Summary
SUMMARY

Introduction

Ecosystems are the basis of the world’s ultimate life-support systems. Ecosystem health is crucial for the success and survival of humans. Ecosystems have a changeable nature and a stable ecosystem is not static, but face changes that can often be defied by the ecosystem. However, some bigger (human-driven) interference cannot be defied, causing ecosystem degradation. It is therefore valuable to understand the current state of the ecosystem and the consequences of potential disruptions. The analysis of food web structures has become a commonly accepted method to determine the state of ecosystems. A food web is a diagram depicting who eats whom in ecosystems. When assessed over time or space, food web structures can instruct us about the effects of disturbances and biodiversity loss, show the sensitivity of species and their connectance.

Reconstruction of food webs, with help of stable isotopes analysis, can be used as a means to study the state of an ecosystem. Stable isotopes of nitrogen and carbon are powerful and frequently used tools to reconstruct food webs. Stable isotopes are used to determine the food web position of species or species groups, making it possible to create a two-dimensional food web. The stable nitrogen isotope (δ¹⁵N) is used to elucidate the trophic structure, displayed on the vertical axis in a food web. The stable carbon isotope (δ¹³C) provides information on the input of carbon sources at the base of the food web and can thus infer the energy transfer through food webs, displayed on the horizontal axis in a food web (pyramid).

At first sight, the Wadden Sea might seem rather species-rich, but this is – at least relative to historical references – far from true. The last 1000 years, the Wadden Sea ecosystem last part of her food web complexity, often caused by human influences. Conservation and recovery became key priority for nature management in the Wadden Sea. Key processes that lead to and at the same time indicate the evolvement into a stable and healthy Wadden Sea ecosystem are thought to be: (1) recovery of the ecosystem engineering sea grass beds, intertidal blue mussel beds and even oyster beds who had a very important role for the total food web and (2) the re-appearance of top-predators. It is valuable to gain insight in the current state and recovery of the Wadden Sea ecosystem. Studying the (change of the) shape of the food web structure of the Wadden Sea can unravel the dependency of the system to changes in species(numbers) and dietary changes. A food web reconstruction of the Wadden Sea ecosystem can help predicting how the Wadden Sea will react to disturbances or restoration and is crucial for timely intervention.

This thesis describes the complexity of food webs, analysed mainly with help of stable isotopes. Who eats whom in an ecosystem, and can this be translated to a food web that integrates time and space? How can food web studies by valuable? I searched for the possibilities to use the food web position of indicator species as an indicator for the (spatially) variable state of the Wadden Sea food web.
SUMMARY

Structure of the food web

In Chapter 2 we show how a food web is formed and changes through time. This is studied by a reconstruction of the food web of the salt marsh of the Wadden Island Schiermonnikoog, with a focus on the role of external nutrient input. Making use of a hundred year old salt marsh succession, we could study the food web from a zero to hundred year old salt marsh. We found that the young salt marsh is still very dependent of the input of external nutrients from the adjacent intertidal Wadden Sea. On the young salt marsh, detritivores (organisms feeding on excreted and dead organic matter) are fed by the external nutrient source, the Wadden Sea, and the detritivores are eaten by carnivores. Later in succession the food web becomes 'classic', with an intern nutrient cycle, where plants are eaten by herbivores, who are eaten by carnivores and where detritivores consume the all wasted matter and thereby make it a closed food web cycle. The (initial) structure of a food web therefore requires interaction of nutrients and energy flows between ecosystems.

In order to understand the marine Wadden Sea ecosystem it is valuable to know how autonomous this ecosystem is and by which nutrient sources it is fed, such as external sources or benthic or pelagic algae (resp. from outside the Wadden Sea ecosystem, on the bottom living marine algae and in the sea water floating algae). In Chapter 3 we show that the Wadden Sea ecosystem is mainly internally fed by local benthic algae and that the above-lying food web is mainly dependent on this benthic energy. Besides, we found a high spatial heterogeneity in carbon isotope values of benthic algae. This emphasizes the importance of spatially sampling the benthic and pelagic algae, in order to create a reliable (base of the) food web. Detailed representations of the Wadden Sea food web are therefore difficult to represent.

Constraints of food web and isotope analysis

We found that, beside the spatial heterogeneous base of the food web, more complicating factors hinder us to provide a representative draft of the Wadden Sea food web. Being, changes through time, ontogeny, age and mobility of species, species with dependency of multiple ecosystems and the complexity of measuring methods. In Chapters 4, 6 and 7 we studied how a food web position can be estimated.

In Chapter 4 we show that the base of the food web is also spatially heterogeneous for nitrogen isotopes and that the horizontal position of species in a food web are dependent of correctly estimating this (mean) base of the food web. Mobility and the underlying benthic or pelagic baseline(s) of a species define whether we can correctly estimate a trophic position. Whether spatial variation should be taken into account, when estimating the trophic position, varies between species depending on mobility and underlying benthic or pelagic baseline(s).
SUMMARY

Also the ontogeny of an individual can be decisive for the food web position. For illustration, we see in Chapter 7 that nitrogen isotope values increase with cockle size. Knowledge about the size of cockles that a cockle-consuming organism eats is therefore of influence for the estimation of a trophic position. Furthermore we show that a species can have a varying food web position, depending on its ontogenetic phase.

A correct measuring method will be crucial for the estimation of a correct food web position. (1) Individuals within a species can have different diets. (2) Different tissues of one individual give a diet description varying from the last days to the last months or years and thereby the isotope values of different tissues will likely vary. (3) The measuring process in the laboratory can also affect the isotope value and thus the estimation of a food web position. Do we measure the bulk sample, some lipids or only just a few amino acids? In Chapter 7 we show with help of grey mullets how a trophic position is dependent on measuring methods. What measuring method is most suitable depends on the research question.

In Chapter 6 we show that some species use the Wadden Sea ecosystem only temporarily. Sanderlings change diets while migrating. On arrival in the Wadden Sea they still contain tissue from former locations where they foraged along the migration route. This research shows that food webs of temporary (migrating) species in an ecosystem occupy a special position in a food web. They import external organic matter (feces), their measured isotopic values and diet can thus still show information from former foraging locations and their stay is merely temporarily. We simultaneously show how powerful isotope analysis can be, for by performing one isotope measurement (of two tissues) from one individual sampled at location C we were able to trace the migration schedule of this individual from location A to B to C.

Species in a food web are far from static, not even under undisturbed conditions. Therefore, we would really like to describe how food webs change over time and space. To a certain extent we can account for temporal and spatial variation, since higher trophic organisms often have a higher life expectancy and a higher mobility, species higher in the food web will partly equalize the differences on a smaller scale. Though sessile species, who occur mostly at the bottom of the food web, do not level-out differences and here profound differences in food web position may exist through time and space. In order to analyse the nuanced processes that play a role in disturbances or recovery, a detailed view of the ecosystem is requisite and a general description of the food web will be inadequate. My conclusion in the general discussion is therefore that the food relations in an ecosystem may be more complex than can be represented by a single food web.
SUMMARY

Power of isotope analyses in food web studies

Yet, we can learn (and have learned a lot) from food web studies analysed with help of stable isotopes. Firstly, the use of indicator species can be significant for specific food relations in an ecosystem. Isotope measurements can give insight in misunderstood processes within part of the food web. In Chapter 5 we show how spoonbills can function as indicator species for the state of the young (flat)fish in the shallow intertidal zone of the Wadden Sea. The last decennia spoonbills returned as a breeding bird to the Wadden islands. The circumstance on these islands seem rather ideal; with enough breeding areas, even increasing numbers of breeding colonies, very low degrees of predation and disturbance, seemingly unlimited extends of foraging area and even an increase in shrimp (the repeatedly reported main prey species). We studied the often stated assumption that shrimp are the main prey of spoonbills while breeding in the Wadden Sea, by analysing the diet of spoonbill chicks by regurgitate and isotope analyses. Both methods showed that not shrimp but small (flat)fish are the main prey during the breeding season. Unlike shrimp, small flatfish have been reported to be rather scarce in the Wadden Sea the recent years, which is likely the cause of the flattening spoonbill population and the decreasing chick survival in the Wadden Sea ecosystem. We predict that recovery of the young (flat)fish densities in the shallow parts of the Wadden Sea will be reflected in the diet of spoonbill chicks. Spoonbills can thus function as an indicator species for the (flat)fish stocks in the shallow intertidal Wadden Sea.

In Chapter 7 the power of isotope analysis in food web studies is shown by a diet study of bar-tailed godwits and red knots. Isotope analyses prove an elegant method to determine which worm species is preferred by bar-tailed godwits. The prey quality of red knots appears to be made clear in a $\delta^{13}C-\delta^{15}N$ bi-plot with a sliding scale from left to right. We found that experienced red knots have a diet consisting of qualitatively higher prey species. It thus seems that researchers and nature managers can get insight in prey bivalve availability for knots (cockles, mud snails and Baltic tellin) by studying the carbon and nitrogen isotopes of red knot blood. Red knots could like a indicator species for the availability of high quality shellfish.

Secondly, a general food web can be used to compare ecosystems. In chapter 7 we compare five intertidal ecosystems in Europe and West-Africa along the East-Atlantic migration route. The intertidal areas the Wadden Sea and Banc d’Arguin seem to be differently regulated, with less agricultural influences and a less marine signal. The intertidal area of the Tagus estuary seems enriched by external inland nitrogen sources. Although the five intertidal areas show differences, there are certainly also similarities such as a broad base of primary sources (a wide $\delta^{13}C$ range).
SUMMARY

Conclusion

In summary, it appears to be very difficult or impossible to represent a time and space integrated view of who-eats-whom in an ecosystem (a complete food web). This is because too many complicating factors play an important role in describing all food relations in one food web, such as; temporal change, mobility of species, differences within species (e.g. diet changes due to ontogeny and size), species who are dependent of multiple ecosystems and complexity of measuring methods. A food web can be valuable to study generalities, for example when comparing ecosystems. Furthermore, the study of individual food web positions (of indicator species) can serve as indicators for the variable state of the Wadden Sea food web.

I end my thesis with a somewhat philosophical and hopefully unfounded pessimistic view on what will happen with the small remains of the Zuiderzee, called the Wadden Sea. I cherish this piece of The Netherlands and admire her resilience, but fear the nonchalance with which man influences nature.