CHAPTER 1

General introduction

Jeltje Jouta
CHAPTER 1

With awe I look at the Wadden Sea. So stirred, so much pressure, so impressionable, yet tough. Perhaps – currently – in another state than what it has been before, but still impressive. With growing amazement I have come to realize how good she\textsuperscript{1} manages to stay afloat, how flexible she must be. \textit{“But why does his heart not stop beating?! Why does it not stop?!”} These are the last two sentences of a story by Edgar Allen Poe, the story touched me and I therefore refer to it in my thesis title. In this thesis I search for indicators that represent the state of health of the Wadden Sea ecosystem.

Pardon me! Ecosystem health?

An ecosystem is a complex set of relationships formed by the interactions of living sources and their physical environment. Ecosystems are the worlds’ ultimate life-support and ecosystem health is crucial for the success and survival of humans (Karr 1996, McCann 2000), which is likely the cause of the urge to understand and protect ecosystems and explains the wish to keep an ecosystem in a strong, resilient, pristine and healthy state\textsuperscript{2}.

Ecosystems have a changeable nature and a stable ecosystem is not static, but faces changes that can often be defied by the ecosystem (McCann 2000). Ecosystems assemble over time, developing via succession from a simple and young pioneer stage towards a complex and old climax stage. During succession natural, more or less predictable and orderly changes occur in the species composition and food web structure of a community over time (Odum 1969, Pandolfi, Sven Erik & Brian 2008). Note that the standards of ecosystem health are different when comparing a pioneer and climax ecosystem. An ecosystem in a pioneer stage is thus not (necessarily) in a worse ecosystem health compared to a climax stage. Natural dynamics are a not a reason either to

\begin{itemize}
\item \textsuperscript{1} For me the Wadden Sea is feminine (and most French people will likely agree), but note that the old man of Edgar Allan Poe was masculine.
\item \textsuperscript{2} The term ‘ecosystem health’ is criticized for unjustly comparing to human health (e.g. Suter 1993), yet I will use this term intuitively. As you might have noted, I feel like comparing the state of ecosystems with the state of human beings that can both be described as young, old, erratic, stable, poor, rich, healthy or unhealthy. Being healthy contributes to the chance to survive. Just as there is a desire to keep all your loved ones healthy, we also want to keep an ecosystem healthy and alive (possibly imprimit for the survival of mankind). Differences between ecosystem health and human health are profound, for instance, humans have clear boundaries such as a skin while ecosystems clearly have not. The main argument against using the term ecosystem health is because of the absence of a fixed index. Despite the existence of many ecosystem measures, no standard set of ecosystem measures are defined to indicate ecosystem health.
\item Note that ecological health and ecosystem health are not the same. The term ecological health is used in medicine to refer to exposure of chemicals in an environment, like pesticides or smoke. Whereas ecosystem health concerns the structural and functional condition of biological systems (Karr 1996, Rapport, Costanza & McMichael 1998).
\end{itemize}

10
assign a state of an ecosystem the label ‘unhealthy’. However, human exploitation of nature can impact an ecosystem so violently that, as a consequence, the ecosystem faces degradation. The ecosystem can react in three ways; the degradation can be (a) temporary because the ecosystem shows resilience or (b) temporary since it is followed up by restoration of the ecosystem with help of human efforts, or (c) permanent. In the second and third case, degradation results in an ecosystem with a lower ecosystem health. But how do we qualify ecosystem health?

Numerous measures for ecosystem health are developed and among them are named; biodiversity, net primary production, species richness, landscape mosaics, flow of energy, number of links in a food web and shape of food webs (Xu, Tao, Dawson et al. 2001, Hooper, Chapin, Ewel et al. 2005, Boero & Bonsdorff 2007, Costanza, Fisher, Mulder et al. 2007, Mancinelli & Vizzini 2015, Bird, Perissinotto, Miranda et al. 2016). These ecosystem measures can be translated or merged into bigger qualitative terms such as the comprehensive definitions of the ‘state of an ecosystem’, ‘ecosystem functioning’ or ‘ecosystem health’ (Hobbs & Norton 1996, Slocombe 1998). Despite the existence of many ecosystem measures, no standard set of ecosystem measures are yet defined to indicate ecosystem health. In this thesis I attempt to use food web structure as an ecological measure for ecosystem health.

Food webs

Food is one of the most important factors in life, and that is how Charles Elton (1927) invented food webs and appointed them as a valuable way to describe and compare ecosystems. The analysis of food web structures has become a commonly accepted method to determine the state of ecosystems and provide complex yet manageable representations of biodiversity, species interactions, ecosystem structure and ecosystem function (Dunne, Williams & Martinez 2002). When assessed over time or space, food web structures can instruct us about the effects of biodiversity loss, including secondary and cascading extinctions, and show the sensitivity of species and their connectance (Dunne et al. 2002).

A food web is a diagram depicting who eats whom in ecosystems. Figure 1.1 depicts a conceptual food web, with primary producers such as plants or algae positioned at the bottom of the food web, which are eaten by primary consumers (herbivores) such as beetles, geese or mud snails, which are eaten by mesopredators like passerine birds or fish of intermediate size and finally at the top of the food web are the top predators such as raptors and dolphins. Food webs can be ordered in trophic levels, shown in table 1.1, with the trophic level of an organism being determined by the number of ‘who-eat-who’ feeding links that have passed.

Note that, although the detritivorous pathway plays a critical role in organizing and sustaining ecosystem (Odum 1969, Moore, Berlow, Coleman et al. 2004), I sim-
plified figure 1 by simply drawing arrows from food web elements to ‘detritivore 1’, thereby skipping the step of ‘dead organic matter’. Although the detritivorous pathway recycles energy of dead organic matter, most energy is transformed into heat and lost in the system (Krebs 2001). With increased trophic level, the flow of energy therefore typically becomes smaller, resulting in a pyramid shape, called a food pyramid.

Most ecosystems are regulated by top-down and bottom-up control or by the interaction of the two, meaning that the ecosystem is respectively regulated by predation control and by nutrients and primary productivity, or by both (Menge 2000, Eriksson, van der Heide, van de Koppel et al. 2010). In marine systems, the joint effect of fisheries and eutrophication should be considered very seriously in marine nature management (Eriksson et al. 2010).

![Figure 1.1: Conceptual food web in a pyramid form.](image)

**Table 1.1: Organisation of food webs.**

<table>
<thead>
<tr>
<th>Trophic Level</th>
<th>Primary Producers</th>
<th>‘Plants &amp; Algae’</th>
<th>Top Predator 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>First trophic level</td>
<td>Primary producers</td>
<td>‘Plants &amp; Algae’</td>
<td>Top predator 1</td>
</tr>
<tr>
<td>Second trophic level</td>
<td>Primary consumers</td>
<td>Herbivores</td>
<td></td>
</tr>
<tr>
<td>Third trophic level</td>
<td>Secondary consumers</td>
<td>Carnivores¹</td>
<td></td>
</tr>
<tr>
<td>Fourth trophic level</td>
<td>Tertiary consumers</td>
<td>Mesopredator ²</td>
<td>Higher carnivores³</td>
</tr>
</tbody>
</table>

1: Insects parasitoids can also be part of this group.
2: Although most food webs are limited to four trophic levels, fifth or more trophic levels may occur, with the position of top predators logically shifting to the highest level.
3: Insect hyperparasites can also be part of this group. (Krebs 2001)
GENERAL INTRODUCTION

Food webs can intertwine and can either have a more or less closed or an open nutrient cycle. Whereas in closed systems herbivores and detritivores depend on locally regulated nutrient cycling, in open systems external nutrient input are a major influence driving of the food web. Moreover mobile species, such as migratory birds, can shift between ecosystems, hereby linking several food webs. Although the shape of food webs is typically pyramid-shaped, external input nutrient input and ecosystem transcending processes might result in other food web shapes, with for instance more emphasis in the top part of the food web. Reconstruction of food webs, with help of stable isotopes analysis, can be used as a means to study the state of an ecosystem (Augusto, Tassoni, Ferreira et al. 2015, Mancinelli et al. 2015, Bird et al. 2016).

Before I examine ways to assay the structure of food webs using stable isotopes, we need to share the caveat that food relationships are an important, but not the only one, relationship making up an ecosystem. There are additional non-trophic ecological interactions such as parasitism, competition, mutualism and ecosystem engineering which also strongly feed back on ecosystems and even food web structure (Olff, Alonso, Berg et al. 2009, van der Zee, van der Heide, Donadi et al. 2012).

Stable isotopes

Stable isotopes of nitrogen and carbon are powerful and frequently used tools to reconstruct food webs (Peterson, Howarth & Garritt 1985, Post 2002). 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 (Figure 1.2). In food web ecology, food web reconstructions based on stable isotopes mainly yields to qualitative food webs. The stable nitrogen isotope $^{15}$N is used to elucidate the trophic structure, displayed on the vertical axis in a food web, while the stable carbon isotope $^{13}$C 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) (Figure 1.2) (Peterson & Fry 1987; Post 2002, Middelburg 2014).

The trophic position of consumers can be estimated by level of the two isotopes relative to a fixed standard, hence we talk about $\delta^{15}$N (delta $^{15}$N) and $\delta^{13}$C. The level of the $\delta^{15}$N value of consumers relative to the $\delta^{15}$N value of the primary sources of the food web, often show an ‘enrichment’ by $\sim 3.4\%$ in $\delta^{15}$N per trophic level. $\delta^{13}$C does not show ‘enrichment’; instead the $\delta^{13}$C of plants varies because of different $\delta^{13}$C values in inorganic carbon substrate (atmospheric carbon dioxide or dissolved inorganic carbon) and because of the involvement of different carbon isotope fractionations during C3 or C4 photosynthesis pathways. Thus, in contrast to nitrogen, the ratio of carbon isotope ($\delta^{13}$C) does not change substantially as carbon moves through the food web, making $\delta^{13}$C ideal to determine the ultimate sources of consumers (Peterson et al. 1987, Post 2002, Middelburg 2014).
**Figure 1.2:** A food 'pyramid'.

**Figure 1.3:** Ecosystem health, showing trophic diversity (vertical) and the reliance of sources by the system (horizontal diversity) represented in a stable isotopic bi-plot.
GENERAL INTRODUCTION

The state of an ecosystem, expressed by the diversity of an ecosystem, can be depicted by a food web structure or food pyramid (Figures 1.2 and 1.3). In such a food web representation, trophic diversity is expressed by vertical diversity, while the range of sources where an ecosystem relies on is expressed by horizontal diversity (Figure 1.3). The horizontal and vertical diversity of a food web structure, together, are indicative for ecosystem health or the state of an ecosystem (Olff et al. 2009). As shown in Figure 1.3, ecosystem health is visible in the size and shape of the contours of the food web structure (here food pyramid) which reflects the diversity of the ecosystem.

Note that, whereas the number of species reflects diversity, the number of feeding links in a food web represents the ecosystem complexity. The horizontal and vertical diversity of a food web structure, thus, does not necessarily describe a complex food web.

The Wadden Sea

The Wadden Sea is one of world’s largest intertidal ecosystems along the coast of The Netherlands, Germany and Denmark (Wolff 2000, Eriksson et al. 2010, Hogan & Monosson 2011).

It is fuelled by a multiple sources, internal benthic and pelagic origins and three external sources are together driving the Wadden Sea ecosystem and are distinguishable with help of δ¹³C values (Benthic: −16.3 ±0.1SE % δ¹³C | Pelagic: −18.8 ±0.1SE % δ¹³C | Lake Lauwersmeer: −28.5 % ±0.3SE % δ¹³C | Salt marsh (here island Schiermonnikoog): −28.3% ±0.9SE % δ¹³C). It provides key habitat to approximately 2700 marine species, including the species that connect the Wadden Sea with ecosystems elsewhere on the globe, i.e. the migratory shorebirds (van de Kam, Ens, Piersma et al. 2004, Reise, Baptst, Burbridge et al. 2010).

At first sight, the Wadden Sea might seem rather species-rich, but this is – at least relative to historical references – far from true. Major changes have occurred in Wadden Sea, mostly due to human impact (Lotze, Reise, Worm et al. 2005, Lotze, Lenihan, Bourque et al. 2006). The Wadden Sea area is depleted by more than 90% of formerly important species, more than half of all seagrass and wetland area is destroyed and water quality dropped, while multiple invasive species increased (Lotze 2005, Lotze et al. 2006, Eriksson et al. 2010). Already a 1000 years, the Wadden Sea faced human impact and mild forms of decline, but the last 150 to 300 years human impact escalated and left its traces in forms of steep acceleration of ecological degradation (Lotze et al. 2005, Lotze et al. 2006). The ecosystem changed towards a system with an impoverished food web complexity, which is schematically shown in Table 1.2 (de Jonge, Essink & Boddeke 1993, Wolff 2000, Piersma, Koolhaas, Dekkinga et al. 2001, Lotze 2005, Lotze et al. 2005, Lotze et al. 2006, Eriksson et al. 2010). The two
most destructive changes that both directly and indirectly impeded the complexity of
the Wadden Sea food web were: the disappearance of big top-predators and the strong
decline in the important and once so numerous-present ecosystem engineering sea-
grass meadows and mussel beds at the bottom of the food web, to the point of total
2007, Eriksson et al. 2010).

Table 1.2:

<table>
<thead>
<tr>
<th>Period</th>
<th>Change</th>
<th>Cause</th>
<th>Consequence</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Since ±1100 A.D.</td>
<td>Saltmarsh decrease in area and length</td>
<td>Land reclamation, first by monasteries then by farmers and water board RWS</td>
<td>Less silt sedimentation on saltmarsh. Change in saltmarsh vegetation. Higher water turbidity</td>
<td>Dijkema 1987a</td>
</tr>
<tr>
<td>Since ±1800</td>
<td>Start large-scale loss of big top-predators (porpoise, ray, shark)</td>
<td>Overfishing</td>
<td>Shift in regulation, from top-down to more bottom-up</td>
<td>Wolff 2000, 2005</td>
</tr>
<tr>
<td>Since ±1850</td>
<td>Start sea level rise with ±2 mm/yr in Wadden Sea and North Sea</td>
<td>Climate change, both natural and human induced</td>
<td>Reduced saltmarsh area. Dyke breaches</td>
<td>Behre 2007</td>
</tr>
<tr>
<td>Since 1950</td>
<td>Strong increase planktonic primary producers, possibly followed by slight decrease (from 1990 onwards); no information about epi-phytobenthic primary producers</td>
<td>Initial strong increases in eutrophication of surface water, cause by introduction of fertilizers and agriculture, sewage and industrial discharges. Followed by slight decreases (from 1990) due to better water purification</td>
<td>Amplifying the lack of recovery of seagrass meadows due to turbidity of water. Decrease in sight hunting predators</td>
<td>Philippart, Beukema, Cadee et al. 2007</td>
</tr>
<tr>
<td>Since 1950</td>
<td>Strong increase fishery intensity. Soft-bottom disturbances</td>
<td>Expansion in power of fisheries fleet</td>
<td>Increase water turbidity caused by soft-bottom disturbance. Increase bycatch. Increase total catch</td>
<td></td>
</tr>
</tbody>
</table>
### Table 1.2: Continued.

<table>
<thead>
<tr>
<th>Period</th>
<th>Change</th>
<th>Cause</th>
<th>Consequence</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1965</td>
<td>Start mussel cultivation plots in Wadden Sea (7000ha); harvesting maximal 70-100 million kg/yr (from ca. 1965 onwards), now strongly declined harvest</td>
<td>Disease.Absent spat fall in Zeeland (NL) due to finished Delta Project and diseases</td>
<td>Increase soft-bottom disturbances in sublittoral zone in the Western Wadden Sea</td>
<td></td>
</tr>
<tr>
<td>1969</td>
<td>Loss Lauwerszee as brackish estuary</td>
<td>Construction of the causeway that created lake Lauwersmeer</td>
<td>Loss of brackish species. Freshwater-marine passage</td>
<td></td>
</tr>
<tr>
<td>Since 1980</td>
<td>Rise of mean temperature in The Netherlands, with in total 2 degree/20yrs, a rise that is higher than what is expected based on natural climate cycle</td>
<td>Greenhouse effect, increased emission of CO₂ by increases in fossil fuels</td>
<td>Possibly more predation eg. by shrimp on shellfish because of prolonged predation in winter</td>
<td>Beukema &amp; Dekker 2005, Dekker &amp; Beukema 2007</td>
</tr>
<tr>
<td>Since 1983</td>
<td>Strong rise of invasive shellfish, e.g. the Japanese Oyster Crassostrea gigas and Razor Clam Ensis directus, or Chinese Mitten Crab Eriocheir sinensis</td>
<td>Culturing in nursery beds by oyster farmers. Transport with ballast water</td>
<td>Competition between endemic species and introduced invasive species</td>
<td>Nehls, Diederich, Thielges et al. 2006, Brandt, Wehrmann &amp; Wirtz 2008</td>
</tr>
<tr>
<td>Since 1990</td>
<td>Strong decline of settlement and population size of certain bivalve species, with the ecological extinction of Macoma balthica in the Western Wadden Sea around 2000 (a key stone species until then)</td>
<td>Soft-bottom disturbance by cockle-, mussel- and shrimp fishery which reduces settlement- and survival opportunities. Reduction in high-quality prey for birds</td>
<td>Declines in birds that are dependent on Macoma, such as Red Knots Calidris canutus</td>
<td>van Gils, Spaans, Dekinga et al. 2006</td>
</tr>
</tbody>
</table>
Table 1.2: Continued.

<table>
<thead>
<tr>
<th>Period</th>
<th>Change</th>
<th>Cause</th>
<th>Consequence</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Since 2005</td>
<td>Change of 34 Cockle fishermen from the Wadden Sea to fishing on <em>Spisula</em> in the North Sea. Plans to exploitation of Venus clam fishery in Mauritania</td>
<td>Prohibition of cockle fishery in the Wadden Sea</td>
<td>Unknown effects on the coastal strip of the North Sea</td>
<td></td>
</tr>
<tr>
<td>Since 2006</td>
<td>Increase in provisioning permits to handcockle fishing</td>
<td>Pressure from fisheries sector, evoking employment and tradition</td>
<td>Decrease standing stock of Cockles (not documented)</td>
<td></td>
</tr>
<tr>
<td>2008</td>
<td>Withdrawal by Council of State of permission of mussel seed fishery in the Wadden Sea</td>
<td>Protests of nature organisations, evoking the European rules and precautionary principle</td>
<td>Less soft-bottom disturbance in the sublittoral. Higher availability of young mussels as food for bivalve-eating birds</td>
<td></td>
</tr>
<tr>
<td>Since 2011</td>
<td>Moderation and regulation of hand cockle fishing</td>
<td>Protests of nature organisations and scientists, demonstrating against degradation of benthic fauna</td>
<td>Increase standing stock of Cockles and indirectly also increases in other benthic species</td>
<td></td>
</tr>
</tbody>
</table>

Where management in the Wadden Sea in the past focussed on fishery, shipping, coastal protection and recreation, nowadays nature preservation is an important focus as well. Awareness rose that the Wadden Sea is a unique intertidal area, of great natural importance for many natural processes, not in the least because it functions as a crucial staging area for thousands of birds migrating along the East Atlantic flyway. Nowadays, the Wadden Sea is inscribed on the UNESCO World Heritage List and protected by the Ramsar Convention and the bird, water and habitat directives Natura 2000 (Boere & Piersma 2012). Conservation and recovery became key priority for nature management in the Wadden Sea.

Success was booked by prohibition of cockle fishery, manifested by a reviving benthic fauna after several years of recovery, shown by increasing numbers of the bivalve
species *Macoma balthica* (Compton et al. 2016). However, despite other restoration efforts – such as reintroduction of the two crucial ecosystem engineers, water quality improvement and recovery for seals – the Wadden Sea is not yet restored to a flourishing system with high complexity and species numbers (Piersma et al. 2001, Eriksson et al. 2010, van der Veer, Koot, Aarts et al. 2011, van Roomen, Laursen, van Turnhout et al. 2012). Key processes that lead to and at the same time indicate the evolution into a stable and healthy Wadden Sea ecosystem – thus into a ‘healthy’ and complex state – are thought to be (1) recovery of the two important ecosystem engineering species who had an very important role for the total food web, being the recovery of large fields of (a) stable intertidal blue mussel *Mytilus edulis* beds and (b) sea grass beds *Zostera noltii* and *Z. marina* and (2) the re-appearance of top-predators (Lotze et al. 2005, 2006, Eriksson et al. 2010).

**Issues**

The shape of the food web structure of the Wadden Sea can unravel the dependency of the sources that drive the Wadden Sea ecosystem, showing for instance the dependence on the particularities of the primary sources of an ecosystem (horizontal diversity). A food web structure can be symmetric showing an equal dependency of all primary producers, or it can be build up skewed with the top of the food web hanging to the left or right, showing the dependence of primary producers in the food web (Figure 1.4). Figure 1.4 presents the theoretical shape of the food web of a marine intertidal system, showing the skewness to the left and right as a respectively pelagic or benthic dominated food web.

The contours of a food web structure can thus determine the flow of energy through an ecosystem and may help us forecast what it means if particular food web elements increase or decrease in numbers or shift in diet. The dependency of primary producers on the above-lying food web, thus the skewness of the contours of the food web structure, can be help to understand (with downstream efforts to improve) the state of the ecosystem. If, for instance, there is an interest in the recovery of toppredators in the system, it is helpful to understand what these toppredators would feed upon and determine what primary producers should drive this energy flow (Figure 1.1 and Figure 1.4). A food web structure can thus help predicting how a system will react to disturbances or restoration (Dunne et al. 2002, Pimm 2002, Catry, Lourenco, Lopes et al. 2016).

The aim and urge to understand and validate the processes that should lead to restoration of the Wadden Sea are supported by scientists, local governments and nature management organisations of national, European and global level. The goals are high, the set time is short. Overall, the main goal is to find and effectuate keys that lead to higher complexity and biodiversity (Eriksson et al. 2010). Characterisation of
Chapter 1

![Diagram showing food pyramids for pelagic and benthic food webs.](image)

**Figure 1.4:** Food pyramids for pelagic and benthic food webs.

the Wadden Sea food web would be helpful in finding, effectuating and monitoring the keys to restore the Wadden Sea in its former healthy, flourishing and complex state.

Food web reconstruction could be helpful in following the changes in the Wadden Sea and crucial in timely intervention (Eriksson et al. 2010). Bearing in mind the wish to restore the Wadden Sea ecosystem in its former (pristine) state, if solid information about the food web structure of the former state is lacking, the characterization of a disturbed ecosystem is especially valuable when comparing it to other intertidal ecosystems. Assessing the food web structure of ecosystems creates the ability to compare ecosystems and search for generality of ecosystem health in food web structures.
GENERAL INTRODUCTION

Quantitative comparison between (the food webs structure of) ecosystems are still rare, while being extremely insightful and thus valuable. As an example, the study of Catry et al. (2016) made a quantitative comparison between the food web structure of four important intertidal ecosystems for migratory birds along the East Atlantic flyway, including Tagus estuary in Portugal, Sidi Moussa in Morocco, Banc d’Arguin in Mauritania and Bijagós archipelago in Guinea-Bissau. Differences and similarities between the structure of these intertidal systems became clear (Catry et al. 2016). The geographically more northern oriented intertidal Wadden Sea ecosystem bordering the Netherlands, Germany and Denmark is similarly comparable to the other four intertidal ecosystems in Catry et al. (2016) (see also the General Discussion of this thesis).

In this thesis I search for the possibility to establish whether we can use indicator species to inform us about the contemporary state and structure of the food web of the Wadden Sea. An indicator species is a strategically chosen species whose state reflects the state of other species in the area, and their mutual trophic relationships. Although the population and survival trends of an indicator species is regularly used to quantify the state of (part of) the ecosystem, we here mainly focus on changes in the food web position of the indicator species, which indicates changes in the part of the food web structure where the indicator species is indicative for.

There are multiple types of indicator species, but here the term ‘indicator species’ should probably be defined as a ‘food web position indicator species’ and we assess the food web position of the indicator species by using stable isotopes (Krebs 2001, Carignan & Villard 2002). By studying the food web position of several indicator species, each indicator species can monitor part of the food web and together can give insight in the (changing) state of the total ecosystem. It can help answering how to restore the Wadden Sea and can give insight in the underlying mechanism of the failing or successful conducted restoration attempts. For instance, in the Wadden Sea, a higher trophic indicator species could shift towards more benthic food sources (shown in lower δ¹³C values), indicating that (part of) the ecosystem is now more benthic orientated, which infers recovery of the benthic mud flats.

The research question that I will therefore try to answer: Can we characterize the spatially variable food webs of the Wadden Sea food web with help of stable isotopes, and is it possible to identify useful indicator species to document future food web changes?

Thesis outline

To demonstrate the power of the approach, Chapter 2 presents a reconstruction of the food web of a terrestrial part of the entire Wadden Sea ecosystem, the saltmarsh.
CHAPTER 1

Using a unique and well-established ‘chronosequence’ of the Schiermonnikoog salt-marsh, we were able to reconstruct food web changes over time from food web changes over space. We show that baby saltmarshes to a significant extent are externally fed from the marine component of the Wadden Sea ecosystem.

In order to understand the marine Wadden Sea ecosystem, it is valuable to understand how autonomous the Wadden Sea is and whether the system is supported by local benthic, pelagic primary sources or by external sources. Distinguishing between these energy sources is essential for our understanding of ecosystem functioning. In Chapter 3 we show that the Wadden Sea ecosystem is a primarily internally fuelled, benthic-driven system and show the dependency of benthic sources for species that live in the Wadden Sea, clarifying most of the food web structure on the horizontal axis that represents stable carbon isotopes. The other component of the food web structure, the trophic vertical axis, is highlighted in chapter 4 and 5.

In Chapter 4 we show that in order to calculate trophic positions it is important to use a justified baseline, acknowledging species specific information such as mobility and primary source (benthic /pelagic) and acknowledge spatial heterogeneity in baselines. Knowing the basic ingredients, we can generate food web structures and assign indicator species for parts of the food web structure that can elucidate potential spatial differences in the state of the ecosystem. Assigning indicator species for this area could help monitoring ecosystem health.

In Chapter 5 we assess whether Spoonbills are a suitable indicator species. They are, but what for? Rather than being an indicator of the size and composition of the whole food pyramid, Spoonbill diets assessed by stable isotopes (and verified by analyses of regurgitates) are indicator of the presence of small flatfish in the shallow intertidal Wadden Sea.

Recalling the connectedness within the entire Wadden Sea ecosystem (Chapter 2), in Chapter 6 we zoom out to beyond the Wadden Sea and study its international (and indeed intercontinental) connections. We develop an estimation model with which, based on a single blood sample, we can quite accurately assign the temporal occurrence of two subsequent diet switches of individual shorebirds.

In Chapter 7 I come back to review these results, and conclude that this work has perhaps raised more questions than it did answer. The reconstruction of food webs is more complicated that we had anticipated. For example, the estimations of trophic positions requires information on the spatial heterogeneity in isotope values of the resources and the mobility of the consumers. I conclude that indicators of ‘health’ of the Wadden Sea ecosystem are best represented by the particular functional relationships between resources and consumers which are now relatively well-understood (as for spoonbills, see Chapter 5).
GENERAL INTRODUCTION