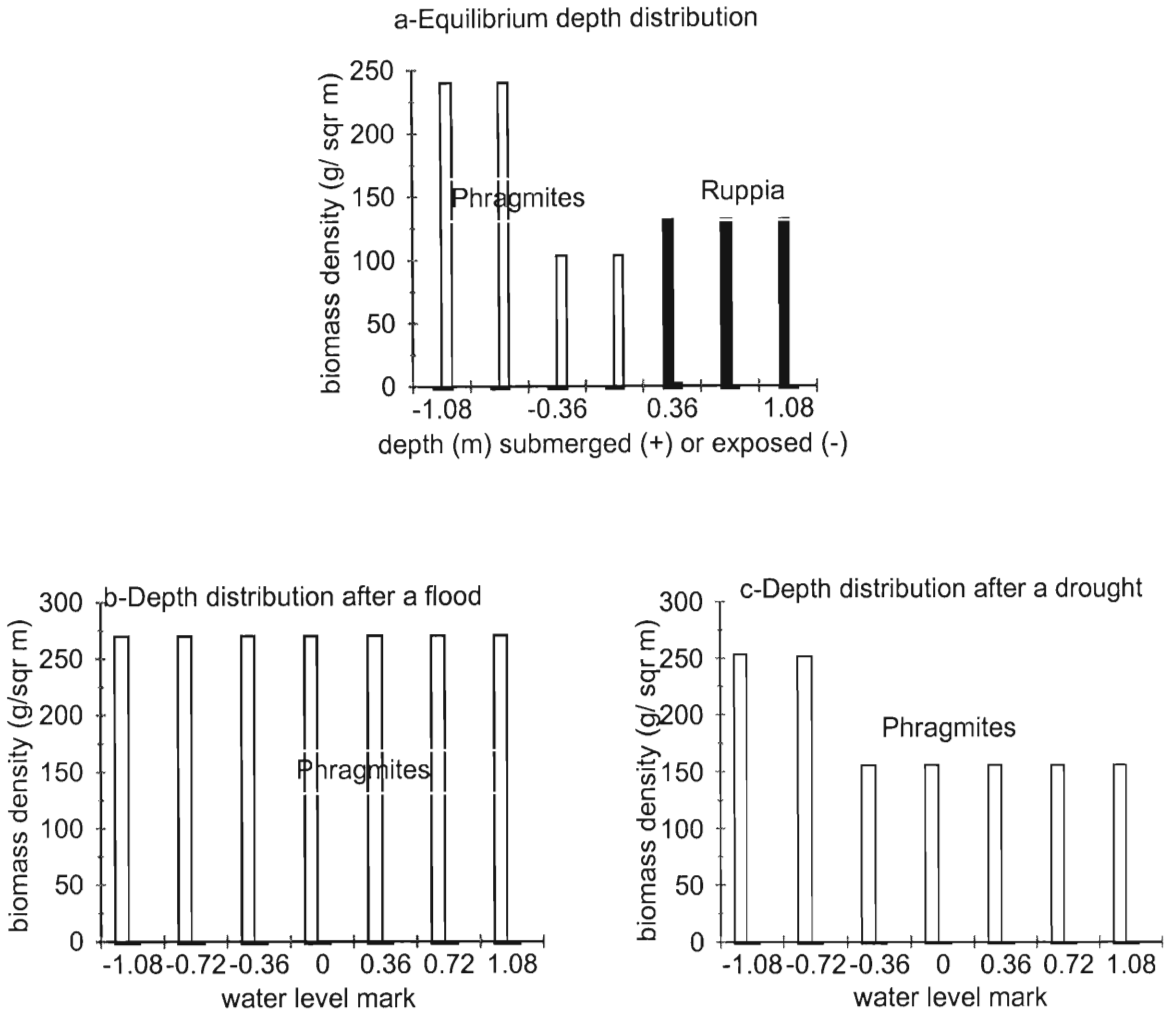

Figure 4.22. Depth distribution of *Phragmites* and *Ruppia* in the upper reaches of the Great Brak estuary for (a) the natural runoff scenario, (b) after a flood, (c) after a drought. In both cases *Phragmites* encroaches into the *Ruppia*-dominated section of the estuary.

4.8.3 Pre-dam Runoff Scenario: MAR = 24.5 x 10^6 $m^3.yr^{-1}$

This scenario represents a reduction in runoff attributable to the construction of farm dams and consumptive use by irrigation. The purpose of the scenario is to determine whether these impoundments significantly alter the state of the estuary from its natural condition. Under the pre-dam scenario, the mouth is open for between 50% and 70% of the time, with the mouth closing for 3 to 5 months during dry periods. Thus the mouth is closed for a longer time than the natural situation (the mouth was closed for no longer than one month). We therefore need to determine how the change in the mouth condition affects the spatial location of the macrophytes and their response to flood conditions or drought conditions.

Since the average salinity in the upper reaches predicted by the physical models is 5 ppt., *Phragmites* can be expected to survive in the upper reaches. However, we cannot conclude offhand how the salinity fluctuations will affect the survival of *Phragmites*. Model results show that *Phragmites* does not survive under this release policy.

4.8.3.1 Equilibrium States

The equilibrium states for the single macrophyte communities are shown in table 4.23.

Table 4.23. The equilibrium states for *Zostera* and *Ruppia* in the Great Brak estuary for pre-dam runoff conditions for the single macrophyte communities. For the equilibrium states biomass density fluctuates periodically over a period of one year. The maximum and minimum periodic biomass density is shown. All the states are stable in the absence of other macrophytes. *Phragmites* does not survive under the pre-dam scenario.

Location in estuary	State	Macrophyte biomass density ($g.m^{-2}$)
R2	*Zostera*	$Z \in (256,258)$
R4	*Zostera*	$Z \in (171,185)$
	Ruppia	$R \in (233,234)$
R8	*Zostera*	$Z \in (32,33)$
	Ruppia	$R \in (162,163)$

The difference between this runoff scenario and the natural runoff scenario is that in the absence of *Ruppia*, the estuary will become marine-dominated. If *Ruppia* is present, then the middle (R4) and upper reaches (R8) will become *Ruppia* dominated. Another difference between the pre-dam runoff scenario and the natural run-of scenario is that *Phragmites* does not survive under the pre-dam runoff scenario whereas it is present under the natural runoff scenario.

4.8.3.2 Spatial Distribution

If we assume that both *Ruppia* and *Zostera* are initially present throughout the estuary, then applying the pre-dam release policy will result in the boundary between *Zostera* and *Ruppia* under the pre-dam occurring 1.5 km from the mouth, with *Zostera* surviving below 1.5 km from the mouth, and *Ruppia* surviving from 1.5 km from the mouth to the upper reaches. This boundary is 0.5 km up from the natural boundary. The division between *Zostera* and *Ruppia* is shown in figure 4.23.

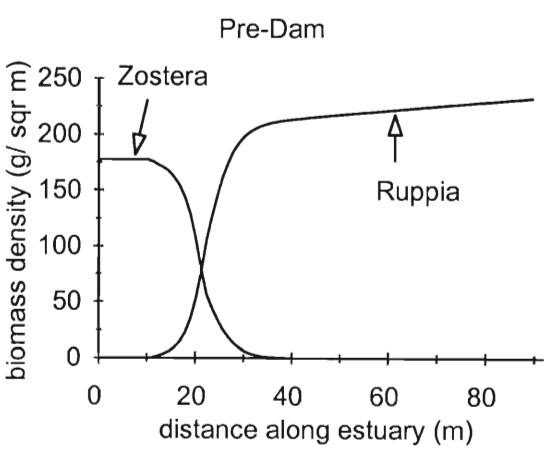

Figure 4.23. Under pre-dam runoff conditions for the Great Brak estuary, if *Ruppia* and *Zostera* are initially present in the estuary, then the division between *Zostera* and *Ruppia* occurs 1.5 km from the estuary mouth.

4.8.3.3 The Effect a Flood or Drought on the Equilibrium States

The results for the disturbance scenarios are shown in tables 4.24 and 4.25.

Table 4.24. The response of the pre-dam equilibrium states to a drought. The biomass density after the drought is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state.

Location	State	Before ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
R2	Z only	$Z \in (256, 258)$	Z=21.7	1 year 1 month	No
R4	Z only	$Z \in (171, 185)$	Z=29	210 days	No
	R only	$R \in (233, 234)$	R=20	1 year, 330 days	No
R8	Z only	$Z \in (32, 33)$	Z=23	1 year, 2 months	No
	R only	$R \in (162, 163)$	R=52	1 year, 1 month	No

Table 4.25. The response of the pre-dam equilibrium states to a flood. The biomass density after the flood is shown. The recovery time is the time the system takes to return to the equilibrium state, if the system returns to the equilibrium state.

Location	State	Before ($g.m^{-2}$)	After ($g.m^{-2}$)	Recovery time	New State?
R2	Z only	$Z \in (256, 258)$	Z=46	210 days	No
R4	Z only	$Z \in (171, 185)$	Z=60	90 days	No
	R only	$R \in (233, 234)$	R=12	1 year, 210 days	No
R8	Z only	$Z \in (32, 33)$	Z=0		Yes, Z=0
	R only	$R \in (162, 163)$	R=8	1 year, 270 days	No

The results show that there is no switch in equilibrium states after a drought or a flood has been imposed on the pre-dam runoff scenario, except the equilibrium state where *Zostera* is

present in the upper reaches. Results show that *Zostera* is eliminated during the 1 in 50 year flood. This may be a useful result for the following reason: If the Great Brak estuary is marine dominated, then imposing a flood will eliminate the marine component in the upper reaches. If a small amount of *Ruppia* is introduced into the upper reaches, this will ensure that the upper reaches do not become marine dominated again (i.e. the upper reaches will settle to the stable *Ruppia* dominated state).

4.8.4 Post-dam Runoff Scenario: MAR = 10 x 10^6 $m^3.yr^{-1}$

The physical models predict that the estuary mouth would be open for between 30% and 50% of the year. So this scenario has the longest period of mouth closure.

Model results show that the only stable equilibrium state is *Zostera* present throughout the estuary. The periodic equilibrium biomass of *Zostera* is stable, and is between 259 $g.m^{-2}$ and 260 $g.m^{-2}$, 267.2 $g.m^{-2}$ and 267.7 $g.m^{-2}$, and 283 $g.m^{-2}$ and 283 $g.m^{-2}$ in the lower, middle and upper reaches respectively.

If *Zostera* is absent, then *Ruppia* can survive in the middle and upper reaches with an equilibrium biomass density of 131 $g.m^{-2}$ and 142 $g.m^{-2}$ respectively.

The response of *Zostera* to a drought under post-dam runoff conditions is on average a 12% reduction in biomass in the lower, middle and upper reaches. The recovery time after the drought is on average 150 days, with the mouth having a faster recovery time of 120 days.

The response of *Zostera* to a flood under post-dam runoff conditions is on average a 66% reduction in biomass in the lower, middle and upper reaches. The recovery time after the flood is on average 270 days, with the lower reaches having a faster recovery time of 210 days.

Ruppia biomass density decreases to 34 $g.m^{-2}$ and 35 $g.m^{-2}$ after a flood in the middle and upper reaches respectively, with a recovery time of 1 year 3 months and 1 year 5 months respectively. During a drought, *Ruppia* biomass density decreases by 16% for the middle and upper reaches and takes 5 months and 6 months to recover in the middle and upper reaches respectively.

4.8.5 Implications for Management

A reduction in freshwater flow favours the encroachment of *Zostera*. The purpose of this study is to determine the colonisation rate of *Zostera* in the Great Brak estuary due to the imposition of pre-dam runoff releases and post-dam runoff releases.

Results were obtained by applying the pre-dam and post-dam runoff scenarios to the natural runoff scenario. Under natural runoff conditions, the boundary between *Zostera* and *Ruppia* occurs approximately 1 km up from the estuary mouth. Results (table 4.26) show that after 3 years of pre-dam conditions, this boundary has moved 23 m up the estuary, while after 3 years of post-dam runoff conditions, *Zostera* has encroached 36 m up the estuary. The reason for the difference in spread rates is due to two factors.

(1) Values of the salinity multipliers for *Zostera* for the pre-dam and post-dam scenarios are different: The average salinity growth and mortality multipliers for *Zostera* (along the boundary between *Zostera* and *Ruppia*) are 0.767 and 0.115 respectively for the pre-dam scenario, and 0.992 and 0.014 respectively for the post-dam scenario. Thus the salinity growth multiplier of *Zostera* is greater under post-dam runoff conditions than pre-dam runoff conditions, and the salinity mortality multiplier is smaller under the post-dam regime than under the pre-dam regime. This contributes to a greater encroachment rate under post dam runoff conditions than under pre-dam runoff conditions, and

(2) The salinity growth and mortality multiplier for *Ruppia* along the section modelled is 0.99 and 0.023 respectively for the pre-dam scenario, and 0.74 and 0.129 respectively for the post-dam scenario. Therefore the slower growth rate and the greater mortality rate of *Ruppia* under post-dam conditions contributes to a faster colonisation rate of *Zostera*.

Table 4.26. The response of the natural system in figure 4.21 to one and three year periods of *pre-dam* and *post-dam* runoff conditions in the Great Brak estuary.

Condition	natural	pre-dam		post-dam	
		after 1 yr	after 3 yr	after 1 yr	after 3 yr
max biomass Z ($g.m^{-2}$)	100	180	180	180	180
max biomass R ($g.m^{-2)}$	170	180	180	80	30
relative boundary position (m)	0	+3	+23	+12	+36

Under pre-dam conditions, the encroachment of *Zostera* will stop approximately 500 metres up from the natural boundary. However, under post-dam runoff conditions, *Zostera* will colonise the upper reaches because phase-plane analysis showed that *Zostera* can survive in the upper reaches, even if *Ruppia* is initially present.

The total biomass of *Zostera* and *Ruppia* along the Great Brak estuary was calculated for the stable equilibrium states. This is presented in figure 4.24 below where the biomass is reflected as a percentage of the biomass under natural runoff conditions.

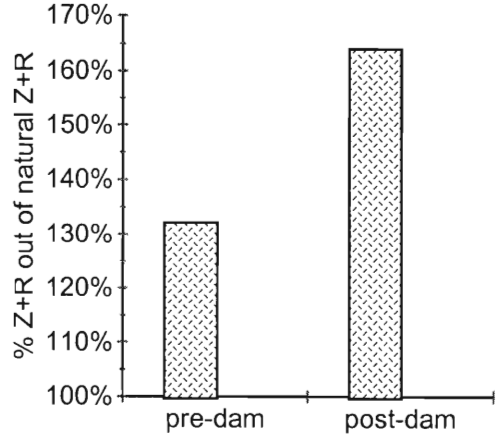

Figure 4.24. The ratio of total *Zostera* and *Ruppia* biomass in the Great Brak estuary for the stable equilibrium states as a percentage of the corresponding biomass under natural runoff conditions.

The graph in figure 4.24 shows that the post-dam scenario and the pre-dam scenario have a greater total biomass of *Zostera* and *Ruppia* than the natural runoff scenario. The stable equilibrium state for the post-dam runoff scenario is a marine-dominated state with *Zostera* present from the mouth to the head of the estuary. The natural runoff scenario is better than the post-dam runoff scenario in that natural runoff results in a multi-species estuarine ecosystem with both *Zostera* and *Ruppia* present along various sections of the estuary. However, the post-dam runoff scenario is better than the natural runoff scenario in that it has a higher total biomass, comprising *Zostera* only, than the total biomass of *Zostera* and *Ruppia* under natural runoff conditions.

4.8.6 Comparison of Results with Expert System Results

Selected results for the scenarios from the expert system model are presented. The results show the plant response to the mean salinity, water level and current velocity for each runoff scenario. This means that extreme salinities and variations in the conditions of the mouth are not taken into account.

The results of the expert system model show that under the natural and pre-dam runoff scenarios *Zostera* would not be found in the upper reaches (R8) of the estuary (table 4.27, growth rate adjustment scores are negative). The mathematical model predicts that *Zostera* can survive in the upper reaches (R8) under pre-dam runoff conditions provided *Ruppia* is absent. Under the pre-dam runoff scenario, at station R8, the average salinity is 5.3 ppt. *Zostera* does not survive under these salinities. However, the salinity fluctuates between 18 ppt. and 0.7 ppt. for the pre-dam runoff scenario. The mathematical model incorporates the daily salinity changes and predicts that *Zostera* can survive.

Results from the expert system model showed that optimal *Zostera* growth would occur under post-dam conditions. This agrees with the mathematical model results.

Table 4.27. Growth rate adjustment scores for the submerged macrophyte *Zostera capensis* at different stations in the Great Brak estuary for the runoff scenarios.

Runoff scenario	Stations			
	R2	R4	R6	R8
Natural runoff	7	10	2.7	-4.4
Pre-dam runoff	7	10	10	-4.5
Post dam runoff	7	10	10	10

Growth rate adjustment scores for *Ruppia* did not differ for the different runoff scenarios (table 4.28), and results indicate that *Ruppia* can survive in the lower, middle and upper reaches. In the absence of *Zostera*, the mathematical model predicted that *Ruppia* was not able to survive in the lower reaches. This is because the model includes dynamic changes in the mouth condition, whereas the expert system model is static and the predictions are based on the average salinity, water level and current velocity.

Table 4.28. Growth rate adjustment scores for the submerged macrophyte *Ruppia cirrhosa* at different stations in the Great Brak estuary for the runoff scenarios.

Runoff scenario	Stations			
	R2	R4	R6	R8
Natural runoff	7	10	10	10
Pre-dam runoff	7	10	10	10
Post dam runoff	7	10	10	10

The expert system model predicts that *Phragmites* can survive under all release policies. The mathematical model predicts that *Phragmites* only survives under the natural runoff scenario. This is because the mathematical model incorporates daily variations in the salinity.

4.8.7 Discussion of Results for the Great Brak Estuary

Zostera, *Ruppia* and *Phragmites* coexist for the natural runoff scenario only. That is, any impoundment in the catchment of the Great Brak estuary will result in a loss of *Phragmites*

habitats. This result is different from the Kromme estuary where *Zostera*, *Phragmites* and *Ruppia* can survive impoundments with a mean annual runoff of 20% MAR.

For the natural runoff scenario, *Phragmites* and *Ruppia* can coexist in the upper reaches. However, the imposition of a flood or drought results in *Phragmites* encroachment into the *Ruppia* dominated areas, resulting in the disappearance of *Ruppia* in the upper reaches. If *Phragmites* is absent then *Ruppia* can survive the disturbance, so the disappearance of *Ruppia* when *Phragmites* is present is due to interactions between *Phragmites* and *Ruppia* beds. The recovery time for *Phragmites* after a flood or drought is 7 months and one month respectively. The recovery times for *Zostera* and *Ruppia* after a flood or drought for the natural runoff scenario varied between one and three years.

Without *Zostera*, *Ruppia* can survive under all runoff scenarios. If *Zostera* is present, then *Ruppia* survives under natural and pre-dam runoff conditions only. For the natural runoff scenario, *Ruppia* survives from 1 km up from the mouth to the upper reaches. For the pre-dam runoff scenario, *Ruppia* survives from 1.5 km up from the mouth to the upper reaches. The recovery times for *Zostera* and *Ruppia* after a flood or drought under pre-dam runoff conditions are less than those for the natural runoff scenario, and vary between 3 months and 1 year 11 months, with *Zostera* overall having faster recovery times than *Ruppia*.

If *Zostera* is present, then *Ruppia* does not survive under the post-dam runoff scenario, and the estuary therefore becomes marine dominated. The recovery time for *Zostera* after the disturbance scenarios is less than one year for the post-dam runoff scenario.

Achieving a marine dominated estuary for the pre-dam runoff scenario is possible provided *Ruppia* is absent from the estuary. However, if a flood is imposed on this system, then *Zostera* is eliminated from the upper reaches. So if the estuary is dominated by *Zostera* under pre-dam runoff conditions, then a flood may be used to eliminate *Zostera* from the upper reaches. If *Ruppia* is then introduced in the upper reaches it will survive because stability analysis showed that the equilibrium state of *Ruppia* in the upper reaches is stable for the pre-dam scenario.

Results showed that *Zostera* encroachment rate increased with an increase in impoundment. For example, three years of pre-dam and post-dam runoff conditions resulted in a *Zostera*

encroachment rate of 23 m and 36 m respectively. Impoundments also diminish the effect of floods on *Zostera*: In the lower reaches, for example, *Zostera* biomass density decreased by 89%, 82%, and 66% during a flood for the natural runoff scenario, the pre-dam scenario and the post-dam scenario respectively.

4.9 Conclusion

The macrophyte model was used to determine the spatial and temporal response of the plants to freshwater inflow in two South African estuaries. The results showed that the outcome for a particular scenario may vary depending on the initial conditions. If a flood or drought disturbance was imposed on certain scenarios, then this resulted in a switch from one equilibrium state to another equilibrium state. In general the recovery time after the disturbance scenario increased with a decrease in freshwater impoundment. That is, impoundments appear to reduce the dynamic nature of estuaries. The model was used to determine the encroachment rate of *Zostera* as freshwater flow decreased. Results showed that not only is this rate dependent on the volume of freshwater inflow (the greater the impoundment, the greater the encroachment rate), but it is also dependent on how much *Ruppia* is present in the estuary: *Ruppia* slowed the encroachment rate of *Zostera*. Some results did not agree with the expert system model results. This is because the expert system model does not include dynamic changes in the physical conditions.

The plant expert system model, the mathematical models in this thesis, and the hydrodynamic models used to obtain the physical data for the plant models, were part of a project designed to determine the freshwater requirements of estuaries. The project focussed on the physical changes associated with freshwater flows, and on the ecological implications on the downstream estuary. A model of mud prawn and fish recruitment also formed part of the ecological models with the plant models. Details of the progress of this collaborative research project and results are contained in Slinger (1994, 1995, 1996). The project highlighted the need for long term monitoring of estuaries in South Africa. The application of the models to two case study estuaries in South Africa, namely the Kromme and Great Brak estuaries, was successful, and can be applied to further estuaries when data becomes available (the physical models require certain basic data before their implementation can be considered, for example water level recordings, hydrological cycles and mouth monitoring).

CHAPTER 5

TECHNICAL ANALYSIS

The purpose of this chapter is to examine the sensitivity of the cellular automata model in the light of the purpose of the model. Thus we need to examine how the results for the freshwater runoff scenarios depend on the assumptions which were made in the model derivation.

An illustration of why a technical analysis is necessary is the following: Model results from chapter 4 showed that the critical freshwater flow requirement to the Kromme estuary was 20% MAR: Freshwater allocations lower than this would result in a marine dominated estuary, while freshwater allocations above this volume would lead to a diverse ecosystem. However, if this result is sensitive to variations in say the model parameters, then freshwater managers should not select a policy of an annual allocation of 25% MAR because this may lead to a different outcome to that predicted by the model. In this case, a higher volume should rather be chosen in order to take the sensitivity of the model to parameter changes into account.

The technical analysis is performed on the cellular automata model. One of the aims of the technical analysis is to answer questions such as how does using a different cell size effect the results for the runoff scenarios. The model was simulated on a grid with small cells in relation to the length of the estuary (length of cell side = 0.4 m, length of Kromme estuary = 13.7 km, length of Great Brak estuary = 7.4 km). The reason why a small cell size was selected was so that the dynamics of the intertidal plants could be modelled. This required a small cell size in order to include the water level fluctuations. (The difference between the daily high and low water level mark was on average not greater than 1 m). However if for a particular runoff scenario the dynamics of the intertidal zone is not important, then we could increase the cell size and model a greater length of the estuary. However, before we do this we need to be aware of the consequences of changing the cell size on the model results.

The results for the case studies were based on the assumption that spread occurred radially, irrespective of neighbour biomass density. It is important to know how the encroachment rate would change if spread is not radial. The encroachment rate shows how fast an area would be

colonised, and is important in low freshwater flow scenarios where *Zostera* encroaches up the estuary and displaces brackish communities. If the technical analysis indicates that the predicted spread rate for the run off scenarios depends on the spread mechanism, then this could have severe implications on management decisions which allow *Zostera* to encroach for a certain period of time, or which are expecting the estuary to become marine dominated within a certain number of years.

Being parameters measured in the field and laboratory, the specific growth rate and specific mortality rate of *Zostera*, *Ruppia* or *Phragmites* may not be correct. A technical analysis is therefore used to determine how variations in the parameter values change the results of the runoff scenarios for the Kromme and Great Brak case studies.

If the technical study shows that the results for the various release policies change if a model function or parameter is varied, then this does not mean that the model is not a useful tool in freshwater decision making processes. The model was derived based on the data which was available. As more data becomes available the model can be refined, and calibrated to additional field results. For the present state of the model, freshwater managers need to know whether or not the outcome to the release policies is sensitive to the model assumptions so that in the decision making process, both the outcome and the sensitivity may be taken into account.

5.1 Analysis of Model Sensitivity to Cell Size

The choice of a cell width of 0.4 m in the cellular automata model of estuarine macrophytes was not the only one possible, and therefore an analysis of the effect of cell size on model results is necessary. An important result from the model is the encroachment rate. Therefore we need to know the effect on this rate if a different cell size had been used for the runoff scenarios. We start with a theoretical analysis, following which a scenario-based case study for various cell sizes is conducted in order to determine the relationship between cell size and encroachment rates and colonisation patterns.

For this analysis the equations for above- and below-ground biomass are not considered. The equations analysed are the cellular automata equations because they are the equations responsible for the spread.

5.1.1 Theoretical Analysis

For this analysis we use rectangular grids rather than hexagonal grids in order to keep the analysis simple. The purpose of this study is to determine whether the model predictions change for a different cell size. We are not concerned with accuracy in results, hence the shape of the cell, namely rectangular or hexagonal, is irrelevant. The aim is to determine only if there is a difference in predictions for different cell sizes.

Consider the scenarios in figures 5.1 a and b. Let figures 5.1 a and b correspond to scenario A and scenario B respectively.

Let:
the area of the rectangle in figure 5.1a between 0 and L be A,
the area of each rectangle in figure 5.1b, between 0 and 1/2 L, and 1/2 L and L, be 1/2A,
the carrying capacity (maximum biomass density) of the rectangle figure 5.1a be K, and
the carrying capacity (maximum biomass density) of each rectangle in figure 5.1b, between 0 and 1/2 L, and 1/2 L and L, be 1/2 K.

For initial biomass in the shaded region in the figures, the cellular automata model predicts that expansion across L in figure 5.1a will occur when the biomass density in the rectangle between 0 and L is equal to

$$\textit{expansion across } L \textit{ when biomass density} = \frac{1}{3}K = g_1.K \qquad (5.1)$$

where g_1 is the growth function of the CA model and is defined in figure 3.6 pp.60. Note that we have not used the full CA model. We have only examined the portion of the CA model that determines total growth (internal and expansion) from a cell.

The corresponding expansion from the cells in (b) will occur when the total biomass density across the region between 0 and L in figure 5.1b is

$$\textit{expansion across } L \textit{ when biomass density} = \frac{1}{2}K.\frac{1}{3} + e + \frac{1}{2}K.\frac{1}{3} = \frac{1}{3}K + e \quad (5.2)$$

where e is the increase in biomass density in the rectangle between 0 and 1/2 L once expansion has occurred across 1/2 L in figure 5.1 b.

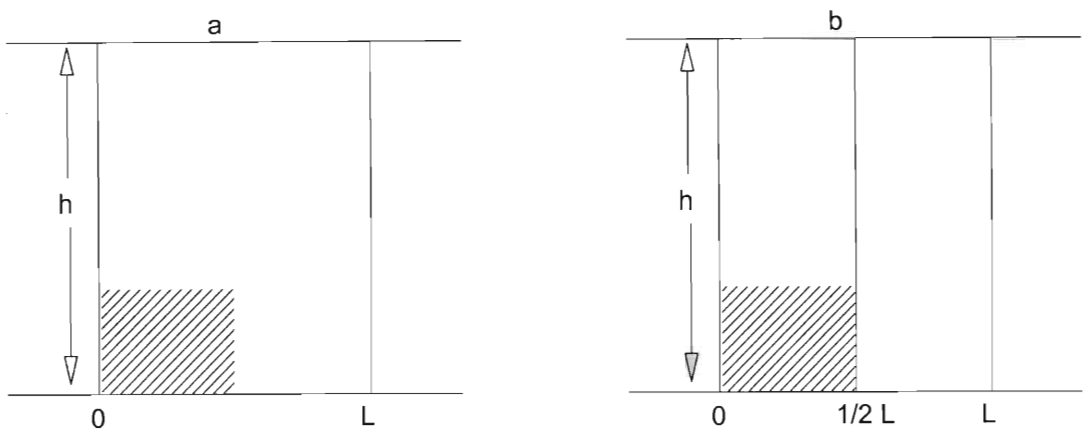

Figure 5.1. For the same initial biomass density, the CA model predicts that the total biomass density between 0 and L in (b) is greater than the biomass density between 0 and L in (a) when expansion into the region R occurs.

Since

$$\frac{1}{K} + e > \frac{1}{K}$$

where e is the increase in biomass density in the rectangle between 0 and 1/2 L once expansion has occurred across 1/2 L in figure 5.1 b, the biomass density in scenario B is greater than that in scenario A when expansion across L occurs. So the larger the cell size, the lower the biomass density when expansion across a particular point occurs. The following section explores this aspect of model behaviour further, and determines how the encroachment rate is related to cell size.

5.1.2 Scenario Analysis

Model simulations are conducted in order to determine how results vary with cell size. In particular, the simulations are used to examine the encroachment rate and biomass density distribution for various cell sizes. The model simulations are run in Turbo Pascal. The assumptions for the investigation are:

K	= 10 biomass units per unit area,
maximum specific growth rate	= 1 biomass unit per biomass unit per year,
maximum specific mortality rate	= 1 biomass unit per biomass unit per year,
time step	= one day,
initial biomass	= 10 biomass units per unit area, evenly distributed over an area of 1.1 m by 1.2 m in the top left corner of the grid (i.e. the (0,0) th cell). If it is necessary to split biomass density across p number of cells, then each cell is assigned a biomass density of 10/p,
gm_{ij}	= 1, and
dm_{ij}	= 0.

We assume that the physical conditions are ideal for growth so that the model predicts the maximum amount of spread and the maximum amount of local growth possible. This would then give the worst case scenario in terms of differences in results predicted using the various cell sizes. For comparison with the estuarine macrophyte model, biomass is density is in units of $g.m^{-2}$ and length is in units of m.

The range of cell sizes for the analysis are shown in table 5.1.

Table 5.1. The cell sizes used in the study to determine the effect of cell size on biomass dynamics. x is the width of the hexagon side and y is the height of the hexagon.

Cell area	x	y
0.4	0.41	0.4
0.73	0.60008	0.6
1.07	0.69	0.684
2.63	1.1402	1.14
3	1.201	1.2
4.66	1.5008	1.5
6.15	1.75003	1.75
8.25	2.001	2
9.1	2.13002	2.13
12.61	2.5001	2.5
18.46	3.001	3

For each scenario, the model is run until the initial biomass reaches a Y target cell, i.e. until initial biomass spreads across a specified distance towards the right. The distance selected is 10 m, so that for the largest cell spread has to occur across at least two cells in order to reach the target distance. This is where inaccuracies are introduced in the analysis: For example, for a grid with successive cells with y_i=9.5 and y_{i+1}=10.2, there is some doubt as to when biomass crosses the 10 m point. Thus, in selecting a target cell the following rules are adopted:

(a) If y_i = 10 m then y_i is the target cell,

(b) If y_i < 10 m and y_{i+1} > 10 m then if the mean of y_i and y_{i+1} > 10 m then y_i is the target cell, otherwise y_{i+1} is the target cell.

Once the target cell is reached, the time and the biomass covering the region from the (0,0) th cell to (X,Y) th cell is recorded where X denotes the x co-ordinate of the target cell and Y

denotes the y co-ordinate of the target cell. The X target cell is defined as the closest hexagon in the vertical direction to 10 m. This cell is chosen as follows:

(a) If $x_i = 10$ m then x_i is the target cell, otherwise

(b) If $x_i < 10$ m then x_{i+1} is the target cell, otherwise

(c) If $x_i > 10$ m then x_i is the target cell.

The target cells for the scenarios are given in table 5.2.

Table 5.2. Target cells for the scenarios defined in table 5.1 (p. 155). The target cells are given in italics. The target cell is the closest cell to 10 m in the x or y direction. See the text for an explanation of how the target cell is determined. Adjacent cells are included to illustrate that the simulation results are not accurate because there is seldom a cell with a 10 m co-ordinate.

Cell area (m^2)	x target cell (m)	y target cell (m)
0.4	$x_{25} = 10.00$	$y_{20} = 10.00$
0.73	$x_{17} = 10.20$, $x_{18} = 10.80$	$y_{16} = 9.78$, $y_{17} = 10.39$,
1.07	$x_{14} = 9.58$, $x_{15} = 10.26$	$y_{13} = 10.15$, $y_{14} = 10.93$
2.63	$x_8 = 9.12$, $x_9 = 10.26$	$y_8 = 9.24$, $y_9 = 10.4$
3	$x_8 = 9.59$, $x_9 = 10.79$	$y_7 = 8.74$, $y_8 = 9.99$
4.66	$x_6 = 8.99$, $x_7 = 10.49$	$y_6 = 9.33$, $y_7 = 10.88$
6.15	$x_5 = 8.75$, $x_6 = 10.50$	$y_5 = 8.78$, $y_6 = 10.54$
8.25	$x_4 = 8.00$, $x_5 = 10.00$	$y_4 = 8.25$, $y_5 = 10.32$
9.1	$x_4 = 8.52$, $x_5 = 10.65$	$y_4 = 8.55$, $y_5 = 10.68$
12.61	$x_4 = 10.00$	$y_3 = 7.57$, $y_4 = 10.09$
18.46	$x_3 = 9.00$, $x_4 = 12.00$	$y_3 = 9.23$, $y_4 = 12.31$

The simulations are used to determine the time taken to expand across the target length and the corresponding biomass density distribution across the length for the various cell sizes. The

results show that the larger the cell size, the faster the outward expansion rate (figure 5.2). The graph in figure 5.2 shows that this relationship is exponential or hyperbolic.

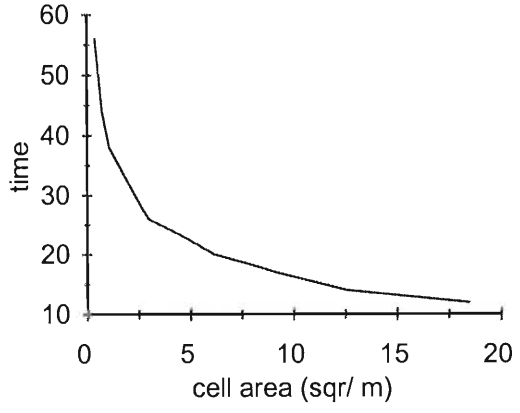

Figure 5.2. The graph of cell area verses the time taken to expand approximately 10 m.

To examine the resulting biomass density the results for three cell sizes are analysed, namely cell areas of 3 (length of side = 1.2), 6.15 (length of side = 1.75) and 12.61 (length of side = 2.5). Results show that after two years there is a biomass density of

(a) 23, between 2.5 m horizontally and 2.4 m vertically,
(b) 39 between 3.51 m horizontally and 3.5 m vertically, and
(c) 47 between 5.04 m horizontally and 5 m vertically respectively.

Similarly, after four years the total biomass density cover for the respective cell sizes is

(a) 46 (distribution area unchanged from that at two years),
(b) 69 (distribution area unchanged from that at two years), and
(c) 104 (distribution area 7.6 m horizontally and 7.5 m vertically).

Therefore not only do grids with large cells result in faster encroachment rates, but they also result in a higher biomass density cover at a specified time. This is due to the density-dependent growth function g_1 in the model equations: The smaller the cell area, the more

intense the competition for space, therefore the smaller the rate of biomass increase. When the cellular automata model was applied to the Kromme and Great Brak estuaries it had already been calibrated to allow for this concern. The method used to calibrate the model is described in the following section.

5.1.3 Model Calibration

5.1.3.1 Method

Results from the previous study showed that model predictions vary with cell size. In particular the time taken to expand over a certain distance and the resultant biomass density at a particular time depends on the size of the cells. The purpose of this study is to determine whether the parameters in the cellular automata model can be scaled to make the dynamics independent of cell size. The difference between a grid with large cells and a grid with small cells is that for the same model parameters, the outward expansion rate is faster in the grid with large sites than in the one with small sites. That is, either biomass in the large cells grows too quickly, or biomass in the small cells grows too slowly. This is a result of the density-dependent growth function g_1 in the model rules.

For the calibration, biomass density is scaled to a value between zero and one. Zero state shows an empty cell and a state of one shows that a cell has reached carrying capacity. We assume that the vegetation can spread up to 27 m radially in one year under ideal conditions. (To ease comparison with the estuarine macrophyte model, biomass density is in units of $g.m^{-2}$ and length is in units of m). The purpose of this investigation is to determine whether the specific growth and mortality rates can be scaled in such a way to produce a spread rate of 27 m per year for a grid with any cell size, and to produce the same resulting biomass distribution for a grid with any cell size, given that the only information available is the maximum yearly spread rate. The reason we choose to calibrate in this manner is that the only quantitative information regarding spread of estuarine macrophytes is the yearly observed spread rate (Adams and Talbot 1992; Talbot and Bate 1987).

The model rules are rewritten as

$$g(b_{ij}) = \alpha gm_{ij} b_{ij} g_1(b_{ij})[1 - g_2(b_{ij})] + \sum_{k,l \in n_{ij}} \frac{1}{6} \alpha gm_{kl} b_{kl} g_1(b_{kl}) g_2(b_{kl}) g_3(b_{ij}) \quad (5.3)$$

$$m(b_{ij}) = \frac{\beta}{4} dm_{ij} b_{ij} \quad (5.4)$$

where:

b_{ij}	is the calibrated biomass density on a scale between zero and one,
gm_{ij}	is the rate of growth of biomass density in the (i,j) th cell,
dm_{ij}	is the rate of mortality of biomass density in the (i,j) th cell,
n_{ij}	is the neighbourhood set of the (i,j) th cell, and
α and β	are the maximum expansion parameters.

Recall in chapter 4 the mortality rate for the runners was written as:

$$dm_{ij} = \frac{\beta}{4}.U(i,j,t).[g_4(U[i,j,t]) + sdm(sal_{ij}) + wldm(wl_{ij}) + ddm(depth_{ij})]$$

where

β	is the maximum specific mortality rate ($g.g^{-1}.day^{-1}$), and
U	is the runner density on a scale between zero and one.

The reason the maximum specific mortality rate is divided by 4 is so that under the worst case scenario, when all the mortality multipliers are equal to one, the mortality rate is equal to the maximum mortality rate.

In terms of the model, a maximum spread rate means that conditions are optimal for growth. Therefore the growth multiplier is equal to its maximum value, i.e. $gm_{ij}=1$, and the mortality multiplier is equal to its minimum value, i.e. $dm_{ij}=0$.

The cell sizes used for the scenarios have widths that vary between 0.2 m (area = 0.103 m^2) to 8 m (area = 164.66 m^2). For the investigation initial biomass density distribution is 10 $g.m^{-2}$ evenly distributed over an area of 1.1 m by 1.2 m in the top left corner of the grid. If distributing biomass across p number of cells is necessary, then each cell is assigned a biomass of 10/p.

For each scenario, the value of α in (5.3) is varied until the model yields a radial spread rate of 27 m per year. The method from the section 5.1.2 is used to determine when 27 m is reached. That is, if there is a cell with a y-co-ordinate of 27, then that cell is the target cell, otherwise if $y_i < 27$ m and $y_{i+1} > 27$ m then if mid point of $y_i > 27$ m then y_i is the target cell, otherwise y_{i+1} is the target cell.

Table 5.3 shows the values of α for different cell sizes that yield a radial spread rate of 27 m per year. Note that the larger the cell, the smaller α. Thus to achieve the same spread rate for grids with different scales, the parameter α must be small for grids with large cells so that the growth in these cells is diminished, thus reducing the normally fast spread rate associated with large cells. For grids with small cells, α must be high to increase the growth in small cells and speed up the normally slow spread rate associated with small cells.

Table 5.3 shows that there is a hyperbolic relationship between the width of the hexagon and α, with their product equal to 0.2 + e where e is less than 0.05 (figure 5.3). These results suggest that for vegetation that spreads 27 m in one year, any cell size between the range studied may be used for the CA model provided the product of the expansion parameter and cell width is 0.2 + e where $e < 0.05$.

Table 5.3. The relationship between cell size and the expansion parameter α in equation (5.3). The first column shows the cell width, the second column shows the calibrated value of α, and the third column is the product of α and the cell width.

Cell width	α	α*width
0.365	0.68	0.248
0.729	0.28	0.204
1.094	0.188	0.206
1.458	0.14	0.204
1.73	0.12	0.208
2.734	0.075	0.205
5.469	0.04	0.219
10.938	0.0214	0.234
14.583	0.017	0.248

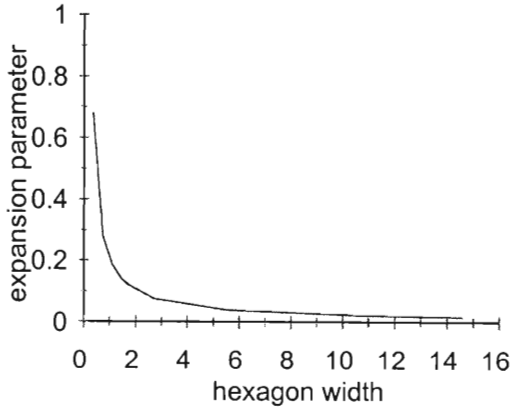

Figure 5.3. The graph of the expansion parameter α and the cell width. The relationship is hyperbolic.

The predicted distance spread for the calibrated model for grids with cells of width 0.365 (area 0.103), 0.73 (area 0.412), 1.458 (area 1.647), 2.734 (5.789) and 5.469 (area 23.156) are plotted in the bar graph in figure 5.4. The grid with the largest cell size, shows the greatest variation

from the distance predictions. However, an encroachment distance after one year of 25.405 m in the horizontal direction for the largest cell size is not necessarily 25.405 m because the next y co-ordinate is 29.639, so the recording 25.405 m means that biomass is distributed between 25.405 and 29.639. The graph shows that for the largest cell size, after one month biomass has not spread from the first cell (the distance spread is zero). However, the first cell on this grid covers a distance to 4.234.

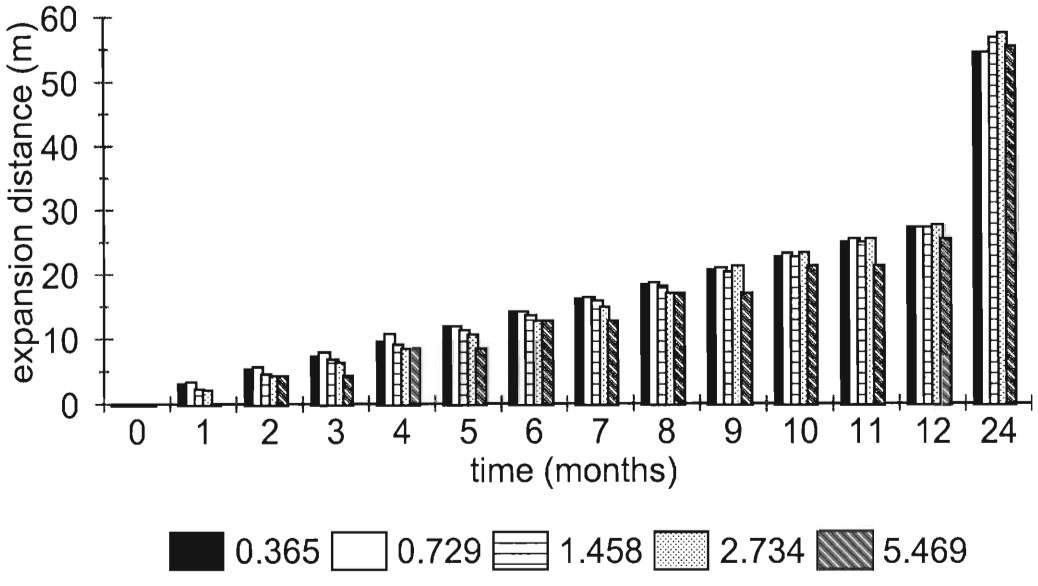

Figure 5.4. Graph of the distance spread for grid sizes given in the legend. The grid sizes correspond to the hexagon width.

The effect of the calibration on the biomass distribution is shown in table 5.4. The biomass in the table is the total biomass (in biomass units) after a spread of 27 m. The total biomass is calculated along a strip of height 3.65 m and length 27 m. The runner density is calibrated on a scale between zero and one. To convert this into biomass units we multiply the runner density by the maximum carrying capacity ($g.m^{-2}$) and by the cell area (m^2).

Table 5.4. The biomass for the scenarios (defined in the first row by the hexagon width). The biomass is the biomass between the distance spread in the horizontal direction and a height of 3.646 m.

Time	Hexagon Width (m)				
	0.365	0.729	1.458	2.734	5.469
0	1.15	1.16	1.16	1.16	1.16
1	8.44	7.15	4.48	4.11	3.7
2	15.44	14.14	10.97	8.34	9.96
3	22.09	20.64	17.32	13.55	13.43
4	28.7	27.03	23.83	19.16	15.51
5	35.33	33.41	30.45	25.01	19.45
6	41.95	39.78	37.2	30.86	27.55
7	48.55	46.14	43.88	37.28	33.81
8	55.13	52.52	50.69	43.13	37.97
9	61.74	58.88	57.45	50.13	43.3
10	68.35	65.27	64.34	56.1	52.56
11	74.97	71.68	71.19	63.04	57.19
12	81.57	78.08	78.02	69.35	62.52

Thus the calibration has not changed the effect that cell size has on biomass distribution: At a particular time, grids with small cells will predict a higher biomass distribution than grids with large cells. This however is not a major factor in the model of estuarine macrophytes because the spread model is only used to describe runner density. Macrophyte biomass dynamics are described by separate equations. That is, the main purpose of the CA model is to predict the right encroachment rate. The dynamics of the existing macrophyte beds are determined by separate equations for above- and below- ground biomass.

5.1.3.2 Implications for the Macrophyte Model

The macrophyte model in chapter 4 was calibrated using the method outlined above. Observations show that the macrophytes can achieve a maximum spread rate of approximately 12 m per year. For the macrophyte model, a value of $\alpha = 0.14$ (equation 5.3) yielded the required encroachment rate. Assigning $\beta = 0.14$ (equation 5.4) yielded spread rates less than or equal to this rate.

The existence of the calibration technique now means that a different cell size can be used and still generate the same spread rate. This is useful when a large area of the estuary needs to be modelled: The cell size may be increased, the expansion parameters calibrated accordingly, and the encroachment rate will remain unchanged.

5.1.4 The Effect of a Different Form of Spread on the Calibrated Model

The results for the Kromme and Great Brak case studies apply to the situation where spread is assumed to occur radially, irrespective of the density of neighbour cells. The purpose of this section is to determine how a different form of spread affects the encroachment rates for the various scenarios.

A theoretical analysis follows to determine whether obtaining different results with a different mechanism of spread is possible. The equations for the above- and below- ground components are not taken into account in the theoretical analysis because the purpose is only to examine how the cellular automata results change as a result of a different spread mechanism.

5.1.4.1 Theoretical Analysis

Low density spread is defined as spread that occurs to the neighbour cell with the lowest density. If there are two cells of equal low density, then equal spread occurs to both cells. For the scenarios from section 5.1.3, model results show that more distance is covered in the same time for low density spread than radial spread (figure 5.5). This is to be expected: In low density spread biomass expands to the cells with lowest competition for space, thereby reducing the biomass lost to competition for space. In radial spread however, more biomass will be lost to competition for space because expansion equally favours high and low density cells. This means that in low density spread, the rate of biomass increment will be greater than

in radial spread and thus the expansion rate will be higher in low density spread than radial spread. For the scenario shown in figure 5.5, the greatest difference is 34% between radial and low density spread after 2 years.

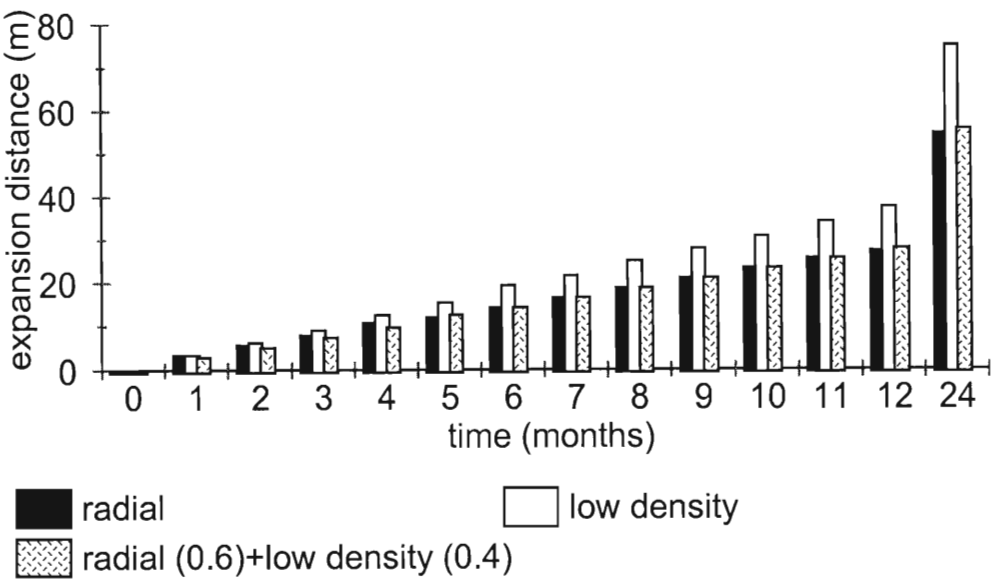

Figure 5.5. A comparison between the distance spread for radial, low density and radial + low density spread. Vegetation that favours low density areas will first expand further than vegetation that expands equally into all adjacent areas. The results in this figure apply to the scenario with a cell width of 0.729.

Rather than considering low density spread only, in their CA model of vegetation spread, Van Tongeren and Prentice (1986) use a weighted spread function: Spread favours low density cells up to a maximum value, thereafter spread is radial. This prevents a large spread rate in one direction only. These effects are incorporated in the model by assuming that 60% of the spread is radial and 40% of the spread favours low density areas. The results shown in figure 5.5 show that there is little difference between the weighted spread and radial spread. (The biggest difference is 11.3% at time = 4).

So a different spread mechanism can lead to different encroachment rates. An important aspect of the scenario-based case studies for the Kromme estuary and for the Great Brak estuary was the impact that perturbations have on release policies. One of these perturbations was a drought for varying periods. Under such conditions, *Zostera* colonised the upper reaches.

Because we are not sure exactly how the macrophytes spread, being aware of how the encroachment rates and the time taken to colonise the upper reaches would change under a different spread mechanism is important. These results should be taken into account when freshwater management decisions are made. In this way, a decision is always based on the worst possible outcome, such as, for example whichever spread mechanism gives the maximum spread rate of *Zostera* into the upper reaches

5.1.4.2 Implications for the Macrophyte Model

The results for the Kromme and Great Brak case studies were derived from the cellular automata model where the assumption was that spread to adjacent sites occurred radially. The purpose of this section is to determine whether a different form of spread will change the encroachment rates for the results of the case studies.

Based on results from the theoretical analysis, the alternative spread mechanism considered is low density spread. This was selected because the theoretical results showed that the greatest difference in predictions occurred between low density spread and radial spread rather than with a combination of radial and low density spread.

5.1.4.2.1 Kromme Case Study

The disturbance scenarios, namely no periods of freshwater inflow, resulted in the encroachment of *Zostera* up the estuary. We therefore examine the effect of the low density spread on the encroachment of *Zostera* under this release policy. The scenarios considered are those which are above the critical volume of freshwater, namely the natural runoff scenario, 40% MAR and 20% MAR. Scenarios with less than 20% MAR resulted in a *Zostera*-dominated estuary.

Natural runoff scenario

The encroachment rate of *Zostera* is 5 m and 29 m after one and three year periods of no freshwater inflow for radial spread (figure 5.6). Under low density spread, the corresponding spread rates for *Zostera* are 28 m and 63 m after one and three year periods of no freshwater inflow (figure 5.6). This is a difference of on average 17 m per year between the radial and low density spread predictions. *Zostera* is known to spread up to a maximum of 12 m per year, so

an encroachment rate of 29 m in one year for low density spread does not seem correct. However, recall that the model has been calibrated to a maximum radial spread of 12 m per year, so obtaining a higher spread rate under low density spread is possible.

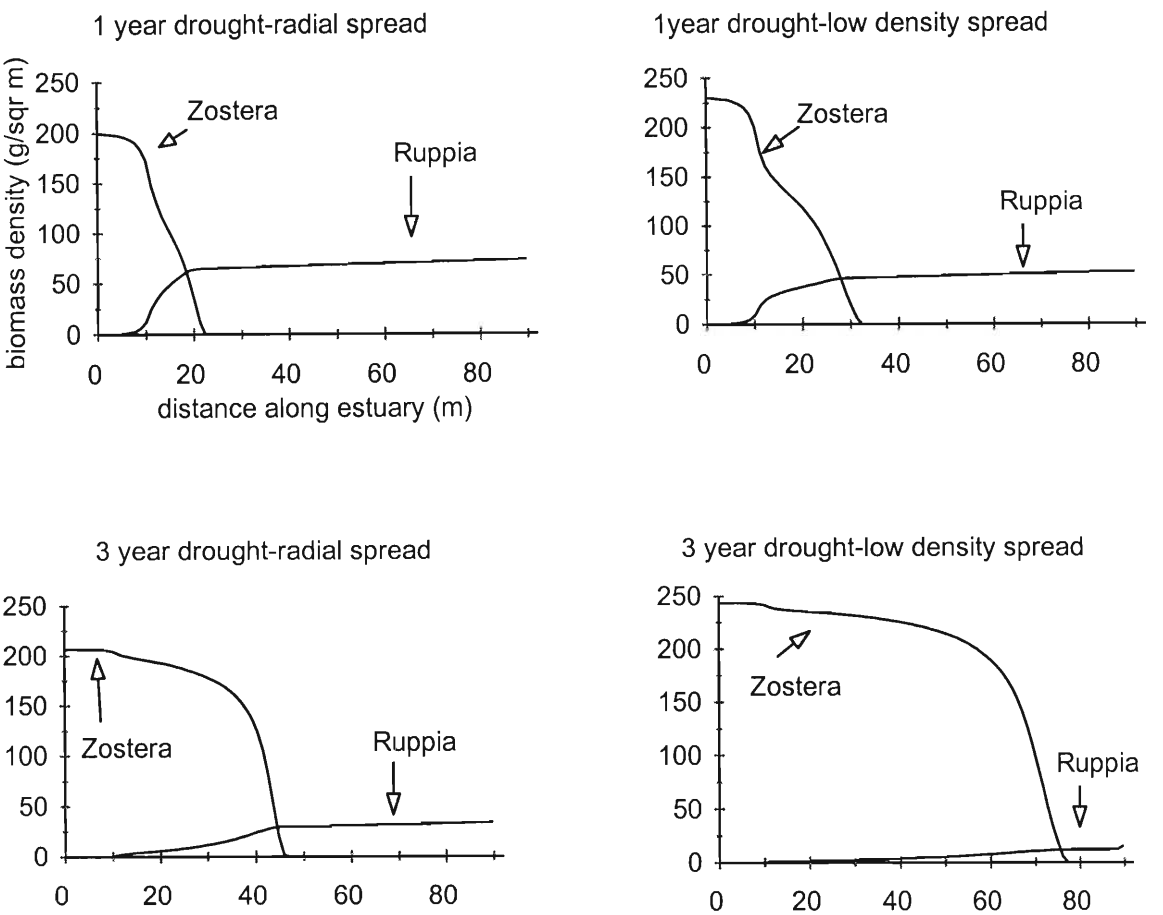

Figure 5.6. The biomass distribution of *Zostera* and *Ruppia* in the Kromme estuary after one and three year periods of no freshwater inflow on the natural runoff scenario. The section shown occurs 6 km from the mouth. Results are shown for radial and low density spread.

Intermediate runoff scenario: 40% MAR

The response of the system to the disturbance scenarios is determined for the new spread rule. These results are presented in figure 5.7. The encroachment rate of *Zostera* is the same after one year of no freshwater inflow for both forms of spread. However the *Zostera* frontier is more convex for low density spread than for radial spread. After three years of no freshwater

inflow, *Zostera* has spread further up the estuary for low density spread than for radial spread and has a higher biomass density for low density spread than radial spread.

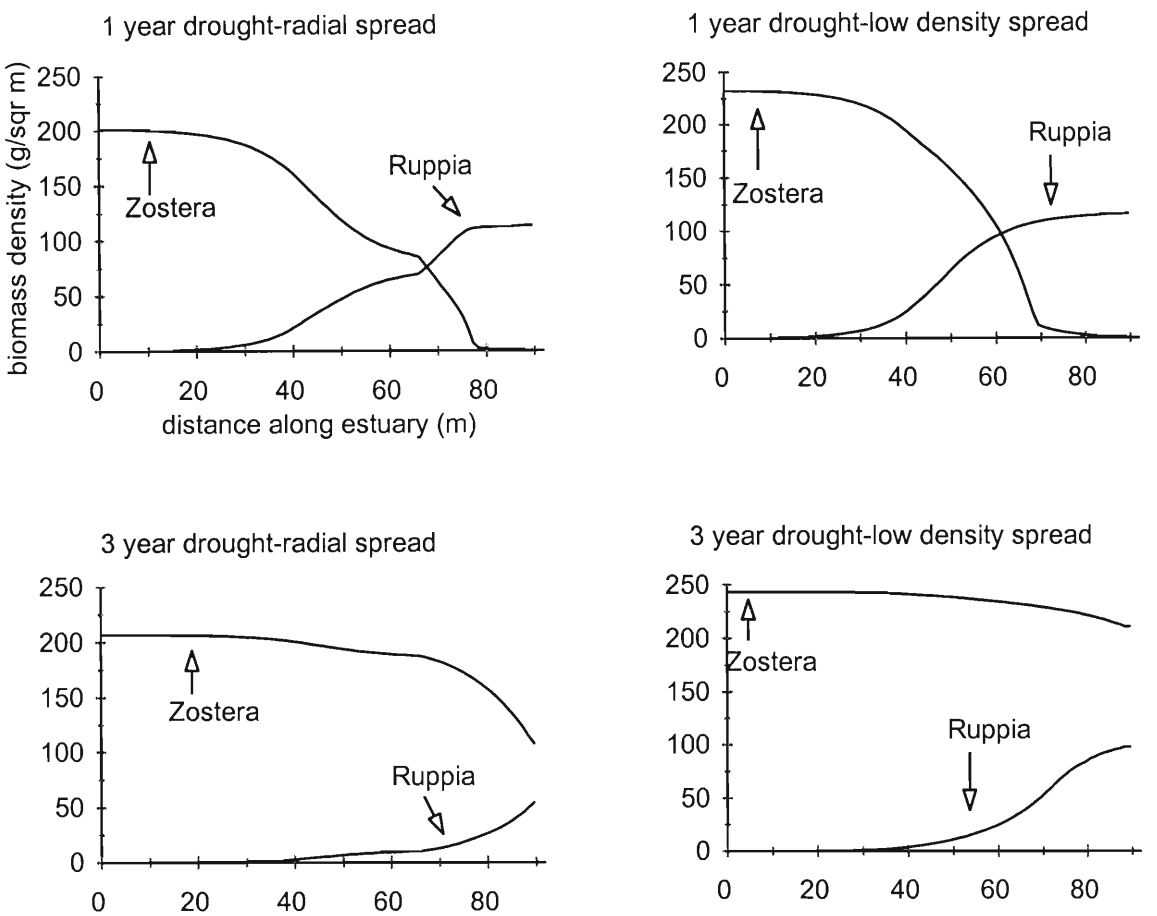

Figure 5.7. The biomass distribution of *Zostera* and *Ruppia* in the Kromme estuary after one and three year periods of no freshwater inflow on the intermediate runoff scenario (40% MAR). The section shown occurs 7.2 km from the mouth. Results are shown for radial and low density spread.

Intermediate runoff scenario: 20% MAR

The results for this scenario are shown in figure 5.8. The shape of the *Zostera* frontier is different for low density and radial spread after one year of no freshwater inflow. Under radial spread *Zostera* encroaches to 90 m and there is a sharp decrease in *Zostera* biomass close to this point. Under low density spread *Zostera* encroaches beyond the 90 m point and there is

a gentle decrease in *Zostera* biomass along the frontier. Because there is a difference in *Zostera* biomass for the two forms of spread, there is also a difference in the distribution of *Ruppia*. After one year of no freshwater inflow, the maximum *Ruppia* biomass density is approximately 100 $g.m^{-2}$ and 25 $g.m^{-2}$ for low density and radial spread respectively. After three years of the same conditions, *Ruppia* has completely died back under radial spread whereas it is still present under low density spread.

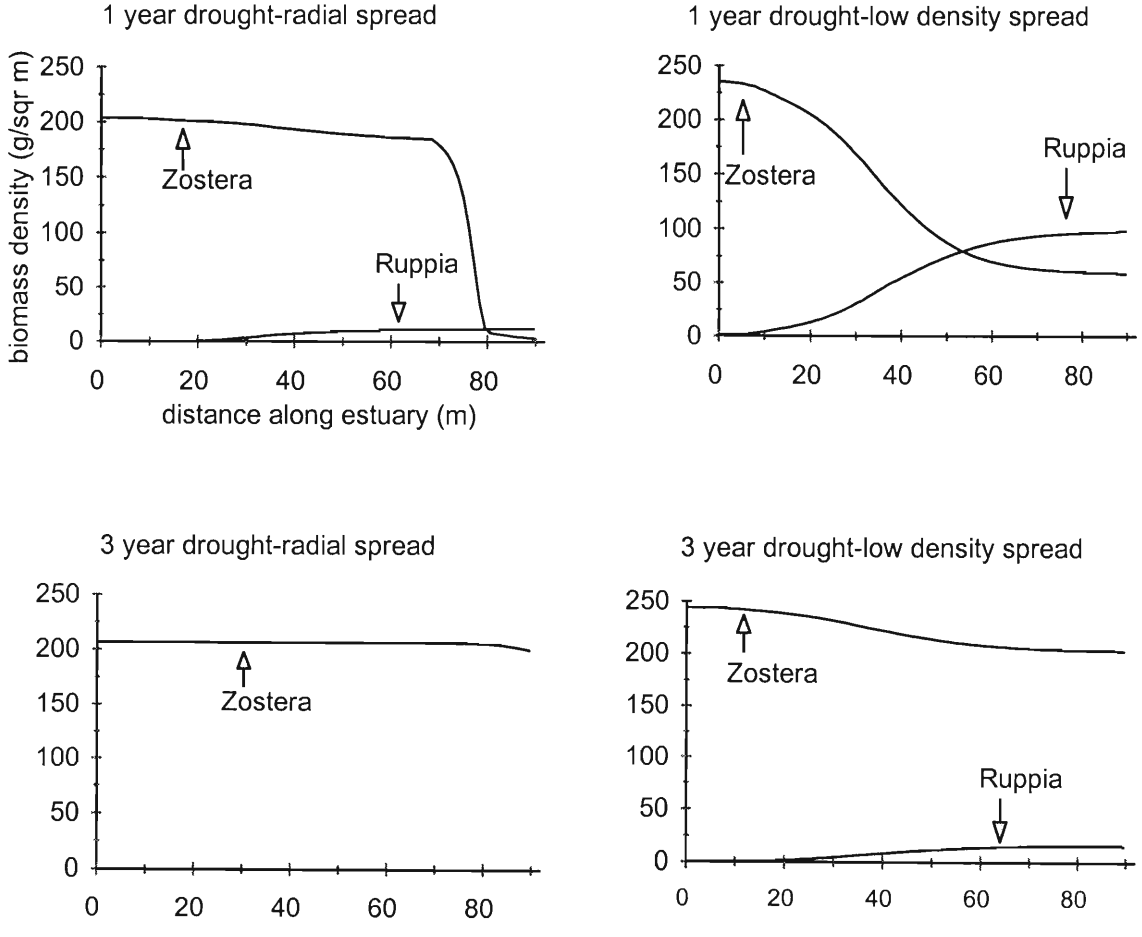

Figure 5.8. The biomass distribution of *Zostera* and *Ruppia* in the Kromme estuary after one and three year periods of no freshwater inflow on the intermediate runoff scenario (20% MAR). The section shown occurs 8.5 km from the mouth. Results are shown for radial and low density spread.

5.1.4.2.2 Great Brak Case Study

We examine the effect of the new spread mechanism on the natural system response to pre-dam conditions. We choose to examine this scenario to determine whether the difference between radial and low density spread for the Great Brak estuary is similar to the corresponding difference for the Kromme estuary.

Natural runoff scenario response to pre-dam runoff conditions

After one and three years of pre-dam conditions, *Zostera* encroaches 3 m and 23 m respectively up the estuary for radial spread. Similarly for low density spread, *Zostera* encroaches 10 m and 44 m. The graphs in figure 5.9 show these results. There is very little difference in the maximum biomass of *Zostera* and *Ruppia* for the different spread structures.

5.1.4.2.3 Discussion

Changing the structure of spread in the model from radial to low density resulted in an increase in encroachment rates. For all the scenarios, with low density spread, the frontier of *Zostera* had a gentle slope and extended further up the estuary, whereas the frontier under radial spread decreased sharply and stopped short of the frontier from low density spread. In selecting a release policy therefore, not only do we need to be aware of disturbances, but we need to bear in mind the fact that obtaining a different result in terms of spread rates and biomass patterns is possible if the spread mechanism is not radial. Ultimately the outcome is the same for the disturbances, namely that *Zostera* colonises the upper reaches, but what is important is that the time taken for this to occur will be much faster for low density spread than radial spread.

Another important consideration is the effect of interspecies competition. Although the effect of low density spread is a greater encroachment rate of *Zostera* under low freshwater flows, for some scenarios this resulted in the survival of *Ruppia* where before it completely died back (Kromme, 20% MAR, figure 5.8, p. 169). This was because there was a wider distribution of *Zostera* but with a lower biomass density, therefore there was less inter-species competition.

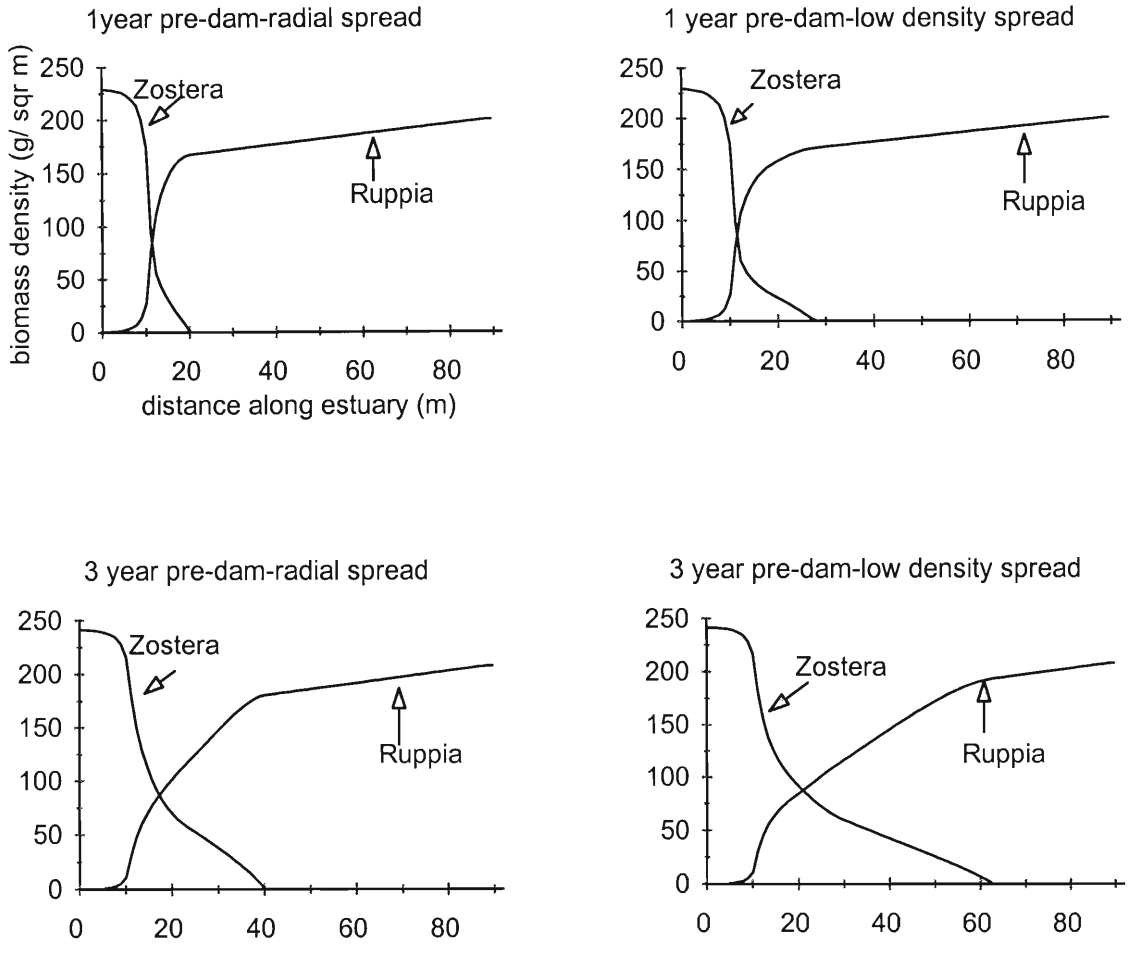

Figure 5.9. The biomass distribution of *Zostera* and *Ruppia* in the Great Brak estuary after one and three year periods of pre-dam runoff conditions on the natural runoff scenario. The section shown occurs 1 km from the mouth. Results are shown for radial and low density spread.

5.1.5 Effect of Cell Size on the Sensitivity of the Model Functions

The purpose of this section is to determine how cell size affects the sensitivity of the model functions, i.e. can it be stated in general that results are less sensitive (i.e. vary in terms of biomass density or distribution patterns) to changes in the model functions in grids with small cells than in ones with large cells? For the analysis three cell sizes from the scenarios in the calibration section 5.1.3 (see table 5.3, p. 160) are selected, namely cell width equal to 0.729, (called small size), 1.458 (≈0.729*2), (called middle size), and 2.734(≈1.458*2), (called large size). The assumption is that the vegetation modelled spreads 27 m per year, thus the expansion parameter for the three scenarios is equal to 0.28, 0.14 and 0.075 respectively (from section 5.1.3). The model functions considered in the sensitivity analysis are:

g_1 measures the effect of cell density on the maximum growth rate of the cell,

g_2 measures the overlap of a cell to its neighbours, and

g_3 is the density dependent growth in a cell.

The functions used for the model simulations in the previous chapter are called the reference functions. The effect of various magnitudes of vertical shifts in the reference functions on model output is examined (figures 5.10 to 5.12). A vertical shift is calculated by setting

$$f^*(x) = f(x)[1 \pm a]$$

where f(x) is the reference function, f*(x) is the new function and a (>0) is the percentage vertical shift. The maximum and minimum values of the shifted functions are one and zero respectively, i.e. if the calculated shift yields values greater than one or less than zero, then the function is defined to be one or zero at these points.

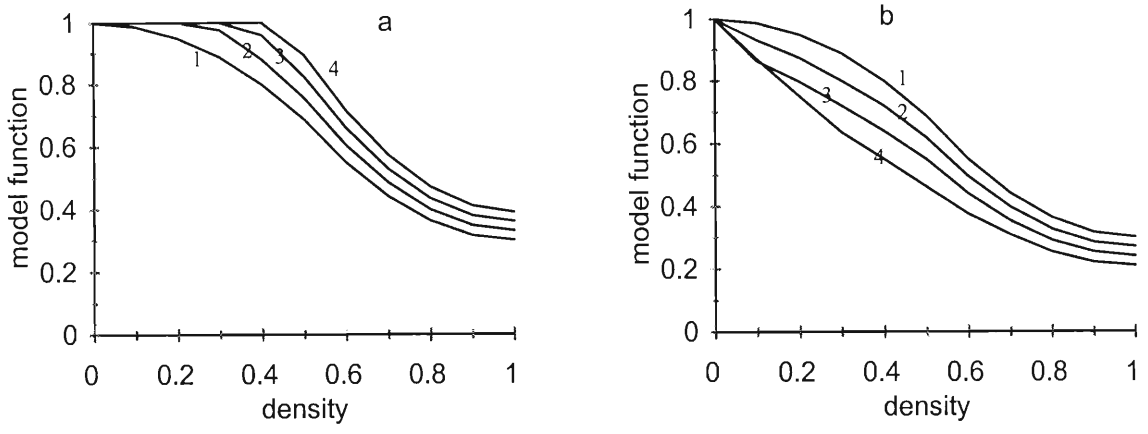

Figure 5.10. The changes in the model function g_1 used to determine the sensitivity of the model in relation to grid size. Figures a and b show positive and negative vertical shifts of 10%, 20% and 30% respectively. 1 = no shift, 2 = 10% shift, 3 = 20% shift, and 4 = 30% shift. The asymptotes in (a) are 0.3, 0.33, 0.36, and 0.39. The asymptotes in (b) are: 0.3, 0.27, 0.24 and 0.21. In (b) the shifted curves for densities less than 0.6 were not calculated using the normal shift formula: This is because the value of the function at zero density is one, therefore the values of the shifted functions were graded to achieve a smooth curve.

Figures 5.10 a and b show the shifts in g_1 considered for the investigation. The curves in figure 5.10a represent vertical shifts of +10%, +20% and +30%. The lower curve is the reference function. The horizontal asymptote changes from 0.3 to 0.33 (+10%) to 0.36 (+20%) to 0.39 (+30%). Figure 5.10b shows vertical shifts of -10%, -20% and -30%, where the upper curve is the reference function. The horizontal asymptote changes from 0.3 to 0.27 (-10%) to 0.24 (-20%) to 0.21 (-30%) for these shifts. Horizontal shifts lead to similar functions and are therefore not considered in the analysis.

The shifts for g_2 are shown in figures 5.11. Vertical shifts are only considered because horizontal shifts lead to graphs that are close to the ones derived from the vertical shifts.

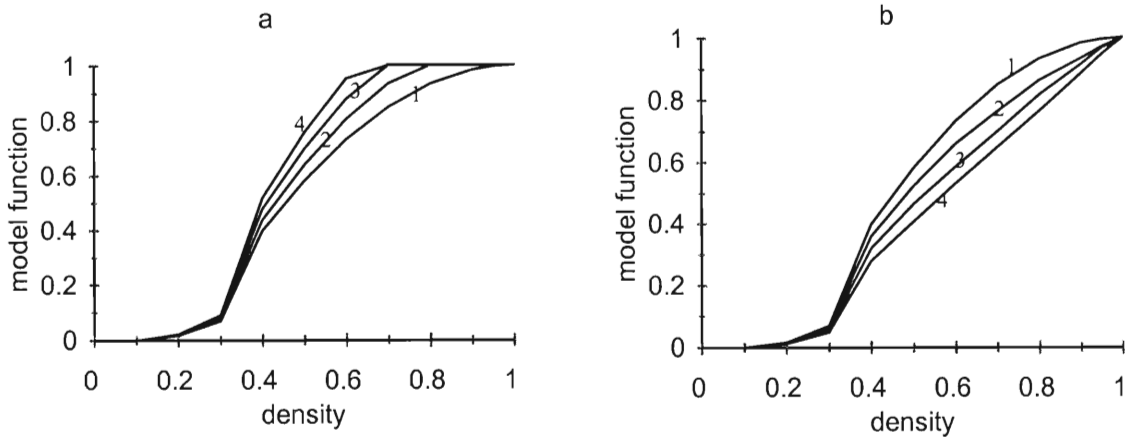

Figure 5.11. The changes in the model function g_2 used to determine the sensitivity of the model in relation to grid size. Figures a and b show positive and negative vertical shifts of 10%, 20% and 30% respectively. 1 = no shift, 2 = 10% shift, 3 = 20% shift, and 4 = 30% shift. The shifted functions were graded slightly at high densities to achieve a function value of one when density equals one.

The shifts for g_3 are shown in figures 5.12. Vertical shifts are only considered because horizontal shifts lead to graphs that are close to the ones derived from the vertical shifts.

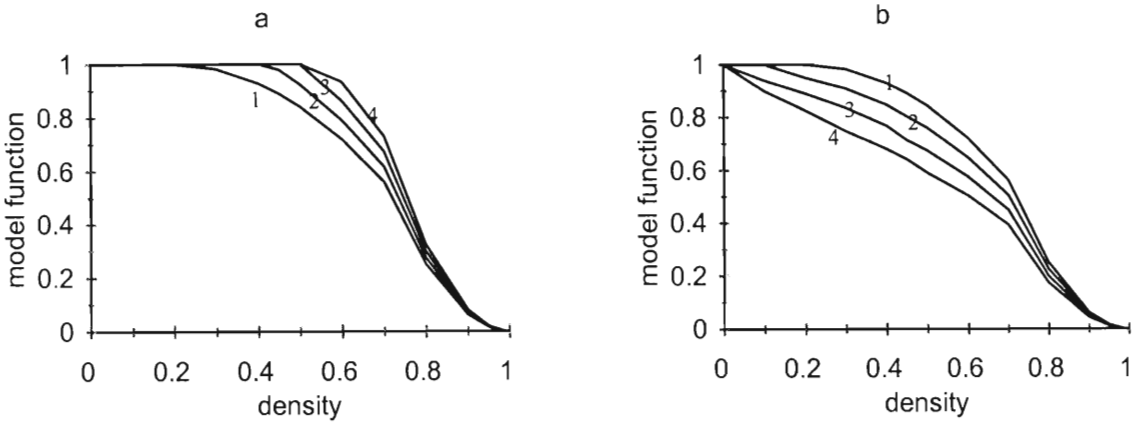

Figure 5.12. The changes in the model function g_3 used to determine the sensitivity of the model in relation to grid size. Figures a and b shows positive and negative vertical shifts of 10%, 20% and 30% respectively. 1 = no shift, 2 = 10% shift, 3 = 20% shift, and 4 = 30% shift. The shifted functions were graded slightly at high and low densities to achieve smooth curves.

For each shift the initial conditions are that biomass density per unit carrying capacity is equal to 0.2*1.65 (cell area is in units of length squared and carrying capacity is in units of biomass density per length squared). This biomass is distributed evenly across an area spanning one middle sized cell in the top left corner of the grid. This means that for the grid with:

(a) large size cells, $(x_0,y_0) = 0.2$,

(b) middle size cells, $(x_0,y_0) = 0.7$ and

(c) small size cells,$(x_0,y_0)=(x_1,y_1)=(x_2,y_0)=(x_0,y_2)=0.7$.

To compare the results for the different size grids, the results are converted so that a cell by cell comparison can be made. That is, the cell results of the middle and small grids are converted to large size grid results. This comparison is done along a strip of height 0.613 length units (this is the height of a cell in the largest grid). The strip is chosen to be between x_2 and x_3 in the largest grid (figure 5.13 a). The equivalent strip for the middle sized grid occurs between x_4 and x_6 (figure 5.13 b) and for the smallest size grid occurs between x_{10} and x_{14} (figure 5.13 c).

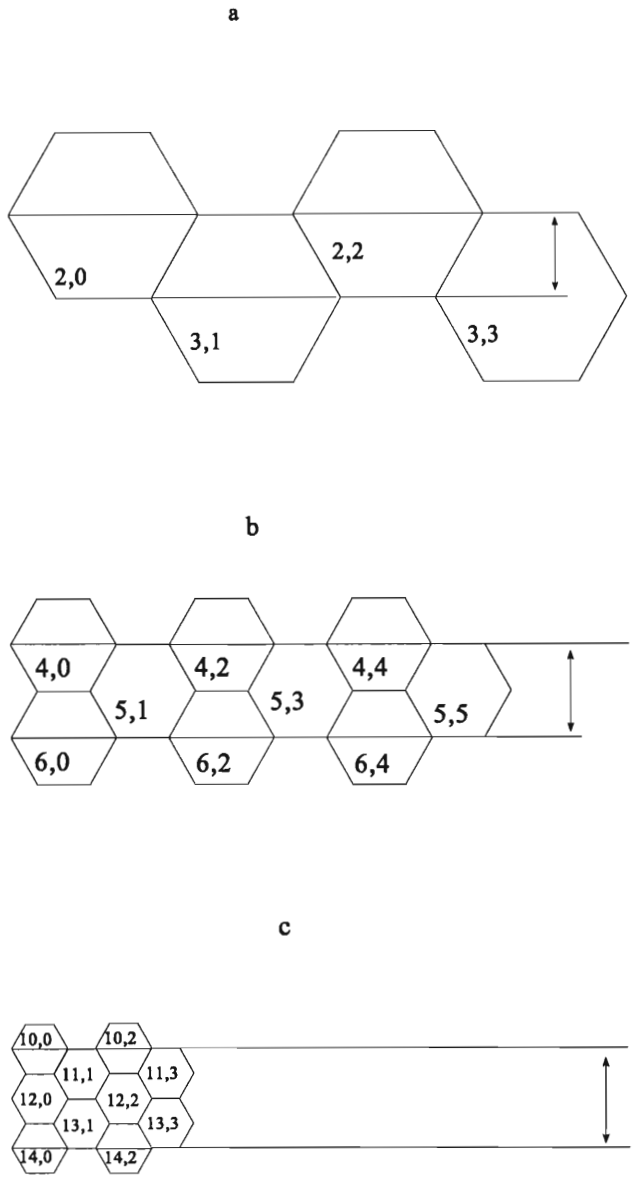

Figure 5.13. To compare results for the different sized grids, biomass along the strip shown by an arrow in the figures is considered. For the grid in (b), cells marked (4,0), (5,1) and (6,0) form the large cell (2,0) in (a), whereas in (c) all the cells shown is the cell (2,0) in (a).

The cell by cell biomass distribution along the strip for the large grid from H(2,0) therefore consists of

$$\frac{1}{2}B(x_2,y_0),\ \frac{1}{2}B(x_3,y_1),\ \frac{1}{2}B(x_2,y_2),\ \frac{1}{2}B(x_3,y_3),\ldots,$$

$$,\ldots,\ \frac{1}{2}B(x_3,y_{m-1}),\ldots,\ \frac{1}{2}B(x_2,y_m)$$

To compare this biomass pattern formation with that of the small and middle grids, the cell by cell distribution for the middle and small grids is converted to the large cell size. For the middle sized grid, this means that, for example, the upper half of H(4,0), the whole of H(5,1) and the lower half of H(6,2) span the area covered by the 1/2H(2,0) in the large grid (see figure 5.13b, p. 176). Thus, the equivalent cell by cell distribution for the middle sized grid is determined from

$$\frac{1}{2}B(x_4,y_{2i}) + B(x_5,y_{2i+1}) + \frac{1}{2}B(x_6,y_{2i}) \text{ for } i = 0,..,\frac{m-2}{2}$$

where m is even.

Similarly for the small grid, the equivalent cell by cell biomass is determined from

$$\frac{1}{2}B(x_{10},y_{4i}) + B(x_{12},y_{4i}) + \frac{1}{2}B(x_{14},y_{4i}) + B(x_{11},y_{4i+1}) + B(x_{13},y_{4i+1}) + \frac{1}{2}B(x_{10},y_{4i+2}) +$$

$$+ B(x_{12},y_{4i+2}) + \frac{1}{2}B(x_{14},y_{4i+2}) + B(x_{11},y_{4i+3}) + B(x_{13},y_{4i+3}) \text{ for } i = 0,..,\frac{m-4}{4}$$

where m is even.

The results for 10% and 30% shifts in the model functions g_1, g_2 and g_3 are shown in tables 5.5 a and b respectively. In the first row of the table a plus or minus sign shows a positive or negative shift in the function. The letters L, S and M in the table mean large, medium and small grid sizes. In the tables:

Average:	means the average of the cell by cell differences in biomass between shifted results and reference results for the strip in figure 5.13 (p. 176) (the averages are calculated on the converted grids),
Maximum:	is the corresponding maximum cell by cell difference in the converted grid,
% cells differ:	is the number of cells which differ from the reference values as a percentage of the total cells in the converted grid,
% actual cells differ:	is the number of cells which differ from the reference values as a percentage of the total cells in the actual grid, and
difference source	is the difference in biomass distribution from the reference biomass: The source biomass is on the left, and plus followed by minus indicates that biomass is greater than the reference biomass close to the source and that biomass is less than the reference biomass further away from the source.

The results show that the larger the cell size, the greater the percentage cells that differ in biomass to the reference biomass when one of the model functions is shifted. In particular, for the grid with largest cell size, variation from the reference scenario starts to occur close to the source or initial biomass. The smaller the grid size, the further away from the source biomass this difference starts to occur, but the corresponding rate of cell by cell change is then greater in the small cells than in the large ones. That is, although a grid with large cells predicts differences from the reference cells close to the source biomass, the rate of increase in this difference away from the source biomass is low. A grid with small cells has a greater rate of variation in cell biomass but further away from the source biomass.

In general the maximum and average cell by cell difference increases with an increase in cell size for a shift in the model functions.

Table 5.5 a. Table showing sensitivity of results in relation to cell size. + = + 10% vertical shift, - = -10% vertical shift. Average = average biomass difference between shifted results and reference results. Maximum = cell maximum biomass difference. % cells differ is calculated in the converted grids, whereas actual % cells differ is calculated from the original grids. The difference in biomass distribution away from the source is shown in the last row, e.g. --++ means that the cell biomass close to the source is less than the corresponding reference biomass, and vice versa as distance from source increases. L, M, S = large, medium and small sized grids respectively.

Condition		g_1 +	g_1 -	g_2 +	g_2 -	g_3 +	g_3 -
average	S	0.225	0.36	0.105	0.151	0.03	0.06
	M	0.117	0.726	0.117	0.137	0.02	0.06
	L	0.13	0.731	0.113	0.122	0.02	0.04
maximum	S	1.621	1.534	0.695	1.071	0.06	0.232
	M	1.268	2.594	1.268	0.96	0.04	0.338
	L	1.165	2.74	1.165	1.572	0.159	0.311
% cells differ	S	73.3%	85.7%	71.4%	85.7%	84.6%	85.7%
	M	40%	42.9%	42.9%	42.9%	61.5%	64.3%
	L	26.7%	35.7%	28.6%	28.6%	46.2%	42.9%
actual % cells differ	S	73.3%	85.7%	71.4%	85.7%	84.6%	85.7%
	M	38.1%	46.2%	38.1%	33%	46.2%	61.9%
	L	22.3%	25.2%	22.2%	17.6%	27.2%	36%
difference from source		----	++++	----	--++	++--	++++

Table 5.5 b. Table showing sensitivity of results in relation to cell size. + = + 30% vertical shift, - = -30% vertical shift. Average = average biomass difference between shifted results and reference results. Maximum = cell maximum biomass difference. % cells differ is calculated in the converted grids, whereas actual % cells differ is calculated from the original grids. The difference in biomass distribution away from the source is shown in the last row, e.g. --++ means that the cell biomass close to the source is less than the corresponding reference biomass, and vice versa as distance from source increases.

Condition		g_1 +	g_1 -	g_2 +	g_2 -	g_3 +	g_3 -
average	S	0.228	0.75	0.243	0.176	0.03	0.211
	M	0.25	1.154	0.403	0.321	0.02	0.219
	L	0.219	1.365	0.232	0.426	0.02	0.182
maximum	S	1.621	2.46	1.621	2.461	0.06	1.216
	M	2.067	3.096	2.882	3.096	0.06	1.5
	L	2.725	3.213	2.814	3.213	0.124	2.052
% cells differ	S	100%	100%	100%	100%	69.2%	100%
	M	40%	64.3%	42.9%	64.3%	61.5%	71.4%
	L	26.7%	50%	28.6%	57.1%	46.2%	50%
actual % cells differ	S	100%	100%	100%	100%	100%	85.7%
	M	42.2%	64.1%	44.4%	64.1	76.9%	61.9%
	L	27.9%	44.8%	44.4%	44.8%	41.6%	36%
difference from source		----	++++	----	++++	++++	++---

5.2 Analysis of Model Sensitivity to Changes in Specific Growth and Mortality Rates

The effect of 30% variations in the specific growth and mortality rates of above- and below-ground biomass is examined on the Kromme and Great Brak case studies. In particular, we examine the outcome on the spatial distribution of the macrophytes.

For the natural runoff scenario for the Kromme estuary, previous results showed that the boundary between *Zostera* and *Ruppia* occurred 6 km up from the mouth. Under 30% variations in the specific growth and mortality rates, results showed that the boundary between *Zostera* and *Ruppia* shifted at most 3 m up or down the estuary. Similarly for the intermediate runoff scenario (40% MAR), the boundary between *Zostera* and *Ruppia* shifted at most 38 m under 30% variations in the specific growth and mortality rates. For the intermediate runoff scenario (20% MAR), results indicated that the boundary shifted at most 16 m under 30% variations in the specific growth and mortality rates.

Under the alternative releases for the Kromme estuary, if the specific growth rate of *Phragmites* is decreased by 30%, or the specific mortality rate of *Phragmites* is increased by 30%, then *Phragmites* does not survive in the upper reaches for these runoff policies. Previous results showed that *Phragmites* would survive under these releases.

Results from chapter 4 show that *Zostera* and *Ruppia* coexist in a section of the Great Brak estuary approximately 1 km from the mouth for the natural runoff scenario. Under 30% variations in the specific growth and mortality rates, results showed that the boundary shifted at most 15 m. Similarly, under the pre-dam scenario, the corresponding shift in the boundary is at most 14 m.

5.3 Conclusion

A calibration technique was developed so that any cell size could be used to give a desired spread rate. However, caution must be taken when using grids with large cells relative to the maximum spread rate of the vegetation because sensitivity to shifts in the model functions increases with cell size. Thus if the model functions cannot be validated, then a small sized grid should be used to give less error as a result of using incorrect model functions. Therefore,

for the macrophyte model, the cell size was chosen to be small relative to the yearly spread rate, though using a larger cell size may have been more feasible because of the size of estuaries. So selecting a small cell size ensured that errors in predictions as a result of errors in model functions were kept to a minimum magnitude. A larger cell sized grid could have been used for the macrophyte model, but at the expense of model results not being as accurate as a result of possible mistakes in defining the model functions. A small cell size was chosen initially to monitor the dynamics of plants along the intertidal zone. The effects of varying the specific growth and mortality rates by one third did not change the spatial distribution of *Zostera* and *Ruppia*.

The effect of applying low density spread rather than radial spread expectedly proved to cause an increase in encroachment rates under periods of no freshwater inflow. This may affect management decisions that are based on allowing a macrophyte to encroach up to a particular point. This highlights the need for further field testing and subsequent model validation.

The technical analysis has provided an indication of how well the macrophyte model performs. It has provided a method of calibration such that a different grid size may be used. This is particularly useful if large areas need to be modelled: The cell size may be increased with no effect on the encroachment rate. The analysis showed that encroachment rates and inter-species dynamics vary if different model assumptions or parameters are used. This shows the need for further research and field testing of the competition between different macrophytes, and how the presence of one macrophyte would alter the encroachment of an invading plant. As more data becomes available, the model can be improved and further calibrated with field observations.

CHAPTER 6

CONCLUSION

In South Africa the demand for freshwater has resulted in increased abstraction of water in the catchment. This results in a reduced or altered pattern of river flow to the downstream estuary, and this holds serious consequences for the estuarine ecosystem. This study developed three mathematical models to predict the effects of alterations in river inflow to estuarine macrophytes. The models can evaluate the freshwater requirements of estuarine macrophytes by determining how the plants respond as a consequence of a management action such as artificial breaching or a water release policy. The development of these models therefore contributed to the assessment of the freshwater requirements of estuaries and to the planning of regional and national water resource developments.

While some aspects of the models developed in this study have not been tested, it should be noted that the models are based entirely on the current understanding of estuarine ecosystems in South Africa. The study of estuarine macrophytes in South Africa is relatively new, having started in the early 1980's. Therefore in the development phase of the model, and in the validation phase, we were able to identify and initiate further research.

The model was derived under the assumption that vegetative spread occurred equally to the neighbouring cells, despite the surrounding physical conditions or neighbouring biomass densities. The sensitivity analysis showed that the encroachment rate increased if the model incorporated encroachment that favoured low density areas first. The consequences for the management decisions are higher encroachment rates of marine macrophytes under reduced freshwater flows (worst case scenario), or increased spread of freshwater macrophytes in the upper reaches under increased freshwater flow (best case scenario). A programme of laboratory and field monitoring of expansion rates has been discussed with biologists to give better insight into the most appropriate choice of some model formulations regarding the effects of density and physical conditions on vegetative spread.

There are relatively few studies on the competitive interactions among *Zostera*, *Ruppia* and *Phrgamites*. Research on the rate of change in plant community structure due to competition, succession or interaction with other species would enable a more rigorous validation of the model.

Previous methodologies for determining the freshwater requirements of estuaries in South Africa focussed on providing yearly estimates of runoff totals (Jezewski and Roberts 1986; CSIR 1994). These estimates did not provide an indication of the seasonal or monthly distribution of the annual allocation. In other parts of the world, only the United States has appeared to have directed substantial research effort at formulating techniques for determining the freshwater requirements of estuaries. Two distinct approaches have evolved, one applicable to estuaries flowing into the Gulf of Mexico (Texas Department of Water Resources 1982), and one for the San Francisco Delta-Bay area (San Francisco Estuary Project 1993). The method adopted for the San Francisco Delta-Bay is focussed on a single index, namely salinity. Although salinity attributes are necessary for the continued functioning of an estuarine ecosystem, it is also important to determine whether these physical conditions can support the estuarine fauna and flora. The approach developed for estuaries flowing into the Gulf of Mexico provides a link between freshwater inflow and harvesting of fish (representing recruitment success). However, the models are based on time series data of which there is no comparable data in South Africa.

Therefore, the models in this thesis have enhanced the state of decision support for determining the freshwater requirements of estuaries, not only locally, but also globally. They are the first mathematical models to predict the freshwater requirements of estuarine macrophytes. The models can predict the plant response to variations in the frequency and volume of freshwater runoff. In addition, the cellular automata models gave spatial predictions and we can therefore assess various water releases in the light of the distribution of the plants both along the length of the estuary as the mouth to head salinity gradient changes, and along the intertidal zone as water level fluctuations vary.

The macrophyte models formed part of an integrated group of models designed to assess both the biotic and the abiotic consequences of various freshwater releases. It is anticipated that

these models will provide a basis for further improvements in estuarine modelling. To further integrate the physical models in this decision support system and the plant models, research on estuarine plant responses to freshwater controlled physical factors must continue. This will enable additional physical factors to be incorporated in the model, and consequently allow for improved predictions as more factors are taken into account in the model.

In addition, the macrophyte models could include more plants (e.g. salt marsh, emergent macrophytes) as information becomes available, and plants could be added as new classes, (e.g. mangroves and macroalgae. To monitor rehabilitation problems, the plant models could be extended to describe the effect of salinity or inundation on seedling establishment and growth. At present the models describe the growth of existing macrophyte beds as this is the main mechanism of colonisation into new areas.

Not only have estuaries in South Africa been affected by diminished freshwater supply, but there is growing concern in the international literature regarding the reduction of freshwater flow to estuaries, particularly in semiarid regions such as Australia (Ruello 1973) and parts of the United States (Chapman 1977, p. 20). So as data becomes available, the models developed in this thesis may be applied to additional estuaries, not only in South Africa, but also in other parts of the world, and thereby contribute to estuarine management both locally and globally.

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