

**Effects of warm and dry years
on the habitat suitability of
Zostera noltii in the Dutch
Wadden Sea**



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Summary

Estuaries experience changes in both climate and human induced environmental conditions. In the last couple of years, it becomes more and more evident that climate change is accompanied by so-called extreme events. As seagrasses are seen as indicators of the conditional status of estuarine ecosystems, pressure put upon these systems by extreme events could be displayed in a decrease in seagrass occurrence. Moreover, seagrasses are also classified as ecosystem engineers.

In the Dutch Wadden Sea until the 1930s, seagrass growth was abundant. However, after mass mortality due to the wasting disease and changes in hydrology, recolonization did not occur. As an aid to identify problems of recolonization of areas by seagrasses, habitat suitability maps have been made. Yet, these maps consider average conditions over time and as climate is changing, this may not be the case. Moreover, the effects of extreme events can hamper recolonization and could attribute to unforeseen negative impacts on this recolonization. So, to be able to have successful management strategies for safeguarding or recolonization of the Dutch Wadden Sea by seagrasses, one should know what present day *and* future threats are for seagrass survival. Because the Royal Netherlands Meteorological Institute predicts an increase of warm and dry year for the coming years, the focus of this study is on how warm and dry years, alternating with average years, will affect the potential habitat suitability of *Zostera noltii* in the Dutch Wadden Sea.

As a tool the HABITAT model is used, knowledge rules on how environmental conditions determine habitat suitability and how seagrass could influence those environmental conditions are required. The knowledge rules are derived from several earlier studies that contain knowledge rules on the relation between habitat suitability of *Zostera noltii* and averaged environmental conditions and without plant-system feedback. For feedback mechanisms between *Zostera noltii* and environmental conditions, the knowledge rules are extended by means of a literature study.

From the results, it is concluded that warm and dry years have a negative impact on the habitat suitability index of *Zostera noltii* in the Dutch Wadden Sea compared to average years. The direct and indirect effects of increased temperature contributed the most to this effect. However, for both types of years, the most limiting factor is the low light availability for *Zostera noltii* and the lack of temporarily uncovered flats. Moreover, the results show that even at present year to year variations in environmental conditions can affect the habitat suitability of *Zostera noltii* in the Dutch Wadden Sea significantly, which has implications for restoration projects now and, with ongoing climate change, in the future.

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1 Introduction

Estuaries are under influence of both rivers and sea and therefore experience a range of different pressures that originate from both land and sea, like nutrient inputs, changing salinity and tides. Many of these pressures are climate and human induced (Schanz and Asmus, 2003; Orth et al., 2006; Björk et al., 2008; and many others). Climate change may lead to altered abiotic and biotic conditions due to changes in temperature, precipitation and evaporation, which can impact ecosystems to a certain degree (Ruddiman, 2008). Next to gradual climate change, the frequency of extreme events, such as dry years, heavy storms, are also likely to increase (Van den Hurk et al., 2009). In current literature, the main idea is that the effects of extreme events may have greater impact on ecosystems than gradual climate change. Extreme events can be defined as the 10 and 90 percentile of the occurrence of certain climatic factors, like temperature or the amount of precipitation (Meehl et al., 2000). Furthermore, the effect of an extreme event is dependent on the resilience of an ecosystem. If an ecosystem experience has low resilience, the occurrence of an extreme event can be more devastating than when the same extreme event occurs in an ecosystem that has high resilience (Meehl et al., 2000).

When looking at climate scenarios of the Royal Netherlands Meteorological Institute, the occurrence of warm and dry years, defined by precipitation shortage and temperature, will increase over the coming years. At present the occurrence of warm and dry years, like 2003 occur one out of ten years. Around 2050 a frequency of occurrence of once every two years of these type of years is foreseen (Van den Hurk et al., 2009). Warm and dry years impact estuaries by changes in fresh water inflow and temperature. These changes alter the hydrological cycle, which modify estuarine characteristics, like salinity, turbidity, nutrient budgets, residence time, stratification, primary productivity and seasonal oxygen depletion (Justić et al, 2005; see figure 1).

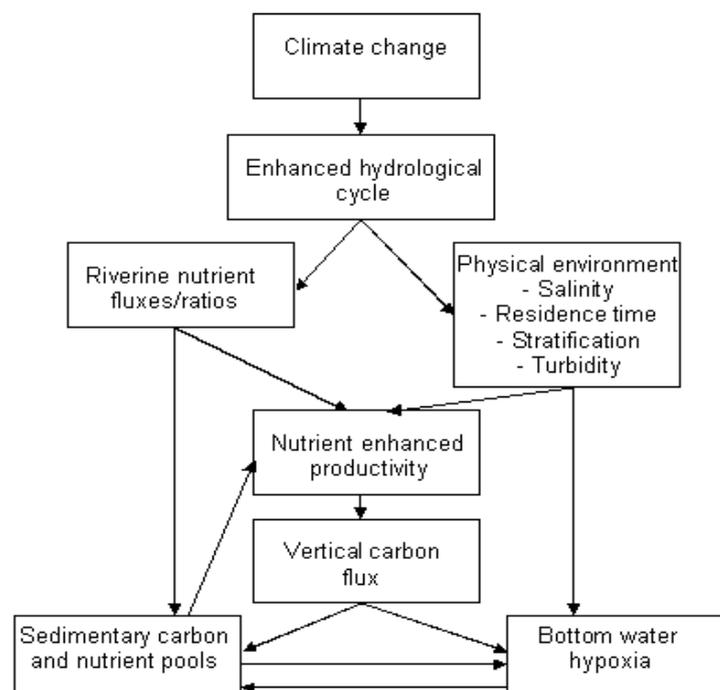


Figure 1.1: Effect chain of effects of climate change on estuaries (after Justić et al, 2005).

Because seagrasses are valued for their intrinsic biodiversity and concurrent importance as habitats for recreationally and commercially valued fish, crustacean and mollusk species *and* are known to be susceptible to many known pressures, seagrasses function often as indicators of estuarine health (Ward et al., 1998). Another important characteristic of seagrasses is that they act as a CO₂-sink. On a worldwide scale, seagrasses contain roughly 12% of the CO₂ stored in the ocean (Duarte and Cebrian, 1996). Over the last decennia worldwide declines of seagrass meadows have been reported (Orth et al., 2006 and references therein) and are often believed to be caused by increased human induced nutrient input (Burkholder et al., 1992 and 1994) and human induced physical damage that occurs for instance due fishing and just the removal of seagrass (Daby, 2003; Neckles and Short, 2005). However, also climate induced changes, such as altered temperatures and salinities, are believed to exert pressure on seagrasses (Bulthuis, 1987; Katwijk et al., 1999; Orth et al., 2006). Waycott et al. (2007) indicated what factors are likely to change with ongoing climate change and how they affect survival of seagrasses (see table 1.1).

Table 1.1 Expected impacts of climate changes on seagrasses worldwide (from Waycott et al., 2007).

Impact	Direction of change
Temperature	Loss and community shifts
Sea level rise	Loss
Disturbance (e.g. storms)	Loss, some gains and community shifts
Light and UV	Small potential loss but largely unknown
CO ₂ and pH	Unknown, small theoretical potential for loss and gain
Ocean circulation	Loss, gain, community shifts
Rainfall and river flood plumes	Loss and community shifts

Until the 1930s extensive seagrass meadows were present in the Dutch Wadden Sea. However, after the wasting disease and changes in hydrology because of the new-built "afsluitdijk", nowadays the seagrass meadows that are present in the Wadden Sea are very small (see Erftemeijer, 2005 for more detail). The meadows contain the seagrass species *Zostera marina* or *Zostera noltii* (Erftemeijer, 2005). The almost lack of recolonization of the Dutch Wadden Sea by seagrasses is believed to be caused by, amongst other things, the mere absence of seagrasses (because of their function as ecosystem engineers) (Van Katwijk et al., 1997; Van der Heide, 2009), the low availability of seeds, the occurrence of storm surges, periodically ice cover and the turbidity and high energy of the Wadden Sea itself (pers comm. P. Erftemeijer).

The two species present in the Dutch Wadden Sea differ in their dominant reproduction strategies and could therefore be impacted differently by climate change and extreme events, like for instance a warm and dry year. *Zostera noltii* reproduces primarily by vegetative propagation. Those propagules need to have sufficient energy and balanced nutrient supply to survive the autumn and winter period to be able to grow in May of the next year (Philipart, 1994). *Zostera marina*, at the other hand, reproduces mainly by seed dispersal: during the growing season energy is stored in seeds and when the plants start to decrease, those seeds start to disperse. Here, wind direction and strength is the dominant force to where those seeds will eventually settle (Erftemeijer and Van Beek, 2005).

Over the last couple of years, modeling efforts have been carried out to predict the potential habitat for seagrasses in the Dutch Wadden Sea, the lagoon of Venice and Krammer-Volkerak, see for example De Jong et al., 2005; Erftemeijer and Van de Wolfshaar, 2006; Haasnoot and van de Wolfshaar, 2006. When predicting potential habitat, so-called knowledge rules are used. Those knowledge rules are derived from knowledge on the habitat requirements and tolerance thresholds of seagrasses and reflect average and static environmental conditions.

Moreover, these studies consider the habitat suitability of present day situations, for means of exploring the chance of success of recolonization projects (De Jong et al., 2005) or to unravel the factors that are limiting seagrass growth (Erftemeijer and Van de Wolfshaar, 2006). Both are relevant, but changes in climate, both gradual and abrupt, could also cause pressure on the occurrence or the surviving of seagrasses (Orth et al., 2006). To be able to have successful management strategies for safeguarding or recolonization of seagrasses, one should know what the present day *and* future threats are for seagrass growth. The focus of this study is therefore: how warm and dry years, alternating with averaged years, will affect the potential habitat suitability of *Zostera noltii* in the Dutch Wadden Sea. This study is a first attempt to show how to incorporate climate change and feedback of seagrasses on its own environment in a habitat suitability model. This type of modeling can give a clue of the relevance of management options for seagrass surviving and recolonization.

The choice of *Zostera noltii* instead of *Zostera marina* is made because of the dominant reproduction strategies: the direct effect of environmental conditions on the perennial populations of *Zostera noltii* makes it easier to transmit effects to the following year, regarding habitat suitability. For the seed dispersal of *Zostera marina* a wind field needs to be constructed and knowledge of the factors on seed germination is needed.

2 Materials and Methods

For this study the HABITAT model is used (see appendix 7.1 for more detailed information), which requires knowledge rules on how environmental conditions determine habitat suitability and on how seagrasses can influence those environmental conditions. The knowledge rules were derived from the studies of Erftemeijer and Van de Wolfshaar (2006) and De Jong et al (2005), which contain knowledge rules on average conditions and without plant-feedback. For feedback mechanisms between *Zostera noltii* and environmental conditions the knowledge rules are extended by means of a literature study. The used knowledge rules are described below.

The focus of this study on warm and dry and normal years, require input maps that are characteristic for both types of years. When one looks at meteorological data, the year 2003 is characterized as a warm and dry year and the year 2005 as a normal year (Royal Netherlands Meteorological Institute, 2011; and Appendix 7.2). From this starting point, data were requested from the Data Information Service on extinction, salinity, temperature and tides for the Wadden Sea and the years 2003 and 2005. As there are only 10 to 14 measuring points within the Wadden Sea the data is interpolated using the inversed distance weighted method within Arc GIS. Current velocity, sediment characteristics and bathymetry are considered the same for both type of years. Current velocity because the Wadden Sea is a tide dominated estuary and the input of fresh water is considered to be relatively small (pers. comm. A. van Dongeren). As input data model output of a Delft3D Waddensea model of the period 2005-2009 is used (from A. Luijendijk). Sediment and bathymetry are considered the same out of practical reasons. Sediment data is available from the "Waddenzee atlas" (<http://www.waddenzee.nl>) as this is the most up to date and comprehensive source, but only one year is available. For the bathymetry, data from the Data Information Service is used. However, as the bathymetry is measured in different sections in sequential years a composition of the different measurements is made. All input maps have a resolution of 20 by 20 meters.

2.1 Knowledge rules

2.1.1 Available light

Energy availability is reflected for light that can reach *Zostera noltii*. As such, light is one of the key elements for seagrass' germination, growth and survival (Hemminga and Duarte, 2000), and determines the lower limit of seagrass occurrence (Giesen et al., 1990, Nielsen et al., 2002; Kemp et al., 2004). The actual amount of light available depends on several conditions, like: the concentration of suspended matter and the concentration of phytoplankton and macroalgae (Erftemeijer and Van de Wolfshaar, 2006). The importance of light as parameter is illustrated by the fact that the effect of increased turbidity and concurrent a decrease in light penetration of the water is believed to be the main driver of major losses in seagrass meadows worldwide (Shepherd et al., 1989; Green and Short, 2003). The percentage of light that reaches the sediment says something about the habitat suitability of that spot for *Zostera noltii* and generates a habitat suitability index (HSI) for light availability (figure 2.1; Erftemeijer and Van de Wolfshaar, 2006). In general, in HABITAT a HSI of 0.7 is considered as good HSI and means that the chance of indeed finding *Zostera noltii* on that spot is considerable. Note that for a total HSI more environmental conditions are taken into account and that a HSI of 0.7 and higher for light availability only says something about this environmental factor.

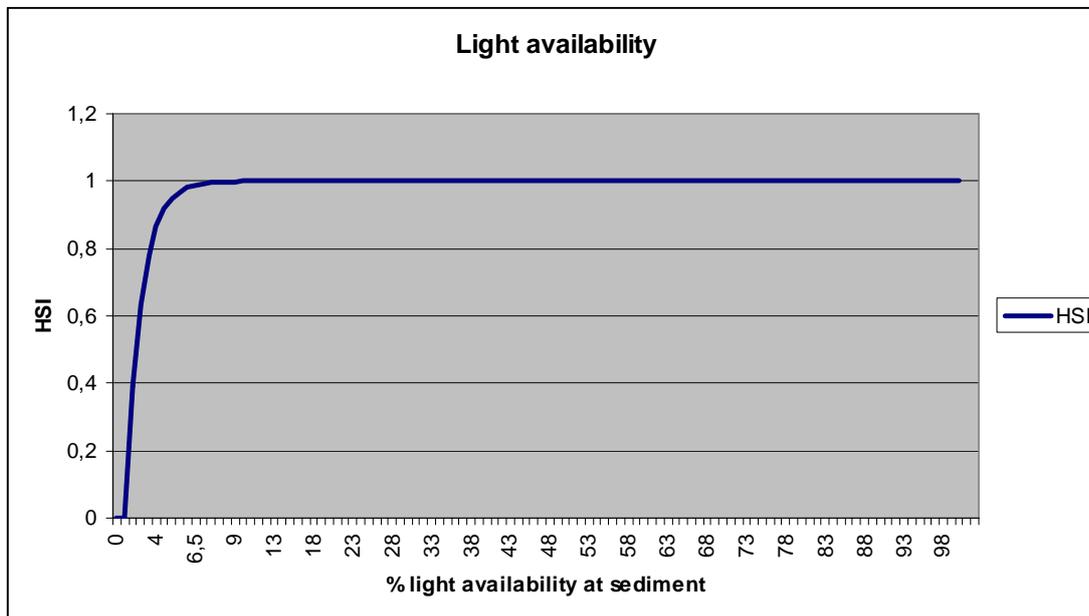


Figure 2.1: the habitat suitability index (HSI) for *Zostera noltii* as the % of light that is available at the sediment (Erftemeijer and Van de Wolfshaar, 2006).

As mentioned earlier, the amount that reaches the sediment is depended on the organisms and substances within the water column. As in warmer and drier years estuaries often encounter more eutrophication (Justic et al., 2005) that influence light availability, this should be taken into account. In literature, several formulas are present that describe the amount of light hitting the sediment (SI), depending on different proxies, like attenuation coefficient and secchi depth but also in terms of concentration of nitrate or ammonium. After a study of the results of 6 different relations between proxies and the percentage of light available at the sediment and the actual appearance of seagrass in the Wadden Sea, the formula developed by Duarte et al (1991) is used (for more detailed information see 7.3):

$$SI = 1.86/\text{attenuation coefficient} \quad (1)$$

When *Zostera noltii* starts to grow, it decreases suspended matter in the water column by reducing stream velocity thereby enhancing sedimentation. Moreover, *Zostera noltii* stabilizes the sediment by means of roots, decreasing the amount of sediment available for erosion (Schanz and Asmus, 2003). These processes make it evident that *Zostera noltii* exert feedback on light availability. However, for modeling purposes problems arise as no data is found that quantify this effect, as such guesses on the effect of *Zostera noltii* on light climate are made. Because *Zostera noltii* starts to grow from rhizomes, periodically less light is needed during the growing season (Workshop report, 2006) as well as with progress of time light availability is improved by the existence of *Zostera noltii* itself (Philippart, 1994). As such the rough assumption is made that when rhizomes are present from the foregoing year 15% less light is needed. The 15% is only a guess and could turn out to be too large, but no quantifications on this feedback has been found in literature and therefore a pragmatic solution has been chosen

2.1.2 Desiccation

The period of emersion during low tide is important for *Zostera noltii* because it determines in general the upper limit of colonization by means of desiccation (Erftemeijer, 2004).

The percentage of emersion, which is used to derive the HSI, is calculated for the Wadden Sea by:

$$E = (\arccos * ((H - W)/A) / \pi) * 100\% \quad (2)$$

Where E stands for the percentage of time sediment is emerged during tide (%), H the depth of the sediment (cm), W the mean water level (cm) and A the amplitude of the tide (cm) (Mulder, 1996). The percentage per time period *Zostera noltii* need and can withstand desiccation is given by Erftemeijer and Van der Wolfshaar (2006) (figure 2.2).

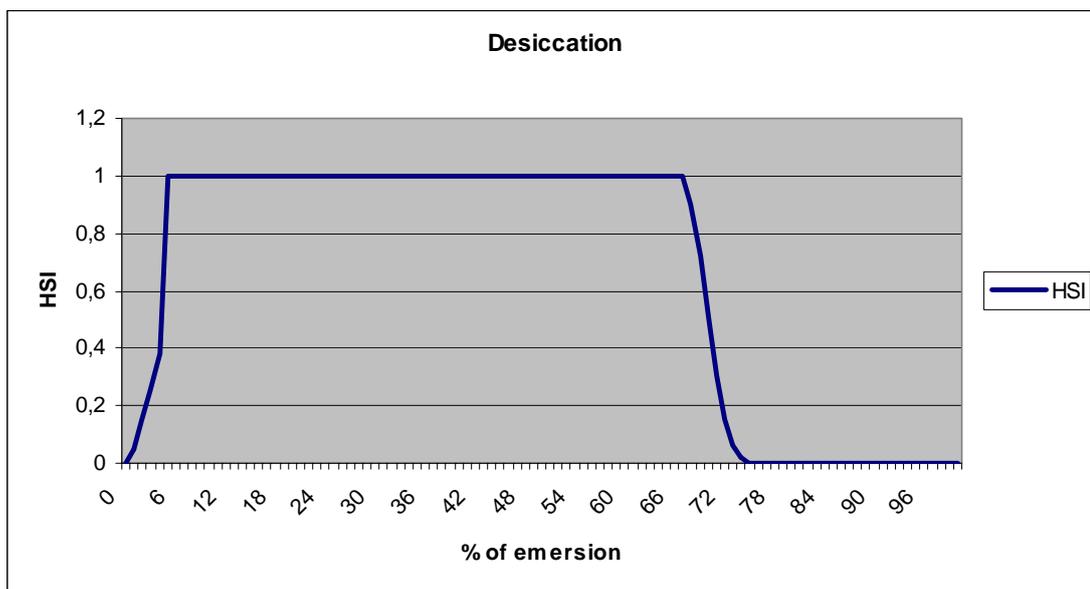


Figure 2.2: the period of emersion needed for *Zostera noltii* (Erftemeijer and Van de Wolfshaar, 2006).

As the percentage of light that hits the sediment determines the lower limit of *Zostera noltii* occurrence and desiccation the upper limit, those two parameters determine the range where *Zostera noltii* can occur. The parameters that are presented below interfere with the habitat suitability within this range.

2.1.3 Temperature

Worldwide optimum temperatures and temperature ranges differ for the same seagrass specie, as it becomes adapted to its local environment. Nonetheless, it seems that the upper limit is intraspecific, but the optimum and minimum temperature differ. Borum et al. (2004) stated that the minimum temperature for *Zostera noltii* can be under the freezing point and the review of Bulkholder et al (2007), gives an optimum range between 10-20°C and a non-surviving temperature of around 30°C. From this knowledge, the HSI for temperature for *Zostera noltii* is derived according to figure 2.3.

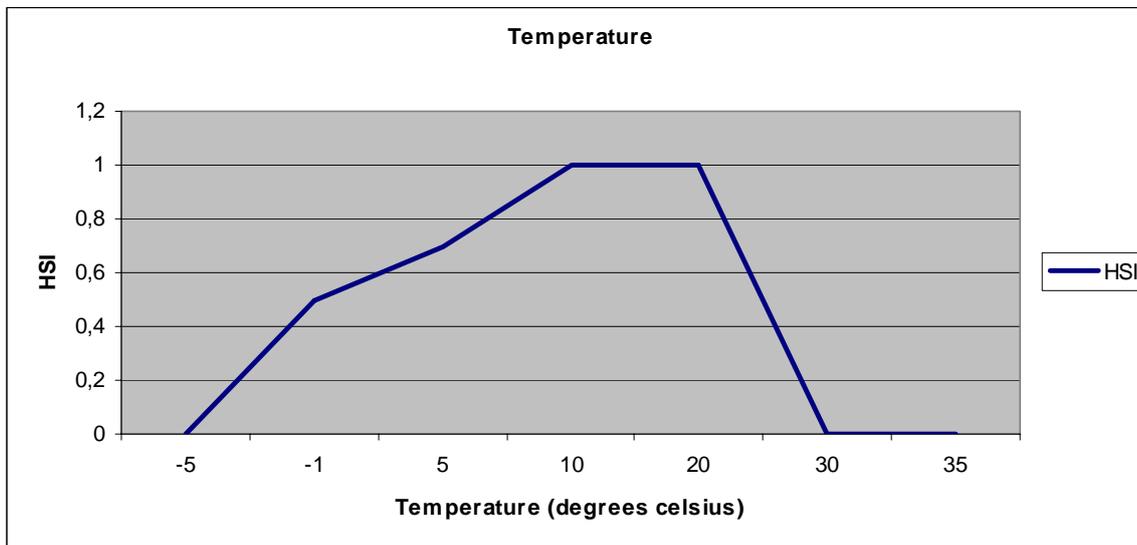


Figure 2.3: temperature HSI for *Zostera noltii* (adapted from Borum et al., 2004 and Bulkholder et al., 2007).

Additionally, temperature can act directly and indirectly on *Zostera noltii*. As presented in figure 2.3, values below and above certain temperatures directly affect *Zostera noltii* by means of enzyme activity. Indirectly, temperature can interfere with the habitat suitability by stimulating growth when light is not limiting but hampering it when light availability is limiting (Bulthuis, 1987). However, as little data is available to get any quantification for this relationship, the interaction between temperature and light availability is not incorporated in the model. Another indirect pathway is via ammonium enrichment and the effect on root growth. As temperature increase, more and more ammonium is released from the sediment, which can lead to such high concentrations that N toxicity can take place (see paragraph 2.1.4) (Van Katwijk et al., 1997; Touchette and Bulkholder, 2007).

2.1.4 N toxicity

Nitrogen can become toxic in nutrient rich environments, like the Wadden Sea, as *Zostera noltii* does not have product inhibition. This means that nitrogen assimilation, an energetic costly process, takes place as long as nitrogen availability remains high enough for uptake. Because of the ongoing uptake of nitrogen, internal imbalances occur regarding the amount of nitrogen and carbon can occur. Ultimately, this leads to depletion of the carbon pool and creates energy problems (Van Katwijk et al., 1997, 2000; Touchette and Burkholder, 2007). As excessive ammonium loads can put stress upon *Zostera noltii* growth, other parameters, which are on itself suitable for *Zostera noltii* growth, could also become stressful. According to De Jong et al. (2005), ammonium stress exacerbates sensitivity to salinity levels and temperature interferes with the ammonium loads released from the sediment as higher temperatures increase ammonium loads.

In their study, De Jong et al. (2005) give, next to the combined effect of salinity and ammonium concentrations on the habitat suitability (see table 2.1), regression formulas that indicate the ammonium flux from the sediment towards the water column for spring and summer/autumn conditions, depending on sediment structure and temperature.

$$\text{Humus content} = 0.17 * \text{lutum content} * 1.5 * 10^4 \quad (3)$$

In which humus and lutum content are depicted as weight percentages, the constant $1.5 * 10^4$ is a conversion factor used to derive organic matter values in g m^{-3} and 0.17 is a scaling constant.

$$\text{NH}_{4\text{flux}} = -6.67 \cdot 10^{-4} - 3.36 \cdot 10^{-8} \cdot \text{humus content} + 5.5 \cdot 10^{-5} \cdot \text{silt} - 3.7 \cdot 10^{-6} \cdot \text{temperature} \quad (4)$$

$$\text{NH}_{4\text{flux}} = -8.6 \cdot 10^{-4} + 7.69 \cdot 10^{-8} \cdot \text{humus content} + 1.27 \cdot 10^{-4} \cdot \text{silt} + 1.27 \cdot 10^{-4} \cdot \text{temperature} \quad (5)$$

Table 2.1: HSI ammonium flux and salinity (De Jong et al., 2005).

Salinity (PSU)	Ammonium flux (kg ha ⁻¹ yr ⁻¹)			
	0 – 50	50 – 100	100 – 150	> 150
≤ 16	0	0	0	0
17-22	1	1	1	1
23-27	1	1	1	0.8
28-30	1	0.8	0.6	0.4
≥ 31	1	0	0	0

Where NH₄ flux is in mol/m²d, humus content in g/m³, silt in weight percentage and temperature in °C. As is the case in the study of De Jong et al. (2005), a calibration factor of 1.5 on the summer/autumn situation is used. A comparison between the output maps of this study and of the study of De Jong et al (2005) show small differences due to different sediment maps, but in general the maps are quite similar.

Zostera noltii exert feedback on ammonium loads, because while growing ammonium is taken up from the sediment as a source of nitrogen. From literature it is deduced that with a measured average growth of about 55 gC/m² (Phillippart et al., 1994) and a N content of 3 % dry weight in eutrophic systems (Duarte, 1991) in the growing season 16,5 kg N/ha is removed from the system and incorporated in the above and belowground biomass of *Zostera noltii*. It is assumed that when HSI > 0.7 *noltii* can grow and therefore, on those spots, ammonium load is reduced by 16,5 kg/ha.

2.1.5 Salinity

Field and lab results show that seagrasses can withstand a wide range of salinities, but only for short periods. Their long-term salinity ranges are more narrow (Hillman et al., 1989). In this study the knowledge rules developed by Erfteimeijer and Van de Wolfshaar (2006), are used (figure 2.4).

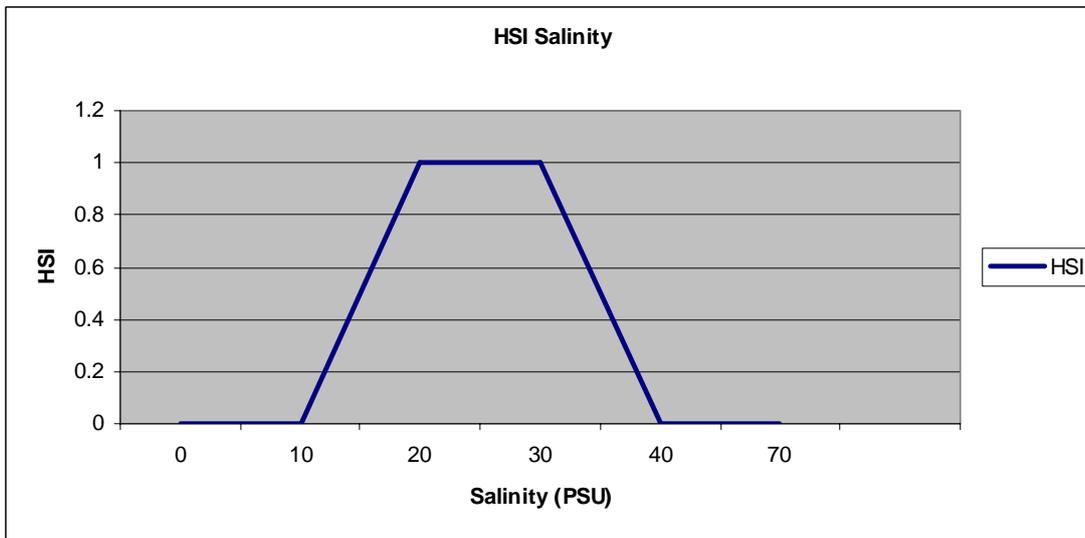


Figure 2.4: Salinity HSI for *Zostera noltii* (Erftemeijer and Van de Wolfshaar, 2006).

2.1.6 Current velocity

Water motion force can have several effects on seagrass growth. The force can be to severe thereby preventing seagrass establishment or when seagrasses are present, damaging the plants physically. On the other hand, increasing current velocities can decrease the boundary layer thus facilitating nutrient uptake and therefore too low current velocities can hamper nutrient uptake (Fonseca and Kenworthy, 1987; Koch, 2001) (figure 2.5). Seagrass meadows, especially those of the larger seagrass species, are known for their current velocity reducing characteristics; however, as *Zostera noltii* is rather small and flexible, its effect on current velocity is negligible. However, as it is moved flat by current velocity, it prevents the energy to reach the sediment thereby decreasing the amount of sediment available for erosion (pers comm. L. van Duuren).

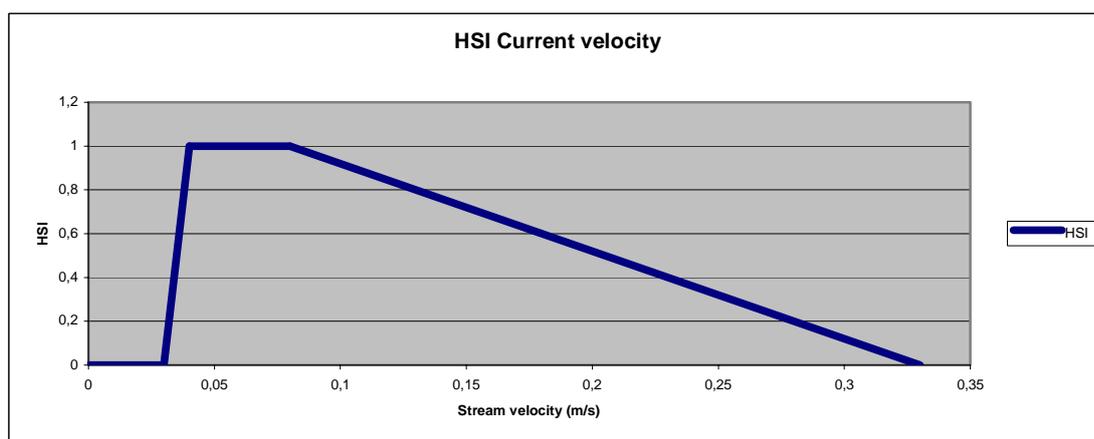


Figure 2.5: Current velocity HSI for *Zostera noltii* (Erftemeijer and Van de Wolfshaar, 2006).

2.1.7 Sediment type

Seagrasses are mostly encountered on sandy to muddy sediments. Sediments with higher organic matter, which are likely to support high bacterial activity, are less suitable because of more reduced conditions (De Jong and De Jonge, 1989; Philipart, 1994). The used knowledge rule is taken from Erftemeijer and Van de Wolfshaar (2006), see figure 2.6.

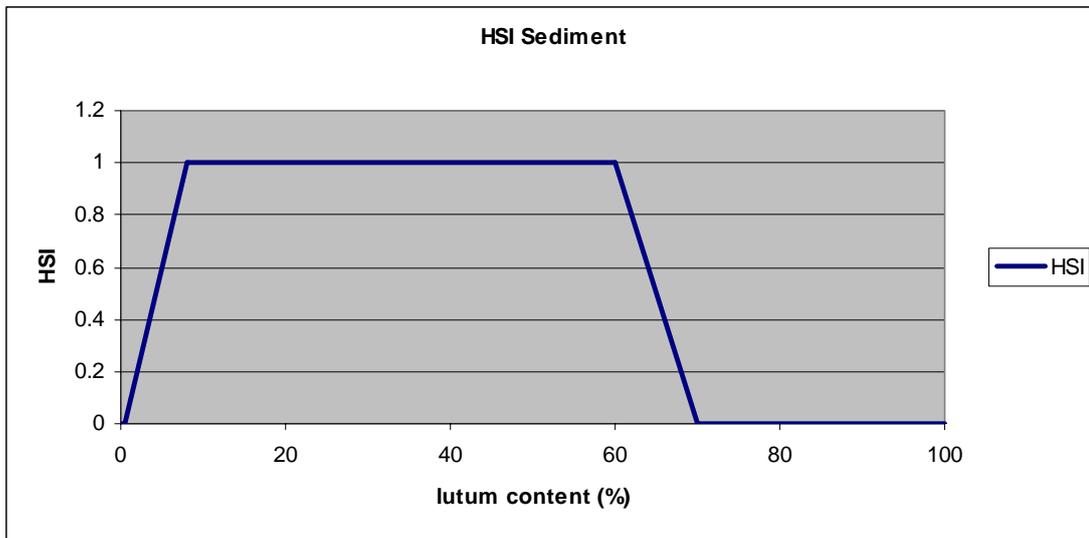


Figure 2.6: Sediment composition HSI for *Zostera noltii* (Erftemeijer and Van de Wolfshaar, 2006).

2.2 Outline of the model

The knowledge rules mentioned above make up the HSI model used for this study. Recapitulating: light availability and desiccation make up the bandwidth of occurrence where *Zostera noltii* can grow, the other environmental parameters narrow habitat suitability further. The amount of ammonium load from the sediment is influenced by temperature and sediment type and the HSI of N toxicity is interfered by salinity. Moreover, *Zostera noltii* feedbacks on light availability and the ammonium load by its presence. See figure 2.7 for the outline.

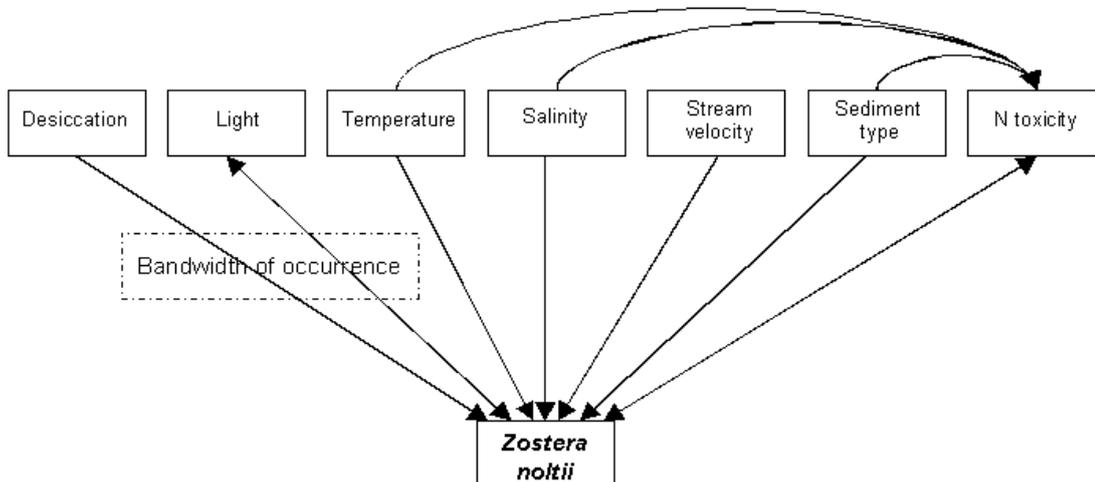


Figure 2.7: Model outline.

2.3 Coupling years in a semi static model

In this study, HABITAT is used as a semi static model, which means that the output of one year is the input for the next year. Therefore, a specific characteristic should transfer the information of the HSI from one year to the next. One option is to use the HSI of the end of the year, however, this implies that the limiting year for HSI is the ultimate result that does not yield insight in how warm and dry and normal year alternating impacts on the HSI of *Zostera noltii*. In the Wadden Sea, *Zostera noltii* expands by vegetative development, where nutrients and energy of the foregoing year is stored into rhizomes. Seagrass shoots and the expansion of seagrass is steered by rhizomes growth (Marba and Duarte, 1998), and could therefore be

used as “system memory” of the foregoing year. In the study of Borum et al. (2004) spreading rates of different European seagrasses are presented. One of them is *Zostera noltii* and its spreading rate is in the range of 0.44-1.68 meter per year. As in HABITAT knowledge rules a habitat suitability index of around 0.7 is considered as a value above which the chance the species occurs in reality is good (good to very good habitat suitability), the work around is that spreading of *Zostera noltii* occurs by means of HSI larger than 0.65 (lower limit). Thus, if HSI is 0.65 or higher, spreading occurs, and depends on the value of the HSI: the better the HSI the more *Zostera noltii* spreads. However, as the maps used in HABITAT are 20 x 20 meter rasters, it is not possible to use the realistic spreading distances stated above. Therefore, a pragmatic solution is used: the smallest possible spread occurs for HSI class 0.65-0.75: 20 meters, the second class, 0.75-0.85 has a spreading of 40 meters, the third class, 0.85-0.95, has a spreading of 60 meters and the class of HSI 0.95-1.0 has a spreading radius of 80 meters. In this way, HSI classes are differentiated. This expansion of *Zostera noltii* is of importance as system memory for the next year when regarding light availability and nitrogen uptake.

2.4 Scenarios

Three scenarios, next to a control run, are run to explore the effect of dry and warm and normal years on the HSI of *Zostera noltii*. A first scenario is run in which 2 normal years are followed by a warm and dry year which is followed by again 2 normal years. In this way, it becomes visible what the impact of a warm and dry year is: is the situation the same after 2 years after a warm and dry year compared to two normal years that are not preceded by a warm and dry year? The second scenario gives insight if and if so how the HSI is changed by having in year 2 a warm and dry year followed by 2 normal years and then again a warm and dry year. In comparison to scenario 1, this shows if several warm and dry years have an impact on the recovery time of the HSI (comparing scenario 1 year 3 to scenario 2 year 5). The last scenario has alternating normal and warm and dry years. This is in accordance with the climate scenarios for 2050 presented by Van den Hurk et al (2009) and gives insight in the resilience of the HSI of *Zostera noltii* when warm and dry years become more common. Table 2.2 gives an overview of the scenarios.

Table 2.2: overview of scenarios.

Scenario	year 1	year 2	year 3	year 4	year 5
Control	Normal	Normal	Normal	Normal	Normal
1	Normal	Normal	Warm and dry	Normal	Normal
2	Normal	Warm and dry	Normal	Normal	Warm and dry
3	Normal	Warm and dry	Normal	Warm and dry	Normal

3 Results

For all three scenarios, the runs started with a normal year. The output maps of HIS, limiting factors and expansion by *Zostera noltii* for this first year are given in figure 3.1. This provides an indication where *Zostera noltii* can grow, what the main limiting factors are and how spreading occurs in the model. As the maps do look alike, the maps are depicted in appendix 7.4. Furthermore, in appendix 7.4 maps are showed that illustrate the differences between succeeding years regarding habitat suitability. In this chapter, statistics on changes in HSI and limiting factors are showed, more detailed statistics are given in appendix 7.5.

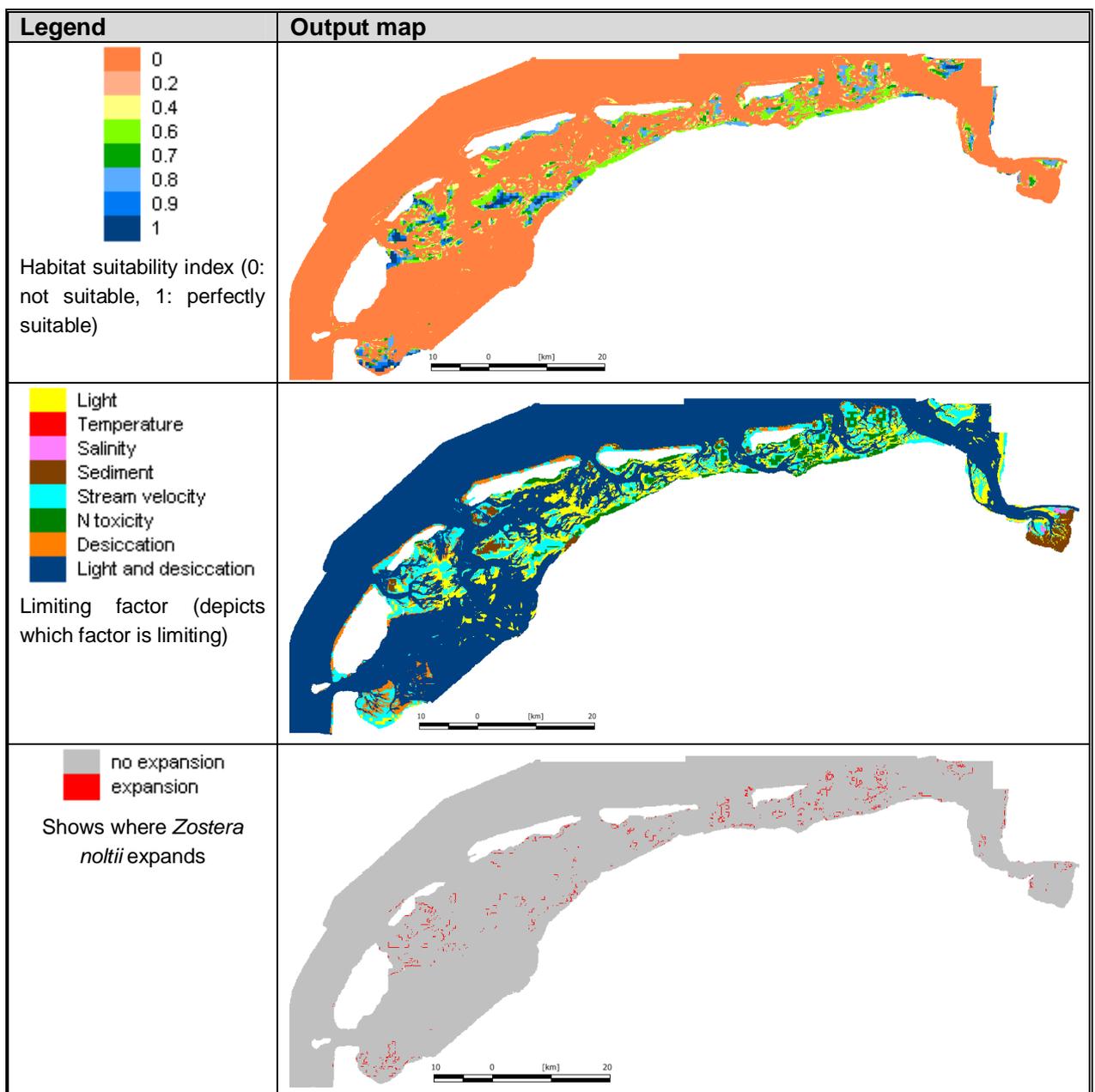


Figure 3.1: overview of HSI, limiting factor and expansion maps of the first year used in all three scenarios.

3.1 Control run

In the control run it is visible that the class of good HSI (>0.7) cover 4.66% of the total area in the first year. The area slightly increases to 4.91% in the fourth and fifth year of the model run. Mediocre HSI (0.5-0.7 HSI) decreases during the simulation and unsuitable to little suitable HSI (<0.5) increases somewhat. The last two years show rather similar coverages of the different HSI classes (table 3.1).

Table 3.1: overview of area share (%) of HSI for the five simulated years.

Year	Year 1 (normal)	Year 2 (normal)	Year 3 (normal)	Year 4 (normal)	Year 5 (normal)
HSI Legend					
[0,0.2>	86.14%	86.08%	86.06%	86.06%	86.06%
[0.2,0.4>	2.52%	2.47%	2.45%	2.44%	2.43%
[0.4,0.6>	3.20%	3.69%	3.65%	3.63%	3.61%
[0.6,0.7>	3.48%	2.88%	2.94%	2.97%	2.99%
[0.7,0.8>	1.59%	1.68%	1.71%	1.72%	1.72%
[0.8,0.9>	2.25%	2.35%	2.35%	2.35%	2.35%
[0.9,]	0.82%	0.84%	0.84%	0.84%	0.84%
Total	100.00%	100.00%	100.00%	100.00%	100.00%

Stabilization is also the case for the importance of limiting factor Light in combination with desiccation is the most limiting factor (73%), as light availability is often too low and lots of the area does not denude during low tide, which is a requirement for *Zostera noltii* growth. Other important limiting factors are current velocity (11%) and light availability (9%) (see table 3.2). Current velocity showed to be too high for *Zostera noltii* growth, preventing it to colonize new areas. Note: a limiting factor does not mean that *Zostera noltii* cannot grow because the limiting factor is the factor with the lowest HSI but can be close to or even 1

Table 3.2: overview of area share of the limiting factors for the whole Wadden Sea

Year	Year 1 (normal)	Year 2 (normal)	Year 3 (normal)	Year 4 (normal)	Year 5 (normal)
Limiting factor					
Light	9.10%	8.71%	8.67%	8.66%	8.66%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.11%	0.11%	0.11%	0.11%	0.11%
Sediment	2.21%	2.21%	2.21%	2.21%	2.21%
current velocity	10.33%	10.62%	10.65%	10.66%	10.67%
NH ₄ _flux	3.05%	3.20%	3.20%	3.20%	3.20%
Desiccation	2.22%	2.23%	2.23%	2.23%	2.23%
light and desiccation	72.98%	72.92%	72.92%	72.92%	72.92%
Total	100.00%	100.00%	100.00%	100.00%	100.00%

When looking for management options it is interesting to know which limiting factors determine mediocre suitability for *Zostera noltii* growth. Because those factors are almost suitable, they give options to create additional areas having good habitat suitability. Habitat suitability that is by far not suitable is not considered in this view, as it is assumed that it takes more effort to turn an unsuitable area into a suitable area than turning a mediocre suitable area into a suitable area. All statistics can be found in appendix 7.5. Table 3.3 shows that especially current velocity (56%), NH₄-flux and light availability is limiting mediocre HSI to become good HSI. However, care should be taken here because also other factors can render mediocre HSI at the same spot but are just slightly less limiting than the most limiting factor.

Table 3.3: overview of area share when the area is classified as mediocre HSI (%) in limiting factors for the five simulated years.

Year	Year 1 (normal)	Year 2 (normal)	Year 3 (normal)	Year 4 (normal)	Year 5 (normal)
Limiting factor					
Light	10.81%	8.65%	9.06%	9.41%	9.59%
temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.80%	0.93%	0.92%	0.91%	0.91%
Sediment	5.94%	6.93%	6.86%	6.82%	6.80%
current velocity	48.24%	56.79%	56.69%	56.55%	56.47%
NH ₄ -flux	34.16%	26.62%	26.39%	26.23%	26.15%
Desiccation	0.05%	0.07%	0.07%	0.07%	0.07%
light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%

3.2 Scenario 1

In the first scenario, where two normal years are followed by a warm and dry year and after that again two normal years, the effect of warm and dry years as well as feedback of *Zostera noltii* on environmental factors are visible. The first year, the start-up, shows a total good HSI (0.7-1) of 4.66% for *Zostera noltii* within the whole Wadden Sea (table 3.4), which increases to 4.86% in the second year. The area share of good HSI decreases in the succeeding warm and dry year to 3.05% and increases towards 4.81% and 4.89% in the fourth and fifth year, respectively.

Table 3.4: overview of area share (%) of HSI for the five simulated years.

Year	Year 1 (normal)	Year 2 (normal)	Year 3 (warm and dry)	Year 4 (normal)	Year 5 (normal)
HSI Legend					
[0,0.2>	86.14%	86.08%	87.01%	86.09%	86.07%
[0.2,0.4>	2.52%	2.47%	2.23%	2.46%	2.45%
[0.4,0.6>	3.20%	3.69%	3.84%	3.70%	3.64%
[0.6,0.7>	3.48%	2.88%	3.88%	2.94%	2.95%
[0.7,0.8>	1.59%	1.68%	1.17%	1.67%	1.70%
[0.8,0.9>	2.25%	2.35%	1.88%	2.32%	2.35%
[0.9,]	0.82%	0.84%	0.00%	0.82%	0.84%
Total	100.00%	100.00%	100.00%	100.00%	100.00%

Light availability and desiccation is limiting good HSI in the first year the most (73%) followed by current velocity and light availability, 10% and 9%, respectively (see table 3.5). Changes in limiting factors when comparing year 2 to year 1 are just marginal, but current velocity and NH₄-flux become more important as limiting factor. The following year, a warm and dry year, cause the disappearance of spots with very good HSI (class 0.9-1.0). An increase in stress from light availability and N-toxicity (both +2%) appear the main drivers. The normal year succeeding the warm and dry year shows a switch back in limiting factors with an increase of 2% for both current velocity and NH₄-flux and cause light availability to become less important. Year 4 and 5 are looking rather similar concerning limiting factors.

Table 3.5: overview of area share of the limiting factors for the whole Wadden Sea

Year	Year 1 (normal)	Year 2 (normal)	Year 3 (warm and dry)	Year 4 (normal)	Year 5 (normal)
Limiting factor					
Light	9.10%	8.71%	10.49%	8.81%	8.67%
Temperature	0.00%	0.00%	0.44%	0.00%	0.00%
Salinity	0.11%	0.11%	0.01%	0.11%	0.11%
Sediment	2.21%	2.21%	1.97%	2.21%	2.21%
current velocity	10.33%	10.62%	8.06%	10.54%	10.66%
NH ₄ _flux	3.05%	3.20%	5.35%	3.17%	3.20%
Desiccation	2.22%	2.23%	1.61%	2.23%	2.23%
light and desiccation	72.98%	72.92%	72.08%	72.92%	72.92%
Total	100.00%	100.00%	100.00%	100.00%	100.00%

Table 3.6 shows that current velocity (48%), NH₄-flux (34%) and light availability (11%) are most limiting good HSI for the first year. For the succeeding year, current velocity (57%) and sediment (7%) become more important in determining mediocre HSI while light availability (9%) and NH₄-flux (27%) become less important. The warm and dry year shows a change in the most important limiting factor: NH₄ flux becomes most important (50%), followed by current velocity (38%) and light availability (7%). The normal year that succeeds the warm and dry year shows that mediocre habitat suitability is mostly limited by current velocity (56%), NH₄-flux (26%) and light availability (10%). The next normal year show a small increase of importance in limiting mediocre HSI by current velocity (+1%) and a small decrease of light availability (-1%) limiting it.

Table 3.6: overview of area share when the area is classified as mediocre HSI (%) in limiting factors for the five simulated years.

Year	Year 1 (normal)	Year 2 (normal)	Year 3 (warm and dry)	Year 4 (normal)	Year 5 (normal)
Limiting factor					
Light	10.81%	8.65%	7.45%	10.24%	9.23%
temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.80%	0.93%	0.00%	0.92%	0.92%
Sediment	5.94%	6.93%	4.91%	6.82%	6.85%
current velocity	48.24%	56.79%	37.82%	55.85%	56.66%
NH ₄ _flux	34.16%	26.62%	49.80%	26.11%	26.27%
Desiccation	0.05%	0.07%	0.02%	0.07%	0.07%
light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%

3.3 Scenario 2

The second scenario shows, after the initial 4.66% area coverage of good HSI of the first normal year, a drop of 1.64% in good HSI area in the warm and dry year, an increase of 1.79% to 4.81% area coverage of good HSI in the third year, followed by slight increase of good HSI area to 4.89% in the fourth year and finally a drop towards an aerial coverage of 3.06% in the warm and dry fifth year (table 3.7).

Table 3.7: overview of area share (%) of HSI for the five simulated years.

Year	Year 1 (normal)	Year 2 (warm and dry)	Year 3 (normal)	Year 4 (normal)	Year 5 (warm and dry)
HSI Legend					
[0,0.2>	86.14%	87.05%	86.09%	86.07%	87.00%
[0.2,0.4>	2.52%	2.24%	2.47%	2.45%	2.23%
[0.4,0.6>	3.20%	3.84%	3.70%	3.65%	3.82%
[0.6,0.7>	3.48%	3.85%	2.93%	2.95%	3.90%
[0.7,0.8>	1.59%	1.15%	1.67%	1.70%	1.18%
[0.8,0.9>	2.25%	1.87%	2.32%	2.35%	1.88%
[0.9,]	0.82%	0.00%	0.82%	0.84%	0.00%
Total	100.00%	100.00%	100.00%	100.00%	100.00%

Factors that become more limiting in the second year in contrast to the first year at the expense of current velocity, desiccation, light and desiccation, sediment and salinity are NH₄-flux, light availability and temperature, +2%, +1% and +0.5% respectively (see table 3.8). The subsequent two normal years show an initial increase of 1.79% of good HSI in the subsequent year and a smaller increase of 0.08% in the second normal year. The increase is concomitant with a reduction in stress from NH₄-flux, light availability and temperature. For the first normal year, light availability becomes less important, but current velocity becomes more important as limiting factor. Between year 3 and 4 little changes regarding overall limiting factors. The fifth year, a warm and dry year, shows again an increase in importance of NH₄-flux, light availability and temperature as limiting factors.

Table 3.8: overview of area share of limiting factors for the whole Wadden Sea.

Year	Year 1 (normal)	Year 2 (warm and dry)	Year 3 (normal)	Year 4 (normal)	Year 5 (warm and dry)
Limiting factor					
light	9.10%	10.53%	8.81%	8.68%	10.47%
temperature	0.00%	0.44%	0.00%	0.00%	0.44%
salinity	0.11%	0.01%	0.11%	0.11%	0.01%
sediment	2.21%	1.97%	2.21%	2.21%	1.97%
current velocity	10.33%	8.04%	10.54%	10.65%	8.07%
NH ₄ _flux	3.05%	5.33%	3.17%	3.20%	5.35%
desiccation	2.22%	1.61%	2.23%	2.23%	1.61%
light and desiccation	72.98%	72.08%	72.92%	72.92%	72.08%
total	100.00%	100.00%	100.00%	100.00%	100.00%

When looking at mediocre HSI (table 3.9), warm and dry years are most hampered by NH₄-flux followed by current velocity and normal years are most hampered by current velocity followed by NH₄-flux. Moreover, the total mediocre HSI area is higher in warm and dry years than in normal years. Moreover, light availability is less important in warm and dry years than in normal years, however, the importance of light availability is less in the normal year that follows upon a normal year. In this case current velocity becomes more important.

Table 3.9: overview of area share when the area is classified as mediocre HSI (%) in limiting factors for the five simulated years.

Year	Year 1 (normal)	Year 2 (warm and dry)	Year 3 (normal)	Year 4 (normal)	Year 5 (warm and dry)
Limiting factor					
light	10.81%	7.50%	10.03%	9.14%	7.40%
temperature	0.00%	0.00%	0.00%	0.00%	0.00%
salinity	0.80%	0.00%	0.92%	0.92%	0.00%
sediment	5.94%	4.93%	6.84%	6.85%	4.90%
current velocity	48.24%	37.81%	55.95%	56.70%	37.97%
NH ₄ _flux	34.16%	49.74%	26.19%	26.31%	49.72%
desiccation	0.05%	0.02%	0.07%	0.07%	0.02%
light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%

3.4 Scenario 3

The first three years are the same as scenario 2, but the fourth year is in this scenario warm and dry instead of normal. Good HSI decreases with 1.76% to 3.05% when going from year 3 to year 4 and increases back to a HSI of 4.81% in year 5, a normal year. Year 3 and 5 do look alike in limiting factors for the whole Wadden Sea (table 3.11), but when looking at mediocre HSI (table 3.12) differences are visible.

Table 3.10: overview of area share (%) of HSI for the five simulated years.

Year	Year 1 (normal)	Year 2 (warm and dry)	Year 3 (normal)	Year 4 (warm and dry)	Year 5 (normal)
HSI Legend					
[0,0.2>	86.14%	87.05%	86.09%	87.02%	86.09%
[0.2,0.4>	2.52%	2.24%	2.47%	2.23%	2.46%
[0.4,0.6>	3.20%	3.84%	3.70%	3.82%	3.69%
[0.6,0.7>	3.48%	3.85%	2.93%	3.88%	2.95%
[0.7,0.8>	1.59%	1.15%	1.67%	1.17%	1.67%
[0.8,0.9>	2.25%	1.87%	2.32%	1.88%	2.32%
[0.9,]	0.82%	0.00%	0.82%	0.00%	0.82%
total	100.00%	100.00%	100.00%	100.00%	100.00%

Table 3.11: overview of area share of limiting factors for the whole Wadden Sea

Year	Year 1 (normal)	Year 2 (warm and dry)	Year 3 (normal)	Year 4 (warm and dry)	Year 5 (normal)
Limiting factor					
Light	9.10%	10.53%	8.81%	10.49%	8.81%
temperature	0.00%	0.44%	0.00%	0.44%	0.00%
Salinity	0.11%	0.01%	0.11%	0.01%	0.11%
Sediment	2.21%	1.97%	2.21%	1.97%	2.21%
current velocity	10.33%	8.04%	10.54%	8.07%	10.55%
NH ₄ _flux	3.05%	5.33%	3.17%	5.33%	3.17%
desiccation	2.22%	1.61%	2.23%	1.61%	2.23%
light and desiccation	72.98%	72.08%	72.92%	72.08%	72.92%
total	100.00%	100.00%	100.00%	100.00%	100.00%

Limiting good HSI in year 5 is more hampered by light availability than is the case for year 4. When comparing the 2 dry and warm years also little change is visible.

Table 3.12: overview of area share when the area is classified as mediocre HSI (%) in limiting factors for the five simulated years

Year	Year 1 (normal)	Year 2 (warm and dry)	Year 3 (normal)	Year 4 (warm and dry)	Year 5 (normal)
Limiting factor					
light	10.81%	7.50%	10.03%	7.35%	10.47%
temperature	0.00%	0.00%	0.00%	0.00%	0.00%
salinity	0.80%	0.00%	0.92%	0.00%	0.91%
sediment	5.94%	4.93%	6.84%	4.92%	6.80%
current velocity	48.24%	37.81%	55.95%	38.09%	55.72%
NH ₄ _flux	34.16%	49.74%	26.19%	49.63%	26.03%
desiccation	0.05%	0.02%	0.07%	0.02%	0.07%
light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%

3.5 Overall

For all scenario's it shows that going from a normal to a warm and dry year, temperature and N toxicity become more important as limiting factors and when going from a warm and dry year to a normal year light availability, current velocity and salinity become more important as limiting factors. However, for all years light availability in combination with desiccation is the most limiting factor.

Table 3.13 overview of area (m²) of unsuitable (unsuitable and almost not suitable), mediocre and good HSI in the whole Wadden Sea (red means dry years).

Scenario	HSI type	Year 1	Year 2	Year 3	Year 4	Year 5
control	unsuitable	4.01E+09	4.04E+09	4.03E+09	4.03E+09	4.03E+09
	mediocre	2.24E+08	1.93E+08	1.95E+08	1.96E+08	1.97E+08
	good	2.07E+08	2.16E+08	2.18E+08	2.18E+08	2.18E+08
scenario 1	unsuitable	4.01E+09	4.04E+09	4.08E+09	4.04E+09	4.03E+09
	mediocre	2.24E+08	1.93E+08	2.32E+08	1.96E+08	1.96E+08
	good	2.07E+08	2.16E+08	1.35E+08	2.14E+08	2.17E+08
scenario 2	unsuitable	4.01E+09	4.08E+09	4.04E+09	4.03E+09	4.08E+09
	mediocre	2.24E+08	2.31E+08	1.96E+08	1.95E+08	2.33E+08
	good	2.07E+08	1.34E+08	2.14E+08	2.17E+08	1.36E+08
scenario 3	unsuitable	4.01E+09	4.08E+09	4.04E+09	4.08E+09	4.03E+09
	mediocre	2.24E+08	2.31E+08	1.96E+08	2.32E+08	1.97E+08
	good	2.07E+08	1.34E+08	2.14E+08	1.36E+08	2.14E+08

From table 3.13 it shows that after 3 normal years the model already reached a near steady state. Moreover, the first scenario shows that good HSI for *Zostera noltii* needs somewhat more than one year to recover from a warm and dry year as after one year less good HSI area is present and after two years more good HSI is present than was present after the first two normal years. Scenario 2 shows that after one warm and dry year the same area of good HSI is reached in the two normal years that follow. However, the fifth year, a warm and dry year, show a larger area of good HSI than year two, probably because of the larger area with good HSI after year four than is the case after year one. In the third scenario the years that follow upon a warm and dry year show the same results, and the second dry year show a little bit more good HSI area than the first warm and dry year. However, the good HSI area may be same in years three and five, their limiting factors are not. This means that the showed stability in good HSI area may change if more alternating years are added.

4 Discussion

4.1 Analysis

From the results it is clear that warm and dry years render less suitable area for *Zostera noltii* growth. It shows that especially higher NH_4 fluxes and temperature lead to this effect. As such, the effect of temperature is twofold: indirect via increasing the NH_4 flux from the sediment and direct via enzyme inhibition. Normal years are, compared to warm and dry years, more subjected to current velocity, light availability and salinity. The recovery time of habitat suitability in this study is fast. This is because the focus is on *habitat suitability* and not on the actual growth of *Zostera noltii*. Thus, if environmental conditions are good, this means habitat suitability is good and does not mean *Zostera noltii* is growing there. The recovery time in this model has therefore to do with the ability of *Zostera noltii* to feedback on environmental conditions, with the underlying assumption that if HSI is good, the feedback will take place. Of course, when looking on the impact of *real Zostera noltii* the effect of warm and dry years could be more devastating as the actual recolonization is much and much slower.

When looking at the output maps as a whole, light availability is the most limiting factor: around 80% for all years, followed by current velocity and N toxicity. When comparing to the habitat suitability map constructed by De Jong et al. (2005), the amount of suitable area is about 10 times higher in this study. Zooming in on both studies, it showed that the habitat suitability map by De Jong et al. (2005) is mainly limited by desiccation, which is assigned a good HSI if areas are uncovered by water between 40 and 65% of the time. This knowledge rule is constructed for the flexible type of *Zostera marina*, which could explain the difference of the percentage of time allowed used in this study (5-67%). Moreover, in the study of De Jong et al. (2005) light availability is not taken into account. However, the finding that light availability is the mean factor hampering the (re)growth of *Zostera noltii* is acknowledged by other research (Giesen et al., 1990; De Jonge and de Jong, 1992; Van der Heide et al., 2006). Also the relatively high importance of current velocity (if light availability is sufficient, current velocity is often the limiting factor) has been acknowledged (De Jonge and De Jong, 1992; Schanz and Asmus, 2003).

It is good to bare in mind that while looking at limiting factors in this study, that factor is the most limiting, that does not mean that when this factor improves regarding HSI, HSI increases at the same pace as other factors can become limiting. The other way around, when pinpointing a limiting factor, it does not mean that *Zostera noltii* cannot grow, as the value of the limiting factor can be sufficient to sustain a good HSI, but it means that that factor is putting the most stress on survival of *Zostera noltii*.

4.2 Importance

The scope of this study is to explore the effects of warm and dry years in comparison to normal years on the habitat suitability (HSI) of *Zostera noltii* in the Dutch Wadden Sea. As becomes clear from the input data, there exist differences in environmental conditions between warm and dry and normal years. Warm and dry years show higher extinction coefficients, temperatures and ammonium fluxes than is the case for normal years (see appendix 7.6). This is in accordance with the findings of Justic et al. (2005), and shows already some of the natural range an environmental factor can fluctuate over time. As habitat suitability maps consider average conditions that are often averaged over time, normal fluctuations over years are not considered. However, these environmental fluctuations are important when one considers long-term habitat suitability. This is illustrated by the results of this study: warm and dry years impacted the area of good HSI for *Zostera noltii* compared to the HSI in a normal year.

Nonetheless, average habitat suitability maps can give clues on what is going on in the system, for instance: what factor(s) is (are) limiting good habitat suitability. This knowledge can be relevant for restoration or management options (De Jong et al., 2005; Björk et al., 2008). Even so, as environmental factors are changing within and over years, a restoration project in one year can fail because changes in one environmental factor, but can succeed in another year when all environmental factors are in the right range for the growth of *Zostera noltii*. It is good to be aware of this and if a habitat suitability model could not explain project failure, it is interesting to know what limited the growth of *Zostera noltii*, like storm surges, ice cover, foraging birds etc. This knowledge broadens the understanding of the system dynamics. Furthermore, as climate is changing and events of more extreme environmental conditions are becoming more common, restoration projects should keep in mind that the range over which environmental parameters fluctuates is likely to increase, not only in amplitude but also in frequency of occurrence.

4.3 Remarks

As stated earlier, little data was available both in time and space and therefore interpolation was very rough. This leads to a generalized overview of the input data and is by no means specific for place as well as time. Thus, the output is subjected to generalized results and therefore not place specific. An example of too strong time interpolation is algal bloom occurrences, because they can temporarily lead to high extinction coefficients, which hamper the growth of *Zostera noltii*. Moreover, temporal changes in temperature influence ammonium fluxes from the sediment to the water column, which is, especially in dry years, of importance for the determination of the HSI. Another shortcoming of the model is its resolution, which was too large to correctly model the colonization rates stated in literature (Borum et al., 2004). An idea is to pick a small spot where *Zostera noltii* grows and apply higher resolution to fit colonization rates, this is also for validation purposes a fruitful work around.

Another source of inaccuracy is the used knowledge rules: as they are just considering a few parameters and often not the dependencies between them, important parameters that occur not on a regular basis (like storm surges, mowing) or synergy are not taken into account. This leads to omissions of the actual systems, which is of course often the when models are used. In addition to possible mediocre applicability of the used knowledge rules: problems do arise for the impact of feedback from *Zostera noltii* exerts on environmental conditions. Additional literature or even field or lab work is needed. Moreover, the knowledge rule on N toxicity is difficult to quantify as limited data on this process is available (pers comm.. C. Schipper). Therefore, over or under estimation of this flux is very well possible.

To get insight into the goodness of fit of this habitat suitability model, validation is needed. However, as little *Zostera noltii* is present in the Wadden Sea, this can prove difficult. Still, the model predicted good HSI for the places where both *Zostera noltii* and *Zostera marina* are present nowadays. A remarkable observation is that when looking at mapped *Zostera noltii* occurrence in the Wadden Sea, 2003 has higher *Zostera noltii* biomass than 2005 (Erftemeijer, 2005). However, as the foregoing year is also important in determining the biomass for the next year and the occurrence of storm surges and freezing events in winter it is not easily to say what cause the mismatch between model and field results.

5 Conclusion

The presented habitat suitability model showed that warm and dry years have a negative impact on the habitat suitability index of *Zostera noltii* in the Dutch Wadden Sea compared to normal years. It showed that especially the direct and indirect effects of temperature are the ones that contribute most to this effect. This is because higher temperatures increase ammonium flux from the sediment, which leads to N toxicity and also affect enzymatic activity. However, for both type of years, the most limiting factor is the small availability of light reaching the sediment and the lack of denuded areas during tides, followed by too high current velocities. This study shows that year-by-year variations in environmental conditions can affect the habitat suitability of *Zostera noltii* in the Dutch Wadden Sea, which yields implications for restoration projects now and, with ongoing climate change, surely in the future.

6 Literature

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Internet sources:

Watlas, available on the world wide web and last visited on 15-03-2011:

<http://www.waddenzee.nl/Watlas.27.0.html>

7 Appendices

7.1 Habitat instrument

HABITAT is a spatial analysis tool that can be used to analyze the availability and quality of habitats for individual or groups of species and to map spatial units (e.g. ecotopes). Moreover, HABITAT can be used to predict potential damage and/or risks for different kinds of land use caused by human interventions, climate change and autonomous developments.

HABITAT, consists of two parts: software and dose effect relations. The latter describes relations between steering variables and the habitat suitability of a species, species group or ecotope. The software core of HABITAT is based on PCRaster, which facilitates a large variety of spatial analyses. As input GIS maps or filed observations in raster format are required. Dose effect relations calculate the output, being maps or tables.

HABITAT is freely available if newly developed knowledge rules are shared with the HBAITAT community through a knowledge database (<http://habitat.deltares.nl>).

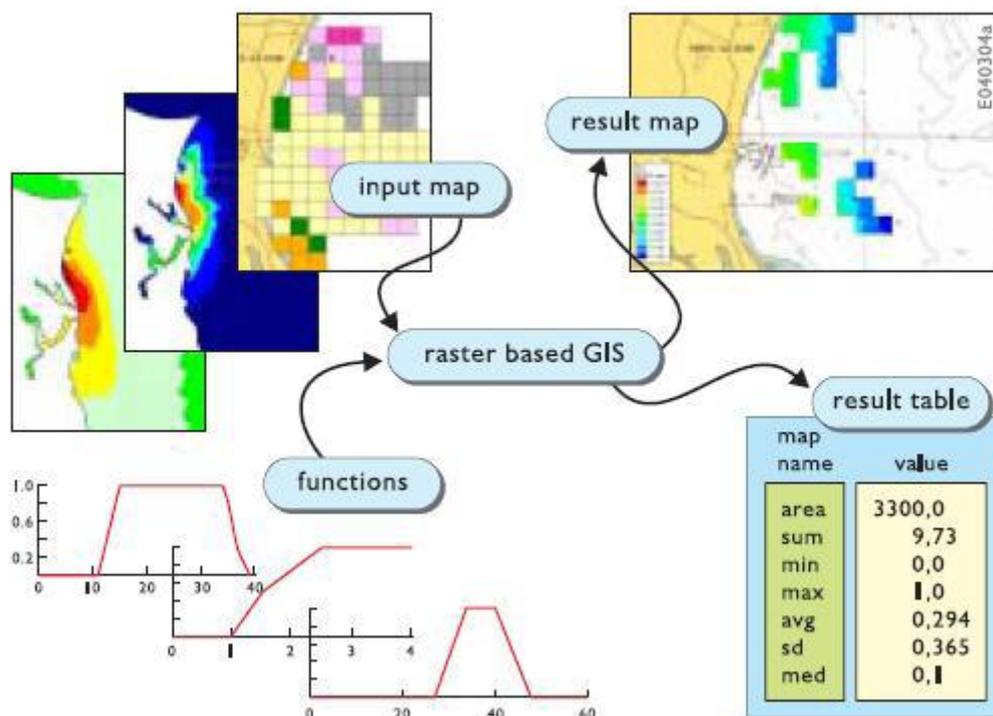


Figure 7.1: outline of the HABITAT tool.

7.2 Weather type description (Dutch)

Beschrijvingen een op een over genomen van het KNMI (2011):

http://www.knmi.nl/klimatologie/maand_en_seizoenoverzichten/#jaar

7.2.1 Warm and Dry Year (2003)

In De Bilt heeft de zon het afgelopen jaar 2022 uren geschinen tegen een langjarig gemiddelde van 1524 uren. Niet eerder sinds het begin van de waarnemingen in 1901 telde een jaar zoveel zonuren. Het oude record stond op naam van 1959 met 1986 uren zonneshijn.

Van de afzonderlijke maanden eindigden er zes in de top 10 van zonnigste overeenkomstige maanden, februari en maart zelfs op de eerste plaats. In De Bilt verliepen slechts 45 dagen geheel zonloos; normaal telt men 76 sombere dagen. Gemiddeld over het land werden 2099 zonuren geregistreerd tegen normaal 1550. Het zonnigst was het langs de westkust met op het KNMI-station De Kooy maar liefst 2194 zonuren.

Een aantal stations noteerden meer zon dan het absolute record voor ons land dat tot nu toe op naam stond van Valkenburg (ZH) waar in 1995 de zon 2054 uren scheen. Het minst scheen de zon in het noordoosten van het land; Nieuw-Beerta registreerde 1971 uren.

Met een gemiddelde temperatuur in De Bilt van 10,3 °C tegen een langjarig gemiddelde van 9,8 °C was 2003 warm. Meest markant was de uitzonderlijke warmte tijdens de zomer; in De Bilt was alleen de zomer van 1947 nog een fractie warmer.

Tabel 7.1: voorkomen van weerskarakteristieken in De Bilt voor het jaar 2003:

2003	Normaal		
6	(8)	ijsdagen	(max.temp. lager dan 0 °C)
75	(58)	vorstdagen	(min.temp. lager dan 0 °C)
116	(77)	warme dagen	(max.temp. 20 °C of hoger)
48	(22)	zomerse dagen	(max.temp. 25 °C of hoger)
11	(3)	tropische dagen	(max.temp. 30 °C of hoger)

Tussen haakjes is het langjarig gemiddelde vermeld.

Het aantal warme dagen was nog nooit eerder sinds 1901 zo hoog geweest. Het aantal zomerse dagen werd alleen in 1947 overtroffen; dat jaar telde er 64. Van 31 juli tot en met 13 augustus was er sprake van een hittegolf, de 34e sinds 1901. De hittegolf leverde in Arcen een aaneengesloten periode van 12 tropische dagen op. Op drie dagen steeg de temperatuur in onder andere Arcen zelfs tot boven de 37 °C; op 7 augustus tot 37,8 °C. Deze waarde behoort tot de hoogste temperaturen die ooit in Nederland zijn waargenomen. De landelijk laagste temperatuur, -16,8 °C, werd gemeten op 9 januari in Nieuw Beerta.

Gemiddeld over het land viel 631 mm neerslag, terwijl het langjarig gemiddelde 797 mm bedraagt. De grootste hoeveelheid neerslag, 754 mm, werd afgetapt in Marknesse, terwijl De Kooy met 509 mm de minste neerslag kreeg te verwerken. In De Bilt viel 613 mm tegen normaal 793 mm. Daarmee eindigde het jaar op de tiende plaats in de rij van droogste jaren sinds 1901. Het droogst was 1921 met slechts 387 mm. Met name de zomer was zeer droog, in De Bilt zelfs de droogste in ruim honderd jaar. De geringe hoeveelheid neerslag in combinatie met de grote verdamping leidde met name in het westen tot een groot neerslagtekort en ernstige droogteproblemen voor o.a. de agrarische sector, het waterbeheer en energieproducenten.

Over 2002 bedroeg de gemiddelde temperatuur in De Bilt 10,8 °C en het aantal uren zonneshijn 1688. Er viel 924 mm neerslag.

7.2.2 Normal Year (2005)

Met een gemiddelde temperatuur in De Bilt van 10,7 °C tegen een langjarig gemiddelde van 9,8 °C was 2005 zeer warm en eindigt op een gedeelde vijfde plaats in de rij van warmste jaren sinds 1901. Alle jaren van deze top 10 zijn na 1988 voorgekomen. Bovendien is 2005 het negende jaar op rij met een temperatuur van boven de 10,0 °C. De opwarming van het Nederlandse klimaat zet hiermee onverminderd door. Vooral in januari, april, september en oktober was de gemiddelde temperatuur hoog: januari eindigde op de zevende, april op de vijfde, september op de achtste en oktober op de tweede plaats in de rij van warmste overeenkomstige maanden sinds 1901. De klimatologische herfst (september, oktober, november) was bovendien de warmste in drie eeuwen. Van 18 tot en met 24 juni was er sprake van een landelijke hittegolf, de 36e sinds 1901. Tijdens deze hittegolf werd het op 20 juni in Gilze-Rijen 34,7 °C, de landelijk hoogste temperatuur dit jaar. De landelijk laagste temperatuur, -20,7 °C, werd gemeten op 4 maart in Marknesse. Het was de laagste temperatuur die ooit in maart in ons land is gemeten.

Tabel 7.2: voorkomen van weerskarakteristieken in De Bilt voor het jaar 2005:

Jaar 2005	Normaal		
3	(8)	Ijsdagen	(max. temp. lager dan 0,0 °C)
48	(58)	Vorst dagen	(min. temp. lager dan 0,0 °C)
88	(77)	Warme dagen	(max temp. 20,0 °C of hoger)
34	(22)	Zomerse dagen	(max. temp. 25,0 °C of hoger)
4	(3)	Tropische dagen	(max. temp. 30,0 °C of hoger)

Het jaar was zeer zonnig met landelijk gemiddeld 1820 uren zonneshijn tegen 1550 uren normaal. In De Bilt werden 1789 zonuren geregistreerd tegen 1524 normaal. Sinds 1901 waren er maar zes jaren nog zonniger.

Van de KNMI-stations was Vlissingen het zonnigst met 1910 uren zonneshijn, Arcen in Limburg het somberst met 1724 uren. Vooral september en oktober verliepen zeer zonnig. In De Bilt eindigde september op de achtste plaats en oktober op de derde plaats in de rij van zonnigste overeenkomstige maanden in ruim een eeuw.

Gemiddeld over het land viel 785 mm neerslag, terwijl het langjarig gemiddelde 797 mm bedraagt. Van de KNMI-stations was Vlissingen met 887 mm het natst, Maastricht met 604 mm het droogst. In De Bilt werd 873 mm geregistreerd tegen 793 mm normaal.

Op 2 en 3 maart lag er na langdurige sneeuwval in een groot deel van het noorden van het land 20 tot ruim 50 cm sneeuw. Een dergelijk sneeuwdek over zo'n groot gebied is uitzonderlijk voor ons land en doet zich waarschijnlijk minder dan eens per 50 jaar voor. 25 november was een zeer natte dag. In een strook van Noord-Holland naar Gelderland viel overvloedige neerslag, lokaal 50 tot ca. 90 mm in 24 uur. In het westen viel de neerslag als regen, in het oosten en later zuiden als sneeuw waarbij zich een sneeuwdek vormde tot lokaal ca. 20 cm met veel overlast tot gevolg.

Over 2004 bedroeg de gemiddelde temperatuur in De Bilt 10,3 °C en het aantal uren zonneshijn 1629. Er viel 859 mm neerslag.

7.3 Description of light availability formulas

In this appendix 6 formulas that describe the percentage of light that is available on the sediment for both a warm and dry year and a normal year are presented for the areas where it is known *Zostera noltii* grows.

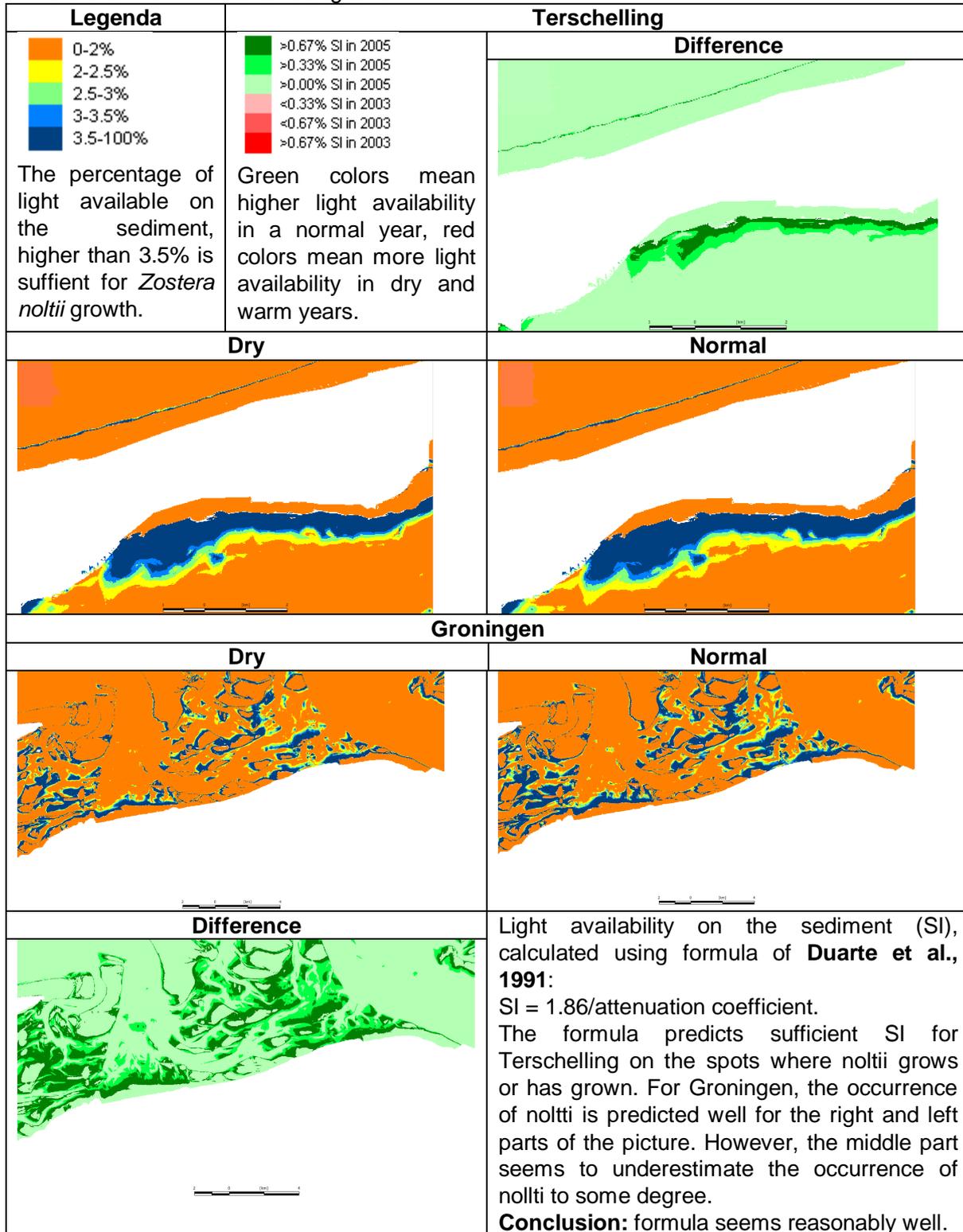


Figure 7.2: description of light availability formula by Duarte et al., 1991.

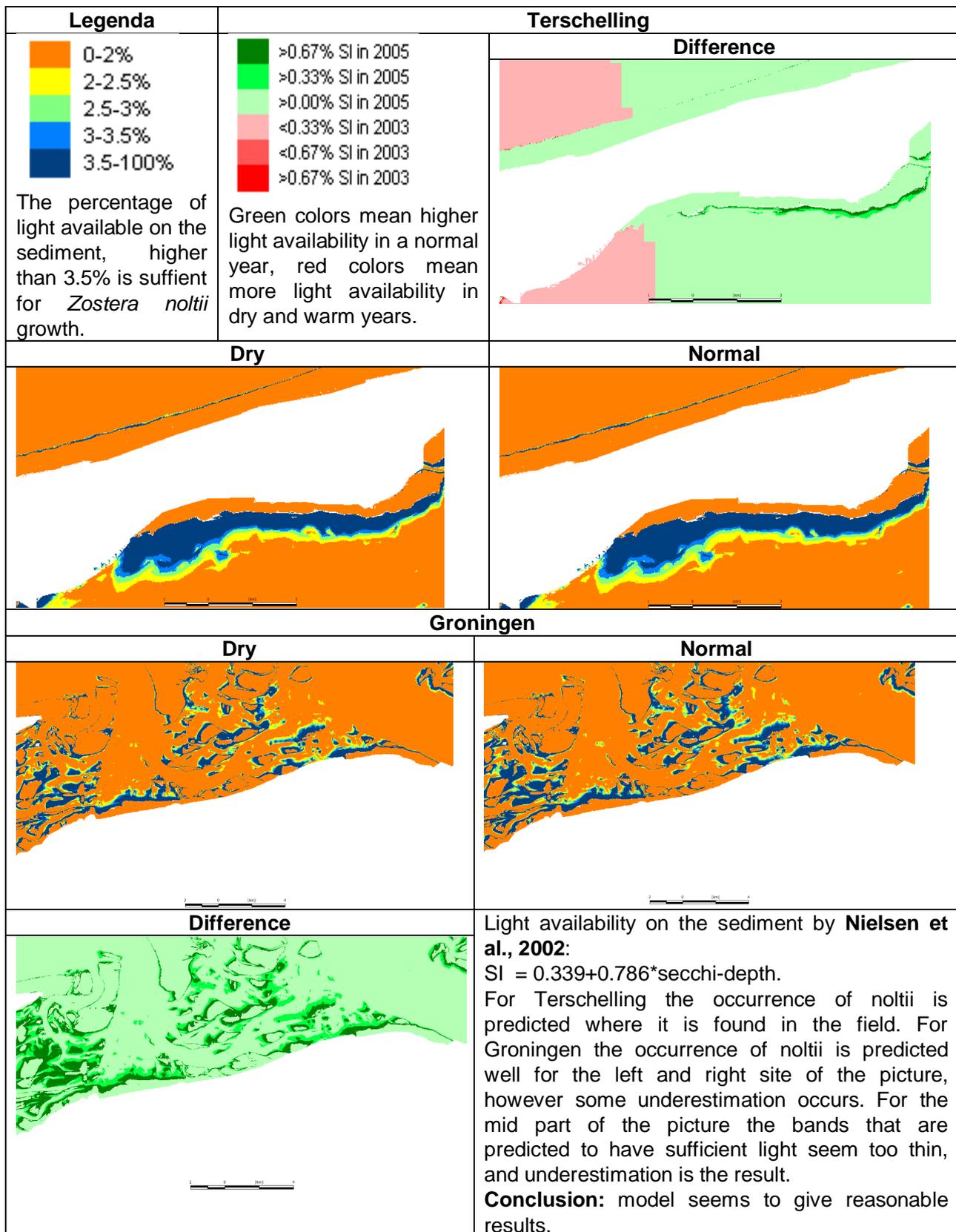


Figure 7.3: description of light availability formula by Nielsen et al., 2002.

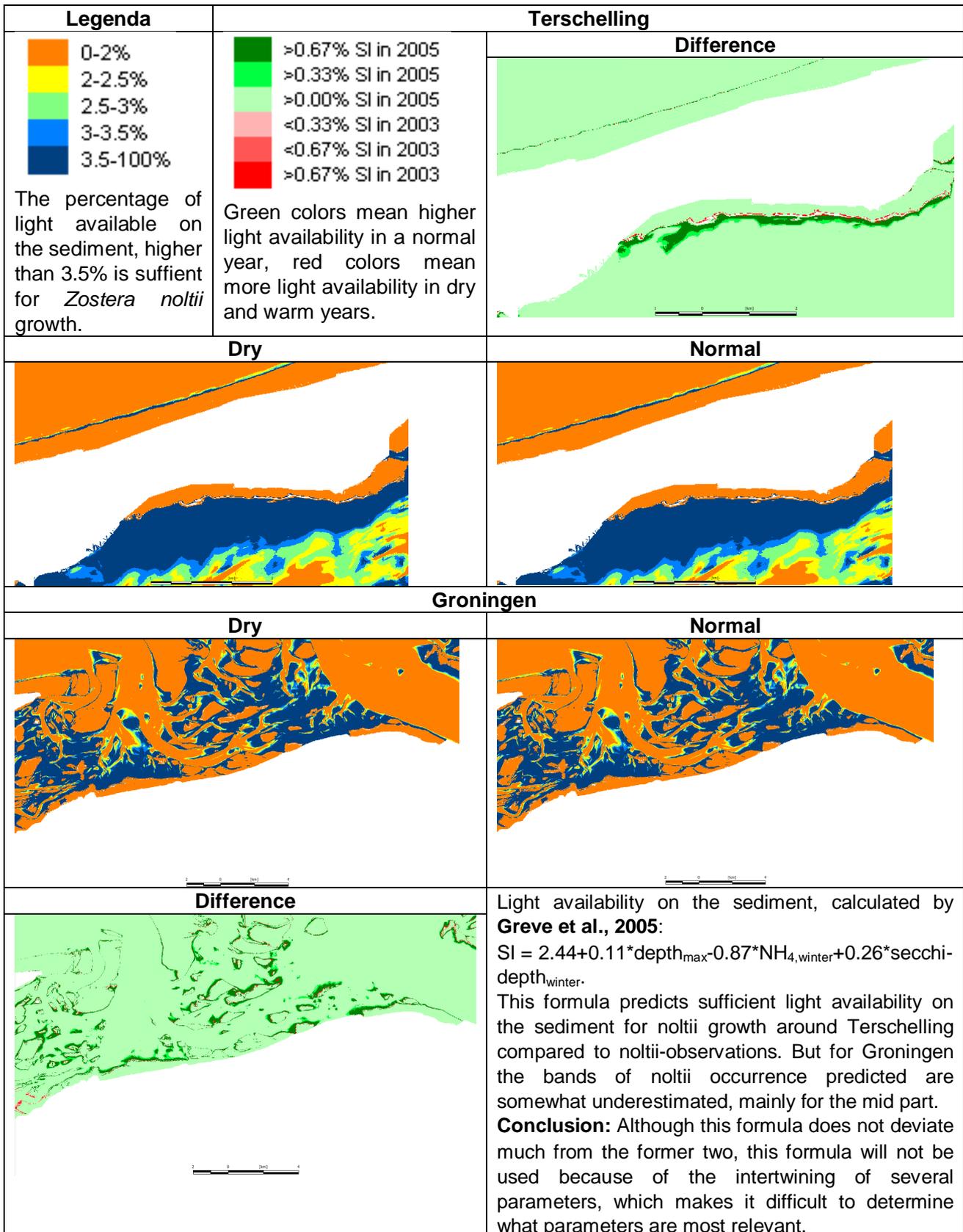


Figure 7.4: description of light availability formula by Greve et al., 2005.

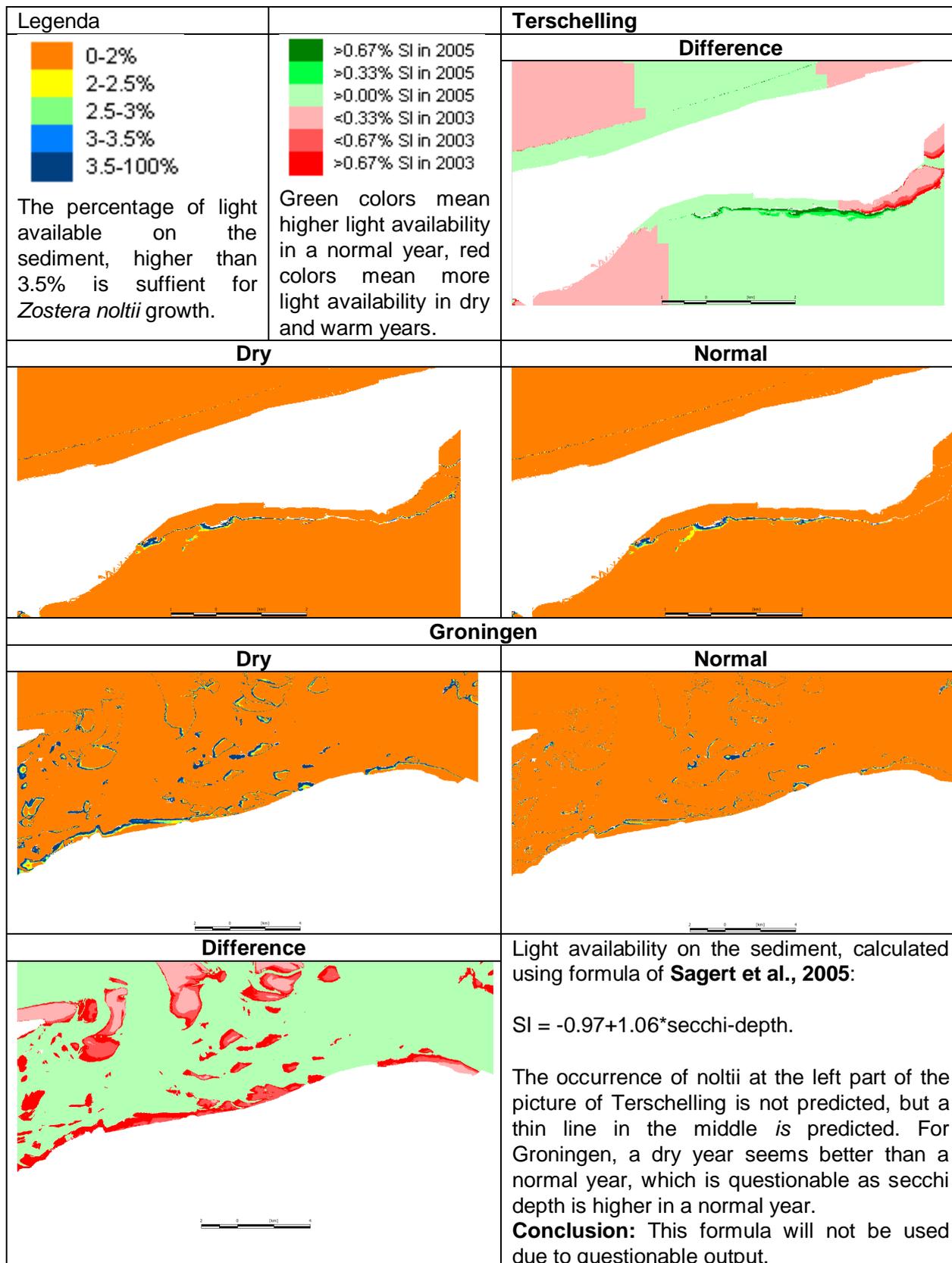


Figure 7.5: description of light availability formula by Duarte et al., 1991.

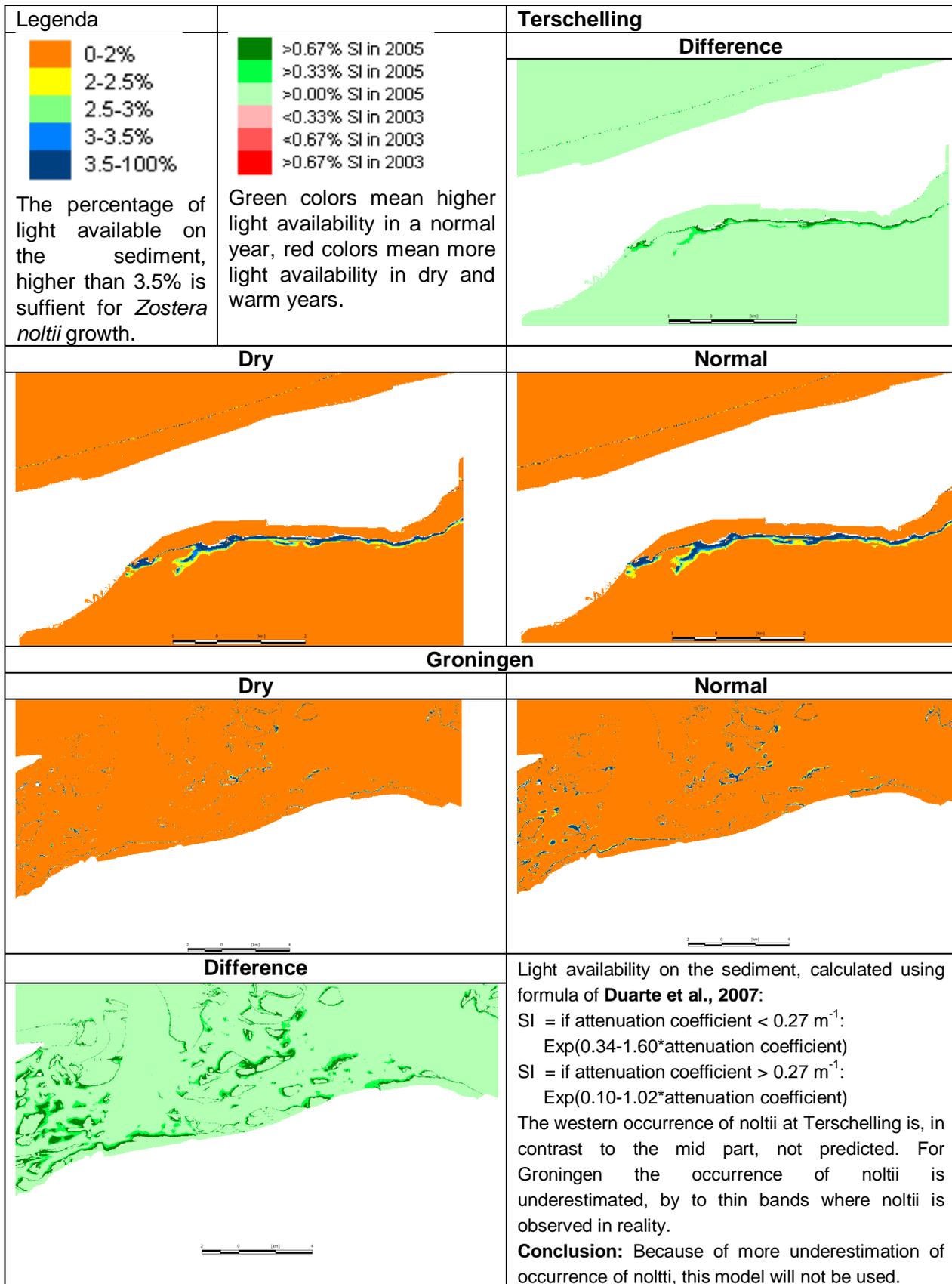


Figure 7.6: description of light availability formula by Duarte et al., 2007.

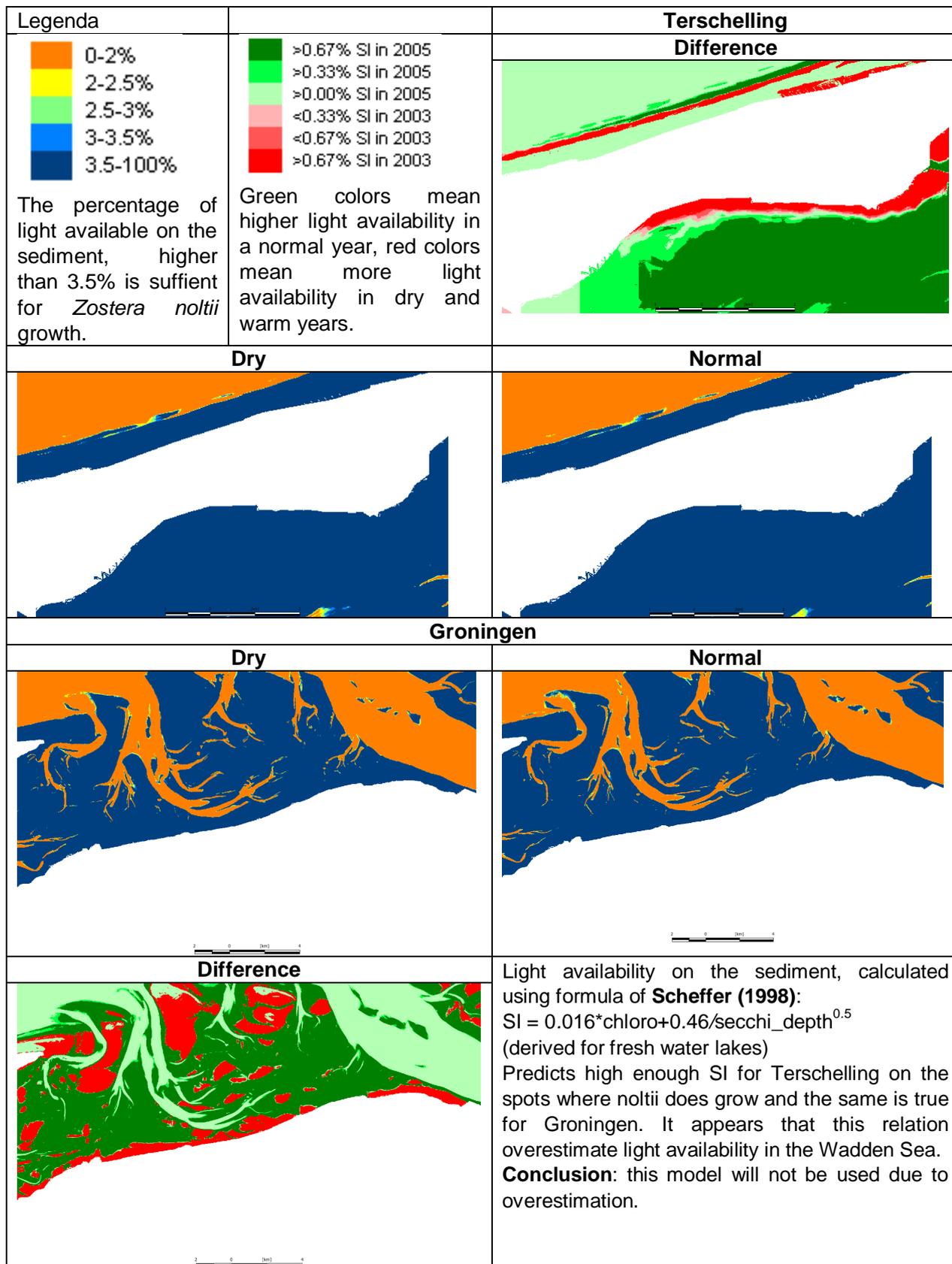
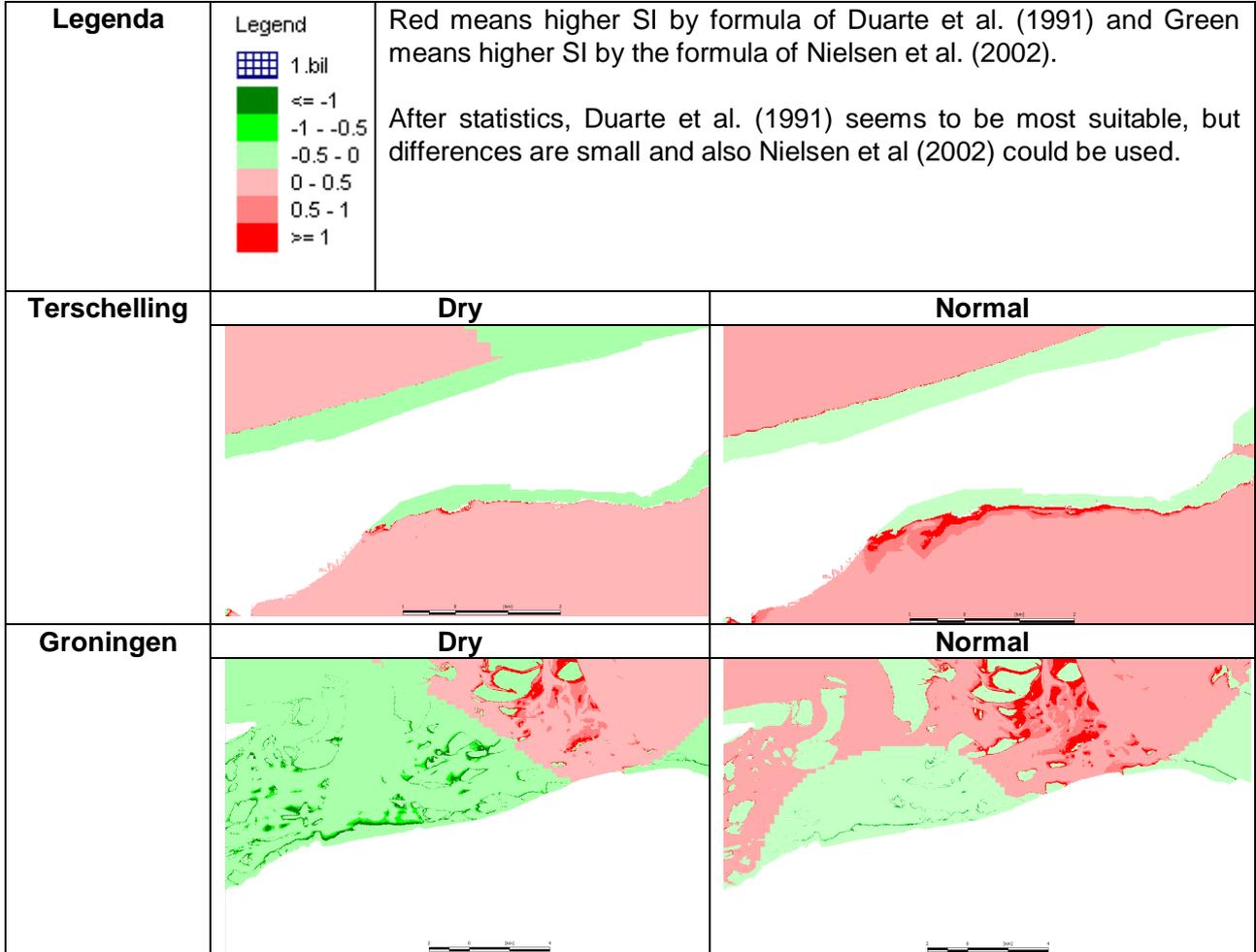


Figure 7.7: description of light availability formula by Scheffer, 1998.

Overall conclusion:



7.4 Output maps

Table 7.3: HSI maps control run

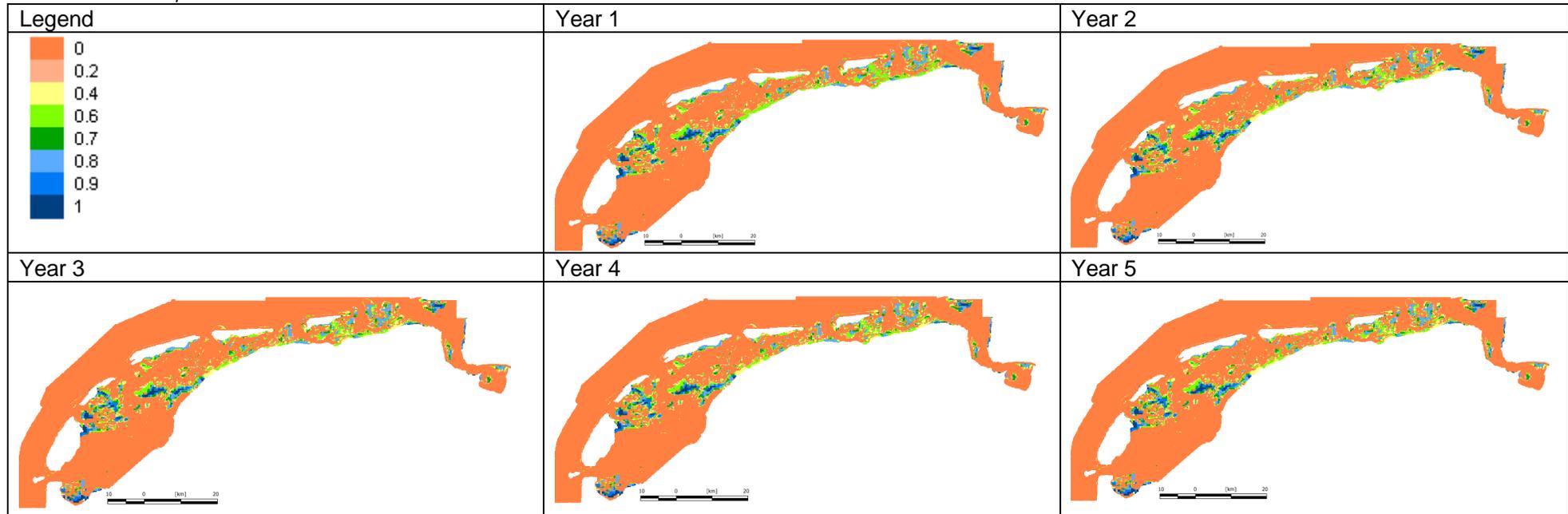


Table 7.4: Limiting factors maps control run.

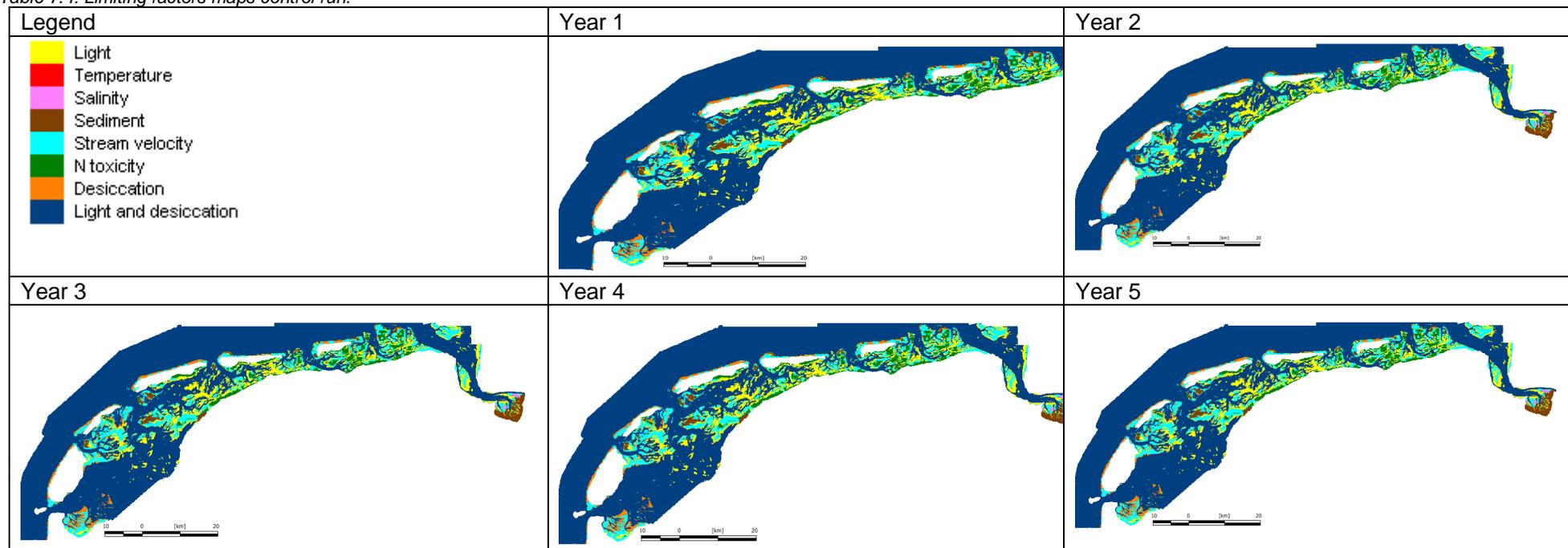


Table 7.5: Difference from year to year in suitable and non-suitable HSI area control run

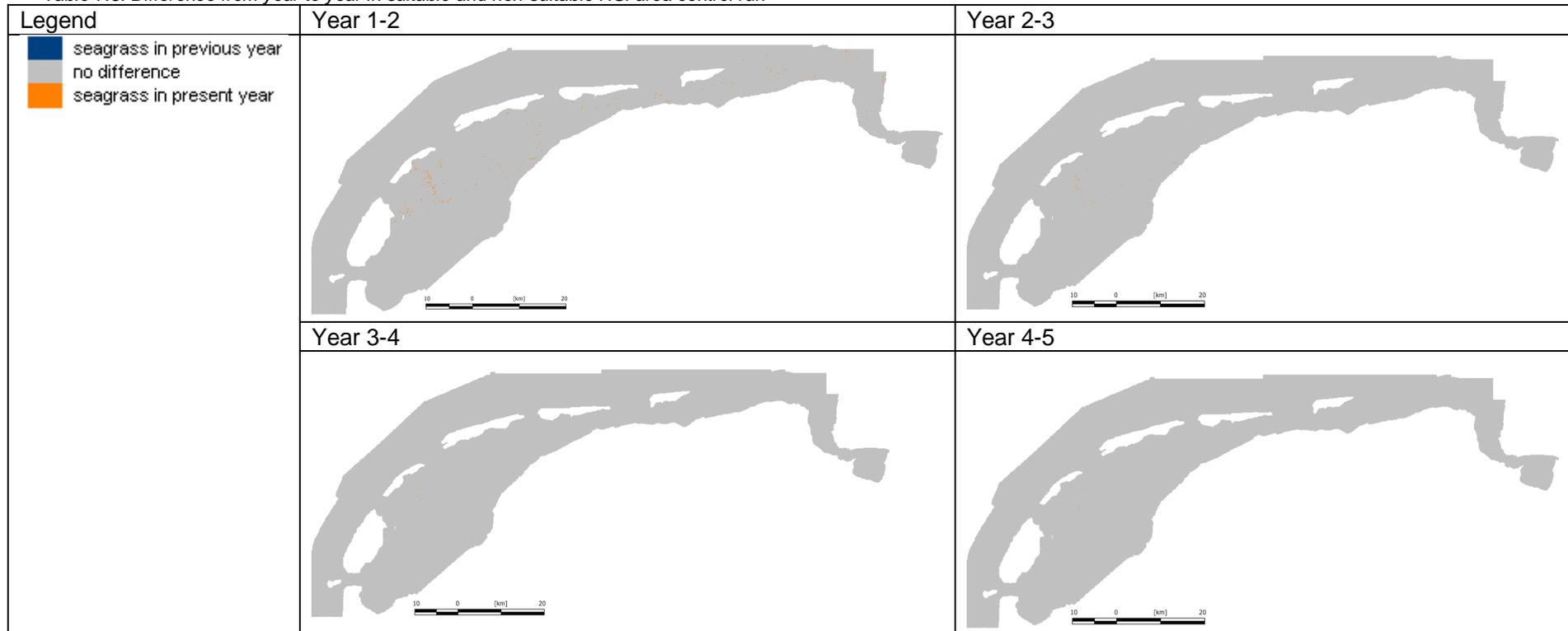


Table 7.6: HSI maps scenario 1

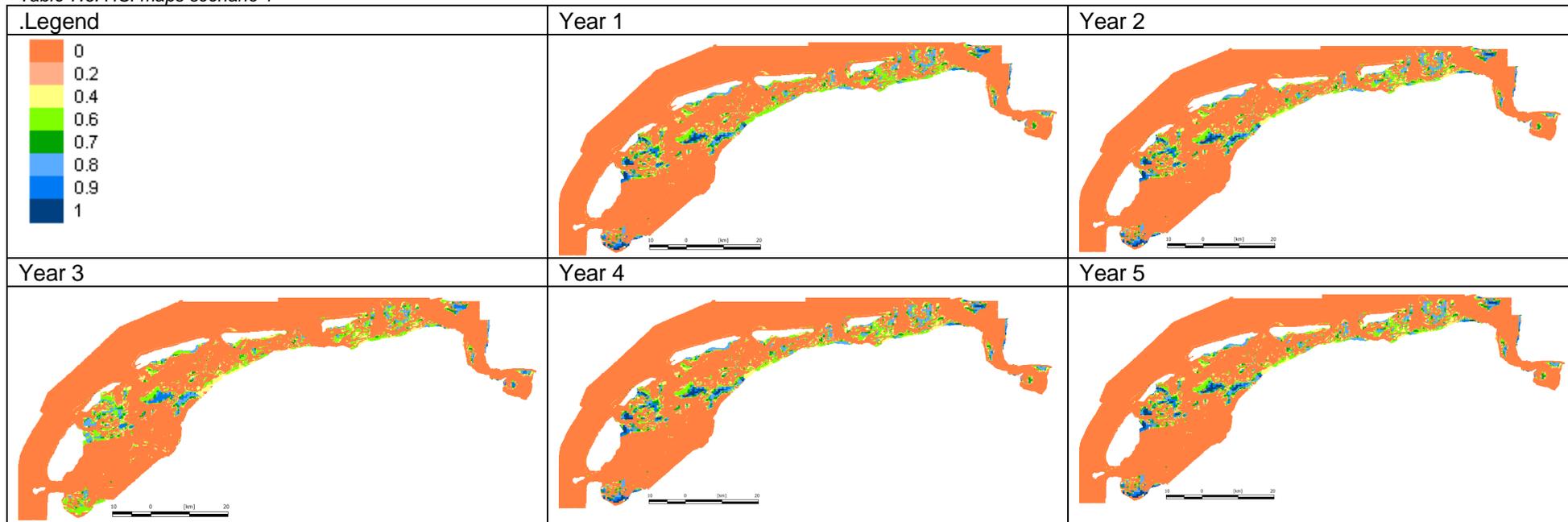


Table 7.7: Limiting factors maps scenario 1.

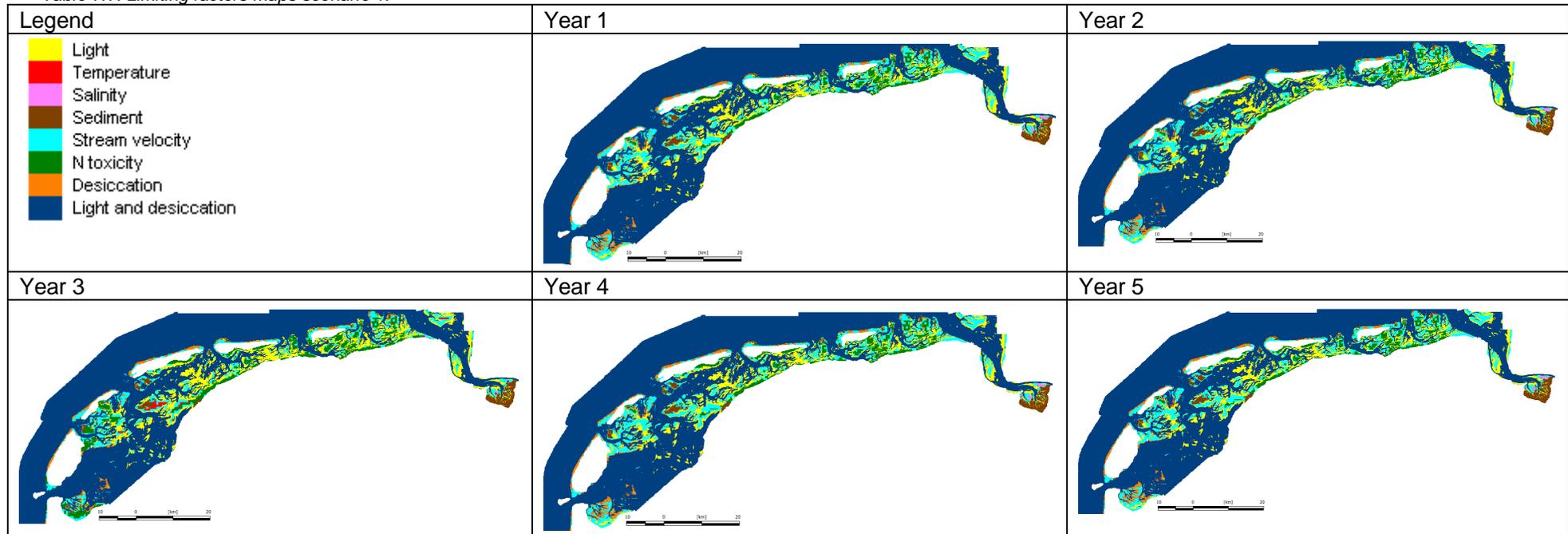


Table 7.8: Difference from year to year in suitable and non-suitable HSI area scenario 1

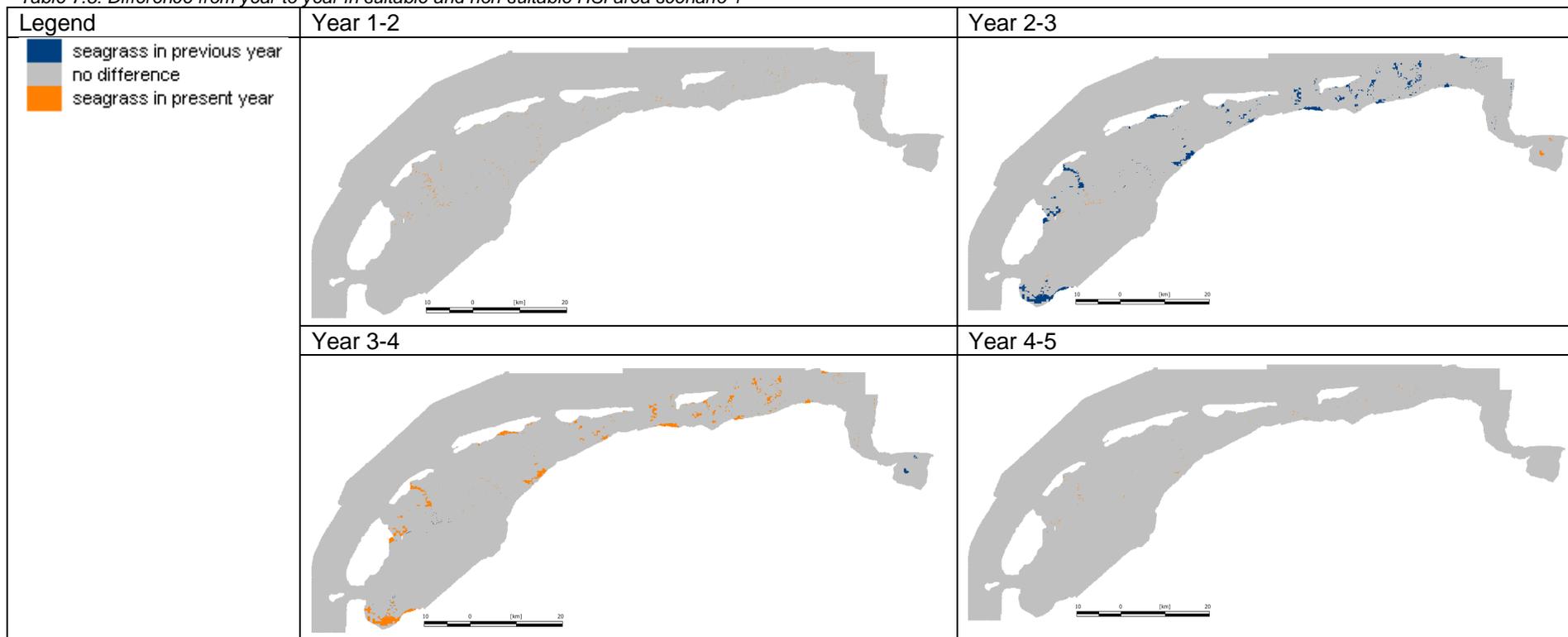


Table 7.9: HSI maps scenario 2

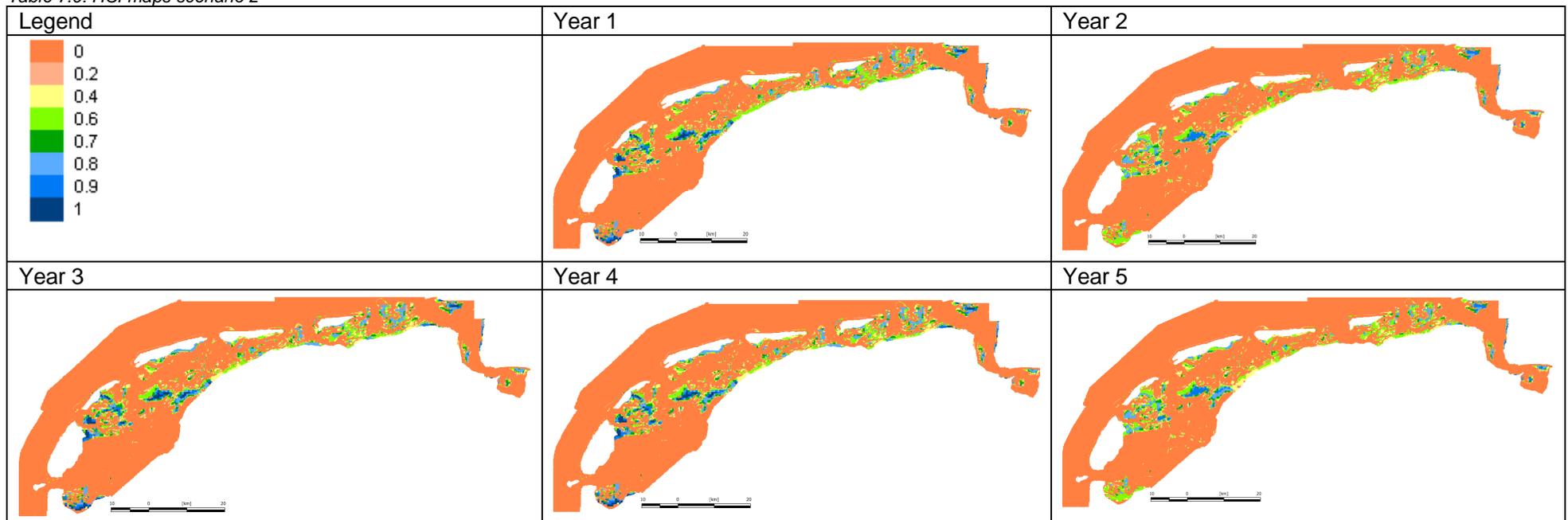


Table 7.10: Limiting factors maps scenario 2.

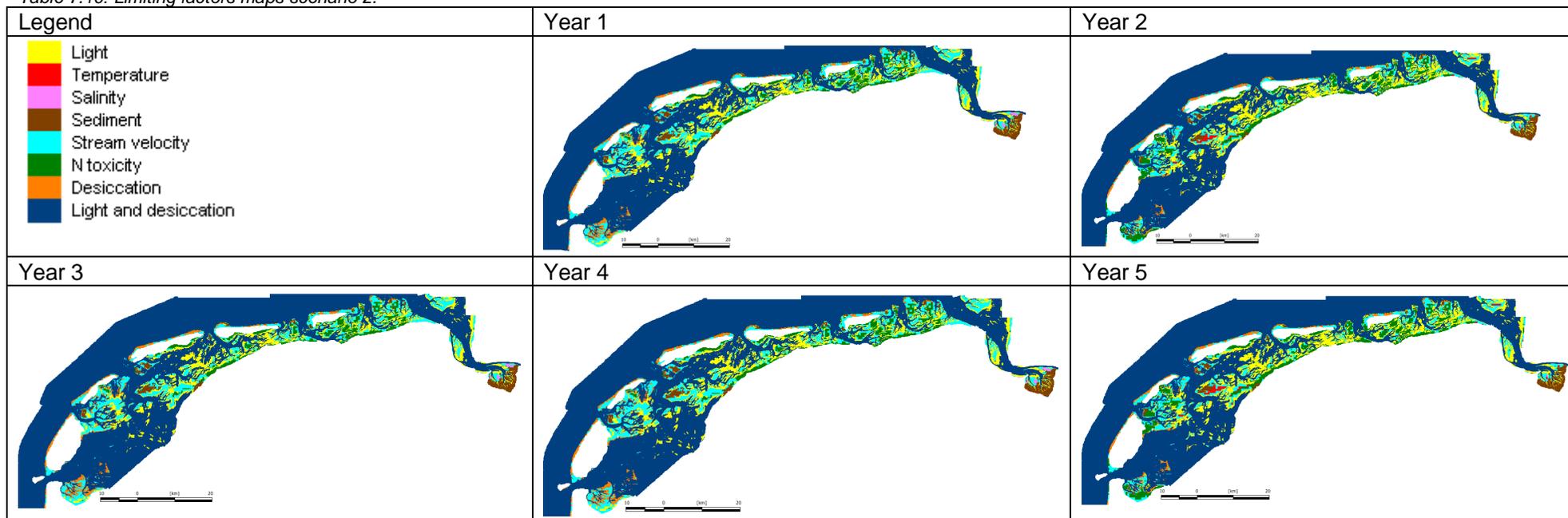


Table 7.11: Difference from year to year in suitable and non-suitable HSI area scenario 2.

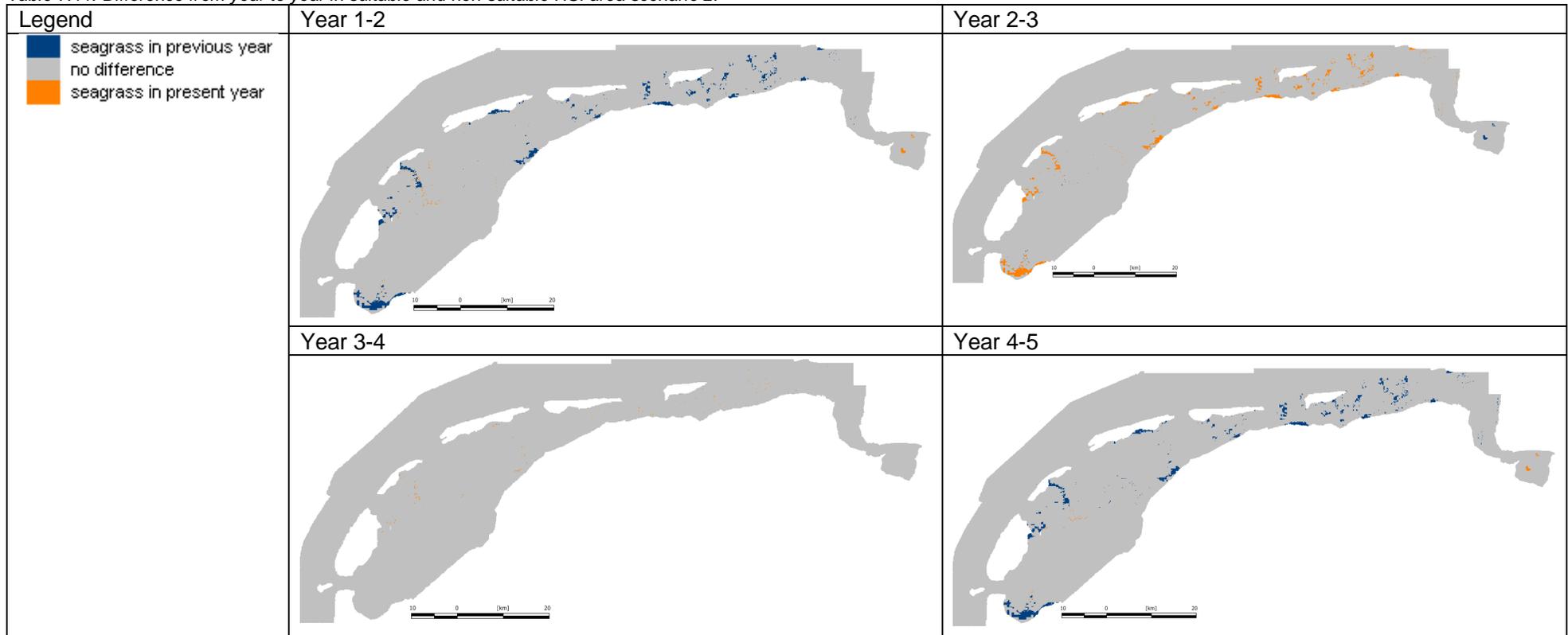


Table 7.12 : HSI maps scenario 3

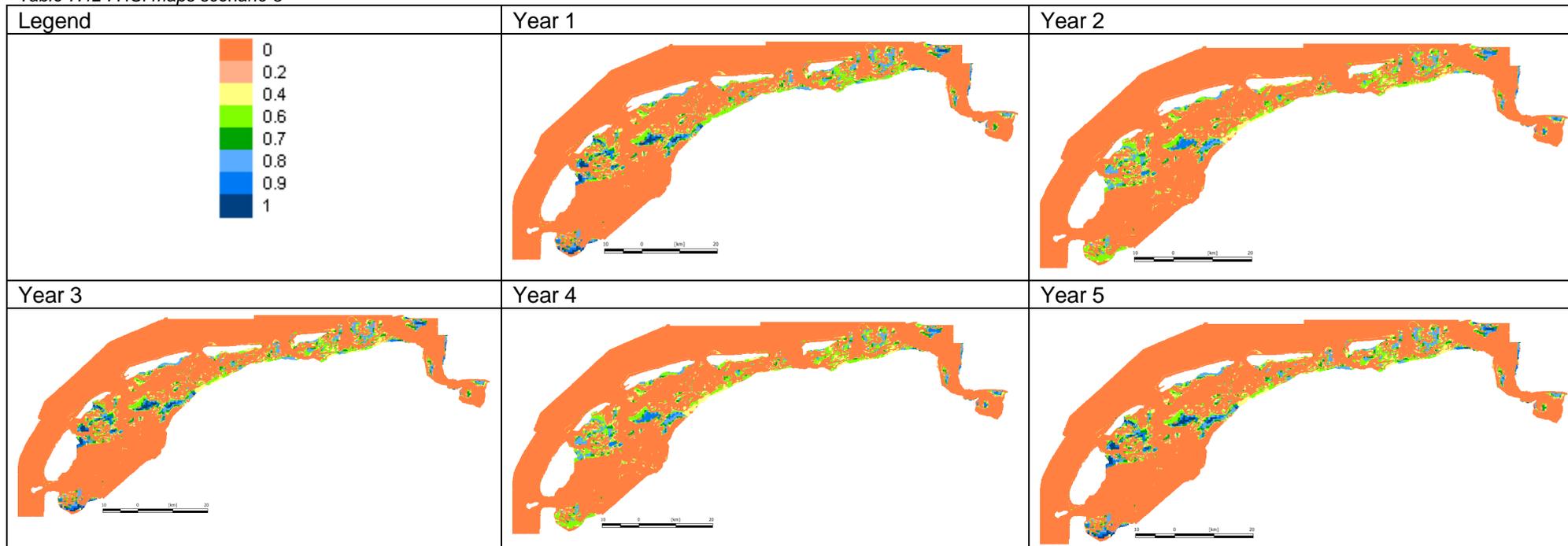


Table 7.13: Limiting factors maps scenario 3.

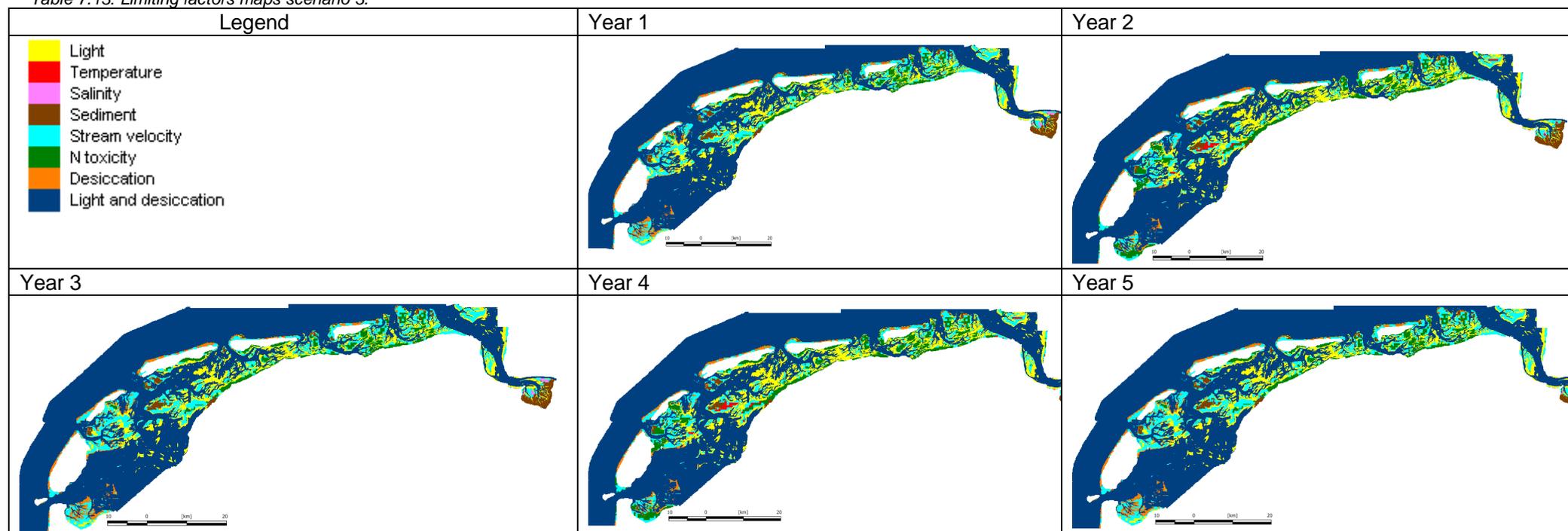
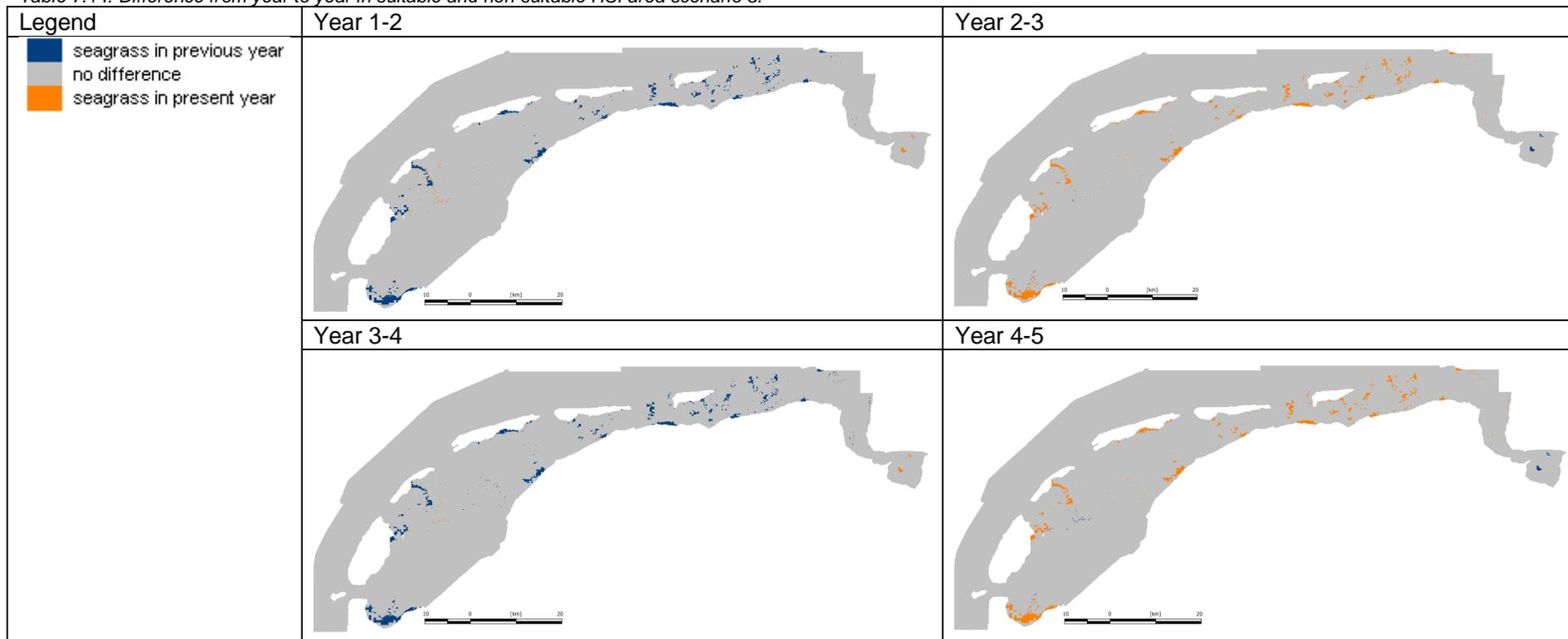


Table 7.14: Difference from year to year in suitable and non-suitable HSI area scenario 3.



7.5 Statistics

Table 7.15: overview of absolute area (m²) in HSI and limiting factor for control.

Absolute	Year1	Year2	Year3	Year4	year5
HSI					
[0,0.2>	3.83E+09	3.83E+09	3.87E+09	3.83E+09	3.83E+09
[0.2,0.4>	1.12E+08	1.10E+08	9.93E+07	1.09E+08	1.09E+08
[0.4,0.6>	1.42E+08	1.64E+08	1.71E+08	1.64E+08	1.62E+08
[0.6,0.7>	1.55E+08	1.28E+08	1.72E+08	1.31E+08	1.31E+08
[0.7,0.8>	7.07E+07	7.48E+07	5.19E+07	7.42E+07	7.57E+07
[0.8,0.9>	1.00E+08	1.04E+08	8.34E+07	1.03E+08	1.04E+08
[0.9,]	3.62E+07	3.73E+07	0.00E+00	3.66E+07	3.73E+07
Total	4.45E+09	4.45E+09	4.45E+09	4.45E+09	4.45E+09
Limiting factor					
Light	4.06E+08	3.87E+08	3.86E+08	3.85E+08	3.85E+08
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	4.86E+06	4.89E+06	4.89E+06	4.89E+06	4.89E+06
Sediment	9.84E+07	9.84E+07	9.84E+07	9.84E+07	9.84E+07
Stream velocity	4.60E+08	4.72E+08	4.74E+08	4.74E+08	4.74E+08
N_toxicity	1.36E+08	1.42E+08	1.42E+08	1.42E+08	1.42E+08
Desiccation	9.88E+07	9.91E+07	9.93E+07	9.93E+07	9.93E+07
Light and desiccation	3.25E+09	3.24E+09	3.24E+09	3.24E+09	3.24E+09

Table 7.16: overview of relative area (%) in HSI and limiting factor for control

relative	Year1	Year2	Year3	Year4	year5
HSI					
[0,0.2>	86.14	86.08	87.01	86.09	86.07
[0.2,0.4>	2.52	2.47	2.23	2.46	2.45
[0.4,0.6>	3.20	3.69	3.84	3.70	3.64
[0.6,0.7>	3.48	2.88	3.88	2.94	2.95
[0.7,0.8>	1.59	1.68	1.17	1.67	1.70
[0.8,0.9>	2.25	2.35	1.88	2.32	2.35
[0.9,]	0.82	0.84	0.00	0.82	0.84
Total	100.00	100.00	100.00	100.00	100.00
Limiting factor					
Light	9.10	8.71	8.67	8.66	8.66
Temperature	0.00	0.00	0.00	0.00	0.00
Salinity	0.11	0.11	0.11	0.11	0.11
Sediment	2.21	2.21	2.21	2.21	2.21
Stream velocity	10.33	10.62	10.65	10.66	10.67
N_toxicity	3.05	3.20	3.20	3.20	3.20
Desiccation	2.22	2.23	2.23	2.23	2.23
Light and desiccation	72.98	72.92	72.92	72.92	72.92

Table 7.17: overview of absolute areas (m²) in limiting factor for control run.

relative	Year1	Year2	Year3	Year4	year5
Suitable HSI					
Light	2.40E+07	2.14E+07	2.26E+07	2.29E+07	2.30E+07
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	3.07E+06	3.09E+06	3.09E+06	3.09E+06	3.09E+06
Sediment	9.31E+06	9.45E+06	9.45E+06	9.45E+06	9.45E+06
Stream velocity	1.15E+08	1.25E+08	1.26E+08	1.26E+08	1.26E+08
N_toxicity	5.55E+07	5.71E+07	5.71E+07	5.71E+07	5.71E+07
Desiccation	1.08E+04	2.20E+04	2.20E+04	2.20E+04	2.20E+04
Light and desiccation	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Mediocre HSI					
Light	2.42E+07	1.67E+07	1.77E+07	1.85E+07	1.89E+07
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	1.79E+06	1.80E+06	1.80E+06	1.80E+06	1.80E+06
Sediment	1.33E+07	1.34E+07	1.34E+07	1.34E+07	1.34E+07
Stream velocity	1.08E+08	1.10E+08	1.11E+08	1.11E+08	1.11E+08
N_toxicity	7.65E+07	5.14E+07	5.15E+07	5.15E+07	5.15E+07
Desiccation	1.19E+05	1.34E+05	1.38E+05	1.41E+05	1.45E+05
Light and desiccation	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Bad HSI					
Light	3.57E+08	3.49E+08	3.45E+08	3.44E+08	3.43E+08
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Sediment	7.58E+07	7.56E+07	7.56E+07	7.56E+07	7.56E+07
Stream velocity	2.37E+08	2.37E+08	2.37E+08	2.37E+08	2.37E+08
N_toxicity	3.76E+06	3.36E+07	3.36E+07	3.36E+07	3.36E+07
Desiccation	9.87E+07	9.90E+07	9.91E+07	9.92E+07	9.92E+07
Light and desiccation	3.24E+09	3.24E+09	3.24E+09	3.24E+09	3.24E+09

Table 7.18: overview of relative areas (%) in limiting factor for control run.

relative	Year1	Year2	Year3	Year4	year5
Suitable HSI					
Light	11.60%	9.91%	10.37%	10.49%	10.53%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	1.48%	1.43%	1.42%	1.42%	1.42%
Sediment	4.50%	4.36%	4.34%	4.33%	4.33%
Stream velocity	55.61%	57.90%	57.65%	57.57%	57.54%
N_toxicity	26.81%	26.39%	26.22%	26.18%	26.17%
Desiccation	0.01%	0.01%	0.01%	0.01%	0.01%
Light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%
Mediocre HSI					
Light	10.81%	8.65%	9.06%	9.41%	9.59%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.80%	0.93%	0.92%	0.91%	0.91%
Sediment	5.94%	6.93%	6.86%	6.82%	6.80%
Stream velocity	48.24%	56.79%	56.69%	56.55%	56.47%
N_toxicity	34.16%	26.62%	26.39%	26.23%	26.15%
Desiccation	0.05%	0.07%	0.07%	0.07%	0.07%

relative	Year1	Year2	Year3	Year4	year5
Light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%
Bad HSI					
Light	8.90%	8.65%	8.56%	8.53%	8.51%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.00%	0.00%	0.00%	0.00%	0.00%
Sediment	1.89%	1.87%	1.87%	1.88%	1.88%
Stream velocity	5.91%	5.88%	5.89%	5.89%	5.89%
N_toxicity	0.09%	0.83%	0.83%	0.83%	0.83%
Desiccation	2.46%	2.45%	2.46%	2.46%	2.46%
Light and desiccation	80.75%	80.32%	80.38%	80.42%	80.43%

Table 7.19: overview of absolute area (m²) in HSI and limiting factor for scenario 1

Absolute	Year1	Year2	Year3	Year4	year5
HSI					
[0,0.2>	3.83E+09	3.83E+09	3.87E+09	3.83E+09	3.83E+09
[0.2,0.4>	1.12E+08	1.10E+08	9.93E+07	1.09E+08	1.09E+08
[0.4,0.6>	1.42E+08	1.64E+08	1.71E+08	1.64E+08	1.62E+08
[0.6,0.7>	1.55E+08	1.28E+08	1.72E+08	1.31E+08	1.31E+08
[0.7,0.8>	7.07E+07	7.48E+07	5.19E+07	7.42E+07	7.57E+07
[0.8,0.9>	1.00E+08	1.04E+08	8.34E+07	1.03E+08	1.04E+08
[0.9,]	3.62E+07	3.73E+07	0.00E+00	3.66E+07	3.73E+07
Total	4.45E+09	4.45E+09	4.45E+09	4.45E+09	4.45E+09
Limiting factor					
Light	4.06E+08	3.87E+08	4.66E+08	3.92E+08	3.86E+08
Temperature	0.00E+00	0.00E+00	1.94E+07	0.00E+00	0.00E+00
Salinity	4.86E+06	4.89E+06	4.89E+05	4.89E+06	4.89E+06
Sediment	9.84E+07	9.84E+07	8.74E+07	9.84E+07	9.84E+07
Stream velocity	4.60E+08	4.72E+08	3.58E+08	4.69E+08	4.74E+08
N_toxicity	1.36E+08	1.42E+08	2.38E+08	1.41E+08	1.42E+08
Desiccation	9.88E+07	9.91E+07	7.15E+07	9.92E+07	9.93E+07
Light and desiccation	3.25E+09	3.24E+09	3.20E+09	3.24E+09	3.24E+09

Table 7.20: overview of relative area (%) in HSI and limiting factor for scenario 1

relative	Year1	Year2	Year3	Year4	year5
HSI					
[0,0.2>	86.14	86.08	87.01	86.09	86.07
[0.2,0.4>	2.52	2.47	2.23	2.46	2.45
[0.4,0.6>	3.20	3.69	3.84	3.70	3.64
[0.6,0.7>	3.48	2.88	3.88	2.94	2.95
[0.7,0.8>	1.59	1.68	1.17	1.67	1.70
[0.8,0.9>	2.25	2.35	1.88	2.32	2.35
[0.9,]	0.82	0.84	0.00	0.82	0.84
Total	100.00	100.00	100.00	100.00	100.00
Limiting factor					
Light	9.10	8.71	10.49	8.81	8.67

relative	Year1	Year2	Year3	Year4	year5
Temperature	0.00	0.00	0.44	0.00	0.00
Salinity	0.11	0.11	0.01	0.11	0.11
Sediment	2.21	2.21	1.97	2.21	2.21
Stream velocity	10.33	10.62	8.06	10.54	10.66
Ammonium flux	3.05	3.20	5.35	3.17	3.20
Desiccation	2.22	2.23	1.61	2.23	2.23
Light and desiccation	72.98	72.92	72.08	72.92	72.92

Table 7.21: overview of absolute areas (m²) in limiting factor for scenario 1

relative	Year1	Year2	Year3	Year4	year5
Suitable HSI					
Light	2.40E+07	2.14E+07	3.60E+06	2.31E+07	2.22E+07
Temperature	0.00E+00	0.00E+00	1.94E+07	0.00E+00	0.00E+00
Salinity	3.07E+06	3.09E+06	4.89E+05	3.09E+06	3.09E+06
Sediment	9.31E+06	9.45E+06	5.16E+06	9.42E+06	9.45E+06
Stream velocity	1.15E+08	1.25E+08	5.65E+07	1.22E+08	1.26E+08
N_toxicity	5.55E+07	5.71E+07	5.02E+07	5.63E+07	5.71E+07
Desiccation	1.08E+04	2.20E+04	0.00E+00	1.68E+04	2.20E+04
Light and desiccation	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Mediocre HSI					
Light	2.42E+07	1.67E+07	1.73E+07	2.01E+07	1.81E+07
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	1.79E+06	1.80E+06	0.00E+00	1.80E+06	1.80E+06
Sediment	1.33E+07	1.34E+07	1.14E+07	1.34E+07	1.34E+07
Stream velocity	1.08E+08	1.10E+08	8.77E+07	1.10E+08	1.11E+08
N_toxicity	7.65E+07	5.14E+07	1.16E+08	5.12E+07	5.14E+07
Desiccation	1.19E+05	1.34E+05	4.12E+04	1.36E+05	1.41E+05
Light and desiccation	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Bad HSI					
Light	3.57E+08	3.49E+08	4.46E+08	3.49E+08	3.45E+08
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Sediment	7.58E+07	7.56E+07	7.09E+07	7.56E+07	7.56E+07
Stream velocity	2.37E+08	2.37E+08	2.14E+08	2.37E+08	2.37E+08
N_toxicity	3.76E+06	3.36E+07	7.19E+07	3.36E+07	3.36E+07
Desiccation	9.87E+07	9.90E+07	7.15E+07	9.91E+07	9.91E+07
Light and desiccation	3.24E+09	3.24E+09	3.20E+09	3.24E+09	3.24E+09

Table 7.22: overview of relative areas (%) in limiting factor for scenario 1

relative	Year1	Year2	Year3	Year4	year5
Suitable HSI					
Light	11.60%	9.91%	2.66%	10.79%	10.21%
Temperature	0.00%	0.00%	14.31%	0.00%	0.00%
Salinity	1.48%	1.43%	0.36%	1.45%	1.42%
Sediment	4.50%	4.36%	3.81%	4.41%	4.35%
Stream velocity	55.61%	57.90%	41.76%	57.01%	57.73%
N_toxicity	26.81%	26.39%	37.10%	26.34%	26.28%

relative	Year1	Year2	Year3	Year4	year5
Desiccation	0.01%	0.01%	0.00%	0.01%	0.01%
Light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%
Mediocre HSI					
Light	10.81%	8.65%	7.45%	10.24%	9.23%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.80%	0.93%	0.00%	0.92%	0.92%
Sediment	5.94%	6.93%	4.91%	6.82%	6.85%
Stream velocity	48.24%	56.79%	37.82%	55.85%	56.66%
N_toxicity	34.16%	26.62%	49.80%	26.11%	26.27%
Desiccation	0.05%	0.07%	0.02%	0.07%	0.07%
Light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%
Bad HSI					
Light	8.90%	8.65%	10.93%	8.64%	8.56%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.00%	0.00%	0.00%	0.00%	0.00%
Sediment	1.89%	1.87%	1.74%	1.87%	1.87%
Stream velocity	5.91%	5.88%	5.25%	5.88%	5.89%
N_toxicity	0.09%	0.83%	1.76%	0.83%	0.83%
Desiccation	2.46%	2.45%	1.75%	2.45%	2.46%
Light and desiccation	80.75%	80.32%	78.57%	80.32%	80.38%

Table 7.23: overview of absolute area (m²) in HSI and limiting factor for scenario 2

absolute	Year1	Year2	Year3	Year4	year5
HSI					
[0,0.2>	3.83E+09	3.87E+09	3.83E+09	3.83E+09	3.87E+09
[0.2,0.4>	1.12E+08	9.96E+07	1.10E+08	1.09E+08	9.90E+07
[0.4,0.6>	1.42E+08	1.71E+08	1.65E+08	1.62E+08	1.70E+08
[0.6,0.7>	1.55E+08	1.71E+08	1.30E+08	1.31E+08	1.73E+08
[0.7,0.8>	7.07E+07	5.11E+07	7.42E+07	7.57E+07	5.23E+07
[0.8,0.9>	1.00E+08	8.33E+07	1.03E+08	1.04E+08	8.34E+07
[0.9,]	3.62E+07	0.00E+00	3.66E+07	3.73E+07	0.00E+00
Total	4.45E+09	4.45E+09	4.45E+09	4.45E+09	4.45E+09
Limiting factor					
Light	4.06E+08	4.68E+08	3.92E+08	3.86E+08	4.66E+08
Temperature	0.00E+00	1.94E+07	0.00E+00	0.00E+00	1.94E+07
Salinity	4.86E+06	4.89E+05	4.89E+06	4.89E+06	4.89E+05
Sediment	9.84E+07	8.74E+07	9.84E+07	9.84E+07	8.74E+07
Stream velocity	4.60E+08	3.57E+08	4.69E+08	4.74E+08	3.59E+08
N_toxicity	1.36E+08	2.37E+08	1.41E+08	1.42E+08	2.38E+08
Desiccation	9.88E+07	7.14E+07	9.92E+07	9.93E+07	7.15E+07
Light and desiccation	3.25E+09	3.20E+09	3.24E+09	3.24E+09	3.20E+09

Table 7.24: overview of relative area (%) in HSI and limiting factor for scenario 2

relative	Year1	Year2	Year3	Year4	year5
HSI					
[0,0.2>	86.14	87.05	86.09	86.07	87.00
[0.2,0.4>	2.52	2.24	2.47	2.45	2.23
[0.4,0.6>	3.20	3.84	3.70	3.65	3.82
[0.6,0.7>	3.48	3.85	2.93	2.95	3.90
[0.7,0.8>	1.59	1.15	1.67	1.70	1.18
[0.8,0.9>	2.25	1.87	2.32	2.35	1.88
[0.9,]	0.82	0.00	0.82	0.84	0.00
Total	100.00	100.00	100.00	100.00	100.00
Limiting factor					
Light	9.10	10.53	8.81	8.68	10.47
Temperature	0.00	0.44	0.00	0.00	0.44
Salinity	0.11	0.01	0.11	0.11	0.01
Sediment	2.21	1.97	2.21	2.21	1.97
Stream velocity	10.33	8.04	10.54	10.65	8.07
Ammonium flux	3.05	5.33	3.17	3.20	5.35
Desiccation	2.22	1.61	2.23	2.23	1.61
Light and desiccation	72.98	72.08	72.92	72.92	72.08

Table 7.25: overview of absolute areas (m²) in limiting factor for scenario 2

relative	Year1	Year2	Year3	Year4	year5
Suitable HSI					
Light	2.40E+07	3.09E+06	2.30E+07	2.22E+07	3.91E+06
Temperature	0.00E+00	1.94E+07	0.00E+00	0.00E+00	1.94E+07
Salinity	3.07E+06	4.89E+05	3.09E+06	3.09E+06	4.89E+05
Sediment	9.31E+06	5.16E+06	9.42E+06	9.45E+06	5.16E+06
Stream velocity	1.15E+08	5.62E+07	1.22E+08	1.26E+08	5.66E+07
N_toxicity	5.55E+07	5.02E+07	5.63E+07	5.71E+07	5.02E+07
Desiccation	1.08E+04	0.00E+00	1.68E+04	2.20E+04	0.00E+00
Light and desiccation	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Mediocre HSI					
Light	2.42E+07	1.73E+07	1.96E+07	1.79E+07	1.72E+07
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	1.79E+06	0.00E+00	1.80E+06	1.80E+06	0.00E+00
Sediment	1.33E+07	1.14E+07	1.34E+07	1.34E+07	1.14E+07
Stream velocity	1.08E+08	8.72E+07	1.09E+08	1.11E+08	8.83E+07
N_toxicity	7.65E+07	1.15E+08	5.12E+07	5.14E+07	1.16E+08
Desiccation	1.19E+05	3.88E+04	1.32E+05	1.40E+05	4.12E+04
Light and desiccation	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Bad HSI					
Light	3.57E+08	4.48E+08	3.49E+08	3.46E+08	4.44E+08
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Sediment	7.58E+07	7.09E+07	7.56E+07	7.56E+07	7.09E+07
Stream velocity	2.37E+08	2.14E+08	2.37E+08	2.37E+08	2.14E+08

relative	Year1	Year2	Year3	Year4	year5
N_toxicity	3.76E+06	7.19E+07	3.36E+07	3.36E+07	7.19E+07
Desiccation	9.87E+07	7.14E+07	9.90E+07	9.91E+07	7.15E+07
Light and desiccation	3.24E+09	3.20E+09	3.24E+09	3.24E+09	3.20E+09

Table 7.26: overview of relative areas (%) in limiting factor for scenario 2

relative	Year1	Year2	Year3	Year4	year5
Suitable HSI					
Light	11.60%	2.30%	10.77%	10.21%	2.88%
Temperature	0.00%	14.40%	0.00%	0.00%	14.26%
Salinity	1.48%	0.36%	1.45%	1.42%	0.36%
Sediment	4.50%	3.84%	4.41%	4.35%	3.80%
Stream velocity	55.61%	41.78%	57.02%	57.74%	41.71%
N_toxicity	26.81%	37.33%	26.35%	26.28%	36.98%
Desiccation	0.01%	0.00%	0.01%	0.01%	0.00%
Light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%
Mediocre HSI					
Light	10.81%	7.50%	10.03%	9.14%	7.40%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.80%	0.00%	0.92%	0.92%	0.00%
Sediment	5.94%	4.93%	6.84%	6.85%	4.90%
Stream velocity	48.24%	37.81%	55.95%	56.70%	37.97%
N_toxicity	34.16%	49.74%	26.19%	26.31%	49.72%
Desiccation	0.05%	0.02%	0.07%	0.07%	0.02%
Light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%
Bad HSI					
Light	8.90%	10.98%	8.65%	8.57%	10.90%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.00%	0.00%	0.00%	0.00%	0.00%
Sediment	1.89%	1.74%	1.87%	1.87%	1.74%
Stream velocity	5.91%	5.24%	5.88%	5.89%	5.25%
N_toxicity	0.09%	1.76%	0.83%	0.83%	1.76%
Desiccation	2.46%	1.75%	2.45%	2.46%	1.75%
Light and desiccation	80.75%	78.53%	80.31%	80.38%	78.59%

Table 7.27: overview of absolute area (m²) in HSI and limiting factor for scenario 3

absolute	Year1	Year2	Year3	Year4	year5
HSI					
[0,0.2>	3.83E+09	3.87E+09	3.83E+09	3.87E+09	3.83E+09
[0.2,0.4>	1.12E+08	9.96E+07	1.10E+08	9.91E+07	1.09E+08
[0.4,0.6>	1.42E+08	1.71E+08	1.65E+08	1.70E+08	1.64E+08
[0.6,0.7>	1.55E+08	1.71E+08	1.30E+08	1.72E+08	1.31E+08
[0.7,0.8>	7.07E+07	5.11E+07	7.42E+07	5.22E+07	7.42E+07
[0.8,0.9>	1.00E+08	8.33E+07	1.03E+08	8.34E+07	1.03E+08
[0.9,]	3.62E+07	0.00E+00	3.66E+07	0.00E+00	3.66E+07
Total	4.45E+09	4.45E+09	4.45E+09	4.45E+09	4.45E+09
Limiting factor					
Light	4.06E+08	4.68E+08	3.92E+08	4.66E+08	3.92E+08

absolute	Year1	Year2	Year3	Year4	year5
Temperature	0.00E+00	1.94E+07	0.00E+00	1.94E+07	0.00E+00
Salinity	4.86E+06	4.89E+05	4.89E+06	4.89E+05	4.89E+06
Sediment	9.84E+07	8.74E+07	9.84E+07	8.74E+07	9.84E+07
Stream velocity	4.60E+08	3.57E+08	4.69E+08	3.59E+08	4.69E+08
N_toxicity	1.36E+08	2.37E+08	1.41E+08	2.37E+08	1.41E+08
Desiccation	9.88E+07	7.14E+07	9.92E+07	7.15E+07	9.92E+07
Light and desiccation	3.25E+09	3.20E+09	3.24E+09	3.20E+09	3.24E+09

Table 7.28: overview of relative area (%) in HSI and limiting factor for scenario 3

relative	Year1	Year2	Year3	Year4	year5
HSI					
[0,0.2>	86.14	87.05	86.09	87.02	86.09
[0.2,0.4>	2.52	2.24	2.47	2.23	2.46
[0.4,0.6>	3.20	3.84	3.70	3.82	3.69
[0.6,0.7>	3.48	3.85	2.93	3.88	2.95
[0.7,0.8>	1.59	1.15	1.67	1.17	1.67
[0.8,0.9>	2.25	1.87	2.32	1.88	2.32
[0.9,]	0.82	0.00	0.82	0.00	0.82
Total	100.00	100.00	100.00	100.00	100.00
Limiting factor					
Light	9.10	10.53	8.81	10.49	8.81
Temperature	0.00	0.44	0.00	0.44	0.00
Salinity	0.11	0.01	0.11	0.01	0.11
Sediment	2.21	1.97	2.21	1.97	2.21
Stream velocity	10.33	8.04	10.54	8.07	10.55
N_toxicity	3.05	5.33	3.17	5.33	3.17
Desiccation	2.22	1.61	2.23	1.61	2.23
Light and desiccation	72.98	72.08	72.92	72.08	72.92

Table 7.29: overview of absolute areas (m²) in limiting factor for scenario 3

relative	Year1	Year2	Year3	Year4	year5
Suitable HSI					
Light	2.40E+07	3.09E+06	2.30E+07	3.86E+06	2.31E+07
Temperature	0.00E+00	1.94E+07	0.00E+00	1.94E+07	0.00E+00
Salinity	3.07E+06	4.89E+05	3.09E+06	4.89E+05	3.09E+06
Sediment	9.31E+06	5.16E+06	9.42E+06	5.16E+06	9.42E+06
Stream velocity	1.15E+08	5.62E+07	1.22E+08	5.66E+07	1.22E+08
N_toxicity	5.55E+07	5.02E+07	5.63E+07	5.02E+07	5.63E+07
Desiccation	1.08E+04	0.00E+00	1.68E+04	0.00E+00	1.68E+04
Light and desiccation	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Mediocre HSI					
Light	2.42E+07	1.73E+07	1.96E+07	1.70E+07	2.06E+07
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	1.79E+06	0.00E+00	1.80E+06	0.00E+00	1.80E+06
Sediment	1.33E+07	1.14E+07	1.34E+07	1.14E+07	1.34E+07
Stream velocity	1.08E+08	8.72E+07	1.09E+08	8.82E+07	1.10E+08
N_toxicity	7.65E+07	1.15E+08	5.12E+07	1.15E+08	5.12E+07

relative	Year1	Year2	Year3	Year4	year5
Desiccation	1.19E+05	3.88E+04	1.32E+05	4.12E+04	1.36E+05
Light and desiccation	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Bad HSI					
Light	3.57E+08	4.48E+08	3.49E+08	4.46E+08	3.48E+08
Temperature	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Salinity	0.00E+00	0.00E+00	0.00E+00	0.00E+00	0.00E+00
Sediment	7.58E+07	7.09E+07	7.56E+07	7.09E+07	7.56E+07
Stream velocity	2.37E+08	2.14E+08	2.37E+08	2.14E+08	2.37E+08
N_toxicity	3.76E+06	7.19E+07	3.36E+07	7.19E+07	3.36E+07
Desiccation	9.87E+07	7.14E+07	9.90E+07	7.15E+07	9.91E+07
Light and desiccation	3.24E+09	3.20E+09	3.24E+09	3.20E+09	3.24E+09

Table 7.30: overview of relative areas (%) in limiting factor for scenario 3

relative	Year1	Year2	Year3	Year4	year5
Suitable HSI					
Light	11.60%	2.30%	10.77%	2.84%	10.79%
Temperature	0.00%	14.40%	0.00%	14.27%	0.00%
Salinity	1.48%	0.36%	1.45%	0.36%	1.45%
Sediment	4.50%	3.84%	4.41%	3.80%	4.41%
Stream velocity	55.61%	41.78%	57.02%	41.72%	57.01%
N_toxicity	26.81%	37.33%	26.35%	37.00%	26.34%
Desiccation	0.01%	0.00%	0.01%	0.00%	0.01%
Light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%
Mediocre HSI					
Light	10.81%	7.50%	10.03%	7.35%	10.47%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.80%	0.00%	0.92%	0.00%	0.91%
Sediment	5.94%	4.93%	6.84%	4.92%	6.80%
Stream velocity	48.24%	37.81%	55.95%	38.09%	55.72%
N_toxicity	34.16%	49.74%	26.19%	49.63%	26.03%
Desiccation	0.05%	0.02%	0.07%	0.02%	0.07%
Light and desiccation	0.00%	0.00%	0.00%	0.00%	0.00%
Bad HSI					
Light	8.90%	10.98%	8.65%	10.93%	8.62%
Temperature	0.00%	0.00%	0.00%	0.00%	0.00%
Salinity	0.00%	0.00%	0.00%	0.00%	0.00%
Sediment	1.89%	1.74%	1.87%	1.74%	1.87%
Stream velocity	5.91%	5.24%	5.88%	5.25%	5.88%
N_toxicity	0.09%	1.76%	0.83%	1.76%	0.83%
Desiccation	2.46%	1.75%	2.45%	1.75%	2.46%
Light and desiccation	80.75%	78.53%	80.31%	78.57%	80.34%

7.6 Input maps

Table 7.18: input map of the bathymetry (cm, positive values represent depth)

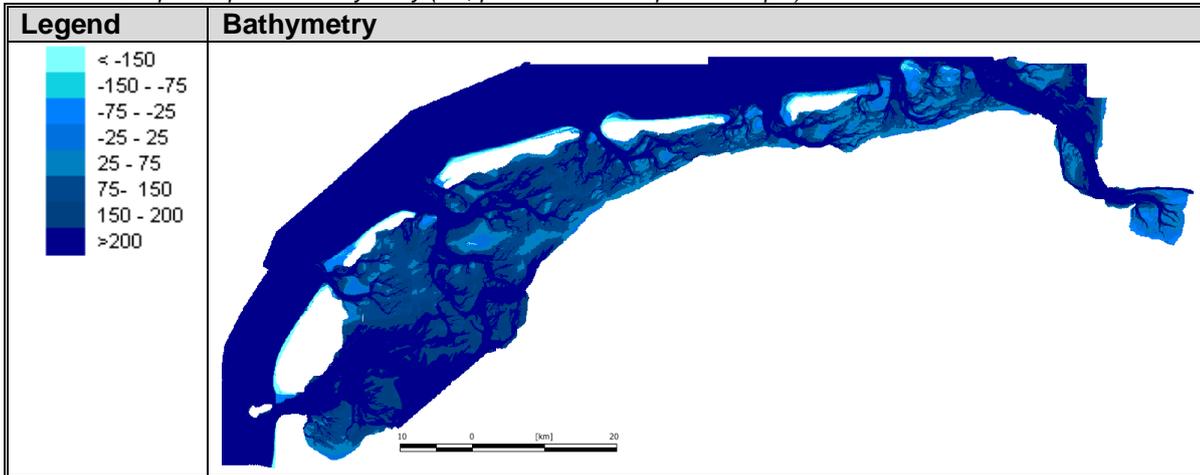


Table 7.19: input map of the sediment composition (% silt)

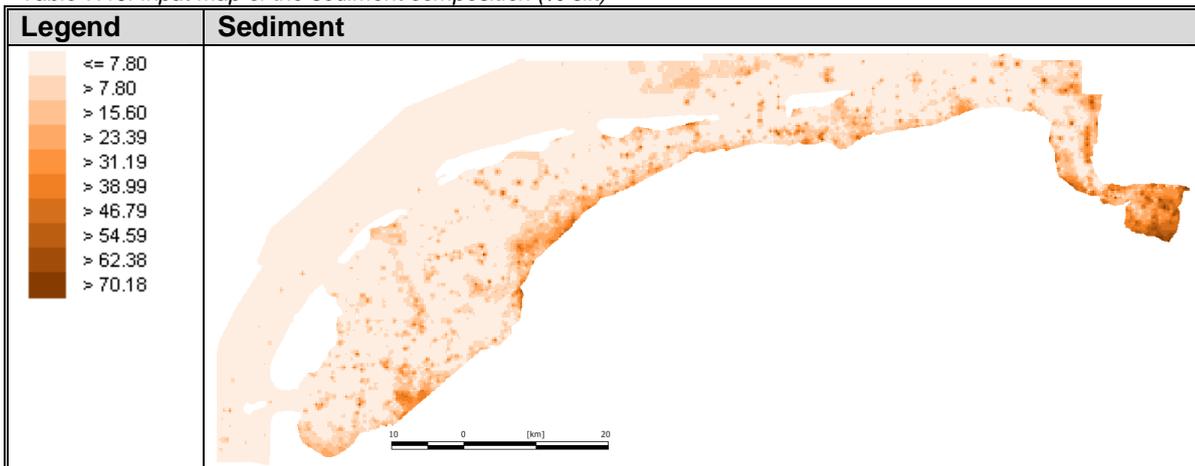


Table 7.20: input map of the mean stream velocity (m/s)

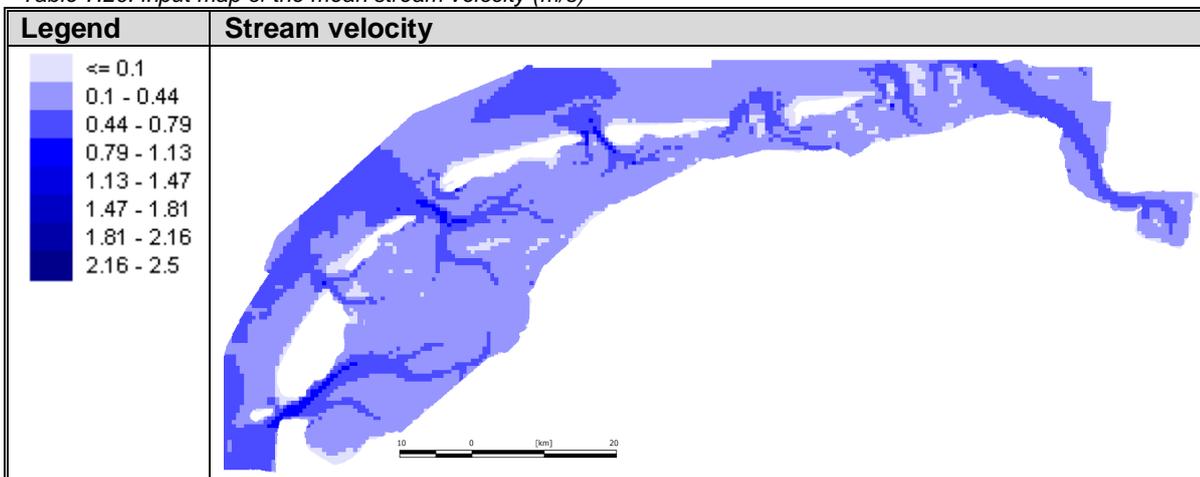


Table 7.21: input maps of the attenuation coefficient for warm and dry and normal years (m^{-1})

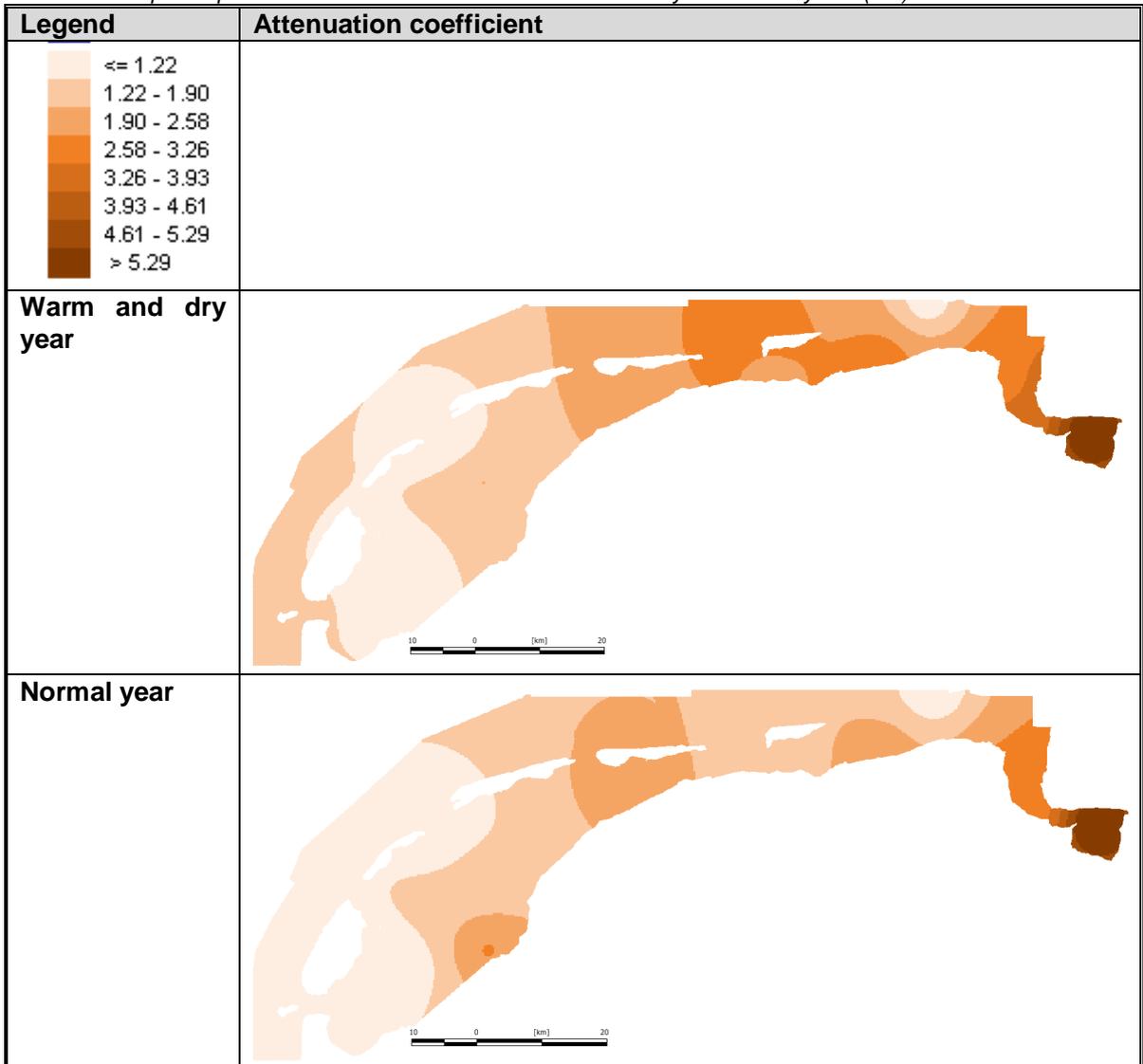


Table 7.22: input maps of the temperature for warm and dry and normal years (°C)

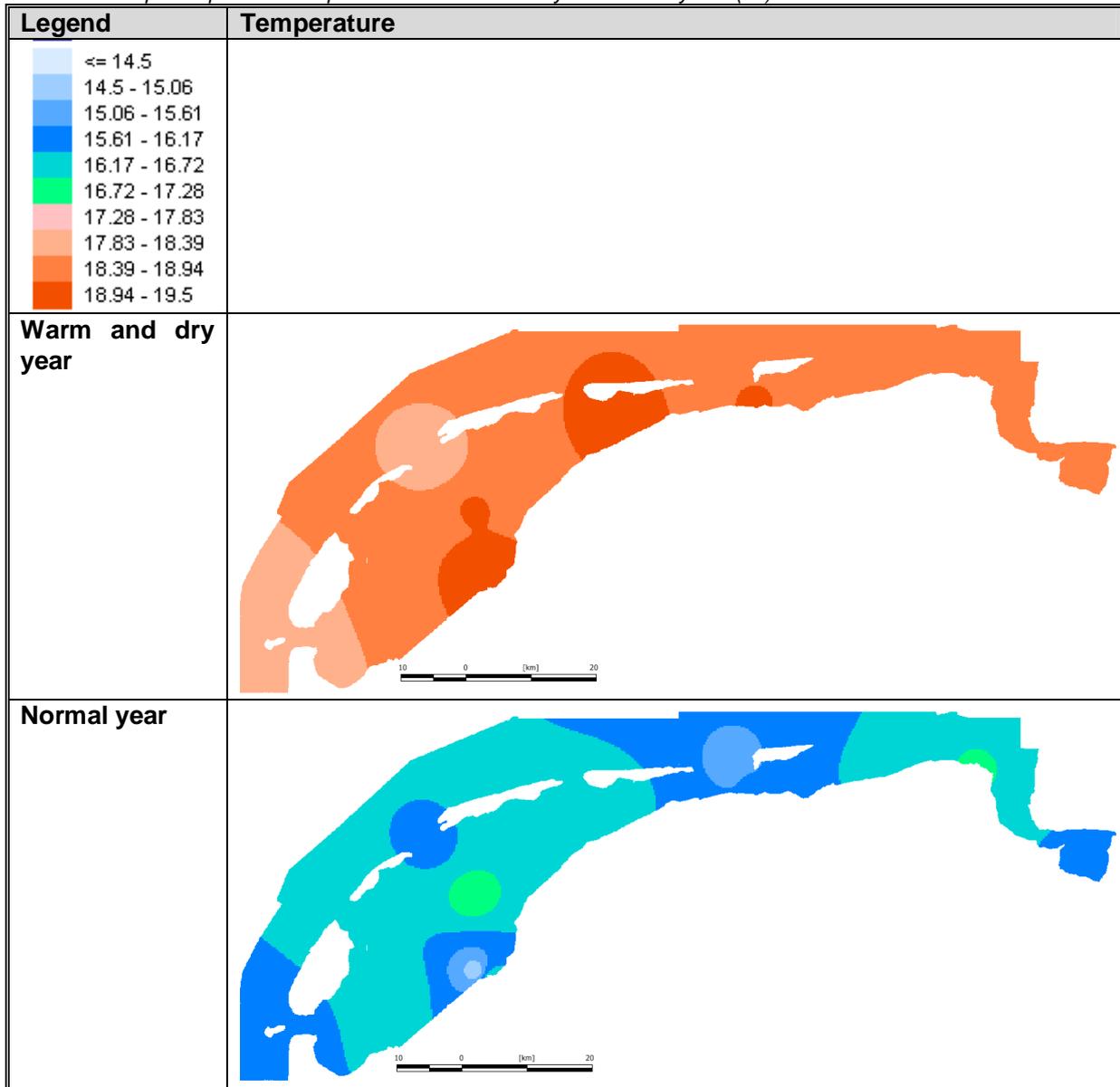


Table 7.23: input maps of the salinity for warm and dry and normal years (psu)

