Feed and fly

-

A model study about the relationship between coastal birds and intertidal food webs

Dissertation

Sabine Horn

Feed and fly
–
A model study about the relationship between coastal birds and intertidal food webs

Dissertation
zur Erlangung des Doktorgrades an der Mathematisch-Naturwissenschaftlichen Fakultät
der Christian-Albrechts-Universität zu Kiel

Vorgelegt von

Sabine Horn

Angefertigt am Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung
Wattenmeerstation Sylt

Kiel, 2016

Cover photos
Flying oystercatchers: Robert Waleczek
Curlew sandpipers: Anna Schareck

Prüfungskomission

PD Dr. Harald Asmus (Erster Gutachter)

Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, List

Prof. Dr. Stefanie M. H. Ismar (Zweite Gutachterin)

GEOMAR, Helmholtz-Zentrum für Ozeanforschung Kiel

Prof. Dr. Mojib Latif (Vorsitz)

GEOMAR, Helmholtz-Zentrum für Ozeanforschung Kiel

Prof. Dr. Stefan Garthe

Forschungs- und Technologiezentrum Westkünste der Christian-Albrechts-Universität zu Kiel

Verteidigt am: 21. 12. 2016

Druckgenehmigung: 21. 12. 2016

Zusammenfassung

Das Wattenmeer ist ein einzigartiger Lebensraum und von essentieller Bedeutung für Millionen von Küstenvögeln, die das Wattenmeer als Hauptnahrungsquelle nutzen. Dennoch ist Beziehung zwischen nahrungssuchenden Vögeln und intertidalen Lebensräumen wenig untersucht und wurde in dieser Arbeit mit Hilfe der Ökologischen Netzwerkanalyse näher betrachtet.

Zunächst wurde die Nahrungsnetzstruktur von sechs eulitoralen Habitaten (i.e. Herzmuschelfeld, Schwertmuschelfeld, Schlickwatt, Miesmuschelbank, Sandwatt, Seegraswiese) analysiert und miteinander verglichen. Alle Habitate besitzen eine ausgeglichene Systemstruktur, was auf die Fähigkeit hindeutet, Belastungen standhalten zu können. Die Habitate unterscheiden sich jedoch in ihrem detaillierten Aufbau. Das Herzmuschelfeld und die Miesmuschelbank weisen eine sehr komplexe Flussstruktur, sowie eine starke Abhängigkeit von Phytoplankton-Importen auf. Das Schwertmuschelfeld ist ein einfach aufgebautes System mit einem effizienten Energietransport. Das Schlickwatt ist aufgrund der einfachen und kurzen Energiekreisläufen und des geringen Recycling anfällig für Störungen. Das Sandwatt und die Seegraswiese sind geprägt durch eine sehr komplexe und redundante Flussstruktur und ein hohes Maß an Recycling. Die Vielfalt unterschiedlicher Habitate im Wattenmeer scheint demnach von großer Bedeutung zu sein, da jeder Lebensraum eine andere Rolle einnimmt und zur Funktion des gesamten Ökosystems beiträgt. Außerdem werden die Habitate in unterschiedlicher Intensität von nahrungssuchenden Vögeln genutzt.

Vögel sind ein wichtiger Bestandteil des Wattenmeer-Nahrungsnetzes. Aufgrund der vielfältigen direkten und indirekten Verbindungen ziehen Veränderungen in der Vogelpopulation Folgen für das gesamte Nahrungsnetz nach sich. Mit einer Abnahme in der Vogelpopulation verkürzen sich die Energietransportwege im Nahrungsnetz und die Energieflüsse sind weniger divers und redundant. Vögel tragen somit maßgeblich zur Stabilisierung des Wattenmeer-Nahrungsnetzes bei. Holistische Studien wie diese können als Grundlage dienen, Bewertungsinstrumente für die Beschreibung des ökologischen Zustandes des Wattenmeer-Nahrungsnetzes zu entwickeln.

Abstract

The Wadden Sea is a unique coastal ecosystem and of outstanding importance for millions of coastal birds which use the intertidal area as a major food source. In this study the importance of habitat diversity and the influence of avian predators on the intertidal food web was determined using Ecological Network Analysis.

Similarities and differences of the food web structure were analyzed for six different intertidal habitats (i.e. cockle field, razor clam field, mud flat, mussel bank, sand flat, seagrass meadow). All systems were in a good trade-off between their degree of order and their redundancy implying a sustainable system structure and resistance in front of perturbations. But the habitats differed in their detailed features. The cockle field and the mussel bank were characterized by a complex and diverse flow structure while being simultaneously strongly dependent on external phytoplankton imports. Razor clam fields were revealed to be simple but very efficient systems. The studied mud flat appeared to be vulnerable to perturbations due to short and simple pathways and little recycling. The sand flat and the seagrass meadow showed a complex and redundant flow structure and a high recycling indicating independence and resistance. Habitat diversity appears to be an important trait for the Wadden Sea food web as each habitat has a distinct role in the whole ecosystem functioning. Furthermore, the diverse habitats are of great importance for foraging bird which might be specialized to one of the habitats.

Birds induce a large impact on the Wadden Sea food web. Due to their various direct and indirect influences, it is likely that changes in the bird population also cause changes in the whole system functioning. A decline in birds results in a decrease of pathway length and a less redundant and diverse flow structure. Birds therefore play an important role in stabilizing the intertidal food web.

The holistic approach of Ecological Network Analysis provides fundamental insight in the Wadden Sea food web structure. Results of this thesis are a useful basis to develop management tools and strategies for assessing the ecological state and the health of this unique ecosystem.

Contents

Chapter 3: Diversity of intertidal food webs – functions and features 109

List of figures

General introduction

Chapter 1: The diversity of benthos and birds in intertidal habitats

Chapter 2: Relationships between fresh weight, dry weight, ash free dry weight, carbon and nitrogen content for selected vertebrates

Chapter 3: Diversity of intertidal food webs – functions and features

Chapter 4: Impact of birds on the intertidal food web – assessed with Ecological Network Analysis

General discussion

List of tables

Chapter 1: The diversity of benthos and birds in intertidal habitats

Chapter 2: Relationships between fresh weight, dry weight, ash free dry weight, carbon and nitrogen content for selected vertebrates

Chapter 3: Diversity of intertidal food webs – functions and features

Chapter 4: Impact of birds on the intertidal food web – assessed with Ecological Network Analysis

Appendix

Even the longest journey
begins with the first step

Lao-Tse

General introduction

General introduction

1. The Wadden Sea

1.1. General description

The Wadden Sea (Fig. 1) is a unique ecosystem in the southeastern part of the North Sea, stretching along the coastline of Denmark, Germany and the Netherlands. From a geological point of view, the area is relatively young (Lozán et al. 1994). At the present place, it emerged about 6,000 years ago migrating in landward direction as the result of special geomorphological and hydrodynamic interactions (Lozán et al. 1994, Gätje and Reise 1998b). A line of barrier islands and sandbanks separates the Wadden Sea from the adjacent North Sea. The Wadden Sea and the North Sea are connected with each other by deep tidal channels branching in smaller inlets and creeks (Wolff 1983). Three large rivers discharge in the Wadden Sea (i.e. Ems, Weser and Elbe). Their inputs in freshwater in the coastal areas induce a gradual decline of salinity from the North Sea influenced areas (i.e. salty water) to the river-influenced areas (i.e. brackish water, Wolff 1983) .

The Wadden Sea is increasingly impacted by human influences (Wolff et al. 2010, Kabat et al. 2012). Land reclamation and the building of dykes lead to a loss of habitat (Wolff et al. 2010). Dredging and extraction of sand and shells to deepen shipping lanes or for land recreation is a severe perturbation of the benthic community (Smardon 2009, Wolff et al. 2010). The large rivers are permanent sources of pollution and nutrients which might cause eutrophication (Smardon 2009, Wolff et al. 2010). Fisheries for fish, shrimp and shellfish affects the populations of the fished species (Smardon 2009, Wolff et al. 2010) and the human-induced introduction of alien species alters the species composition in the Wadden Sea (Kabat et al. 2012). But also the changing climatic conditions influence the ecosystem continuously (Kabat et al. 2012).

However, the major force which forms the Wadden Sea is still the tidal change (Lozán et al. 1994). The area has a total size of about 9,300 km^2 including islands, salt marshes, intertidal flats and tidal inlets (Lozán et al. 1994). About half of the area is exposed twice per day during low tide resulting in a large extent of intertidal flats, which characterize this unique ecosystem. The intertidal flats cover about 4,700 km². It is the largest coherent intertidal area worldwide and therefore one of the most valuable stretches of coastline (Reise et al. 2010, Wolff et al. 2010, Kabat et al. 2012). The extended intertidal flats have remained the most outstanding natural feature of the Wadden Sea (Wolff et al. 2010) and since 2014 the whole area has been proclaimed as a UNESCO World Heritage Site.

Fig. 1: Satellite picture of the Wadden Sea, source: http://www.waddensea-secretariat.org

1.2. Habitat diversity

At first sight, the vast intertidal flats appear to be bare, empty sediments, but the areas are highly productive (Beukema 1976, Asmus and Asmus 1985). Microalgae such as diatoms form thick layers on the sediment surface (Asmus and Bauerfeind 1994) and a rich benthic fauna inhabits the tidal flats supporting millions of coastal birds during their breeding period on their migration along the East Atlantic Flyway (Blew et al. 2015, Koffijberg et al. 2015). Interactions of physical forces turn the extensive intertidal flats into heterogeneous habitats, either characterized by differences in their sediment types or by their dominant species aggregation.

Sandy sediments cover most of the intertidal area (Lozán et al. 1994), often characterized by high abundances of *Arenicola marina* which is constantly reworking the sediment (Volkenborn et al. 2007, Fig. 2 A). Muddy sediments only occur close to the shore where weak hydrodynamics allow the deposition of fine material (Lozán et al. 1994, Fig. 2 B). In sheltered areas, the sediment is often overgrown by dense seagrass meadows consisting of the two species *Zostera noltei* and *Zostera marina* (Fig. 2 C). In contrast to the worldwide trend, there is an expansion of seagrass meadows in the Wadden Sea since the 1990s (Dolch et al. 2013). Seagrass meadows are important shallow water habitats providing shelter and nursery ground for a diversity of species (Dolch et al. 2013). In some parts of the intertidal area, specific bivalve species accumulate and dominate the species composition. Mussel banks, dominated by *Mytilus edulis* and the introduced species *Crassostrea gigas*, form solid epibenthic structures providing a habitat for species depending on a hard substrate to settle (Fig. 2 D). On the other hand, cockle fields and razor clam fields are infaunal habitats, dominated by the common intertidal species *Cerastoderma edule* (Fig. 2 E) and the alien species *Ensis directus* (Fig. 2 F), respectively.

The heterogeneity of habitats is an important requirement for different macrobenthic species to settle as well as for higher predators such as birds that might be specialized to forage in a certain environment.

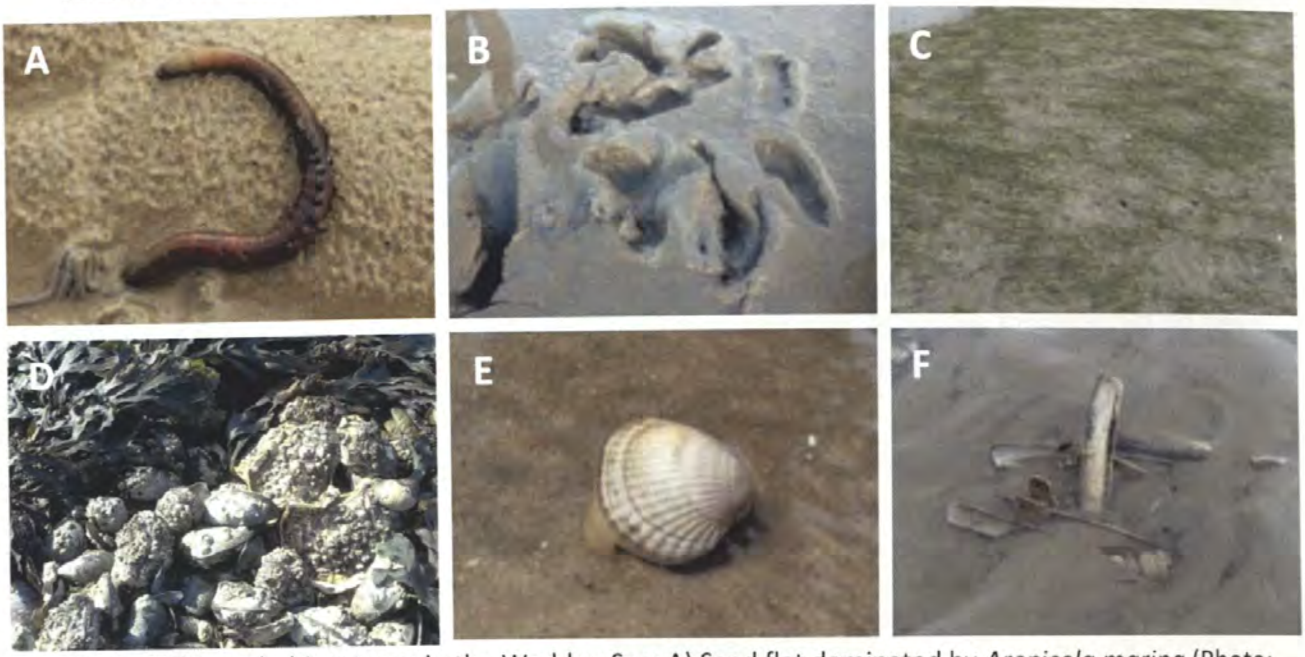


Fig. 2: Different habitat types in the Wadden Sea; A) Sand flat dominated by *Arenicola marina* (Photo: Mike Kuschereitz), B) Mud flat (photo: Sabine Horn), C) Seagrass meadow (photo: Sabine Horn), D) Mussel bank characterized by *Mytilus edulis* and *Crassostrea gigas* (photo: Sabine Horn), E) Cockle field dominated by *Cerastoderma edule* (photo: Mike Kuschereitz), F) Razor clam field characterized by *Ensis directus* (photo: Sabine Horn)

2. Birds in the Wadden Sea

The huge flocks of birds (Fig. 3) are one of the most prominent characteristics of the Wadden Sea (Wolff 1983). Considerable parts or even the total population of 50 different species of waders, gulls, ducks and geese depend on the Wadden Sea which is one of the most important breeding and migration sites (Wolff 1983, Kabat et al. 2012, Koffijberg et al. 2013, Blew et al. 2015, Koffijberg et al. 2015). About 10 to 12 million birds per year use this area to moult, breed and rear their chicks and to rest and refuel their fat reserves during their migration along the East Atlantic Flyway (Wolff et al. 2010, Koffijberg et al. 2015) (Fig. 4). Some of the bird species use the intertidal seagrass meadows and green algae mats as a major food source (e.g. An*as penelope, Branta bernicla).* But most of the

Fig. 3: Flocks of birds feeding in the Wadden Sea (photo: Peter Antkowiak

birds such as waders and gulls are strongly dependent on the benthic fauna inhabiting the tidal flats Birds can take up 25 to 45% of the standing stock of their prey items (Goss-Custard 1980) and are therefore one of the most important predators in the Wadden Sea. The distribution of birds on the tidal flats depnds on the food density and the distance between feeding and roosting area with a preference for high densities and short distances (Wolff 1983).

Furthermore, birds are good bio-indicators to assess the status of an ecosystem (Markert et al. 2003). Birds occupy various positions in the food web especially in higher trophic levels. Chemical pollution or other contaminations in various compartments of the ecosystem would therefore be revealed in the health status of the bird population. In addition, birds have a long life-span and changes in the bird population generally reflect the status of the ecosystem over time (Markert et al. 2003).

Fig. 4: Schematic illustration of the East Atlantic Flyway, the Wadden Sea (red dot) is like the neck of a funnel for birds coming from breeding grounds in North America and Eurasia and travelling down to Africa, source: van de Kam (2004)

In the Wadden Sea, birds are therefore highly protected under several comprehensive regulations and conventions (e.g. EU Bird Directive, Bonn Convention and the Bern Convention, Mendel 2008). Most of these management plans are based on species abundance data which is determined in several counting programs such as ship-based and aerial transect counts, flock surveys and the waterfowl census (Mendel 2008, Markones and Garthe 2011, Blew et al. 2015, Koffijberg et al. 2015).

In the last decades there was a strong decline in a variety of coastal bird species (van Roomen et al. 2012, Blew et al. 2015, Koffijberg et al. 2015, Fig. 5). Reasons for these population decreases are diverse and probably interconnected with each other. Climate change is presumably one of the main drivers inducing sea-level rise and an increase in flooding events. Bird species which breed close to the shoreline or on beaches may suffer from a decrease in reproduction success because nests are regularly flooded and destroyed (van de Pol 2010, Wolff et al. 2010). But also increased mammalian predation threatens the breeding populations (Wolff et al. 2010). In shellfish-feeding species a reduced food supply might play an important role as well (Kabat et al. 2012, Koffijberg et al. 2015).

In addition to the population changes, there are also changes in the migration pattern of the birds. Some species (e.g. geese, ducks) arrive earlier in spring from their winter areas and leave the

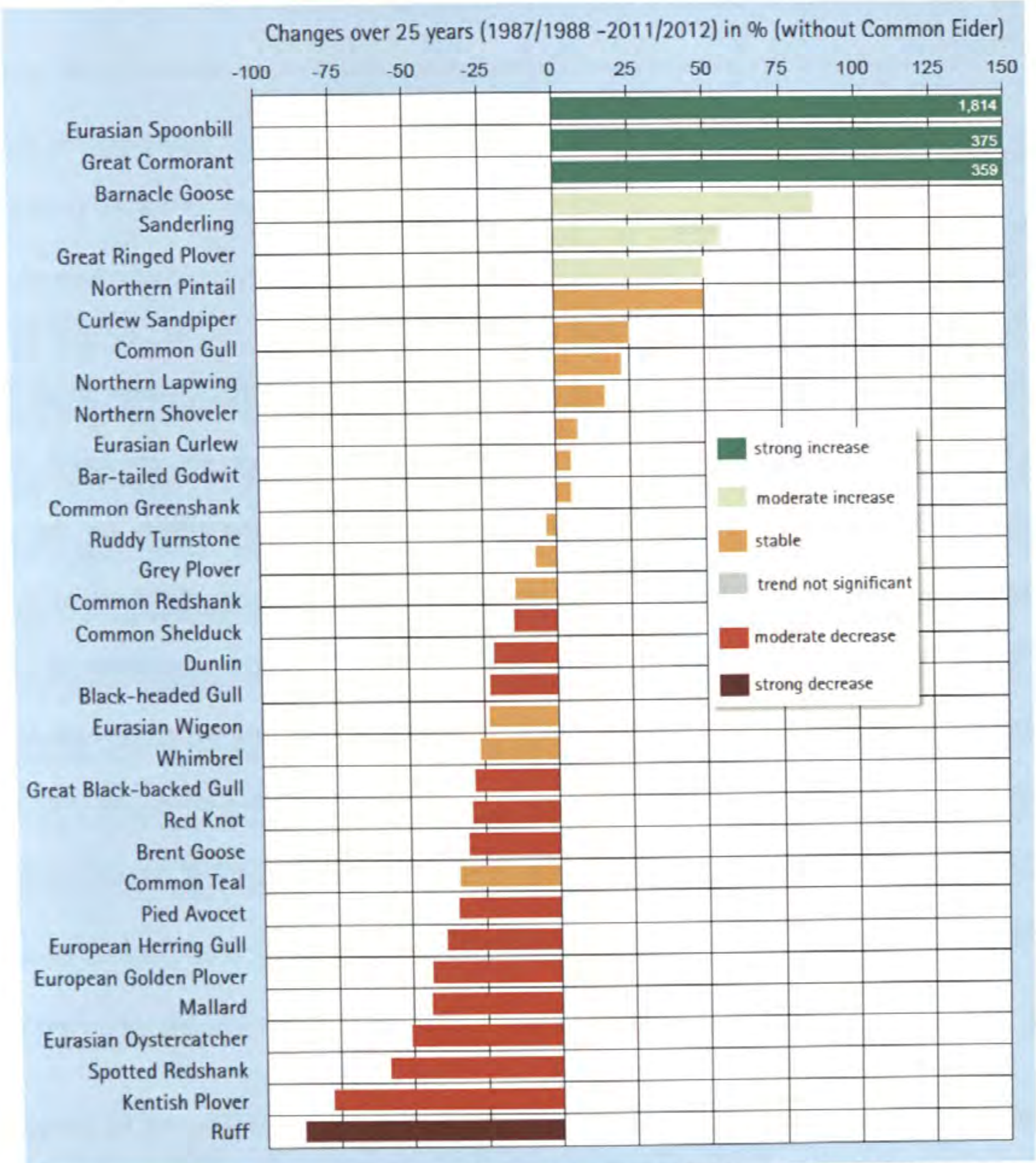


Fig. 5: Long-term and short-term population trends for coastal birds in the Wadden Sea, source: Blew et al. (2015)

Wadden Sea later than before (Wolff et al. 2010) which might cause an increased predation pressure on the intertidal benthic community. Other species tend to leave the Wadden Sea earlier to their Arctic breeding sites due to earlier snow melting (Piersma and Rakhimberdiev, Wadden Sea Day 2016). These species need to take up the same amount of food in a shorter time to refuel their fat reserves. Although birds are one of the most important predators in the tidal flats, little is known about their influence on the intertidal communities. Therefore, it is difficult to assess the impact of population and migration changes of birds on the Wadden Sea ecosystem.

3. Management strategies

3.1. Impacts on the Wadden Sea

The Wadden Sea is exposed to a variety of natural and anthropogenic changes and disturbances which may alter the ecosystem temporally or permanently (Wolff et al. 2010, Doney 2012). Storm events or severe winters with ice shredding on the intertidal surface are consistent natural disturbances which may cause local damages but have no long-lasting effects on the whole ecosystem. On the other hand, there is a diversity of anthropogenic impacts which are permanent stressors for the Wadden Sea ecosystem (e.g. land reclamation, pollution, extraction of oil and fisheries for fish, shellfish and shrimps, Wolff et al. 2010). But also climate driven changes such as sea-level rise and ocean acidification are severe threats for the coastal ecosystem and may induce irreversible damages in the system structure and functioning. Management of coastal habitats is therefore confronted with a variety of very serious challenges (Levin 2009).

3.2. Ecosystem-based management

In order to protect the unique ecological status as a World Heritage Site and its outstanding importance for birds, the Wadden Sea is subjected to extensive protection and management arrangements on national and international (i.e. Framework of Trilateral Wadden Sea Cooperation) levels (Wolff et al. 2010). The main objective of these conservation strategies is to attain a natural and sustainable ecosystem in which natural processes proceed undisturbed (Wolff et al. 2010). Therefore, a comprehensive list of environmental legislation was developed to protect the tidal area with its morphological dynamics and its species composition which supports the huge flocks of coastal birds (Wolff et al. 2010). The most relevant ordinances are the Habitats, Birds and Water Framework Directives which should deal as guidelines to achieve a good ecological status (Meeresumwelt 2012). The characteristics of an ecosystem which is in a good status can be summarized in six different points: the system achieved a homeostasis; the system is free of diseases; there is a high level of diversity and complexity; the ecosystem is resilient and stable in front of perturbations; there is a scope for growth and there is a balance between the system components (Jørgensen et al. 2010).

Large-scale comprehensive ecosystem-based management is therefore crucial to develop and apply ecological indicators which describe the current status of coastal ecosystems in order to assess effective marine conservation and protection strategies (Levin 2009, Jørgensen et al. 2010). In this context, an understanding of the whole functioning of the ecosystem is needed to identify reliable indicators (Levin 2009, Samhouri 2009). Scientific investigations on ecosystem-level are therefore strongly recommended because questions about the ecosystem status cannot be answered by studying single species or populations. An ecosystem is more than just the sum of components (Mann et al. 1989). In contrast to single species or population studies, research on ecosystem-level takes into account all components of system and all their direct and indirect interactions (Pockberger and Asmus 2014). One of the few tools which can allow holistic approaches on ecosystem-scale is the modelling of food web structures which could give insight in the complex interaction within ecosystems and their reaction to stressors and disturbances.

4. Ecological Network Analysis

4.1. The theory of Ecological Network Analysis

Ecological Network Analysis (ENA) can be used to create a holistic representation of the intertidal food web. It provides tools allowing to understand the functioning of the whole ecosystem (Wulff et al. 1989). The methodology is based on economic input-output theory developed by Leontief (1951). Hannon (1973) was the first who applied the principle to ecological systems. The concept of ENA is in detail described in Kay et al. (1989) and Ulanowicz (2004).

The currency of natural systems is energy (Fath 2007). Therefore, ENA pays more attention to energy processes in a system than to single objects such as species (Ulanowicz 2004). The diverse interactions between the species in a particular environment are described as flows of energy between different feeding levels resulting in a simplified representation of the natural system (Heymans et al. 2014, Fig. 6). ENA accounts for the totality of relationship between the systems' various components (Leguerrier et al. 2003) and results in a full picture of all direct and indirect effects in a system based on the systematic application of linear algebra (Ulanowicz 2004).

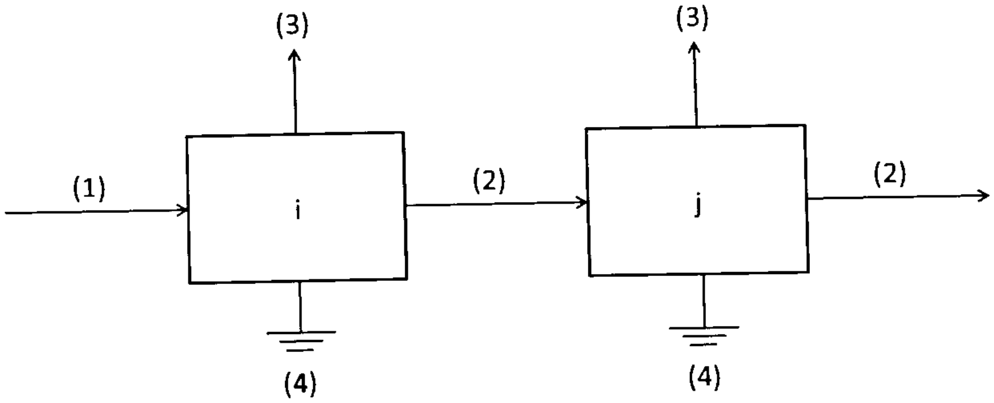


Fig. 6: Four possible classes of energetic flows within a system between prey compartment i and consumer compartment j: (1) exogenous inputs (e.g. solar radiation), (2) intercompartmental exchanges, (3) exports of organic material (e.g. egestion), (4) energy dissipation (e.g. respiration)

In ENA, each component of the network is represented as a compartment which can be a species, a group of species or a functional group (Fath 2007). Information about the biomass stock and the physiological parameters is required for the different compartments (i.e. for autotrophs: gross primary production, respiration and net primary production; for heterotrophs: production, respiration, egestion and consumption, Fath 2007) . Each compartment is then characterized by a production value, energy losses due to respiration and egestion, and energy input based on gross primary production or consumption. The consumption fluxes connect the compartments with each other by quantifying how much energy of prey compartment i enters the consumer compartment j. Therefore, the diet composition of each compartment is needed providing information about who eats whom and by how much (Fath 2007).

ENA is therefore a data intensive technique which is capable to analyze the complex interactions within an ecosystem including all direct and indirect relationships.

4.2. ENA output

Results of ENA are diverse and can be a powerful tool to assess the ecosystems' current status (Saint-Béat 2015). A mature and stable system is assumed to increase in its properties of organization, cycling and in its complexity (Saint-Béat 2015). On the other hand, a system should also maintain reserves of free energy (i.e. overhead) to react to perturbations. A balanced system which is stable in front of perturbations and at the same time efficient in using its energy sources therefore requires both, an adequate amount of organization and overhead of free energy to cope with disturbances (Ulanowicz 2004, Fath 2015, Saint-Béat 2015). Ecological Network Analysis uses a set of algorithms from which several system properties can be derived. These properties are the system attributes which describe the system in terms of its size and activity, developmental status, flow structure (e.g. diversity of flows, number of parallel pathways), cycling properties and trophic organization (Wulff et al. 1989). The attributes can be used to determine environmental issues but also to describe the system's status in terms of maturity, health, stability and stress (Scharler and Baird 2005a, Schückel et al. 2015).

In a complex food web network each component influences each other directly or indirectly. For example, an oystercatcher feeding on cockles is directly dependent on the cockle compartment. However, because the cockles filter phytoplankton the oystercatcher also depends on phytoplankton due to an indirect connection. These hidden relationships are often difficult to assess but ENA provides comprehensive dependency matrices with quantitative information about all connections – direct and indirect ones – in the network. Such calculations allow an estimation of how a change in one compartment of the system affects the other compartments.

Results from ENA are therefore of great importance for ecosystem-based management as they can provide information about the current ecological status of whole ecosystems. It might therefore be possible to include ENA indices as health indicators in the Water Framework Directives to assess the state of marine ecosystems (Saint-Béat 2015).

5. Focus of the thesis

5.1. Study site

The present study is located in the German part of the Wadden Sea at the western coast of the federal state of Schleswig-Holstein between the islands Amrum, Föhr and Langeness (Fig. 7). The area has a total size of 655.4 km² with 286.3 km² of intertidal flats. The tidal range is on average 3.0 m. Mean temperature varies from 16 °C in summer to 5.9 °C in winter. The salinity ranges from 30.1 in summer to 28.5 in winter.

Two large tidal inlets enter the study site, the Norderaue in the north between the islands Föhr and Langeness and the Süderaue in the south of Langeness. Both inlets have a permanent water exchange with the open North Sea.

The intertidal area of the study site is characterized by six different habitat types (Fig. 2, Fig. 7). Most of the area is covered by sand flats (62.7%) followed by seagrass meadows (13.0%). 12.3% of the site consists of razor clam fields. Mud flats cover 9.3% of the study site and only small areas are represented by cockle fields (2.4%) and mussel banks (0.2%).

The studied area is of great importance for a variety of coastal bird species which use the islands as roosting and breeding sites and the intertidal flats for foraging (Koffijberg et al. 2013).

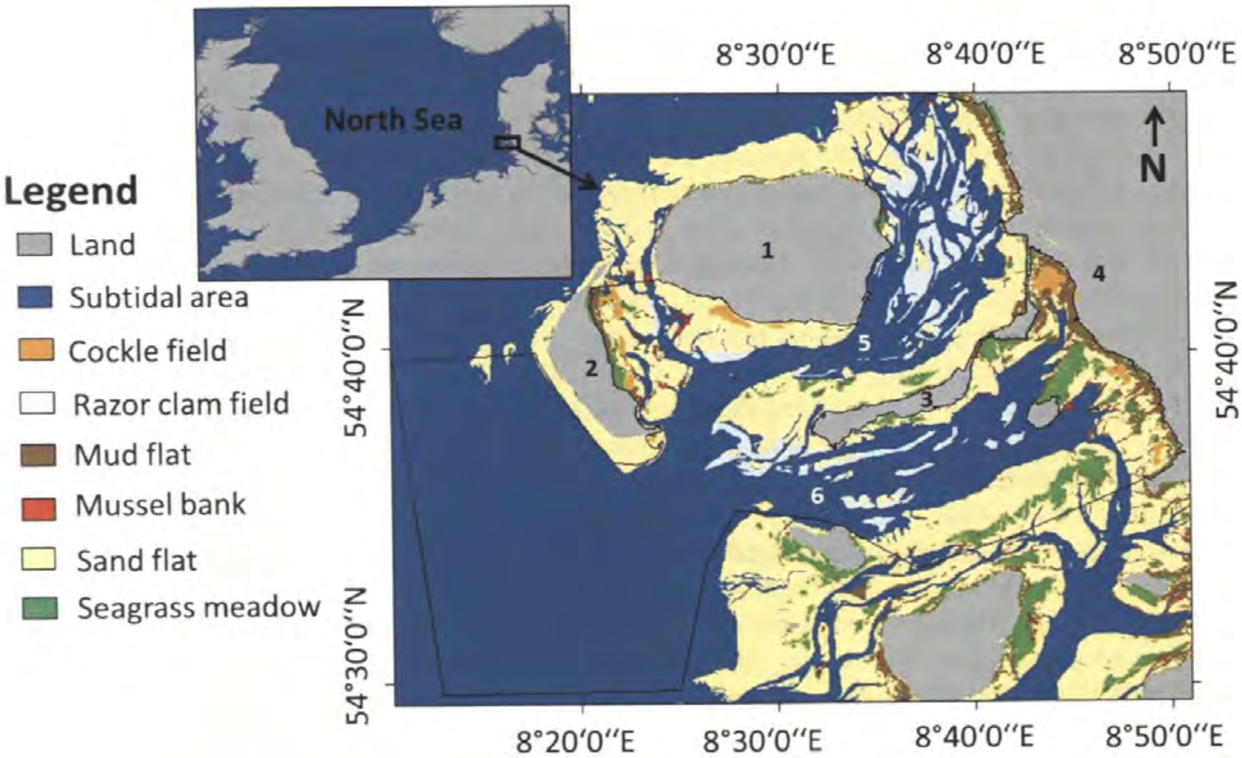


Fig. 7: Location and habitat distribution of the study site; the black frame delimits the border of the studied area; 1) Föhr, 2) Amrum, 3) Langeness, 4) Mainland coast, 5) Norderaue, 6) Süderaue; map changed after Brockmann Consult GmbH © 2014 (picture processing) and Landsat-8 USGS © 2014 (original data)

5.2. Objectives

The present thesis focuses on the influence of birds on six intertidal habitats of the Wadden Sea. Birds were included in food web models to assess the impact of avian predation pressure on the ecosystem. This study is one of the first of its kind as birds are rarely included in food web studies because they are highly mobile and difficult to incorporate in quantitative analysis. The thesis is divided in four chapters dealing with distinct objectives:

Chapter 1: The first chapter focuses on the characterization of the six selected habitats of the Wadden Sea (i.e. cockle field, razor clam field, mud flat, mussel bank, sand flat and seagrass meadow). These habitats were represented by their species composition, abundance and biomass of benthic flora and fauna. In addition, foraging birds were counted in each of the habitats.

Chapter 2: Missing relationships between different biomass units (e.g. relationship between fresh weight and carbon content) were determined in the second chapter for several species of birds from the Wadden Sea. Indeed, bird data is usually assessed in abundance while ecological networks use standardized biomass units (e.g. carbon) to describe the flows of energy in the system.

Chapter 3: The intertidal area of the Wadden Sea is a heterogeneous mosaic of different habitats each functioning in a distinct way and with a different importance for foraging birds. In chapter 3 food web models of six intertidal habitats were created using Ecological Network Analysis. Similarities and differences in the systems' functioning were determined to assess characteristic features of the habitats.

Chapter 4: Birds exert intense predation pressure on intertidal organisms during their breeding and migration periods. However, it is widely unknown how birds and the ecosystem they live in influence each other. An Ecological Network Analysis for the entire study site was conducted in order to assess the current state of the studied ecosystem and to get insight in the impact of birds in the intertidal food web.

6. References

Asmus, H., and R. Asmus. 1985. The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. HELGOLANDER MEERESUNTERSUCHUNGEN **39**:273-301.

Asmus, R., M., , and E. Bauerfeind. 1994. The microphytobenthos of Königshafen - spatial and seasonal distribution on a sandy tidal flat. HELGOLANDER MEERESUNTERSUCHUNGEN **48**:257-276.

Beukema, J., J. 1976. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. Netherlands Journal of Sea Research **10**:236-261.

Blew, J., K. Günther, B. Hälterlein, R. Kleefstra, K. Laursen, and G. Scheiffarth. 2015. Trends of Migratory and Wintering Waterbirds in the Wadden Sea 1987/1988-2011/2012.

Dolch, T., C. Buschbaum, and K. Reise. 2013. Persisting intertidal seagrass beds in the northern Wadden Sea since the 1930s. Journal of Sea Research.

Doney, S., Ruckelshaus, M, Duffy, JE, Barry, JP, Chan, F, English, CA, Galindo, HM, Grebmeier, JM, Hollowed, AB, Knowlton, N, Polovina, J, Rabalais, NN, Sydeman, WJ, Talley, LD. 2012. Climate Change Impacts on Marine Ecosystems. Annual Reviews **4**:11-37.

Fath, B., D., Scharler, U., M., Ulanowicz, R., E., Hannon, B. 2007. Ecological network analysis: network construction. Ecological Modelling **208**:49-55.

Fath, B. D. 2015. Quantifying economic and ecological sustainability. Ocean & Coastal Management **108**:13-19.

Gätje, C., and K. Reise. 1998. Ökosystem Wattenmeer: Austausch-, Transport-und Stoffumwandlungsprozesse. Springer, Berlin.

Goss-Custard, J. 1980. Competition for food and interference among waders. Ardea **68**:31-52.

Hannon, B. 1973. The structure of ecosystems. Journal of theoretical biology **41**:535-546.

Heymans, J. J., M. Coll, S. Libralato, L. Morissette, and V. Christensen. 2014. Global patterns in ecological indicators of marine food webs: a modelling approach. Plos One **9**:e95845.

Jørgensen, S. E., L. Xu, and R. Costanza. 2010. Handbook of ecological indicators for assessment of ecosystem health. CRC press.

Kabat, P., J. Bazelmans, J. van Dijk, P. M. Herman, T. van Oijen, M. Pejrup, K. Reise, H. Speelman, and W. J. Wolff. 2012. The Wadden Sea Region: Towards a science for sustainable development. Ocean & Coastal Management **68**:4-17.

Kay, J. J., L. A. Graham, and R. E. Ulanowicz. 1989. A detailed guide to network analysis. Pages 15-61 Network Analysis in Marine Ecology. Springer.

Koffijberg, K., K. Laursen, B. Hälterlein, G. Reichert, and J. Frikke. 2013. Trends of Breeding Birds in the Wadden Sea 1991-2009.

Koffijberg, K., K. Laursen, B. Hälterlein, G. Reichert, J. Frikke, and L. Soldat. 2015. Trends of Breeding Birds in the Wadden Sea 1991-2013. Wadden Sea Ecosystem.

Leguerrier, D., N. Niquil, N. Boileau, J. Rzeznik, P.-G. Sauriau, O. Le Moine, and C. Bacher. 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. Marine Ecology Progress Series **246**:17-37.

Leontief, W. W. 1951. Input-output economics. Sci Am **185**:15-21.

Levin, P., Fogarty, MJ, Murawski, SA, Fluharty, D. 2009. Integrated Ecosystem Assessments: Developing the Scientific Basis for Ecosystem-Based Management of the Ocean. PLoS Biology **7**:23-28.

Lozán, J. L., E. Rachor, K. Reise, H. Von Westernhagen, and W. Lenz. 1994. Warnsignale aus dem Wattenmeer: wissenschaftliche Fakten. Blackwell Wissenschafts-Verlag.

Mann, K. H., J. G. Field, and F. Wulff. 1989. Network analysis in marine ecology: an assessment. Springer.

Markert, B., A. Breure, and H. Zechmeister. 2003. Biomonitoring with birds. Bioindicators & Biomonitors:677.

Markones, N., and P. D. S. Garthe. 2011. Marine Säugetiere und Seevögel in der deut-schen AWZ von Nord-und Ostsee-Teilbericht Seevögel.

Meeresumwelt, G. d. 2012. Umsetzung der Meeresstrategie-Rahmenrichtlinie. Bund- Länder Messprogramm.

Mendel, B. 2008. Profiles of seabirds and waterbirds of the German North and Baltic Seas: distribution, ecology and sensitivities to human activities within the marine environment. Bundesamt f. Naturschutz.

Pockberger, M., and H. Asmus. 2014. Empfehlungen zur Anwendung von Ökosystemanalysen zur Beurteilung des Nahrungsnetzes im Wattenmeer in der Meeresstrategie Rahmenrichtlinie.

Reise, K., M. Baptist, P. Burbridge, N. Dankers, L. Fischer, B. Flemming, A. Oost, and C. Smit. 2010. The Wadden Sea-a universally outstanding tidal wetland. The Wadden Sea 2010. Common Wadden Sea Secretariat (CWSS); Trilateral Monitoring and Assessment Group: Wilhelmshaven.(Wadden Sea Ecosystem; 29/editors, Harald Marencic and Jaap de Vlas) **7**.

Saint-Béat, B., Baird, D., Asmus, H., Asmus, R., Bacherd, C., Pacellaa, S., R., Johnsona,G., A., Davida, V., Vézinaf, A., F., Niquila, N. 2015. Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review. Ecological indicators **52**:458-471.

Samhouri, J., F., Levin, P., S., Harvey, C., J. 2009. Quantitative Evaluation of Marine Ecosystem Indicator Performance Using Food Web Models. Ecosystems **12**:1283-1298.

Scharler, U. M., and D. Baird. 2005. A comparison of selected ecosystem attributes of three South African estuaries with different freshwater inflow regimes, using network analysis. Journal of Marine Systems **56**:283-308.

Schückel, U., I. Kröncke, and D. Baird. 2015. Linking long-term changes in trophic structure and function of an intertidal macrobenthic system to eutrophication and climate change using ecological network analysis. Mar Ecol Prog Ser **536**:25-38.

Smardon, R. 2009. The Wadden Sea Wetlands: A Multi-jurisdictional Challenge. Pages 21-56 Sustaining the World's Wetlands. Springer.

Ulanowicz, R. E. 2004. Quantitative methods for ecological network analysis. Computational Biology and Chemistry **28**:321-339.

van de Kam, J. 2004. Shorebirds: an illustrated behavioural ecology. KNNV.

van de Pol, M., Ens, B., J., Heg, D., Brouwer, L., Krol, J., Maier, M., Exo, K., Oosterbeek, K., Lok, T.,Eising, C., M., Koffijberg, K. 2010. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? Journal of Applied Ecology **47**:720-730.

van Roomen, M., K. Laursen, C. van Turnhout, E. van Winden, J. Blew, K. Eskildsen, K. Günther, B. Hälterlein, R. Kleefstra, and P. Potel. 2012. Signals from the Wadden sea: Population declines dominate among waterbirds depending on intertidal mudflats. Ocean & Coastal Management **68**:79-88.

Volkenborn, N., S. Hedtkamp, J. Van Beusekom, and K. Reise. 2007. Effects of bioturbation and bioirrigation by lugworms (Arenicola marina) on physical and chemical sediment properties and implications for intertidal habitat succession. Estuarine, Coastal and Shelf Science **74**:331-343.

Wolff, W. 1983. Ecology of the Wadden Sea. v. 2: Fishes and fisheries, birds, marine mammals, pollution.

Wolff, W. J., J. P. Bakker, K. Laursen, and K. Reise. 2010. The Wadden Sea Quality Status Report-Synthesis Report 2010. The Wadden Sea 2010. Common Wadden Sea Secretariat (CWSS); Trilateral Monitoring and Assessment Group: Wilhelmshaven.(Wadden Sea Ecosystem; 29/editors, Harald Marencic and Jaap de Vlas) **25**.

Wulff, F., J. G. Field, and K. H. Mann. 1989. Network analysis in marine ecology: methods and applications. Springer Science & Business Media.

Chapter 1

Photo flying geese: Robert Waleczek

The diversity of benthos and birds in intertidal habitats

Horn, S[1]

Affiliation

[1] Alfred-Wegener-Institute Helmholtz Centre for Polar- and Marine Research, Wadden Sea Station Sylt Hafenstr. 43, D-25992 List/ Sylt, Germany

Corresponding author: sabine.horn@awi.de

Keywords: species composition, shorebirds, mussel bank, biodiversity, seasonal variation

Abstract:

In the Wadden Sea, benthic species are highly productive and represent an important link between the marine microflora and -fauna and higher trophic levels such as birds. In this study, six intertidal habitats (i.e. cockle field, razor clam field, mud flat, mussel bank, sand flat and seagrass meadow) directly influenced by the open North Sea were studied in terms of their benthic species-composition and their diversity of foraging birds.

Chlorophyll a content of microphytobenthos and biomass of benthic species showed seasonal variations with peaks in summer and autumn, respectively.

The species composition differed between the habitats. The cockle field, the razor clam field and the mussel bank were dominated by bivalve species (i.e. *Cerastoderma edule, Ensis directus, Mytilus edulis*, respectively) whereas the mud flat, the sand flat and the seagrass meadow showed a dominance of gastropods mainly caused by *Peringia ulvae*.

The highest abundances of birds were found on the sand flat and the seagrass meadow but the species composition of foraging birds differed between the habitats.

1. Introduction

The Wadden Sea, which is entirely a World Heritage Site since 2014, is a highly productive intertidal area and of outstanding importance for millions of breeding and migrating coastal birds (Asmus and Asmus 1985, Wolff et al. 2010, Koffijberg et al. 2015). Benthic species accumulate unevenly in specific areas in the intertidal area and form a heterogeneous mosaic of different habitats which are used in variable intensities by foraging birds. The benthos is therefore an important link between the marine microflora and – fauna and higher trophic levels (Wolff et al. 2010). Thus, studies about the benthos composition are a necessary requirement to understand the structure and functioning of the intertidal ecosystem.

However, in the German part of the Wadden Sea, only two benthic datasets with detailed information about species abundance and biomass in different intertidal habitats are available, the first one is from the Sylt-Rømø Bight in the northern Wadden Sea (Baird et al. 2004, Baird et al. 2007, 2012) and the second one is from the Jade Bay in the southern Wadden Sea (Schückel et al. 2015). Both the Sylt-Rømø Bight and the Jade Bay are enclosed basins with a small connection to the open North Sea. No recent data is available for the intertidal area more influenced by the North Sea, although such areas represent large parts of the Wadden Sea.

The present study therefore aims 1) to create a basic data set for benthos in an intertidal area directly influenced by the open North Sea and 2) to determine the diversity of birds feeding in different intertidal habitat types.

2. Material and Methods

2.1. Study site

The study site was located in the north-eastern German Wadden Sea at the western coast of the federal state of Schleswig-Holstein between the islands Amrum, Föhr and Langeness (Fig 1).

In total, the study site covered 655.4 km², with 286.3 km² of intertidal area with an average tidal range of 3 m. The mean water temperature varies from 16.0 °C in summer to 5.9 °C in winter. Mean salinity is 30.1 in summer and 28.5 in winter.

Six different intertidal habitats have been identified in this heterogeneous area, either characterized by a certain sediment type (i.e. mud flat, sand flat) or by a dominating species (i.e. cockle field, razor clam field, mussel bank, seagrass meadow). The sand flats cover most of the intertidal area (62.7%), followed by sea grass meadows (13.0%), which overgrow the bare sediment in some areas. Razor clam fields and soft bottom mud flats cover 12.3% and 9.3% of the area, respectively. Smaller parts of the area are characterized by cockle fields (2.4%) mussel banks (0.2%).

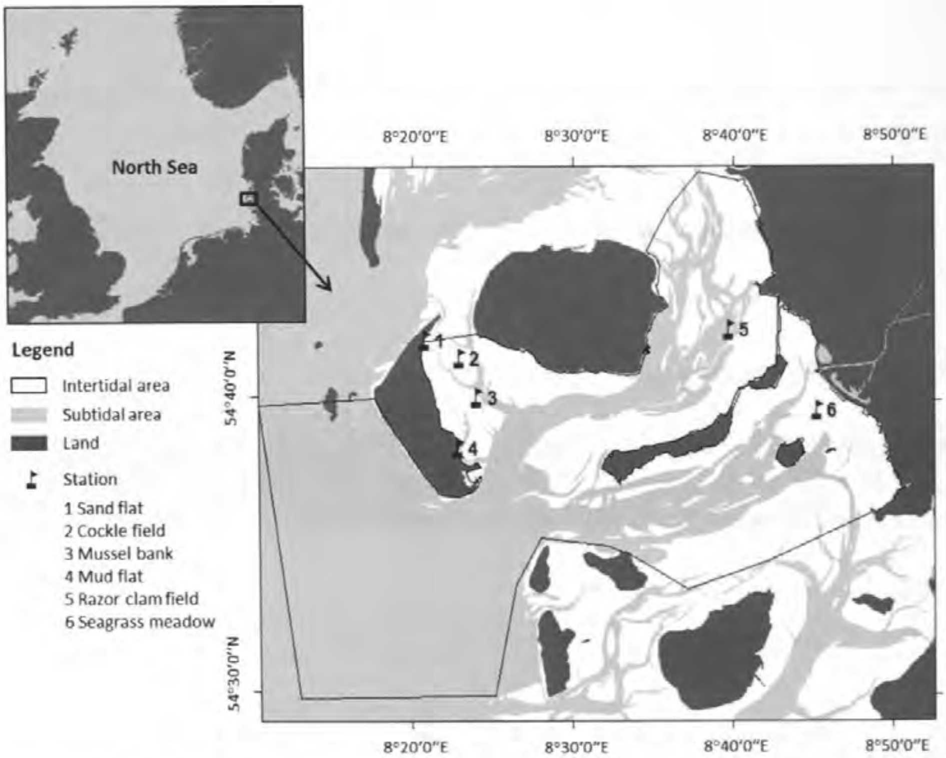


Fig. 1: Location of the study site. The black frame delimits the studied area. Sampling locations in the different habitat types are represented with black flags, map source: Topographic GIS map 2003, issued by National Park Authority, Tönning

2.2. Sampling

Samples were taken seasonally (Spring: March to May, Summer: June to August, Autumn: September to November, Winter: December to February) between summer 2013 and summer 2015 in each of the six habitat types (i.e. cockle field, razor clam field, mud flat, mussel bank, sand flat, seagrass meadow). In each habitat, five to six stations, in 50 m distance from each other, were sampled, following a transect of 200 to 250 m length. To allow quantitative sampling, microphytobenthos, macrophytes and macrobenthos (i.e. epifauna and infauna) were sampled at each station in a 25x25 cm quadrat.

For microphytobenthos (MPB), the first centimeter of the sediment surface was outpaced with a corer (ø 1 cm). The sediment was then freeze-dried and the Chlorophyll a (Chl a) content was measured and calculated (Lorenzen 1967, Edler 1979).

Samples for epifauna and macrophytes were taken by hand within the quadrat. A subsample for infauna was taken with a 10x10 cm corer in 15 cm depth which was sieved through a 0.5 and 1 mm mesh-cascade. Organisms were sorted out of the sample, identified to the most precise taxonomic level and counted.

Biomass was determined for each species of macrofauna and macrophytes. The samples were dried in an oven at 50 °C until constant dry weight and then burned in a furnace at 500 °C for 5 h. Ash free dry weight (AFDW) was calculated by subtracting the ash weight from the dry weight.

In each of the sampled habitats foraging birds were counted seasonally in a predefined area of 0.01 km^2 (cockle field) to 0.16 km^2 (mussel bank) overlapping with the benthos transect. The counts occurred in 10 min intervals for 2 h using a telescope. The birds were identified to species level. Only foraging individuals were taken into account.

2.3. Data analysis

Data was analyzed using the software Primer v6.1 (Plymouth Marine Laboratory). The biodiversity within each habitat was determined using the Shannon-Index (H', 1.1) which takes into account the number of different species (S) and the total number of individuals (N). Additionally, Pielou's evenness (J', 1.2) was calculated to describe the balance between the abundances of the occurring species.

$$H' = -\sum_i p_i * ln(p_i) \quad (1.1)$$

$$J' = \frac{H'}{log(S)} \quad (1.2)$$

With p_i describing the contribution of species i to the total number of individuals N, and S as the number of species in the habitat.

3. Results and discussion

3.1. Primary producers

3.1.1. Microphytobenthos

MPB and macrophytes were the two primary producers present in the samples.

Mean values for microphytobenthos (MPB) were the highest in the mud flat (20.2 mgChl a.m^{-2}) followed by the cockle field (11.1 mgChl a.m^{-2}) and the mussel bank (9.61 mgChl a.m^{-2}). Intermediate values were found in the razor clam field (6.5 mgChl a.m^{-2}) and the sand flat (5.7 mgChl a.m^{-2}). The lowest amount of MPB was measured in the seagrass meadow with 4.5 mgChl a.m^{-2}.

There was no consistent seasonal trend between the studied habitats (Fig. 2). The clear spring bloom which was found by Asmus and Bauerfeind (1994) and Colijn and Dijkema (1981) was only observed in the mud flat, which had the highest Chlorophyll a values in this season. The cockle field, the sand flat and the seagrass meadow reached their MPB Chl a peaks in summer, and the razor clam field and mussel bank in autumn.

In most of the systems lowest values were found in winter (i.e. cockle field, mussel bank, sand flat and seagrass meadow), except for the razor clam field and the mud flat in which the lowest values were found in spring and autumn, respectively.

The differences in MPB Chl a content, and in its seasonal variation in the six habitats, can be explained by differences in the microphytobenthic species assemblages. Although the MPB species composition was not determined in this study, Asmus and Bauerfeind (1994) observed different MPB species composition in three intertidal habitats in the Sylt-Rømø Bight. In addition, differences in the physical forces, sediment characteristics, temperature and exposure time characterizing the six studied habitats, might also have influenced the Chl a content (Asmus and Bauerfeind 1994).

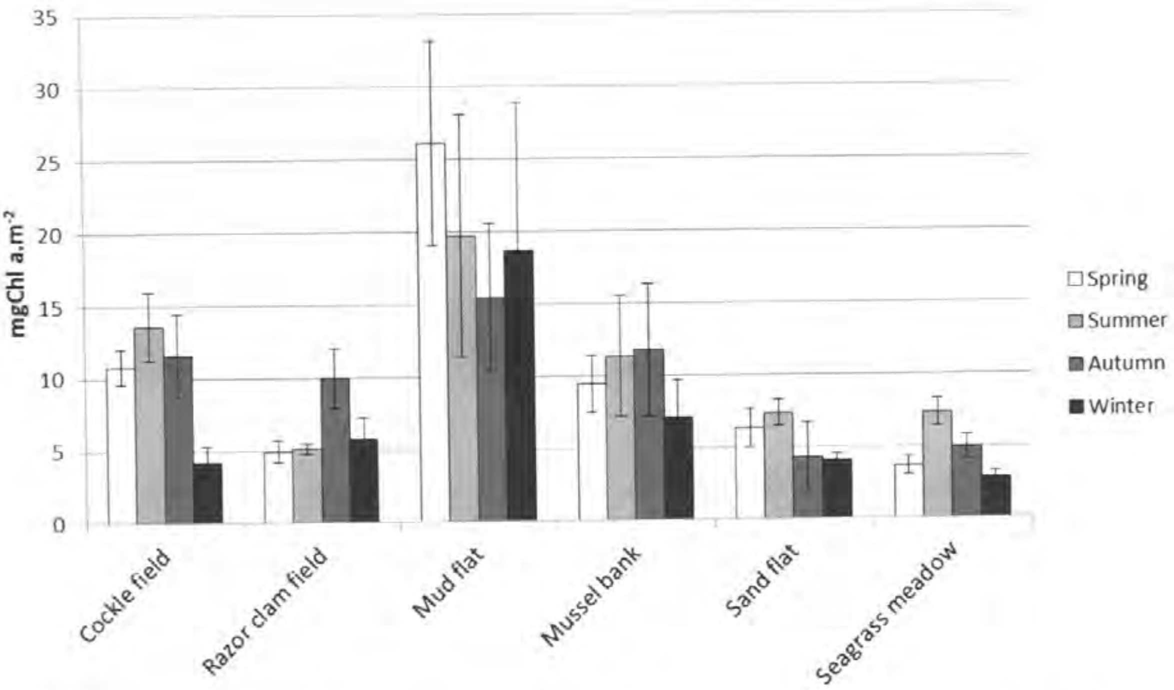


Fig. 2: Seasonal variation of microphytobenthic Chlorophyll a content in the six sampled habitats

3.1.2. Macrophytes

Macrophytes were found in four of the six habitats (i.e. cockle field, mussel bank, sand flat and seagrass meadow). The highest biomass was found on the mussel bank (181,724.5 mgAFDW.m^{-2}) because most parts of the bank were covered by a carpet of *Fucus vesiculosus* which was attached to the hard structure formed by the bivalves.

The seagrass meadow was a macrophyte-dominated habitat with a high biomass of *Zostera noltei* (16,744.9 mgAFDW.m^{-2}).

In the sand flat and the cockle field *Ulva spp.* was randomly distributed on the sediment surface with a mean biomass of 2,319.6 mgAFDW.m^{-2} and 171.5 mgAFDW.m^{-2}, respectively.

3.2. Dominant species of the benthic community

The intertidal area of the Wadden Sea hosts relatively few benthic species in comparison to the subtidal parts (Dekker 1989) due to the high seasonal and spatial variation in abiotic conditions in the ecosystem (Beukema 1976). Therefore, most of the benthic species occurred in all of the six habitats, but varied in abundances and biomass.

3.2.1. Cockle field

The cockle field was mainly dominated by *Cerastoderma edule* (223,191.7 mgAFDW.m^{-2}; Table 1), but also *Macoma balthica* and *Peringia ulvae* were found in a high biomass (11,733.4 mgAFDW.m^{-2} and 19,286.4 mgAFDW.m^{-2}, respectively). The dominant species *C. edule* can be found in the entire intertidal area, but it concentrates in some locations where it can reach densities up to several thousand individuals per square meter (Jensen 1992), which we call cockle fields in this study. These dense accumulations of *C. edule* tend to reduce the abundance of other species, which are not able to cope with the intense bioturbation caused by *C. edule* in the sediment (Flach 1996).

3.2.2. Razor clam field

The razor clam field is characterized by a high concentration of the alien species *Ensis directus* (21,302.8 mgAFDW.m^{-2}; Table 1) which invaded the Wadden Sea in the late 1970s probably transported in ballast water (Tulp et al. 2010). Only few other species in low abundances were found in this habitat, probably due to the location of the razor clam field in the lower part of the intertidal which is characterized by harsh abiotic conditions.

3.2.3. Mud flat

The highest biomass values in the mud flat were found for *Peringia ulvae* (29,738.9 mgAFDW.m^{-2}), followed by *Cerastoderma edule* (27,085.5 mgAFDW.m^{-2}) and *Carcinus maenes* (11,880.0 mgAFDW.m^{-2}, Table 1). *P. ulvae* is a typical grazing species in the intertidal area of the Wadden Sea (Beukema 1976) and probably benefits from the high amount of MPB which was found in the mud flat.

3.2.4. Mussel bank

The mussel bank is formed by aggregations of *Mytilus edulis*. Therefore, *M. edulis* contributes the most to the total biomass with 504,714.1 mgAFDW.m^{-2} (Table 1). Since the introduction of *Crassostrea gigas* in the 1980s in the Wadden Sea by shellfish culture, the mussel banks are overgrown by *C. gigas* which uses the mussels to settle. (Diederich et al. 2005). Nowadays, *C. gigas* is therefore the second characteristic species of the mussel bank, with a relatively high biomass of 73,190.5 mgAFDW.m^{-2}.

3.2.5. Sand flat

P. ulvae and *Arenicola marina* represent the highest biomass in the sand flat (65137.0 mgAFDW.m^{-2} and 11305.0 mgAFDW.m^{-2}, respectively; Table 1). These two species are typical inhabitants of sandy habitats. Indeed, comparable results were already described for sand flats in the Sylt-Rømø Bight in the northern Wadden Sea (Asmus 1982).

3.2.6. Seagrass meadow

Seagrass meadows offer shelter to numerous associated benthic species. Furthermore, several species of benthic fish from the North Sea use this habitat as a nursery ground (Reise and Kohlus 2008). But also a variety of benthic species uses seagrass meadows as shelter and food stock. The biomass of the benthic community of the studied seagrass meadow was dominated by *P. ulvae* and *C. edule* (20,542.1 mgAFDW.m^{-2} and 5,799.0 mgAFDW.m^{-2}, respectively, Table 1).

3.2.7. Seasonal variation of the benthic biomass

There were seasonal fluctuations in the benthic biomass of the studied habitats (Fig. 3). In all the habitats, except razor clam field and mussel bank, the highest values of total biomass were reached in autumn with a strong decline in winter, followed by an increase in spring and summer. These results are in accordance with a seasonal study in the Dutch Wadden Sea in which the highest values of biomass were found in late summer and autumn with a decline in winter (Beukema 1974).

In the razor clam field, the highest biomass was found in winter. However, the tidal conditions during autumn sampling did not allow collecting large individuals of *E. directus*. Therefore, the autumn biomass is probably strongly underestimated in this habitat.

The highest biomass for the mussel bank was revealed in spring with lowest values in autumn. The seasonal variation of the mussel bank biomass was mainly caused by *M. edulis*. The patchy distribution of *M. edulis* accumulations on the mussel bank might have influenced the sampling and therefore the results.

Table 1: Species list with mean values for abundance [Ind. m^{-2}] and biomass in AFDW [mg m^{-2}] for all six habitats

		Cockle field		Razor clam field		Mud flat		Mussel bank		Sand flat		Seagrass meadow	
Taxon	Species	Abundance [Ind. m^{-2}]	AFDW [mg m^{-2}]	Abundance [Ind. m^{-2}]	AFDW [mg m^{-2}]	Abundance [Ind. m^{-2}]	AFDW [mg m^{-2}]	Abundance [Ind. m^{-2}]	AFDW [mg m^{-2}]	Abundance [Ind. m^{-2}]	AFDW [mg m^{-2}]	Abundance [Ind. m^{-2}]	AFDW [mg m^{-2}]
Anthozoa	Anthozoa	-	-	-	-	-	-	245	11,829.1	-	-	-	-
Bivalvia	*Bivalvia spp. juv.*	1,800	46.2	-	-	2,317	26.1	100	3.2	19,867	1,038.6	120	1.5
	Cerastoderma edule	20,983	223,191.7	-	-	1,029	27,085.5	182	22,510.8	2,100	6,798.1	110	5,799.0
	Crassostrea gigas	-	-	-	-	-	-	374	73,190.5	-	-	-	-
	Ensis directus	-	-	5	21,302.8	-	-	-	-	-	-	-	-
	Fabulina fabula	-	-	200	11.8	-	-	-	-	-	-	-	-
	Macoma balthica	1,693	11,733.4	150	2,042.5	438	1,930.8	100	8.0	2,068	2,085.1	367	1,257.3
	Mya arenaria	175	703.7	-	-	-	-	-	-	220	3,090.8	-	-
	Mytilus edulis	202	344.5	-	-	-	-	907	504,714.1	8	854.8	-	-
Crustacea	*Austrominius modestus*	-	-	-	-	-	-	1,959	4,380.9	-	-	100	11.6
	Balanidae spp. juv.	-	-	-	-	-	-	2,596	288.1	-	-	100	2.1
	Balanus crenatus	-	-	-	-	-	-	2,084	20,620.0	-	-	-	-
	Bathyporeia sarsi	-	-	200	89.6	-	-	-	-	-	-	-	-
	Bathyporeia spp.	-	-	200	7.8	-	-	-	-	-	-	-	-
	Caprella linearis	-	-	-	-	-	-	2,000	77.0	-	-	-	-
	Carcinus maenas	100	595.0	-	-	100	11,880.0	153	13,193.1	-	-	100	160.4
	Corophium arenarium	100	68.2	200	23.4	100	10.9	100	3.0	100	9.5	383	60.6
	Corophium spp.	-	-	100	1.6	100	2.8	2,000	126.0	-	-	100	2.1
	Corophium volutator	-	-	-	-	100	9.7	-	-	-	-	2,050	1,200.5
	Crangon crangon	100	580.0	100	2,110.0	-	-	8	252.8	-	-	-	-
	Crangon spp.	100	36.7	-	-	-	-	-	-	-	-	-	-
	Crangon spp. juv.	200	35.6	-	-	100	101.3	-	-	-	-	-	-
	Gammaridae spp.	-	-	-	-	-	-	100	0.1	-	-	-	-
	Gammarus locusta	10	17.4	100	3.9	-	-	-	-	-	-	-	-

Table 1 (continued): Species list with mean values for abundance [Ind. m^{-2}] and biomass in AFDW [mg m^{-2}] for all six habitats

	Gammarus spp.	100	55.8	-	-	-	-	-	-	-	-	100	4.4
	Hemigrapsus takanoi	-	-	-	-	-	-	100	8,070.0	-	-	-	-
	Idothea baltica	2	9.8	-	-	-	-	-	-	-	-	-	-
	Iphinoe trispinosa	-	-	100	1.5	-	-	100	12.6	-	-	-	-
	Jaera albifrons	-	-	-	-	-	-	100	2.4	-	-	100	22.2
	Jaera spp.	-	-	-	-	-	-	-	-	-	-	100	3.2
	Lamprops fasciata	-	-	100	1.9	-	-	-	-	-	-	-	-
	Pycnogonum littorale	-	-	-	-	-	-	24	156.0	-	-	-	-
	Semibalanus balanoides	-	-	-	-	-	-	1,547	16,407.8	-	-	-	-
	Urothoe poseidonis	267	108.8	300	77.5	-	-	-	-	-	-	100	31.1
Gastropoda	*Crepidula fornicata*	-	-	-	-	-	-	140	495.5	-	-	-	-
	Lepidochitona cinerea	-	-	-	-	-	-	197	488.8	-	-	-	-
	Littorina littorea	4	1,708.0	-	-	20	1,138.2	260	30,631.2	7	2,199.6	108	1,712.1
	Littorina obtusata	-	-	-	-	-	-	16	601.6	-	-	-	-
	Peringia ulvae	170,539	19,286.4	100	1.4	87,432	29,738.9	300	51.2	65,137	30,198.2	29,033	20,542.1
	Retusa obtusa	340	57.1	100	4.1	633	62.1	-	-	2,171	1,939.0	100	49.9
Nemertea	Nemertea	-	-	-	-	-	-	200	313.8	217	302.2	-	-
Oligochaeta	Oligochaeta	1,217	58.6	257	14.8	12,522	720.8	23,705	5,280.2	11,305	1,666.0	1,734	106.4
Polychaeta	*Ampharete spp.*	-	-	-	-	-	-	100	62.3	-	-	-	-
	Arenicola marina	128	2,799.4	-	-	-	-	100	1,280.0	1,049	8,333.0	24	3,505.6
	Capitella capitata	898	187.2	370	16.3	443	78.6	1,011	572.2	1,422	94.2	451	17.7
	Eteone longa	342	104.7	100	13.0	100	6.8	100	58.3	440	72.0	286	111.2
	Eteone spp.	250	17.1	-	-	200	5.9	200	5.6	100	4.1	-	-
	Heteromastus filiformis	-	-	-	-	-	-	482	90.0	-	-	-	-
	Lanice conchilega	100	155.5	-	-	300	4.8	3,430	9,487.4	-	-	-	-
	Lepidonotus squamatus	-	-	-	-	-	-	40	648.8	-	-	-	-
	Magelona filiformis	-	-	100	24.5	-	-	-	-	-	-	-	-

Table 1 (continued): Species list with mean values for abundance [Ind. m^{-2}] and biomass in AFDW [mg m^{-2}] for all six habitats

Malacoceros fuliginosus	2,000	42.0	-	-	100	32.1	4,451	23,083.7	-	-	-	-
Microphtholmus spp.	200	3.7	100	1.6	-	-	795	9.0	-	-	-	-
Nephtys hombergii	100	1,645.0	100	1,228.4	-	-	100	220.0	-	-	100	2.6
Nephtys spp.	-	-	100	40.8	-	-	-	-	-	-	-	-
Nephtys spp. juv.	150	4.0	200	159.2	-	-	200	122.2	-	-	150	7.3
Nereidoideo	-	-	-	-	-	-	100	1.7	-	-	-	-
Nereis diversicolor	300	924.7	-	-	1,576	7,245.8	2,100	2,228.0	167	784.2	140	604.6
Nereis spp. juv.	275	1,576.8	-	-	200	1.8	100	1.6	100	1.4	258	55.3
Nereis virens	-	-	-	-	100	8,690.0	-	-	-	-	-	-
Paroonis fulgens	-	-	133	4.9	-	-	-	-	-	-	-	-
Phyllodoce moculata	-	-	-	-	-	-	100	59.1	100	44.8	-	-
Phyllodoce mucosa	354	448.0	-	-	-	-	1,320	977.7	220	349.8	-	-
Phyllodoce spp.	-	-	-	-	-	-	-	-	100	820.0	-	-
Polydoro cornuta	-	-	-	-	-	-	-	-	-	-	100	4.7
Polydoro spp.	-	-	-	-	100	18.7	100	123.3	-	-	-	-
Polynoidae spp.	-	-	-	-	-	-	-	-	100	8.5	-	-
Pygospio elegans	985	79.0	584	28.5	588	41.8	200	7.6	673	50.8	1,932	99.0
Scoloplos armiger	583	66.8	244	329.9	300	42.9	725	109.7	2,843	4,762.0	1,043	524.1
Spio martinensis	-	-	333	24.0	-	-	-	-	-	-	-	-
Spio spp.	-	-	100	3.8	100	5.5	-	-	-	-	-	-
Spionido spp.	-	-	-	-	-	-	100	3.0	-	-	-	-
Spiophones bombyx	100	49.4	-	-	-	-	200	7.0	-	-	-	-
Streblospio benedicti	-	-	-	-	150	9.8	-	-	-	-	100	4.5
Tharyx killoriensis	578	43.4	-	-	1,583	139.2	100	11.3	100	3.2	1,210	158.6
SUM	205,273	266,783.2	4,677	27,569.7	110,730	89,030.7	55,752	752,877.0	110,613	65,509.7	40,598	36,061.9

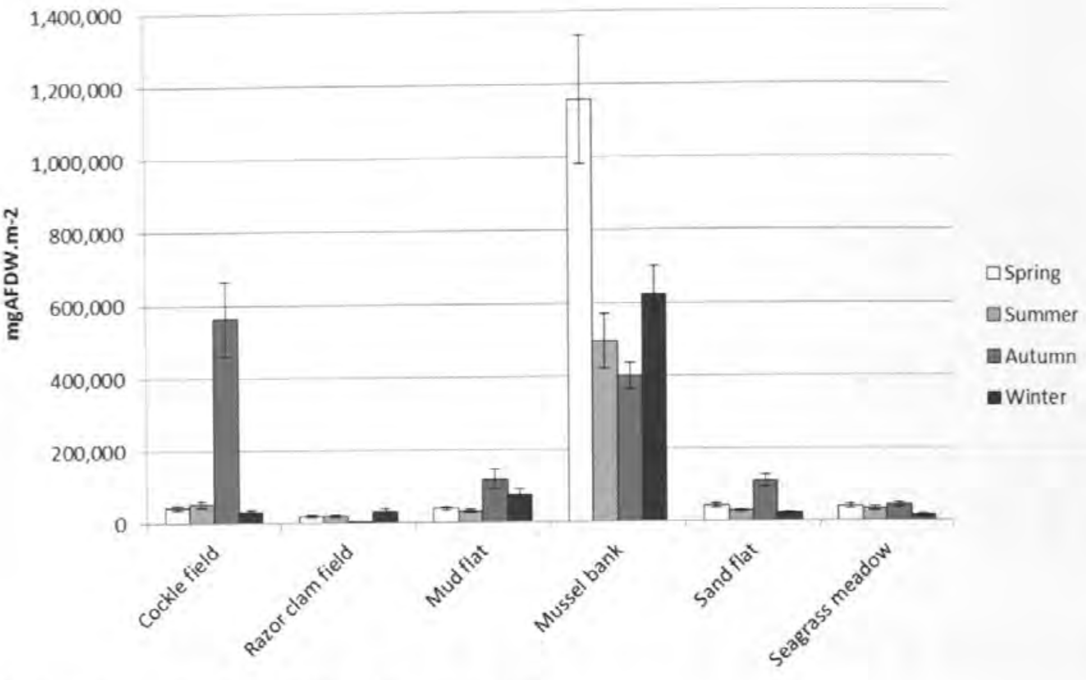


Fig. 3: Seasonal variation of benthic biomass

3.3. Species richness

The species number, diversity (H´) and the evenness (J´) differed between the six habitats. The number of species was the highest in the mussel bank (50 species) and the lowest in the sand flat (24 species; Table 2). The cockle field (34 species), the seagrass meadow (29 species), the razor clam field (27 species) and the mud flat (26 species) had intermediate values.

The total number of individuals of all species together (N) was the highest in the cockle field (205,273 individuals), followed by the mud flat (110,730 individuals) and the sand flat (110,613 individuals) which had similar intermediate values. The number of individuals was 55,752 and 40,598 in the mussel bank and the seagrass meadows respectively. The lowest value was found in the razor clam field (4,677 individuals; Table 2).

The Shannon Index (H´) and Pielou's evenness (J´) followed the same trend between the habitats. Both, the Shannon-Index (H´) and Pielou's evenness (J´) were the highest in the razor clam field indicating a high biodiversity and a high evenness (3.10, and 0.94 respectively). The mussel bank also revealed a relatively high biodiversity (H'=2.46) and evenness (J'=0.63). Intermediate values were found for both indices in the sand flat (H′=1.42 and J′=0.45) and seagrass meadow (H′=1.34 and J′=0.40). The lowest values of both indices were found in the mud flat (H′=0.91 and J′=0.28) and in the cockle field (H′=0.76 and J′=0.22; Table 2).

The high biodiversity and evenness observed in the razor clam field is caused by an intermediate number of different species which occur in similar abundances. This can be related to the harsh abiotic conditions which characterized this habitat. Indeed, razor clam fields often occur in the lower part of the intertidal which is exposed to a high current velocities and sediment mobility. In this unfavorable environment, only few species are able to settle.

The mussel bank, on the other hand, is also characterized by a high biodiversity and evenness but with a high number of different species in high abundances. Comparable results were found for mussel banks in the Dutch Wadden Sea (Beukema 1976). Most of the areas in the Wadden Sea are bare sediments. Mussel banks are one of the few habitats providing a solid epibenthic structure used by several species dependent on hard substrate to settle (e.g. barnacles, oysters, anthozoa). Furthermore, the dense accumulation of *M. edulis* provides shelter for numerous associated species (e.g. *Carcinus maenas*) which then reach higher abundances than in other habitats (Beukema, 1976). The biodiversity and evenness in mussel banks is consequently relatively high.

In contrast, the cockle field and the mud flat are poor in biodiversity and evenness (H'=0.76 J'=0.22 and H'=0.91 J'=0.28, respectively). This might be explained by the high dominance of single species in each of these habitats. The cockle field is strongly dominated by *Cerastoderma edule* and in the mud flat extremely high abundances of *Peringia ulvae* were found. This decreases the biodiversity and particularly the evenness in these habitats.

Table 2: Results of the biodiversity analysis, H'=Shannon-Index, J'=Pielou's evenness

Area	Number of species	Number of individual	H'	J'
Cockle field	34	205273	0.76	0.22
Razor clam field	27	4677	3.10	0.94
Mud flat	26	110730	0.91	0.28
Mussel bank	50	55752	2.46	0.63
Sand flat	24	110613	1.42	0.45
Seagrass meadow	29	40598	1.34	0.40

3.4. Birds

3.4.1. Cockle field

The cockle field was a favored foraging site of *Haematopus ostralegus* and *Tadorna tadorna* (Table 3). Among the eight species observed (Table 3), these two species contributed most to the counted abundances. These results are in accordance with a telemetry study on *H. ostralegus* which showed that this species prefers intertidal areas with high abundances of *Cerastoderma edule* for foraging (Schwemmer et al. 2016a). The high abundances of *T. tadorna* can be explained by the high biomass of *Peringia ulvae* found in the cockle field which contributes in high proportion to their diet (Buxton and Young 1981, Viain et al. 2011).

3.4.2. Razor clam field

Little is known about the importance of intertidal razor clam fields for birds. Indeed, very few studies were done on razor clam fields because first, it invaded the Wadden Sea relatively recently and second, its location on the lower part of the intertidal is difficult to sample. Eight bird species were observed feeding on the studied razor clam field (Table 3). The most abundant species were *Larus argentatus* and *Larus fuscus* which fed on the habitat during the short exposition time of about one hour per tide (personal observation). The gulls dragged the razor clams out of the sediment, opened the shell and ate the meat of the clams. Smaller gull species which were not able to get the clams out of the sediment such as *Larus canus* or *Chroicocephalus ridibundus* often conducted kleptoparasitism on the prey items already open by *L. argentatus* and *L. fuscus*.

E. directus was also found in faeces and stomach content of *Somateria mollissima* and *Melanitta nigra* (Tulp et al. 2010). Therefore, there might be an increasing importance of this alien species as a food source for benthivorous birds, although neither *S. mollissima* nor *M. nigra* was observed in this study, probably because they prefer subtidal *E. directus* populations for foraging.

3.4.3. Mud flat

L. canus and *Limosa lapponica* dominated the species assemblage of the mud flat consisting of 16 different species (Table 3). It was the only habitat type which was visited by *Recurvirostra avosetta* for foraging. The mud flat is characterized by a soft sediment structure which is easy to penetrate and therefore the ideal feeding ground for long-beaked species such as *R. avosetta* and *L. lapponica*.

3.4.4. Mussel banks

The lowest number of individuals was found on the mussel bank (1.25E-04 $\mathrm{Ind.m^{-2}.h^{-1}}$; Table 3). *Hoematopus ostralegus* was the most abundant of the 12 different species which were counted in the mussel bank. This is in accordance with the diet of *H. ostralegus* encompassing a large proportion of *M. edulis* (Nehls et al. 1997). *M. edulis* is also known to be one of the main food sources of *S. mollissima,* which forages during high tide on mussel banks and dive to catch the bivalves (Nehls 1989).

Because the bird counts were conducted during low tide, only a small number of *S. mollissima* was counted on the mussel bank and the predation pressure of this species was probably highly underestimated.

Table 3: Mean values of all bird counts in the six intertidal habitats with values for abundance [Ind.m^{-2}.h^{-1}] and biomass in fresh weight [mg.m^{-2}.h^{-1}], biomass values were calculated using mean fresh weight values (Bezzel 1985, FTZ unpublished data)

	Cockle field		Razor clam field		Mud flat		Mussel bank		Sand flat		Seagrass meadow	
Species	**Abundance [Ind.m^{-2}.h^{-1}]**	**Biomass [mg.m^{-2}.h^{-1}]**	**Abundance [Ind.m^{-2}.h^{-1}]**	**Biomass [mg.m^{-2}.h^{-1}]**	**Abundance [Ind.m^{-2}.h^{-1}]**	**Biomass [mg.m^{-2}.h^{-1}]**	**Abundance [Ind.m^{-2}.h^{-1}]**	**Biomass [mg.m^{-2}.h^{-1}]**	**Abundance [Ind.m^{-2}.h^{-1}]**	**Biomass [mg.m^{-2}.h^{-1}]**	**Abundance [Ind.m^{-2}.h^{-1}]**	**Biomass [mg.m^{-2}.h^{-1}]**
Anas acuta	-	-	-	-	-	-	-	-	-	-	-	-
Anas penelope	-	-	-	-	-	-	-	-	3.17E-03	2,158.1	3.95E-03	2,689.3
Anas platyrhynchos	-	-	-	-	1.71E-05	25.3	5.10E-06	7.6	1.29E-04	190.7	1.76E-04	260.7
Arenaria interpres	-	-	-	-	-	-	8.40E-06	1.2	3.37E-05	4.6	3.13E-05	4.3
Branta bernicla	-	-	-	-	1.20E-04	173.6	-	-	1.24E-04	179.3	7.38E-04	1,070.0
Calidris alpina	-	-	-	-	2.48E-04	12.2	-	-	8.92E-05	4.4	9.15E-03	450.9
Calidris canutus	-	-	-	-	-	-	-	-	5.71E-04	77.1	3.36E-03	453.9
Charadrius hiaticula	-	-	-	-	-	-	-	-	6.60E-05	4.1	-	-
Chroicocephalus ridibundus	9.96E-05	23.8	3.28E-05	7.8	3.01E-04	71.8	6.94E-06	1.7	9.89E-05	23.6	5.28E-04	126.2
Haematopus ostralegus	5.99E-04	278.5	2.34E-05	10.9	9.88E-05	45.9	2.69E-05	12.5	4.59E-04	213.1	1.15E-03	533.0
Larus agentotus	5.22E-05	50.1	1.98E-04	189.8	3.07E-05	29.5	7.97E-06	7.7	9.69E-05	93.1	1.06E-04	102.1
Larus canus	5.69E-05	23.4	2.43E-05	10.0	3.34E-05	13.8	1.57E-05	6.5	1.02E-04	42.1	4.54E-05	18.7
Larus fuscus	-	-	3.53E-05	28.5	1.71E-05	13.8	-	-	-	-	-	-
Larus marinus	-	-	2.34E-05	39.1	-	-	-	-	-	-	-	-
Limicola falcinellus	-	-	-	-	-	-	-	-	-	-	3.75E-05	1.4
Limosa lapponica	2.24E-04	73.8	4.82E-05	15.9	3.21E-04	105.9	2.44E-05	8.0	1.56E-03	514.5	5.30E-04	175.0
Numenius arquata	1.07E-04	62.2	1.82E-05	10.6	2.82E-05	16.4	1.02E-05	5.9	9.87E-05	57.3	3.70E-04	214.7
Numenius phaeopus	-	-	-	-	-	-	-	-	-	-	4.38E-05	19.5
Pluvialis squatarola	-	-	-	-	3.61E-05	8.2	5.21E-06	1.2	2.15E-04	48.7	3.59E-04	81.6
Recurvirostra avosetta	-	-	-	-	6.59E-05	22.5	-	-	-	-	-	-
Somateria mollissima	-	-	-	-	3.13E-05	67.2	7.99E-06	17.2	-	-	-	-
Tadorna tadorna	3.42E-04	384.2	-	-	6.38E-05	71.8	-	-	1.93E-04	217.1	4.89E-05	71.0
Tringa erythropus	-	-	-	-	-	-	-	-	-	-	1.50E-04	24.4
Tringa nebularia	-	-	-	-	1.71E-05	3.1	3.11E-06	0.6	3.09E-05	5.7	1.33E-04	24.4
Tringa totanus	1.33E-04	192.6	-	-	4.34E-05	62.9	3.11E-06	4.5	3.09E-05	44.8	7.44E-05	107.9
SUM	1.61E-03	1,088.6	4.03E-04	312.7	1.47E-03	744.0	1.25E-04	74.4	7.07E-03	3,878.5	2.10E-02	6,429.0

3.4.5. Sand flat

The sand flat had the second highest number of foraging birds (7.07E-03 $\mathrm{Ind.m^{-2}.h^{-1}}$) and 17 species were observed feeding on this habitat (Table 3). *Anas penelope* contributed the most to the bird abundances, followed by *L. lapponica* and *H. ostralegus*. *A. penelope* is a herbivore (Mathers and Montgomery 1998) and probably fed on the macrophytes which were randomly distributed on the sand flat. *L. lapponica* and *H. ostralegus* probably fed on *A. marina* which lives in the sandy sediment (Scheiffarth 2001, Schwemmer et al. 2012).

3.4.6. Seagrass meadow

The highest number of species (19 species) and individuals (2.10E-02 $\mathrm{Ind.m^{-2}.h^{-1}}$) of foraging birds was found on the seagrass meadow (Table 3).

The most abundant species was *Calidris alpina*, followed by *A. penelope* and *Calidris canutus*. The seagrass meadow revealed a high biomass stock of bivalves (e.g. *Cerastoderma edule*, *Macoma balthica*) and worms (e.g. *Nereis diversicolor*) which are favored food items of *C. canutus* and *C. alpina*, respectively (Piersma et al. 1993, Schwemmer et al. 2016b). *A. penelope*, on the other hand, directly feeds on the *Zostera*-stock. Observations in other areas such as the Sylt-Rømø Bight showed a lower abundance of birds on seagrass meadows (Busch 2012). This difference can be explained by the location of the studied habitat. The seagrass meadow in this study was situated in a sheltered area with a long exposure time (about 4 h per tide) and with only few disturbances (e.g. tourism, ships, aerial disturbances) in contrast to the meadows of the Sylt-Rømø Bight situated closer to the shore next to dikes and roads.

3.4.7. Seasonal variation of bird abundances

The highest number of foraging birds was observed in spring and autumn in the sand flat and the seagrass meadow in (Fig. 4). This corresponds to the high abundance of migrating birds (e.g. *A.*

penelope, C. alpina, C. canutus, L. lapponica), which use the Wadden Sea as a stop-over during their migration.

In contrast, in the cockle field and the mud flat number of birds was the highest in summer mainly due to high abundances of *Chroicocephalus ridibundus* and *Haematopus ostralegus* in this season.

The highest abundance of birds in the razor clam field was observed in winter. This might be explained by the decrease in biomass of prey items such as *A. marina* or *C. edulis* which are therefore less available for birds in winter. The birds might then change their foraging habitat to the razor clam field which provides relatively reliable food sources all year long, especially for gulls.

High abundances in winter were also found on the sand flat and the seagrass meadow. Both studied habitats are situated close to the shore and are preferred roosting places of several bird species. The high abundances in winter may therefore reflect easy accessibility of both studied habitats, even during bad weather conditions.

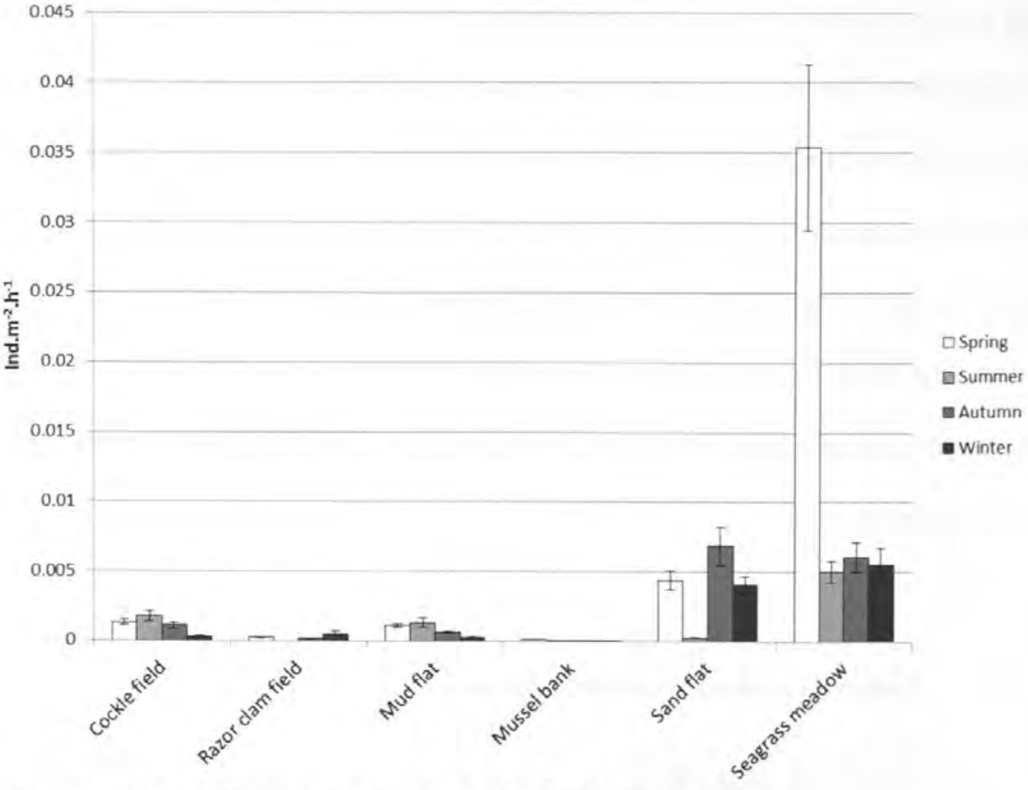


Fig. 4: Seasonal variation of the abundance [Ind.m^{-2}.h^{-1}] of foraging birds

Conclusion

The six studied intertidal habitats differed in their species composition, their biodiversity, the amount of microphytobenthos and their importance for foraging birds. Three of the habitats (i.e. cockle field, razor clam field, mussel bank) were characterized by the biomass of bivalve species (i.e. *Cerastoderma edule, Ensis directus, Mytilus edulis*). In contrast, the mud flat, the sand flat and the seagrass meadow were dominated by the biomass of gastropods mainly due to the high abundance of *Peringia ulvae*.

The highest number of foraging birds was found on the seagrass meadow, followed by the sand flat. The species composition of birds differed between the habitats based on the different feeding strategies and prey preferences of the birds.

This first attempt of an intertidal benthic survey in the Wadden Sea influenced by the open North Sea, showed that the different habitats present in the Wadden Sea might play different role in the Wadden Sea ecosystem as they differ in their species composition and biomass and are therefore used differently by predators.

4. Acknowledgements

This study was funded by the German Federal Ministry of Education and Research in the frame of the German joint research project "STopP – From sediment to top predator" (BMBF, FKZ 03F672B). I'm grateful to Harald and Ragnhild Asmus for their advices and for introducing me to the work in the Wadden Sea. I would furthermore like to thank Leonie Enners for organizing the bird counts in the different habitats. Many thanks to the teams of the vessels "MS Hooge" and "FS Mya II" who enabled access to remote intertidal flats.

5. References

Asmus, H. 1982. Field measurements on respiration and secondary production of a benthic community in the northern Wadden Sea. Netherlands Journal of Sea Research **16**:403-413.

Asmus, H., Asmus, R. 1985. The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. HELGOLANDER MEERESUNTERSUCHUNGEN **39**:273-301.

Asmus, R., M., , and E. Bauerfeind. 1994. The microphytobenthos of Königshafen - spatial and seasonal distribution on a sandy tidal flat. HELGOLANDER MEERESUNTERSUCHUNGEN **48**:257-276.

Baird, D., H. Asmus, and R. Asmus. 2004. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Marine Ecology Progress Series **279**:45-61.

Baird, D., H. Asmus, and R. Asmus. 2007. Trophic dynamics of eight intertidal communities of the Sylt-Rømø Bight ecosystem, northern Wadden Sea. Marine Ecology Progress Series **351**:25-41.

Baird, D., H. Asmus, and R. Asmus. 2012. Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. Marine Ecology Progress Series **462**:143-162.

Beukema, J. 1974. Seasonal changes in the biomass of the macro-benthos of a tidal flat area in the Dutch Wadden Sea. Netherlands Journal of Sea Research **8**:94-107.

Beukema, J., J. 1976. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. Netherlands Journal of Sea Research **10**:236-261.

Bezzel, E. 1985. Kompendium der Vögel Mitteleuropas: Nichtsingvögel. AULA-Verlag.

Busch, N. 2012. Untersuchungen zur Nutzung eulitoraler Seegraswiesen durch Wattenmeervögel während des Frühjahrszuges. Universität Kiel.

Colijn, F., and K. S. Dijkema. 1981. Species composition of benthic diatoms and distribution of chlorophyll a on an intertidal flat in the Dutch Wadden Sea. Marine Ecology Progress Series **4**:9-21.

Dekker, R. 1989. The macrozoobenthos of the subtidal western Dutch Wadden Sea. I. Biomass and species richness. Netherlands Journal of Sea Research **23**:57-68.

Edler, L. 1979. Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Publication-Baltic Marine Biologists BMB (Sweden).

Flach, E. C. 1996. The influence of the cockle, Cerastoderma edule, on the macrozoobenthic community of tidal flats in the Wadden Sea. Marine Ecology **17**:87-98.

Jensen, K. T. 1992. Dynamics and growth of the cockle, Cerastoderma edule, on an intertidal mud-flat in the Danish Wadden Sea: effects of submersion time and density. Netherlands Journal of Sea Research **28**:335-345.

Koffijberg, K., K. Laursen, B. Hälterlein, G. Reichert, J. Frikke, and L. Soldat. 2015. Trends of Breeding Birds in the Wadden Sea 1991-2013. Wadden Sea Ecosystem.

Lorenzen, C. J. 1967. Determination of chlorophyll and pheo-pigments: spectrophotometric equations. Limnology and oceanography **12**:343-346.

Mathers, R., and W. Montgomery. 1998. Behaviour of Brent geese Branta bernicla hrota and wigeon Anas penelope feeding on intertidal Zostera spp. Oceanographic Literature Review **1**:126.

Nehls, G. 1989. Occurrence and food consumption of the common eider, Somateria mollissima, in the Wadden Sea of Schleswig-Holstein. HELGOLANDER MEERESUNTERSUCHUNGEN **43**:385-393.

Nehls, G., I. Hertzler, and G. Scheiffarth. 1997. Stable musselMytilus edulis beds in the Wadden Sea—They're just for the birds. HELGOLANDER MEERESUNTERSUCHUNGEN **51**:361-372.

Piersma, T., R. Hoekstra, A. Dekinga, A. Koolhaas, P. Wolf, P. Battley, and P. Wiersma. 1993. Scale and intensity of intertidal habitat use by knots Calidris canutus in the western Wadden Sea in relation to food, friends and foes. Netherlands Journal of Sea Research **31**:331-357.

Reise, K., and J. Kohlus. 2008. Seagrass recovery in the Northern Wadden Sea? Helgoland Marine Research **62**:77-84.

Scheiffarth, G. 2001. The diet of bar-tailed godwits *Limosa lapponica* in the Wadden Sea: Combining visual observations and faeces analyses. Ardea **89**:481-494.

Schückel, U., I. Kröncke, and D. Baird. 2015. Linking long-term changes in trophic structure and function of an intertidal macrobenthic system to eutrophication and climate change using ecological network analysis. Mar Ecol Prog Ser **536**:25-38.

Schwemmer, P., F. Güpner, N. Guse, and S. Garthe. 2012. Nahrungswahl von Vogelarten der deutschen Nordseeküste. Vogelwarte **50**:141-154.

Schwemmer, P., C. C. Voigt, A. M. Corman, S. Adler, and S. Garthe. 2016. Body mass change and diet switch tracked by stable isotopes indicate time spent at a stopover site during autumn migration in dunlins Calidris alpina alpina. Journal of Avian Biology.

Tulp, I., J. Craeymeersch, M. Leopold, C. van Damme, F. Fey, and H. Verdaat. 2010. The role of the invasive bivalve *Ensis directus* as food source for fish and birds in the Dutch coastal zone. Estuarine, Coastal and Shelf Science **90**:116-128.

Wolff, W. J., J. P. Bakker, K. Laursen, and K. Reise. 2010. The Wadden Sea Quality Status Report-Synthesis Report 2010. The Wadden Sea 2010. Common Wadden Sea Secretariat (CWSS); Trilateral Monitoring and Assessment Group: Wilhelmshaven.(Wadden Sea Ecosystem; 29/editors, Harald Marencic and Jaap de Vlas) **25**.

Chapter 3

Chapter 2

Photo flying geese: Robert Waleczek

Relationships between fresh weight, dry weight, ash free dry weight, carbon and nitrogen content for selected vertebrates

Sabine Horn[1]*, Camille de la Vega[1]*

Journal of Experimental Marine Biology and Ecology 481 (2016) 41-48

Affiliation:

[1] Alfred-Wegener-Institute Helmholtz-Center for Polar- and Marine Research, Wadden Sea Station Sylt Hafenstr. 43, D-25992 List/ Sylt, Germany

***Corresponding authors**: camille.de.la.vega@awi.de; sabine.horn@awi.de

Key words: Sea birds, harbor seals, biomass measures, weight to weight conversion, %C, food web modeling

Abstract:

Top predators are relevant indicators of the ecological status of a system and can have a high impact on food webs. But top predators are difficult to include in network analyses because their biomass in ash free dry weight or carbon content is missing. Regression equations were determined for the relationships between fresh weight and dry weight, ash free dry weight, carbon and nitrogen contents respectively for six of the most abundant bird species in the Wadden Sea (*Calidris canutus, Limosa lapponica, Haematopus ostralegus, Chroicocephalus ridibundus, Larus canus, Anas penelope*) and harbor seals (*Phoca vitulina*). The relationships for all species were interpreted as linear through the origin. Carbon content *vs.* fresh weight ratios for birds ranged from 0.16 ± 0.01 to 0.22 ± 0.02. Carbon content *vs.* fresh weight ratio was 0.17 ± 0.02 on average for harbor seals. This work highlights that the biomass of top predators was often over- or underestimated in previous studies. The determined conversion factors will be useful for future studies to generate more realistic food web models.

1. Introduction

In the last decades, food web models and ecological networks have become useful tools to describe the functioning of large and complex ecosystems encompassing numerous compartments interacting with each other and responding differently to external stressors (Ings et al. 2009). In many studies, network analyses have been used to define ecosystem properties. These properties include the ecosystem structural complexity, the structure and magnitude of the cycling of energy and material, the efficiency of energy transfer within the system, the rates of energy assimilation and dissipation, the trophic structure, the system activity, growth and development (Baird et al. 2004). Results from these models provide significant insights into the fundamental functioning of the ecosystem (Baird et al. 2004) and are very relevant for the management of marine ecosystems (Samhouri et al. 2009).

Abundance and distribution of top predators, such as sea birds and marine mammals, can have a large influence on community structures and on the functioning of the ecosystem they live in (Baird et al. 1985b, Bowen 1997, Moreira 1997). As a corollary, they are good indicators for ecosystem's health (Furness and Camphuysen 1997, Reddy et al. 2001, Bossart 2011). Therefore, there is an increasing need to include marine birds and mammals in ecosystem models, especially in studies about trophodynamic to have a better understanding of food web functioning, allowing improvement of management plans for conservation.

Studies about marine bird and mammal populations are classically based on abundance data (Reijnders et al. 1997, Brasseur et al. 2013, Markert et al. 2013, Galatius et al. 2014, Mandema et al. 2015), which cannot be directly used to study matter or energy flow within ecosystems (Dumont et al. 1975). These abundance data can be converted to fresh weight values using average individual weight corresponding to the studied species. But the use of fresh tissue might lead to large approximations in the organic matter weight, as body water content can vary between taxa. The fresh weight is therefore a bad proxy for biomass comparison. In ecological studies it is a common practice to use standardized biomass units (e.g. dry weight, ash free dry weight, carbon content) allowing comparison of different species biomass from different locations or periods of time (e.g. seasons, years). Most of the mass balanced food web models such as ECOPATH with ECOSIM (Bradford-Grieve et al. 2003, Leguerrier et al. 2007b, Pinkerton et al. 2010) and especially ecological network analyses (Baird et al. 2004, Scharler and Baird 2005b, Fath et al. 2007, Baird et al. 2012, Saint-Béat et al. 2013b) also rely on these consistent and standardized biomass units (e.g. dry weight, ash free dry weight, carbon content).

Although a large database of conversion factors from fresh weight to standardized biomass units is available for macrobenthic invertebrates (Rumohr et al. 1987, Ricciardi and Bourget 1998b), to our knowledge, no such database exists for marine birds and mammals. As a result, including top predators in ecosystem models is very difficult. It is associated with a high degree of uncertainty and relies on large approximations that might bias the model outputs.

The aim of this study was to determine relationships useful for modeling between fresh weight (FW) and dry weight (DW), FW and ash free dry weight (AFDW), FW and carbon content (CC) and FW and nitrogen content (NC). These relationships were determined for six of the most abundant bird species in the Wadden Sea (Blew et al. 2013) (*Calidris canutus,* Linnaeus, 1758; *Limosa lapponica,* Linnaeus, 1758; *Haematopus ostralegus,* Linnaeus, 1758; *Chroicocephalus ridibundus,* Linnaeus, 1766; *Larus canus,* Linnaeus, 1758; *Anas penelope,* Linnaeus, 1758), and for harbor seal (*Phoca vitulina,* Linnaeus, 1758), one of the most abundant marine mammal species in this area (Reijnders et al. 2009).

2. Material and methods

Carcasses of birds and seals were collected along the shore of the eastern German Wadden Sea, between the coastal city Büsum in the South and the island of Föhr in the North (Fig. 1). Only fresh carcasses which did not show any noticeable signs of starvation or diseases were selected for this study.

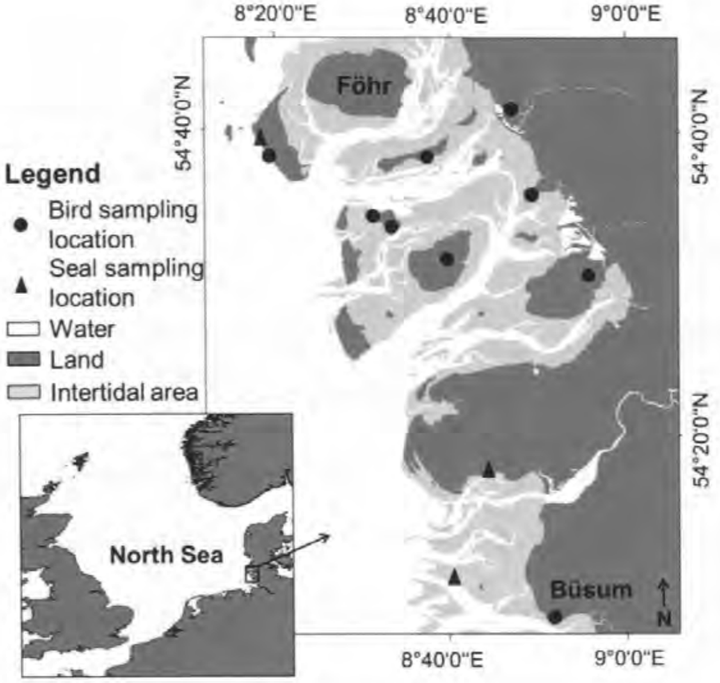


Fig. 1: Location and map of the study area. The circles and triangles refer to the locations where carcasses of birds and seals were respectively found

Seventeen birds from six different species (*C. canutus, H. ostralegus, L. lapponica, C. ridibundus, L. canus, and A. penelope*) were collected by a network of volunteers. Three individuals were collected for each species, except for *A. penelope* for which only two birds were available. Most individuals died due to collision with lighthouses or cars (Table 1). Carcasses were stored frozen in plastic bags at -20 °C until preparation for analyses. Each individual was unfrozen and grinded entirely using a kitchen cutter (RCKC-6000, Royal Catering, 750 watts) in order to get a homogenized mixture composed of all the tissues. Four subsamples were collected from each grinded individual: three for determination of fresh weight (FW), dry weight (DW) and ash free dry weight (AFDW), and one for carbon content (CC) and nitrogen content (NC) analyses.

Table 1: Species, date of collection, total fresh weight of individuals, season and cause of death of the birds

Species #	Date of collection	Total fresh Weight (g)	Season	Cause of death
C. canutus 1	4th Apr. 2014	114.8	Spring	Unknown
C. canutus 2	21st Sep. 2014	119.5	Autumn	Unknown
C. canutus 3	7th Jul. 2014	108.6	Summer	Unknown
L. lapponica 1	2nd Apr. 2004	246.2	Spring	Lighthouse collision
L. lapponica 2	20th Mar. 2007	270.5	Spring	Lighthouse collision
L. lapponica 3	25th Jan. 2007	299.2	Winter	Lighthouse collision
H. ostralegus 1	2nd Jun. 2014	464.7	Summer	Unknown
H. ostralegus 2	27th Mar. 2014	371.7	Spring	Unknown
H. ostralegus 3	27th Apr. 2009	501.3	Spring	Unknown
C. ridibundus 1	27th Sep. 2013	231.7	Autumn	Lighthouse collision
C. ridibundus 2	13th Sep. 2013	198.5	Autumn	Unknown
C. ridibundus 3	3rd Jun. 2012	150.1	Summer	Unknown
L. canus 1	6th May. 2013	521.1	Spring	Unknown
L. canus 2	4th Jul. 2014	332.4	Summer	Vehicle collision
L. canus 3	17th Nov. 2006	442.0	Autumn	Vehicle collision
A. penelope 1	15th Jan. 2002	777.5	Winter	Lighthouse collision
A. penelope 2	11th Nov. 2007	795.7	Autumn	Lighthouse collision

Three harbor seals were collected in 2015 (Table 2) as part of the stranding network established along the German coasts of Schleswig-Holstein (Benke et al. 1998, Siebert et al. 2006). Carcasses were stored frozen in plastic bags at -20°C until necropsies, which were carried out according to the protocol described by Siebert et al. (2007), at the Institute for Terrestrial and Aquatic Wildlife Research of the University of Veterinary Medicine, Hannover Foundation. The different tissues were dissected and weighed (± 0.1 g). The contribution of each tissue to the total fresh weight was determined for each individual. Two subsamples were collected from each tissue and each individual: one for determination of FW, DW, AFDW and one for determination of CC and NC.

Table 2: Seal ID, Date of collection, total fresh weight of individuals, age status, length and gender of the three sampled harbor seals

Seal #	Date of collection	Total Fresh Weight (g)	Age status	Length (cm)	Gender
Phoca vitulina 1	3rd Jun. 2015	83800	Adult	180	Female
Phoca vitulina 2	15th Jun. 2015	85400	Adult	173.5	Male
Phoca vitulina 3	1st Aug. 2015	16200	Juvenile	96.5	Female

The FW of each subsample of birds and seals was measured to the nearest 0.1 mg. Subsamples were dried in an oven at 50°C until constant weight and the DW was measured (± 0.1 mg). Each subsample was then burned in a furnace at 500°C for 5 hours, cooled down in a desiccator and ash weight was measured (± 0.1 mg). AFDW was determined by subtracting the ash weight from the DW. For CC and NC, subsamples were freeze-dried and grinded into a fine powder using a ball mill. An amount of each powder was precisely weighed (± 1 µg) and sealed in a tin capsule. CC and NC were measured using an elemental analyzer (Flash EA 1112, Thermo Scientific, Milan, Italy) at the LIENSs stable isotope facility of the University of La Rochelle, France. Acetanilide (Thermo) and peptone (Sigma-Aldrich) were used as standards for CC and NC calibration.

Relationships between FW and DW, AFDW, CC and NC respectively were plotted for bird species and for each seal tissue. These plots were then made for entire seal individuals taking into account the mass proportions of each tissue in FW. Missing data for some tissues were estimated by assuming that the proportion of the weight of missing tissue is the same as in *Phoca vitulina* 1 (Table 6).

The regression equations for FW and DW, AFDW, CC and NC respectively were calculated for all individuals of bird species combined, for the seal tissues and for entire seals.

3. Results and discussion

3.1. Birds

3.1.1. Relationships among biomass measures

The regression equations of all measured bird individuals revealed linear relationships that pass through the origin between FW and DW, AFDW, CC and NC respectively (Fig. 2, Table 3) and represented 93% (i.e. FW *versus* CC) to 98% (i.e. FW *vs.* DW) of the variation of the measured data points (i.e. R^2, Table 3). Therefore, these equations allow the use of ratios between the different biomass measures and give confidence to extrapolation to heavier and lighter bird species.

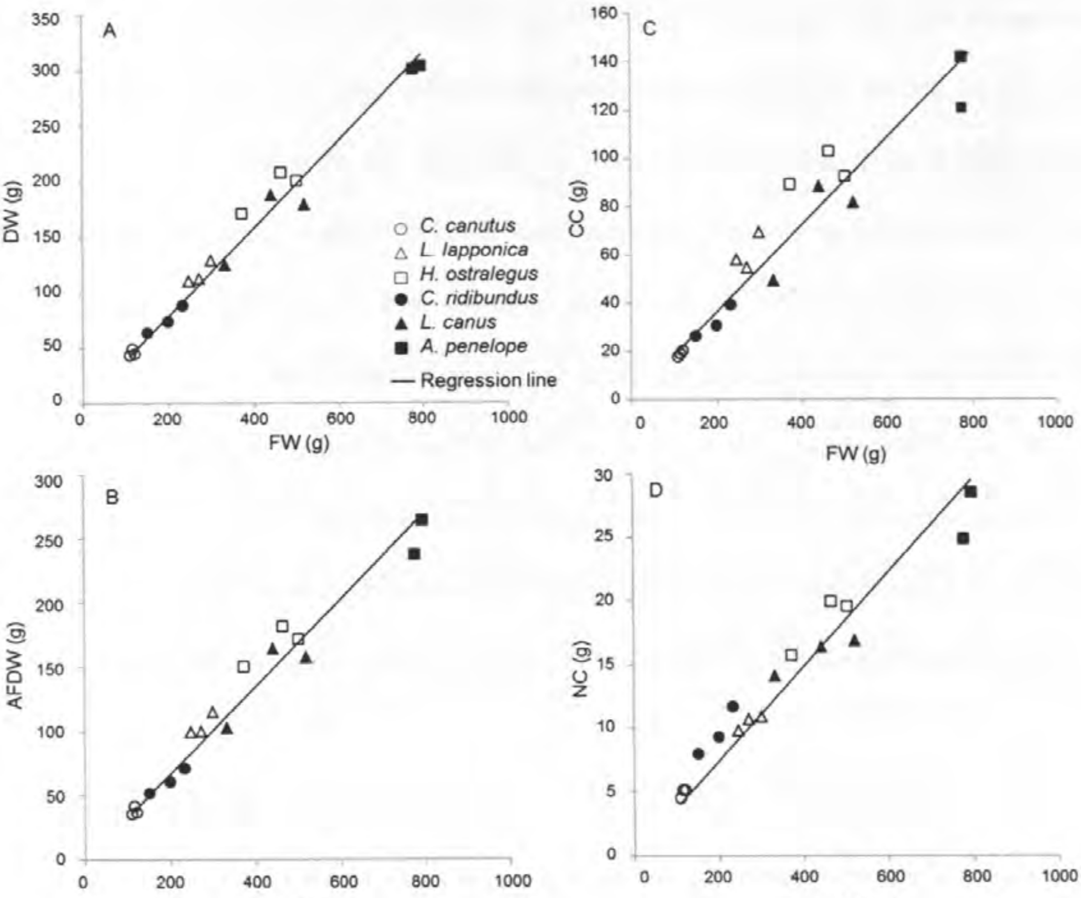


Fig. 2: Relationships between FW and DW, FW and AFDW, FW and CC, FW and NC for all bird species combined. The regression equations are shown in Table 3

The ratios FW *vs.* DW (FW/DW), FW *vs.* AFDW (FW/AFDW), FW *vs.* CC (FW/CC), FW *vs.* NC (FW/NC), DW *vs.* CC (DW/CC), AFDW *vs.* CC (AFDW/CC) and DW *vs.* NC (DW/NC) were then calculated for each replicate of birds to verify the homogeneity of the mixture.

Table 3: Regression equations and R^2 for relationships between FW and DW, FW and AFDW, FW and CC, FW and NC for all bird species combined, for Blubber-skin, Muscle and Bone of seals, and for entire seals

	Regression equation	**R^2**
Birds		
Entire individual	DW(g) = 0.3953 x FW(g)	0.98
	AFDW(g) = 0.3378 x FW(g)	0.97
	CC(g) = 0.1807 x FW(g)	0.93
	NC(g) = 0.0371 x FW(g)	0.95
Seals		
Blubber-skin	DW(g) = 0.5522 x FW(g)	0.97
	AFDW(g) = 0.538 x FW(g)	0.96
	CC(g) = 0.3274 x FW(g)	0.92
	NC(g) = 0.0291 x FW(g)	0.80
Muscle	DW(g) = 0.2821 x FW(g)	1.00
	AFDW(g) = 0.2699 x FW(g)	1.00
	CC(g) = 0.1295 x FW(g)	0.99
	NC(g) = 0.0391 x FW(g)	0.95
Bone	DW(g) = 0.4576 x FW(g)	0.99
	AFDW(g) = 0.3328 x FW(g)	0.97
	CC(g) = 0.1617 x FW(g)	0.95
	NC(g) = 0.0453 x FW(g)	0.87
Entire individual	DW(g) = 0.3396 x FW(g)	1.00
	AFDW(g) = 0.3029 x FW(g)	0.98
	CC(g) = 0.1617 x FW(g)	0.95
	NC(g) = 0.0453 x FW(g)	0.87

3.1.2. Homogeneity of replicates in bird individuals

The intra-individual standard deviations of ratios varied from <0.01 (*L. lapponica* 3) to 0.05 (*C. canutus* 1) for DW/FW and from <0.01 (*C. canutus* 2) to 0.06 (*C. canutus* 1) for AFDW/FW (Table 4). The bird mixture was therefore considered to be homogeneous and representative of the whole individual in terms of body tissue composition, thanks to the very small standard deviations between replicates of a same individual. This grinding method is consequently appropriate for biomass estimation studies in birds.

Table 4: DW/FW, AFDW/FW, CC/AFDW, CC/FW and NC/FW ratios for birds; mean per individual ± standard deviation (n=3) is shown for DW/FW and AFDW/FW

Species #	DW/FW	AFDW/FW	CC/AFDW	CC/FW	NC/FW
C. canutus 1	0.42 ± 0.05	0.36 ± 0.06	0.34	0.16	0.04
C. canutus 2	0.37 ± 0.01	0.31 ± <0.00	0.37	0.17	0.04
C. canutus 3	0.39 ± 0.01	0.33 ± 0.01	0.34	0.16	0.04
L. lapponica 1	0.44 ± 0.01	0.40 ± 0.02	0.48	0.23	0.04
L. lapponica 2	0.41 ± 0.02	0.37 ± 0.01	0.44	0.20	0.04
L. lapponica 3	0.43 ± <0.00	0.39 ± 0.01	0.48	0.23	0.04
H. ostralegus 1	0.45 ± 0.02	0.39 ± 0.01	0.42	0.22	0.04
H. ostralegus 2	0.46 ± 0.01	0.40 ± 0.01	0.46	0.24	0.04
H. ostralegus 3	0.40 ± 0.01	0.34 ± 0.01	0.40	0.18	0.04
C. ridibundus 1	0.38 ± 0.02	0.31 ± 0.01	0.36	0.17	0.05
C. ridibundus 2	0.37 ± 0.01	0.31 ± 0.01	0.34	0.15	0.05
C. ridibundus 3	0.42 ± 0.01	0.35 ± 0.01	0.35	0.17	0.05
L. canus 1	0.34 ± 0.02	0.30 ± 0.01	0.40	0.16	0.03
L. canus 2	0.37 ± 0.02	0.31 ± 0.01	0.33	0.15	0.04
L. canus 3	0.42 ± 0.01	0.37 ± 0.01	0.41	0.20	0.04
A. penelope 1	0.39 ± 0.03	0.30 ± 0.02	0.32	0.16	0.03
A. penelope 2	0.38 ± 0.01	0.33 ± 0.01	0.41	0.18	0.04

3.1.3. Conversion factors of bird species

The DW/FW ratios (mean per species ± standard deviation) ranged from 0.38 ± 0.04 (*L. canus*) to 0.44 ± 0.03 (*H. ostralegus*), the AFDW/FW ratios ranged from 0.32 ± 0.01 (*A. penelope*) to 0.38 ± 0.04 (*H. ostralegus*) and the CC/FW rations ranged from 0.16 ± 0.01 (*C. canutus*) to 0.22 ± 0.02 (*L. lapponica*; Table 5). The bird species were then constituted of 16% to 22% of carbon ($gC.100gFW^{-1}$). This is higher than the value of 10% used by Bradford-Grieve et al. (2003) and the value of 4% used by Leguerrier et al. (2007b) for sea birds in general (Table 5). These authors probably underestimated the bird biomass in their models. On the contrary, Saint-Béat et al. (2013b) and Baird et al. (2004) used a CC/FW ratio of 0.30 (Asmus, personal communication; Table 5), higher than the one measured in this study. As a result, these authors probably overestimated the biomass of birds in their models, and therefore the role of birds in the studied systems. Scharler and Baird (2005b) used a CC/AFDW ratio of 0.50 estimated by McLusky (1989), which is in accordance with the CC/AFDW ratios found in this study ranging from 0.49 ± 0.05 (*C. canutus*) to 0.57 ± 0.03 (*L. lapponica*; Table 5).

NC/FW ratios ranged from 0.03 ± <0.01 (*A. penelope*) to 0.05 ± <0.01 (*C. ridibundus*; Table 5). Studying ecosystem and food web structures using nitrogen as proxy is not common yet, although some nitrogen-based models have been constructed (Baird et al. 2011b). Nitrogen plays an important role in primary production of marine ecosystems being either accumulated in systems such as seagrass beds (Asmus and Asmus 2000b), or being a limiting factor (Vitousek and Howarth 1991). The results of this study of the nitrogen content of top predators will be useful data for the construction of future nitrogen-based ecosystem models.

Table 5: DW/FW, AFDW/FW, CC/FW, CC/DW, CC/AFDW, NC/FW, NC/DW ratios (mean ± standard deviation) for various bird, mammal, macrozoobenthos, and fish taxa. Results from this study are displayed in bold

Species	DW/FW	AFDW/FW	CC/FW	CC/DW	CC/AFDW	NC/FW	NC/DW	References
Birds								
C. canutus	**0.39 ± 0.03**	**0.33 ± 0.03**	**0.16 ± <0.01**	**0.41 ± 0.03**	**0.49 ± 0.05**	**0.04 ± <0.01**	**0.11 ± 0.01**	**present study**
L. lapponica	**0.43 ± 0.02**	**0.38 ± 0.02**	**0.22 ± 0.02**	**0.52 ± 0.03**	**0.57 ± 0.03**	**0.04 ± <0.01**	**0.09 ± 0.01**	**present study**
H. ostralegus	**0.44 ± 0.03**	**0.38 ± 0.04**	**0.21 ± 0.02**	**0.49 ± 0.03**	**0.56 ± 0.03**	**0.04 ± <0.01**	**0.10 ± <0.01**	**present study**
C .ridibundus	**0.39 ± 0.03**	**0.32 ± 0.02**	**0.16 ± 0.01**	**0.42 ± 0.02**	**0.51 ± 0.03**	**0.05 ± <0.01**	**0.13 ± <0.01**	**present study**
L. canus	**0.38 ± 0.04**	**0.33 ± 0.04**	**0.17 ± 0.03**	**0.44 ± 0.04**	**0.51 ± 0.03**	**0.04 ± 0.01**	**0.10 ± 0.01**	**present study**
A. penelope	**0.39 ± 0.01**	**0.32 ± 0.01**	**0.17 ± 0.02**	**0.44 ± 0.05**	**0.52 ± 0.02**	**0.03 ± <0.01**	**0.09 ± 0.01**	**present study**
All birds	**0.40 ± 0.03**	**0.34 ± 0.04**	**0.18 ± 0.03**	**0.45 ± 0.05**	**0.53 ± 0.04**	**0.04 ± 0.01**	**0.10 ± 0.02**	**present study**
All birds			0.10					Bradford-Grieve et al. (2003)
All birds			0.04					Leguerrier et al. (2007b)
All birds			0.30					Baird et al. (2004), Saint-Béat et al. (2013b)
All birds					0.50			McLusky (1989), Scharler and Baird (2005b)
Seals								
P. vitulina	**0.34 ± 0.02**	**0.30 ± 0.04**	**0.16 ± 0.02**	**0.47 ± 0.01**	**0.53 ± 0.02**	**0.05 ± <0.01**	**0.10 ± <0.01**	**present study**
seals			0.10					Bradford-Grieve et al. (2003)
seals		0.35	0.15					Pinkerton and Bradford-Grieve (2008)
Macrozoobenthos					0.58			Gätje and Reise (1998b)
Polychaeta	0.14			0.38				Cauffopé and Heymans (2005a)
	0.20	0.16						Ricciardi and Bourget (1998a)
	0.18	0.13						Rumohr (1987)
Oligochaeta	0.17							Cauffopé and Heymans (2005a)
Gastropoda (including shells)	0.09	0.11						Cauffopé and Heymans (2005a)
		0.09						Rumohr (1987)
Bivalvia (including shells)	0.09	0.06						Cauffopé and Heymans (2005a)
		0.06						Ricciardi and Bourget (1998a)
		0.07						Rumohr (1987)
Crustacea	0.21			0.43				Cauffopé and Heymans (2005a)
	0.20	0.15						Rumohr (1987)
Fish								
Pelagic/Planktivorous (e.g. Clupeids, Sand eel)			0.16					Greenstreet et al. (1997), Heath (2007)
Pelagic/Piscivorous (e.g. mackerel species)			0.18					Greenstreet et al. (1997), Heath (2007)
Demersal/Piscivorous (e.g. Gadoids)			0.10					Greenstreet et al. (1997), Heath (2007)
Demersal/Benthivorous (e.g. flat fish species)			0.11					Greenstreet et al. (1997), Heath (2007)

Table 5: DW/FW, AFDW/FW, CC/FW, CC/DW, CC/AFDW, NC/FW, NC/DW ratios (mean ± standard deviation) for various bird, mammal, macrozoobenthos, and fish taxa. Results from this study are displayed in bold

Gadus morua	0.19 ± 0.01	0.14 ± 0.01						Unpublished data from long term monitoring. Alfred Wegener Institute, Wadden Sea Station, Sylt
Platichthys flesus	0.19 ± 0.01	0.16 ± 0.01						
Pleuronectes platessa	0.17 ± 0.01	0.13 ± 0.01						
Clupea harengus	0.20 ± 0.05	0.16 ± 0.04						
Ammodytes tobianus	0.21 ± 0.01	0.17 ± 0.01						
Terrestrial mammals								
Guinea pig	0.37 ± 5.6					0.03 ± 0.4	0.09 ± 1.9	Pace and Rathbun (1945)
Rat	0.36 ± 0.02					0.04		Pace and Rathbun (1945)
Rabbit	0.29 ± 0.04					0.03		Pace and Rathbun (1945)
Dog	0.41 ± <0.01							Pace and Rathbun (1945)
Cat	0.34					0.03		Pace and Rathbun (1945)

3.2. Seals

3.2.1. Body composition

Blubber-skin tissue made the highest contribution to the total fresh weight of harbor seals, and represented on average 40.4 ± 11.5% (from 29.4%, *Phoca vitulina* 2 to 52.3%, *Phoca vitulina* 1; Table 6). The next highest contributions to total fresh weight were Bone (23.4 ± 7.7%) and Muscle (17.8 ± 6.0%). All the other tissues represented less than 4% of the total fresh weight (Table 6).

3.2.2. Relationships among biomass measures in seal tissues

The regression equations for each of the tissues revealed linear relationships passing through the origin between FW and DW, AFDW, CC and NC respectively. The relationships between the biomass measures and the regression equations were shown only for the tissues which contribute the most to total fresh weight (Blubber-skin, Muscle and Bone; Fig. 3 and Table 3). These equations represented a high percentage of the measured data points variation, ranging from 80% (i.e. FW *vs.* NC) to 97% (i.e. FW *vs.* DW) for Blubber-skin, from 95% (i.e. FW *vs.* NC) to 100% (i.e. FW *vs.* DW and

AFDW*)* for Muscle and from 87% (i.e. FW *vs.* NC) to 0.99% (i.e. FW *vs.* DW) for Bone (i.e. R^2, Table 3). Therefore, ratios between the different biomass measures for the seal tissues can be used

Table 6: Fresh weight of each tissue (g) and contribution of each tissue to total fresh weight (%) for the three sampled harbor seals

	***Phoca vitulina* 1**		***Phoca vitulina* 2**		***Phoca vitulina* 3**	
Sampled tissues	**Fresh weight (g)**	**%**	**Fresh weight (g)**	**%**	**Fresh weight (g)**	**%**
Blubber-skin	43800.0	52.3	25100.0	29.4	6400	39.5
Muscle	14000.0	16.7	20600.0	24.1	2000	12.4
Bone	14600.0	17.4	17800.0	20.8	5200	32.1
Blood	1026.9	1.2	-	-	-	-
Liver	3111.0	3.7	2412.0	2.8	500	3.1
Lungs	1153.0	1.4	1774.0	2.1	631	3.9
Pancreas	144.7	0.2	121.1	0.1	25	0.2
Heart	381.0	0.5	561.0	0.7	160	1.0
Kidney	355.2	0.4	434.7	0.5	127	0.8
Spleen	221.8	0.3	186.5	0.2	59	0.4
Stomach-oesophagus	980.5	1.2	1188.0	1.4	145	0.9
Intestine	1496.0	1.8	-	-	310	1.9
Reproductive system	1320.0	1.6	116.9	0.1	10	0.1
Brain	210.0	0.3	201.6	0.2	-	-

3.2.3. Conversion factors of seal tissues

The DW/FW ratios (mean ± standard deviation) of seal tissues ranged from 0.22 ± 0.04 (Intestine) to 0.55 ± 0.17 (Blubber-skin), the AFDW/FW ratios ranged from 0.21 ± 0.03 (Intestine) to 0.54 ± 0.18 (Blubber-skin), the CC/FW ratios ranged from 0.10 ± 0.02 (Intestine) to 0.33 ± 0.15 (Blubber-skin) and the NC/FW ratios ranged from 0.02 ± 0.01 (Brain) to 0.06 ± 0.05 (Spleen; Table 7). Blubber-skin had the highest DW/FW ratio (Table 7), suggesting a low water content. This is consistent with the predominance of hydrophobic lipids in blubber which are stored in low water content (Pearson 2015). The highest AFDW/FW and CC/FW values were also observed in Blubber-skin suggesting a higher organic matter and carbon content than in the other tissues, which can be explained by the large amount of long chain fatty acids containing 14 to 24 carbons in blubber (Käkelä et al. 1995, Iverson 2009). Brain and Blubber-skin tissues had low NC/FW ratios (0.02 ± 0.01 and 0.03 ± 0.02, respectively), indicating low nitrogen content, which is in accordance with the high lipid content in those two tissues (Henderson et al. 1994). Indeed, most lipids do not contain nitrogen (Mc Mahon et al. 2013). To summarize, fatty tissues, and especially blubber tissue, clearly showed differences in its ratios compared to the other tissues.

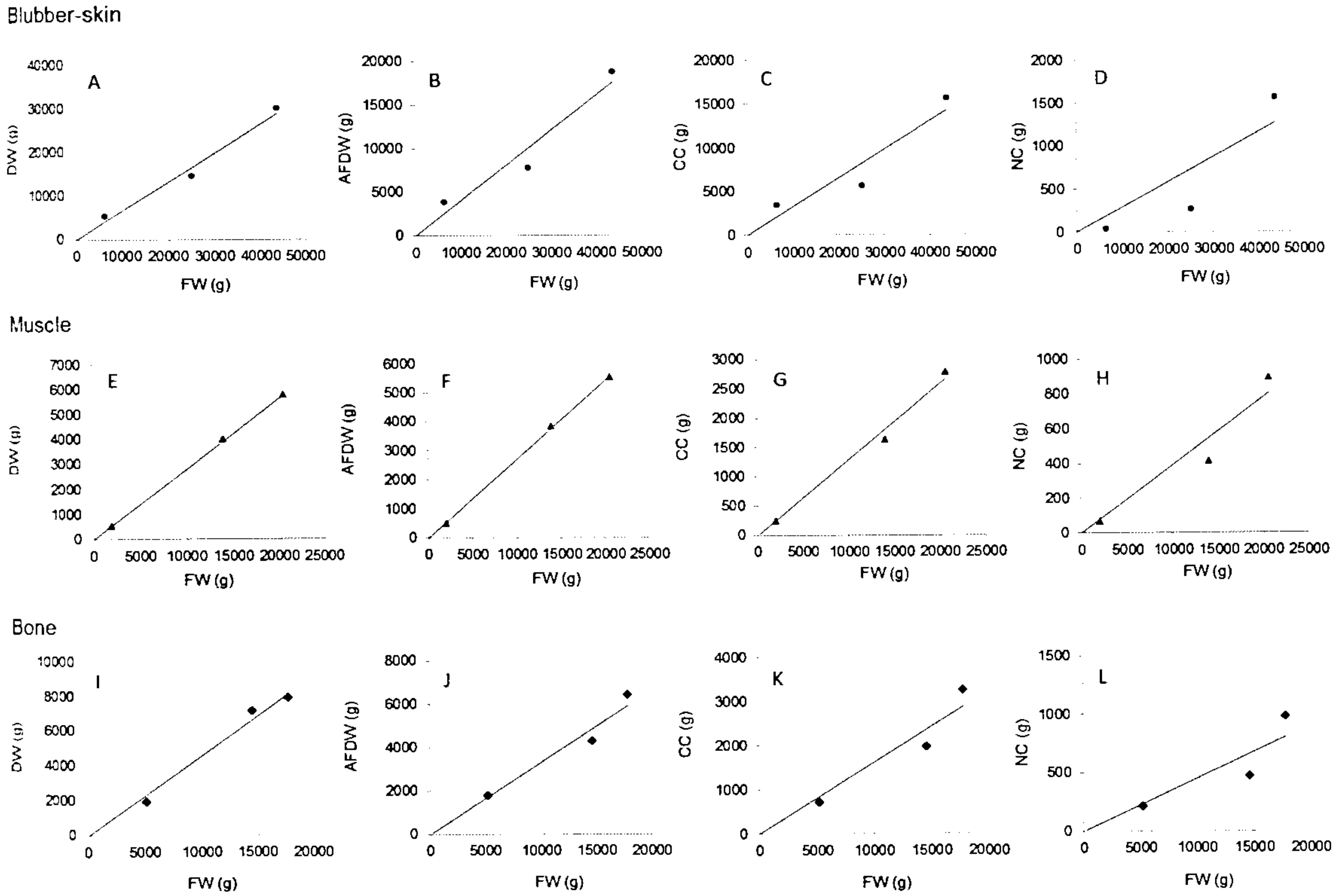


Fig. 3: Relationships for between FW and DW, FW and AFDW, FW and CC, FW and NC for Blubber-skin (A to D), Muscle (E to H), and Bone (I to L) of harbor seals. The regression equations are shown in Table 3

Table 7: Mean and standard deviation of DW/FW, AFDW/FW, CC/FW and NC/FW ratios of the different seal tissues

Tissue	**DW/FW**	**AFDW/FW**	**CC/FW**	**NC/FW**
Blubber-skin	0.55 ± 0.17	0.54 ± 0.18	0.33 ± 0.15	0.03 ± 0.02
Muscle	0.28 ± 0.01	0.27 ± 0.01	0.13 ± 0.01	0.04 ± <0.00
Bone	0.46 ± 0.06	0.33 ± 0.04	0.16 ± 0.03	0.05 ± 0.01
Blood	0.27 ± 0.08	0.26 ± 0.08	0.14 ± 0.04	0.04 ± 0.01
Liver	0.28 ± 0.05	0.26 ± 0.05	0.13 ± 0.02	0.03 ± 0.01
Lung	0.27 ± 0.03	0.25 ± 0.03	0.13 ± 0.02	0.04 ± <0.00
Pancreas	0.24 ± 0.02	0.22 ± 0.01	0.11 ± 0.01	0.03 ± <0.00
Heart	0.24 ± 0.02	0.23 ± 0.02	0.12 ± 0.01	0.03 ± <0.00
Kidney	0.24 ± 0.01	0.23 ± 0.01	0.12 ± 0.01	0.03 ± <0.00
Spleen	0.24 ± 0.01	0.23 ± 0.01	0.12 ± <0.00	0.06 ± 0.05
Stomach-oesophagus	0.25 ± 0.02	0.24 ± 0.03	0.12 ± 0.01	0.04 ± 0.01
Intestine	0.22 ± 0.04	0.21 ± 0.03	0.10 ± 0.02	0.03 ± <0.00
Reproduction system	0.24 ± 0.02	0.23 ± 0.02	0.11 ± 0.01	0.03 ± <0.00
Brain	0.23 ± 0.02	0.22 ± 0.02	0.12 ± 0.01	0.02 ± 0.01

3.2.4. Conversion factor for entire seals

The ratios for entire individuals, calculated taking in account the body composition of each animal, were 0.33, 0.35 and 0.38 for FW/DW, 0.28, 0.32 and 0.36 for FW/AFDW, 0.15, 0.17 and 0.19 for FW/CC and 0.03, 0.04 and 0.04 for FW/NC for *Phoca vitulina* 1, 2 and 3 respectively. The average values for entire seal individuals are displayed in Table 5. The carbon content of each entire animal found in this study (15%, 17% and 19%) was higher than the value of 10% assumed by Bradford-Grieve et al. (2003) (Table 5), who probably underestimated the biomass of seals in their model. Pinkerton and Bradford-Grieve (2008) used 15% for carbon content of fresh weight which is in the order of magnitude of the findings from this study (Table 5).

Using these total ratios, the total DW, total AFDW, total CC and total NC of each entire seal individual were estimated. The relationships between total FW and total DW, total AFDW, total CC and total NC were respectively plotted (Fig. 4) and the corresponding regression equations were computed (Table 3). These regression equations showed linear relationships that pass through the

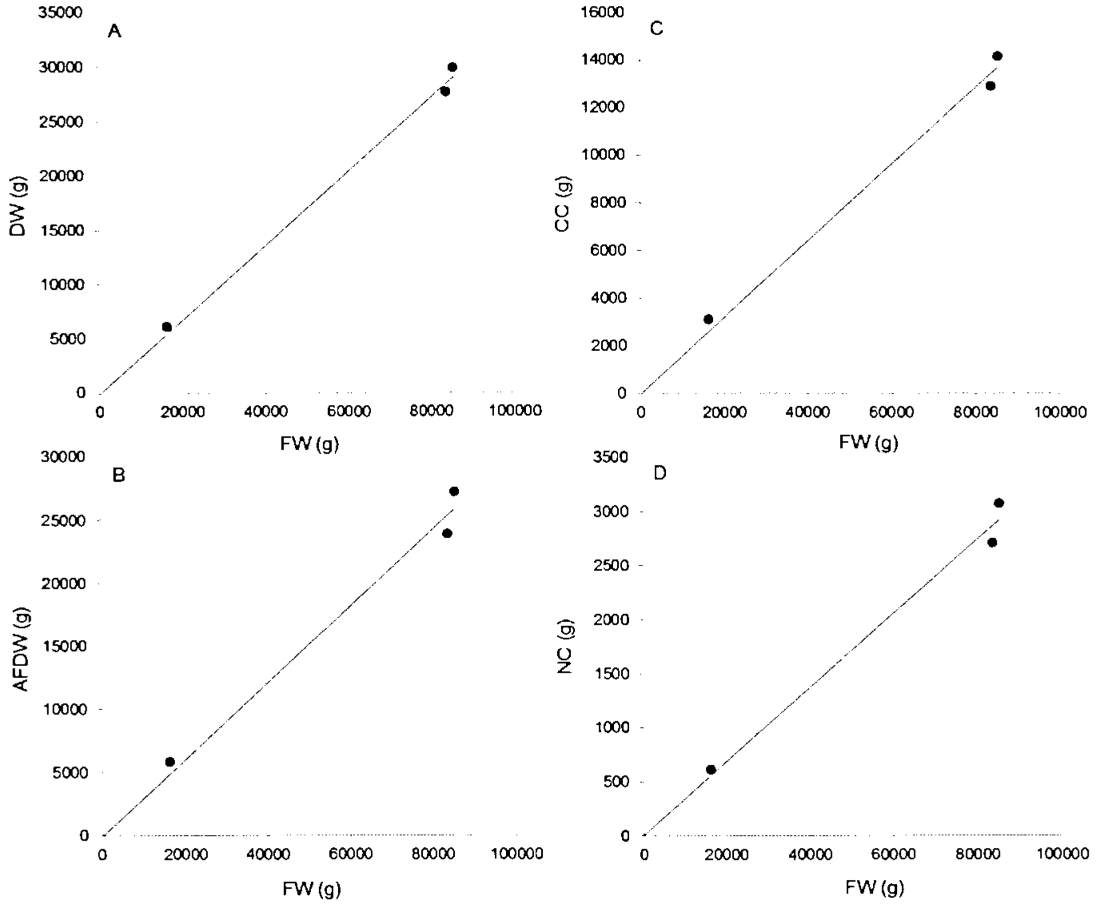


Fig. 4: Relationships between FW and DW, FW and AFDW, FW and CC and FW and NC for entire harbor seal individuals. The regression equations are shown in Table 3

origin between total FW and total DW ($R^2 = 0.99$), total AFDW ($R^2 = 0.98$), total CC ($R^2 = 0.99$) and total NC ($R^2 = 0.99$) respectively (Fig. 4; Table 3). This allows the use of ratios as conversion factors for entire seal individuals.

However, these total ratios must be applied with caution to other studies. Indeed, fatty tissues (e.g. Blubber-skin) in harbor seals were clearly characterized by specific conversion factors differing from those of other tissues (Table 7). This observation implies that variations of the blubber percentage in the body composition would lead to variations of the conversion factors for whole individuals. For pinniped species which undergo huge fasting periods during the reproduction and the molt (Bowen et al. 1992, Atkinson 1997), ratios calculated for each tissue should be preferentially used in relation with the body composition, and particularly the percentage of body fat. The percentage of blubber in phocid seals can be estimated using the following equation determined by Ryg et al. (1990): $\%B = 4.44 + 5693 \times (L \times d) \div FW$ with $\%B$ = % of blubber contribution to total FW, L = the standard length of the seal individual, d = the dorsal blubber thickness and FW = the total FW of the individual.

3.3. Comparison with other taxa

Conversion factors for birds and seals, calculated in this study, were comparable to terrestrial vertebrates (Table 5). The DW/FW ratios of birds and seals were similar to those measured for terrestrial mammal species (i.e. rodent species and rabbits, Table 5) (Pace and Rathbun 1945), suggesting similar body water content. On the other hand, DW/FW ratios measured in this study were clearly higher than those measured in macrozoobenthos taxa (Rumohr et al. 1987, Gätje and Reise 1998a, Ricciardi and Bourget 1998b, Cauffopé and Heymans 2005b) and fish species (Greenstreet et al. 1997) (Table 5), suggesting lower water content in birds and seals. This difference might be related to variations in fat content between the taxa, as fat content is negatively correlated to water content (Friedrich and Hagen 1994). Water content of fish can represent up to 90% of the FW (Dunajski 1980, Friedrich and Hagen 1994) and the typical hydrostatic skeleton of invertebrates (Chapman 1958) also implies high body water content that might also represent up to 90% of the FW (Block 2003). On the contrary, seals have a large proportion of total body weight as fat (Table 6), possibly related to their high DW/FW ratio (Table 7). Furthermore, the presence of keratinous tissue (e.g. claw, hair, feather) – characterized by low water content (10% to 12%) (Taylor et al. 2004) - in birds and mammals might also be responsible for their higher DW/FW ratios. The CC/FW and CC/DW ratios found in this study were higher than the values measured for polychaetes, crustaceans and fish (Table 5), but the small number of available values makes comparisons inconclusive. To summarize, the conversion factors from FW to other biomass measures may vary widely among different taxa and global values should therefore be avoided or carefully applied.

4. Conclusion

This study provides new and essential data about the relationships among biomass parameters and weight conversion factors of top predators, allowing a gap to be filled in ecosystem and food web modelling studies. The relationships between fresh weight and other biomass measures are linear and through the origin for birds and seals. The carbon content of sea birds ranged from 16 ± <0.1% to 22 ± 2% of the fresh weight. The mean carbon content of seals was 16 ± 2% of the fresh weight. Blubber tissue of seals had higher DW/FW, AFDW/FW and CC/FW ratios than the other tissues. Further measurements are necessary to cover a larger number of species and investigating the effect of seasonal variation in body fat content on biomass conversion regressions is an important issue to address. This will allow better estimation of the influence and the role of marine birds and mammals on the ecosystems they live in.

5. Acknowledgements

This study was funded by the German Federal Ministry of Education and Research in the frame of the German-Dutch bilateral Wadden Sea Research "The impact of biological invasions on the food web of the Wadden Sea (INFOWEB)" (FKZ 03F0636A/B) and the German joint research project "STopP – From sediment to top predator" (BMBF, FKZ 03F672B). We are thankful to Ragnhild and Harald Asmus for the supervision of the projects. We would like to thank Ursula Siebert and the team of the Institute for Terrestrial and Aquatic Wildlife Research of University of Veterinary Medicine Hannover Foundation who conducted the seals necropsies as well as the seal hunters for the collection of harbor seals on the beach. We would like to thank Philipp Schwemmer and the colleagues and volunteers of the Research and Technology Centre and the Schutzstation

Wattenmeer e.V. who collected and provided the bird carcasses. We are grateful to Benoit Lebreton and Gaël Guillou for running the carbon and nitrogen analyses at the LIENSs stable isotope facility of the University of La Rochelle. The collection and necropsies of seals were partly funded by the Agency for Coastal Defense National Park and Marine Conservation, as well as The Ministry of Energy, Agriculture, the Environment and Rural Affairs of the Federal State Schleswig-Holstein, Germany.

6. References

Asmus, H., and R. Asmus. 2000. Material exchange and food web of seagrass beds in the Sylt-Rømø Bight: how significant are community changes at the ecosystem level? Helgoland Marine Research **54**:137-150.

Atkinson, S. 1997. Reproductive biology of seals. Reviews of Reproduction **2**:175-194.

Baird, D., H. Asmus, and R. Asmus. 2004. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Marine Ecology Progress Series **279**:45-61.

Baird, D., H. Asmus, and R. Asmus. 2011. Carbon, nitrogen and phosphorus dynamics in nine sub-systems of the Sylt-Rømø Bight ecosystem, German Wadden Sea. Estuarine, Coastal and Shelf Science **91**:51-68.

Baird, D., H. Asmus, and R. Asmus. 2012. Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. Marine Ecology Progress Series **462**:143-162.

Baird, D., P. R. Evans, H. Milne, and P. M. W. 1985. Utilization by shorebirds of benthic invertabrate production in intertidal areas. Oceanogr. Mar. Biol. Ann. Rev. **23**:573-597.

Benke, H., U. Siebert, R. Lick, B. Bandomir, and R. Weiss. 1998. The current status of harbour porpoises (*Phocoena phocoena*) in German waters. Arch. Fish. Mar. Res. **46**:97–123.

Blew, J., K. Günther, B. Hälterlein, R. Kleefstra, K. Laursen, and G. Scheiffarth. 2013. Trends of Migratory and Wintering Waterbirds in the Wadden Sea 1987/1988 - 2010/2011. Wadden Sea Ecosystem No.31. Common Wadden Sea Secretariat, Joint Monitoring Group of Migratory Birds in the Wadden Sea, Wilhelmshaven, Germany.

Block, W. 2003. Water or ice?–the challenge for invertebrate cold survival. Science Progress **86**:77-101.

Bossart, G. D. 2011. Marine Mammals as Sentinel Species for Oceans and Human Health. Veterinary Pathology Online **48**:676-690.

Bowen, W. D. 1997. Role of marine mammals in aquatic ecosystems. Marine Ecology Progress Series **158**:267-274.

Bowen, W. D., O. T. Oftedal, and D. Boness, J. 1992. Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). Physiological Zoology **65**:844-866.

Bradford-Grieve, J. M., P. K. Probert, S. D. Nodder, D. Thompson, J. Hall, S. Hanchet, P. Boyd, J. Zeldis, A. N. Baker, H. A. Best, N. Broekhuizen, S. Childerhouse, M. Clark, M. Hadfield, K. Safi, and I. Wilkinson. 2003. Pilot trophic model for subantarctic water over the Southern Plateau, New Zealand: a low biomass, high transfer efficiency system. Journal of Experimental Marine Biology and Ecology **289**:223-262.

Brasseur, S., B. Diederichs, R. Czeck, L. F. Jensen, A. Galatius, S. Ramdohr, U. Siebert, J. Teilmann, P. Körber, and S. Klöpper. 2013. Aerial surveys of Harbour Seals in the Wadden Sea in 2013 - Is the population growth rate slowing down?

Cauffopé, G., and S. J. Heymans. 2005a. Energy contents and conversion factors for sea lion's prey. Fish. Cent. Res. Rep. **13**:225-237.

Cauffopé, G., and S. J. Heymans. 2005b. Energy contents and conversion factors for sea lion's prey. . Fish. Cent. Res. Rep. **13**:225-237.

Chapman, G. 1958. The hydrostatic skeleton in the invertebrates Biological Reviews **33**:338-371.

Dumont, H. J., I. Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia **19**:75-97.

Dunajski, E. 1980. Texture of fish muscle Journal of Texture Studies **10**:301-318.

Fath, B. D., U. M. Scharler, R. E. Ulanowicz, and B. Hannon. 2007. Ecological network analysis: network construction. Ecological Modelling **208**:49-55.

Friedrich, C., and W. Hagen. 1994. Lipid contents of five species of notothenioid fish from high-Antarctic waters and ecological implications. Polar Biology **14**:359-369.

Furness, R. W., and K. Camphuysen. 1997. Seabirds as monitors of the marine environment. ICES Journal of Marine Science: Journal du Conseil **54**:726-737.

Galatius, A., S. Brasseur, R. Czeck, B. Diederichs, L. F. Jensen, P. Körber, U. Siebert, J. Teilmann, and S. Klöpper. 2014. Aerial surveys of Harbour Seals in the Wadden Sea in 2014 - The highest pup count recorded yet.

Gätje, C., and K. Reise. 1998a. Ökosystem Wattenmeer: Austausch-, Transport-und Stoffumwandlungsprozesse. Springer, Berlin.

Gätje, C., and K. Reise. 1998b. Ökosystem Wattenmeer: Austausch-, Transport-und Stoffumwandlungsprozesse. Springer, Berlin.

Greenstreet, S. P. R., A. D. Bryant, N. Broekhuizen, S. J. Hall, and M. R. Heath. 1997. Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. ICES Journal of Marine Science: Journal du Conseil **54**:243-266.

Heath, M. R. 2007. The consumption of zooplankton by early life stages of fish in the North Sea. ICES Journal of Marine Science: Journal du Conseil **64**:1650-1663.

Henderson, R. J., N. Kalogeropoulos, and M. N. Alexis. 1994. The lipid composition of selected tissues from a Mediterranean monk seal, *Monachus monachus*. Lipids **29**:577-582.

Ings, T. C., J. M. Montoya, J. Bascompte, N. Blüthgen, L. Brown, C. F. Dormann, F. Edwards, D. Figueroa, U. Jacob, and J. I. Jones. 2009. Review: Ecological networks–beyond food webs. Journal of Animal Ecology **78**:253-269.

Iverson, S. J. 2009. Tracing aquatic food webs using fatty acids: from qualitative indicators to quantitative determination. Pages 281-308 Lipids in Aquatic Ecosystems. Springer.

Käkelä, R., R. Ackman, and H. Hyvärinen. 1995. Very long chain polyunsaturated fatty acids in the blubber of ringed seals (*Phoca hispida sp.*) from Lake Saimaa, Lake Ladoga, the Baltic Sea, and Spitsbergen. Lipids **30**:725-731.

Leguerrier, D., D. Degré, and N. Niquil. 2007. Network analysis and inter-ecosystem comparison of two intertidal mudflat food webs (Brouage Mudflat and Aiguillon Cove, SW France). Estuarine, Coastal and Shelf Science **74**:403-418.

Mandema, F. S., J. M. Tinbergen, B. J. Ens, K. Koffijberg, K. S. Dijkema, and J. P. Bakker. 2015. Moderate livestock grazing of salt, and brackish marshes benefits breeding birds along the mainland coast of the Wadden Sea. The Wilson Journal of Ornithology **127**:467-476.

Markert, A., W. Esser, D. Frank, A. Wehrmann, and K.-M. Exo. 2013. Habitat change by the formation of alien Crassostrea-reefs in the Wadden Sea and its role as feeding sites for waterbirds. Estuarine, Coastal and Shelf Science **131**:41-51.

Mc Mahon, K. W., L. L. Hamady, and S. R. Thorrold. 2013. Ocean Ecogeochemistry: A review. Pages 327-374 *in* R. N. Hughes, D. J. Hugues, and I. P. Smith, editors. Oceanography and Marine Biology: an annual review. Taylor and Francis Group.

McLusky, D. 1989. The Estuarine Environment. Page 215 The Estuarine Ecosystem. Glasgow and London: Blackie and Son Ltd, New York: Chapman & Hall 1989.

Moreira, F. 1997. The importance of shorebirds to energy fluxes in a food web of a south European estuary. Estuarine, Coastal and Shelf Science **44**:67-78.

Pace, N., and E. N. Rathbun. 1945. Studies on body composition. 3. The body water and chemically combined nitrogen content in relation to fat content. Journal of Biological Chemistry **158**:685-691.

Pearson, L. E. 2015. Blubber and Beyond: The Role od Lipids in Thermoregulation and Energy Reserves of Phocid Seals. Alaska Fairbanks.

Pinkerton, M., and J. Bradford-Grieve. 2008. Seals: Trophic modelling of the Ross Sea.

Pinkerton, M., J. Bradford-Grieve, and S. Hanchet. 2010. A balanced model of the food web of the Ross Sea, Antarctica. CCAMLR Science **17**:1-31.

Reddy, L., L. A. Dierauf, and F. M. Gulland. 2001. Marine mammals as sentinels of ocean health. CRC handbook of marine mammal medicine: Health, disease and rehabilitation:3-13.

Reijnders, P. J. H., S. M. J. M. Brasseur, T. Borchardt, K. Camphuysen, R. Czeck, A. Gilles, L. F. Jensen, M. Leopold, K. Lucke, S. Ramdohr, M. Scheidat, U. Siebert, and J. Teilmann. 2009. Marine mammals. Thematic Report N°20. In: Marencic, H. and Vlas, J. de, editors. Quality status report 2009. Wadden Sea Ecosystem N°25. Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.

Reijnders, P. J. H., E. H. Ries, S. Tougaard, N. Nørgaard, G. Heidemann, J. Schwarz, E. Vareschi, and I. M. Traut. 1997. Population development of harbour seals *Phoca vitulina* in the Wadden Sea after the 1988 virus epizootic. Journal of Sea Research **38**:161-168.

Ricciardi, A., and E. Bourget. 1998a. Weight-to-weight conversion factors for marine benthic macroinvertebrates. Marine Ecology Progress Series **163**:245-251.

Ricciardi, A., and E. Bourget. 1998b. Weight-to-weight conversion factors for marine benthic macroinvertebrates. Marine Ecology Progress Series.

Rumohr, H., T. Brey, and S. Ankar. 1987. A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. Institut für Meereskunde.

Rumohr, H., Brey, T, Ankar, S. 1987. A Compilation of Biometric Conversion Factors for Benthic Invertebrates of the Baltic Sea. The Baltic Marine Biologists Publication **9**:1-56.

Ryg, M., C. Lydersen, N. H. Markussen, T. G. Smith, and N. A. Øritsland. 1990. Estimating the blubber content of phocid seals. Canadian Journal of Fisheries and Aquatic Sciences **47**:1223-1227.

Saint-Béat, B., C. Dupuy, P. Bocher, J. Chalumeau, M. De Crignis, C. Fontaine, K. Guizien, J. Lavaud, S. Lefebvre, and H. Montanié. 2013. Key features of intertidal food webs that support migratory shorebirds.

Samhouri, J., P. Levin, and C. Harvey. 2009. Quantitative Evaluation of Marine Ecosystem Indicator Performance Using Food Web Models. Ecosystems **12**:1283-1298.

Scharler, U. M., and D. Baird. 2005. A comparison of selected ecosystem attributes of three South African estuaries with different freshwater inflow regimes, using network analysis. Journal of Marine Systems **56**:283-308.

Siebert, U., A. Gilles, K. Lucke, M. Ludwig, H. Benke, K.-H. Kock, and M. Scheidat. 2006. A decade of harbour porpoise occurrence in German waters—Analyses of aerial surveys, incidental sightings and strandings. Journal of Sea Research **56**:65-80.

Siebert, U., P. Wohlsein, K. Lehnert, and W. Baumgärtner. 2007. Pathological Findings in Harbour Seals (*Phoca vitulina*): 1996–2005. Journal of Comparative Pathology **137**:47-58.

Taylor, A. M., R. H. C. Bonser, and J. W. Farrent. 2004. The influence of hydration on the tensile and compressive properties of avian keratinous tissues. Journal of Materials Science **39**:939-942.

Vitousek, P., and R. Howarth. 1991. Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry **13**:87-115.

Chapter 3

Photo flying geese: Robert Waleczek

Diversity of intertidal food webs – functions and features

Sabine Horn[1], Camille de la Vega[1], Ragnhild Asmus[1], Philipp Schwemmer[2], Leonie Enners[2], Stefan Garthe[2], Kirsten Binder[3], Harald Asmus[1]

Affiliation

[1] Alfred-Wegener-Institute Helmholtz Centre for Polar- and Marine Research, Wadden Sea Station Sylt Hafenstr. 43, D-25992 List/ Sylt, Germany

[2] Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany

[3] State Agency for Agriculture, Environment and Rural Areas Schleswig-Holstein, Hamburger Chaussee 25, 24220 Flintbek, Germany

Corresponding author: sabine.horn@awi.de

Keywords: Ecosystem models, network analysis, coastal birds, carbon flow, habitat diversity

Abstract:

The determination of food web structures using Ecological Network Analysis (ENA) is a helpful tool to get insight into complex ecosystem processes. In the World Heritage Site of the Wadden Sea, physical forces form intertidal areas to diverse habitats that differ in their ecological functioning. In the present study, six different intertidal habitats (cockle field, razor clam field, mud flat, mussel bank, sand flat and seagrass meadow) were analyzed using ENA to determine similarities and characteristic differences in the food web structure of the systems. All six systems were well balanced between their degree of organization and their redundancy. However, they differed in their detailed features. The cockle field and the mussel bank exhibited a strong dependency on external imports. The razor clam field appeared to be a rather small system with low energy transfer. In the mud flat, microphytobenthos was used as a main food source and the system appeared to be not fully developed yet. Bird predation was the most pronounced in the sand flat and the seagrass meadow and led to an increase in energy transfer, pathways lengths and parallel trophic cycles in

these habitats. Habitat diversity is an important trait of the Wadden Sea as each subsystem has a specific role in the entire ecosystem and probably improves its overall stability.

1. Introduction

The World Heritage Site of the Wadden Sea is one of the world's most valuable stretches of coastline (Kabat et al. 2012). It consists of vast bare sand and mud flats that emerge twice per day during low tide forming a unique ecosystem (Reise et al. 2010, Kabat et al. 2012). The highly productive intertidal areas are characterized by a rich benthic fauna supporting millions of coastal birds that visit the Wadden Sea for foraging, resting or breeding on the East Atlantic Flyway (Reise et al. 2010, Kabat et al. 2012, Blew et al. 2015, Koffijberg et al. 2015).

The interaction of physical forces and biological activities turn the extensive intertidal flats into heterogeneous habitats either represented by differences in their sediment characteristics or in their dominant species aggregation (Reise et al. 2010). This heterogeneity is an important requirement for different macrobenthic species to find a settling ground as well as for higher predators such as birds or fish that might be specialized to forage in a certain environment.

However, little is known about the ecological functioning of the different habitat types and their role in the ecosystem of the Wadden Sea. Food web modeling and especially Ecological Network Analysis (ENA) are appropriate tools to gain insight into the complexity of system structures. Indeed, ENA accounts for the totality of the interactions between the various components of the system (Leguerrier et al. 2003). ENA allows a simplified representation of the natural system based on flows of energy between different feeding levels resulting in a simplified representation of the natural system (Heymans et al. 2014). The methodology was developed to assess the complex interactions within an ecosystem using a set of algorithms from which several system properties can be derived (Scharler and Baird 2005a, Schückel et al. 2015). Results from ENA provide information that can be used to assess environmental issues but also to describe the system's status in terms of maturity, health, stability and stress (Scharler and Baird 2005a, Schückel et al. 2015).

There were already several approaches to describe intertidal areas using ENA. The food web of the Sylt-Rømø Bight in the northern Wadden Sea was already intensively studied in different energy units and differences in the recycling of carbon, nitrogen and phosphorus have been found in this tidal basin (Baird et al. 2004, Baird et al. 2007, 2008, 2011a). Furthermore, invasive species are known to have settled in the Wadden Sea (e. g. Sylt-Rømø Bight) and they can change the trophic functioning of a system (Baird et al. 2012). Schückel et al. (2015) described the benthic food web of the Jade-Bay (south-eastern Wadden Sea) from the 1930s to the present status and found differences in the functioning of the bay probably caused by climatic changes and anthropogenic impacts such as eutrophication. However, food web studies focusing on birds are very rare as birds are difficult to include in quantitative models due to their mobility. In the French Marénnes-Oléron Bay the influence of migratory shorebirds on the food web structure of mud flats was shown by Saint-Béat et al. (2013a) by regularly counting the birds feeding in the bay. But in the majority of cases, roosting bird data from the coastline is used for modeling (Baird et al. 2004, Baird et al. 2007) that is then interpolated to the intertidal areas. The bird numbers therefore often underlie large approximations as it is not known in which habitats the birds prefer to feed.

In the present study, the structure and functioning of different intertidal habitats was studied in a modeling approach including foraging birds as top predators. The study site is situated between several islands that are known to be important breeding and resting places for various bird species which take up food on the intertidal flats (Reise et al. 2010). Despite its importance for birds, the area is only rarely studied and differs from already investigated intertidal areas in terms of its connection to the open North Sea and its habitat heterogeneity. The main goals of this study were 1) to create food web models of six different habitats in the Wadden Sea that are known to be strongly used by foraging birds and 2) to determine the similarities and differences in the functioning of the distinct systems to find characteristic features for the habitats types.

2. Material and Methods

2.1 Study site

Samples for network construction were collected from summer 2013 to summer 2015 in the German part of the Wadden Sea between the islands Amrum, Föhr, Langeness and the western coast of the federal state of Schleswig-Holstein (Fig. 1, Chapter 1, page 56). The study site had a total size of 655.4 km^2 with an intertidal area of 286.3 km^2. Six different habitats of the intertidal area (i.e. cockle field, razor clam field, mud flat, mussel bank, sand flat and seagrass meadow) were either defined by their sediment type (mud flat and sand flat) or by their dominating species (cockle field, razor clam field, mussel bank and seagrass meadow).

Cockle fields cover about 6.3 $km^2$of the area and are characterized by a very high abundance of the common cockle *Cerastoderma edule* which can reach densities of up to several thousand individuals per m^2 (Jensen 1992). A rather new habitat are the razor clam fields that are formed by aggregations of the immigrant American razor clam *Ensis directus* and are located in wide areas of the lower intertidal (31.5 km^2) and subtidal areas of the study site. Mud flats are soft bottom habitats and occur in sheltered areas with low current velocities close to the shore. About 23.1 km^2 of the area are mud flats (Brockmann Consult GmbH 2014). Mussel banks are small-scaled epibenthic structures dominated by the blue mussel *Mytilus edulis* mixed with the invasive Pacific oyster *Crassostrea gigas* since the late 1980s. Only 0.6 km^2 of the study site represent mussel banks (Brockmann Consult GmbH 2014). The most extended habitat type in the study area are sand flats with 160.3 km^2 (Brockmann Consult GmbH 2014). They are often dominated by dense populations of the lugworm *Arenicola marina*. 33.3 km^2 of the area are overgrown by seagrass meadows (Brockmann Consult GmbH 2014) dominated by the dwarf eelgrass *Zostera noltei* with sparse occurences of the common eelgrass *Zostera marina*.

A transect of 200 to 250 m length that included five to six sampling stations located in a distance of 50 m away from each other was placed in each habitat. Each station was covered by a 25x25 cm frame to define the area for quantitative sampling. Before each sampling the frames were photographed. The samples were taken seasonally to receive the required data for network construction.

2.2 Sampling

In this study, only benthic components, phytoplankton and birds were sampled and included in analyses as the main focus of this study was the interaction between intertidal areas and foraging birds. Each species or group of species was represented by a compartment within the model (Table 1). In the analyzed models birds were the only modules of higher trophic levels. Production used by other predators (i.e. Fish, seals) is therefore included in the export from the particular compartment.

2.2.1 Macrobenthos

Epifauna and macrophytes within each of the 25x25 cm frame were removed from the surface by hand. Infauna was sampled with a 10x10 cm corer about 15 cm deep and afterwards sieved through a 0.5 and 1 mm mesh-cascade. Samples were sorted and organisms were identified to the most precise taxonomic level and counted.

For biomass determination, each species of macrofauna and the macrophytes were dried in an oven at 50°C until constant dry weight. They were then burned at 500°C in a furnace for 5 h. Ash free dry weight (AFDW) was estimated by subtracting the ash weight from the dry weight and further transformed to mg Carbon (C) using the conversion factor 0.58 for invertebrates (Asmus and Asmus 1998).

2.2.2 Microphytobenthos

Samples for microphytobenthos (MPB) were taken by outpacing the first cm of the sediment surface with a corer (ø 1 cm). The sediment was freeze-dried and Chlorophyll a content was measured following the protocol of Edler (1979) and calculated according to Lorenzen (1967). The Chlorophyll a content was multiplied by 50, to convert it to mg C (Riemann et al. 1989).

2.2.3 Phytoplankton

Chlorophyll a data for phytoplankton was taken from a long-term monitoring program conducted monthly in the project area by the State Agency for Agriculture, Environment and Rural Areas of Schleswig-Holstein (LLUR). The data was converted to mg C by multiplying Chlorophyll a values by 50 (Riemann et al. 1989).

2.2.4 Birds

Birds, except for eider ducks (*Somateria mollissima*), were counted depending on weather conditions one to three times per season in each habitat in a predefined area of 0.01 km^2 (cockle field) to 0.16 km^2 (mussel bank) and identified to species level. Counts occurred in 10 min intervals for 2 h. Only the abundance of foraging birds was included for the analyses.

Eider duck data was taken from regular aerial counts and then interpolated to the habitat types they feed on (i.e. mussel bank, cockle field, razor clam field) using the total size of the habitats in the study site and the time the eider ducks spend feeding on the habitat type according to their diet composition.

Abundance of the bird data was transformed to biomass using average body fresh weight values for each species (FTZ, unpublished data, Bezzel 1985) and then converted into carbon units (Horn and de la Vega 2016).

2.2.5 Additional data

In the study site, no data was available for particulate organic carbon in the sediment (sediment POC), suspended particulate organic carbon in the water column (suspended POC), meiofauna (MEI) and bacteria (BAC). To create more realistic food web models these compartments were included in the network using data from similar habitats of the Sylt-Rømø Bight (Baird et al. 2007).

2.3 Network construction

The construction of an ecological network requires information about the standing stock and energy budget of each compartment and about flows between compartments (i.e. who eats whom at what rate?, Fath 2007).

The determination of standing stock data is described above. Averaged values have been used for network construction (Table 1). Energy budgets were taken from recent published and unpublished literature and are summarized with references in Table 1. Diet information for benthic compartments were taken from Baird et al. (2004). Each compartment was balanced in terms of its energy budget following the equations of Parsons et al. (1973)

Gross primary production = Net primary production + Respiration

Consumption = Production + Respiration + Egestion

Several bird species feed on both intertidal areas and terrestrial environments but also on prey items that were not included in the present study such as fish. For those species (i.e. *Anas acuta, Anas penelope, Anas plathyrhynchos, Arenaria interpres, Branta bernicla, Charadrius hiaticula, Chroicocephalus ridibundus, Haematopus ostralegus, Larus argentatus, Larus canus, Larus fuscus, Larus marinus, Numenius arquata, Numenius phaeopus, Tadorna tadorna*), the energy budget was adapted and the consumption value was decreased from 100% to the estimated percentage of time the birds spend feeding on intertidal flats. The diet matrix of the birds is given in Table 2. If a prey item of the diet spectrum of a particular bird species was not available in one of the habitats, the missing consumption flux was equally distributed to the available prey items.

For each of the six habitats a carbon flow model was constructed. Biomass data was expressed in $mgC.m^{-2}$ and respiration, egestion and flows between compartments (i. e. production and consumption rates) as well as imports and exports to and from compartments were given in $mgC.m^{-2}.d^{-1}$.

Number of compartments ranged from 29 in the razor clam field to 48 in the mussel bank. The difference in the number of compartments was due to the restriction of some species to single habitat types and not due to a different degree of aggregation between the systems that might have biased comparisons of the ENA indices (Mann et al. 1989, Baird et al. 1991, Baird and Ulanowicz 1993, Abarca-Arenas and Ulanowicz 2002, Baird et al. 2009). It was shown that an artificial homogenizing of system structure with zero-valued compartments might influence the results as well (Fath et al. 2013). Therefore, we decided to represent the six habitats as they occurred in nature and tolerated the discrepancy in the number of compartments. The results of the models from this study can then be compared.

The total input of each compartment was balanced by the total output. If consumption of a compartment exceeded the production of a compartment of the preceding trophic level, an input was added to this compartment to fulfill the predator's needs. Since this happened mostly due to bird predation it was assumed that the imported prey was consumed outside of the defined habitat, a plausible modus for mobile predators such as birds. Unused production was considered to be exported to one half as prey for compartments not included in this study such as fish or via resuspension during next high tide in terms of MPB. The other half was assumed to become sediment POC and flew back to the system. For phytoplankton, suspended POC and birds, the unused production was completely exported. Excess sediment POC was assumed to be exported from the system due to tidal flushing during storm events in the course of the year.

All six models therefore represented systems in steady-state.

Table 1: Standing stocks in $mgC.m^{-2}$ of the compartments for the six habitats, energy rations applied to calculate the energy budget of each compartment in $mgC.m^{-2}.d^{-1}$ and references of the energy ratios. B=Biomass, GPP=Gross primary production, NPP=Net primary production, P=Production, R=Respiration, E=Egestion, C=Consumption

Compartment	**Cockle field**	**Razor clam field**	**Mud flat**	**Mussel bank**	**Sand flat**	**Seagrass meadow**	**GPP/B**	**R/B**	**NPP/B**		**Source of ratios**
Phytoplankton	605.83	706.80	468.51	605.83	468.51	468.51	0.4205	0.1828	0.2378		Baird et al. (2004)
Macrophyta	428.02	-	-	105,400.21	2,855.20	3,819.14	0.0274	0.0153	0.0121		Baird et al. (2004)
MPB	420.95	309.01	961.51	408.62	296.03	217.53	7.1782	2.4902	4.6880		Baird et al. (2004)
							P/B	**R/B**	**E/B**	**C/B**	
BAC	625.00	625.00	625.00	625.00	625.00	625.00	0.0788	0.1744	0.0610	0.3924	Baird et al. (2007), Baird et al. (2004)
MEI	1,000.00	1,000.00	500.00	500.00	1,000.00	1,000.00	0.0219	0.0834	0.1832	0.2885	Baird et al. (2007), Baird et al. (2004)
Anthozoa	-	-	-	6,860.88	-	-	0.0023	0.0087	0.0013	0.0123	Asmus (1987), Baird et al. (2004)
Cerastoderma edule	129,451.19	-	15,709.57	13,056.26	3,942.88	3,363.42	0.0050	0.0016	0.0184	0.0249	Baird et al. (2004)
Crassostrea gigas	-	-	-	42,450.47	-	-	0.0010	0.0130	0.0008	0.0148	Baird et al. (2012)
Ensis directus	-	12,355.62	-	-	-	-	0.0065	0.0206	0.0014	0.0285	Merkel (2015)
Fobulina fabula	-	6.82	-	-	-	-	0.0082	0.0015	0.0435	0.0533	Baird et al. (2004)
Macoma balthica	6,832.16	1,184.65	1,134.98	6.47	1,811.77	730.11	0.0082	0.0015	0.0435	0.0533	Baird et al. (2004)
Mya arenaria	408.12	-	-	-	1,792.66	-	0.0022	0.0051	0.0037	0.0109	Baird et al. (2004)
Mytilus edulis	199.79	-	-	292,734.20	495.78	-	0.0010	0.0054	0.0009	0.0073	Baird et al. (2004)
Balanidae spp.	-	-	-	24,184.15	-	7.95	0.0033	0.0087	0.0013	0.0133	Baird et. al. 2008
Carcinus+Hemigrapsus	345.10	-	6,890.40	12,332.60	-	93.06	0.0042	0.0063	0.0139	0.0243	Baird et al. (2004)
Crongon spp.	378.33	1,223.80	58.73	146.62	-	-	0.0110	0.0378	0.0110	0.0598	Baird et al. (2004)
Pycnagonum litorale	-	-	-	90.48	-	-	0.0190	0.0268	0.0054	0.0265	Baird et al. (2004)
small crustaceons	150.78	120.18	13.59	128.25	5.48	767.97	0.0040	0.0171	0.0054	0.0265	Baird et al. (2004)
Crepidula fornicata	-	-	-	287.38	-	-	0.0009	0.0062	0.0124	0.0195	Asmus (1987), Baird et al. (2012)
Lepidochitona cinerea	-	-	-	283.50	-	-	0.0050	0.0062	0.0124	0.0235	Asmus (1987), Baird et al. (2004)
Littorina littorea	990.64	-	660.16	18,115.03	1,275.77	993.02	0.0020	0.0062	0.0124	0.0206	Baird et al. (2004)
Peringia ulvae	11,186.09	0.81	17,248.54	29.67	17,514.95	11,914.42	0.0180	0.0060	0.0291	0.0532	Asmus (1987), Baird et al. (2004)

Table 1 (continued): Standing stocks in $mgC.m^{-2}$ of the compartments for the six habitats, energy rations applied to calculate the energy budget of each compartment in $mgC.m^{-2}.d^{-1}$ and references of the energy ratios. B=Biomass, GPP=Gross primary production, NPP=Net primary production, P=Production, R=Respiration, E=Egestion, C=Consumption

Retusa obtusa	33.10	2.38	36.02	-	1,124.62	28.94	0.0039	0.0060	0.0291	0.0391	Baird et al. (2004)
Nemertea	-	-	-	181.98	175.29	-	0.0065	0.0105	0.0380	0.0549	Asmus (1987), Baird et al. (2004)
Oligochaeta	33.97	8.60	418.07	3,062.51	966.26	61.72	0.0027	0.0267	0.0135	0.0736	Baird et al. (2004)
Arenicola marina	1,623.65	-	-	742.40	4,833.16	2,033.25	0.0072	0.0067	0.0339	0.0478	Baird et al. (2004)
Capitella capitata	108.57	9.47	45.61	331.86	54.61	10.29	0.0054	0.0231	0.0567	0.0850	Baird et al. (2004)
Eteone spp.	70.64	7.54	7.37	37.06	44.13	64.49	0.0048	0.0007	0.0084	0.0285	Baird et al. (2004)
Heteramastus filiformis	-	-	-	52.21	-	-	0.0055	0.0104	0.0700	0.0859	Baird et al. (2004)
Lanice conchilega	90.19	-	2.78	5,502.67	-	-	0.0052	0.0100	0.0046	0.0199	Baird et al. (2004)
Lepidonotus squamatus	-	-	-	376.30	-	-	0.0033	0.0105	0.0380	0.0517	Asmus (1987), Baird et al. (2004)
Nephtys spp.	956.39	828.49	-	198.48	-	5.74	0.0110	0.0105	0.0380	0.0595	Baird et al. (2004)
Nereis spp.	1,450.88	-	9,243.83	1,294.15	455.63	382.76	0.0048	0.0117	0.0307	0.0472	Nithart et al. (1999), Baird et al. (2004)
Phyllodoce spp.	259.84	-	-	601.32	704.44	-	0.0027	0.0296	0.0039	0.0360	Baird et al. (2004)
Pygospio elegans	45.80	16.52	24.26	4.41	29.49	57.43	0.0037	0.0170	0.0073	0.0280	Baird et al. (2004)
Scoloplas armiger	38.73	191.36	24.85	63.64	2,761.94	304.01	0.0044	0.0073	0.0189	0.0306	Nithart et al. (1999), Baird et al. (2004)
small polychaetes	55.16	34.16	38.34	13,507.19	4.93	5.34	0.0045	0.0146	0.0084	0.0285	Baird et al. (2004)
Tharyx killariensis	25.15	-	80.73	6.53	1.86	91.98	0.0055	0.0104	0.0111	0.0272	Baird et al. (2004)
Anas acuta	-	-	-	-	-	223.79	0.0029	0.0606	0.0346	0.0981	Baird et al. (2004)
Anas penelope	-	-	-	-	2,883.24	3,592.84	0.0006	0.0179	0.0104	0.0289	Baird et al. (2004)
Anas platyrhynchos	-	-	33.85	7.58	254.81	348.33	0.0006	0.0210	0.0125	0.0341	Baird et al. (2004)
Arenaria interpres	-	-	-	1.12	5.99	5.55	0.0018	0.1072	0.0277	0.1367	Baird et al. (2004)
Branta bernicla	-	-	-	-	239.50	1,429.48	0.0010	0.0250	0.0140	0.0400	Baird et al. (2004)
Calidris alpina	-	-	15.85	-	5.70	584.34	0.0021	0.1198	0.0310	0.1528	Baird et al. (2004)

Table 1 (continued): Standing stocks in mgC.m^{-2} of the compartments for the six habitats, energy rations applied to calculate the energy budget of each compartment in mgC.m^{-2}.d^{-1} and references of the energy ratios. B=Biomass, GPP=Gross primary production, NPP=Net primary production, P=Production, R=Respiration, E=Egestion, C=Consumption

Calidris canutus	-	-	-	-	99.97	588.30	0.0037	0.1963	0.0519	0.2519	Baird et al. (2004)
Charadrius hiaticula	-	-	-	-	5.33		0.0021	0.1198	0.0310	0.1528	Baird et al. (2004)
Chroicocephalus ridibundus	23.43	3.86	94.23	1.63	31.01	165.59	0.0023	0.0537	0.0140	0.0700	Baird et al. (2004)
Haematopus ostralegus	359.25	7.02	79.00	16.12	366.54	916.81	0.0045	0.1040	0.0271	0.1357	Baird et al. (2004)
Larus ogentatus	50.22	95.10	39.37	7.67	124.39	136.35	0.0015	0.0452	0.0121	0.0588	Baird et al. (2004)
Larus canus	23.49	5.01	18.40	6.46	56.25	24.99	0.0018	0.0390	0.0106	0.0514	Baird et al. (2004)
Larus fuscus	-	14.29	18.49	-	-	-	0.0004	0.0117	0.0031	0.0152	Baird et al. (2004)
Larus marinus	-	19.60	-	-	-	-	0.0006	0.0003	0.0078	0.0086	Baird et al. (2004)
Limicola falcinellus	-	-	-	-	-	1.80	0.0021	0.1198	0.0310	0.1528	Baird et al. (2004)
Limosa lapponica	97.85	10.55	187.15	10.67	909.63	309.34	0.0037	0.1593	0.0407	0.2037	Baird et al. (2004)
Numenius arquata	80.20	2.04	28.20	7.66	98.59	369.31	0.0018	0.0551	0.0147	0.0716	Baird et al. (2004)
Numenius phaeopus	-	-	-	-		33.56	0.0018	0.0551	0.0147	0.0716	Baird et al. (2004)
Pluvialis squatarola	-	-	10.62	1.15	63.12	105.75	0.0031	0.0875	0.0219	0.1125	Baird et al. (2004)
Recurvirostra avosetta	-	-	39.82	-	-	-	0.0111	0.1667	0.0444	0.2222	Baird et al. (2004)
Somateria mollissima	38.95	6.81	89.72	206.54	-	-	0.0027	0.1060	0.0271	0.1358	Baird et al. (2004)
Tadorno tadorna	384.99	-	95.91	-	290.08	94.79	0.0024	0.0809	0.0241	0.1074	Baird et al. (2004)
Tringa erythropus	-	-	-	-	-	41.99	0.0036	0.1904	0.0503	0.2443	Baird et al. (2004)
Tringo nebuloria	-	-	4.07	0.55	7.35	31.65	0.0033	0.1767	0.0467	0.2267	Baird et al. (2004)
Tringa totanus	187.19	-	81.47	4.38	58.08	139.89	0.0036	0.1904	0.0503	0.2443	Baird et al. (2004)
sediment POC	19,000.00	19,000.00	19,000.00	19,000.00	19,000.00	19,000.00					Baird et al. (2007)
suspended POC	167.44	167.44	167.44	167.44	167.44	167.44					Baird et al. (2007)

Table 2: Diet matrix of the birds with references, numbers show the percentage contribution of each prey compartment i to the diet of each bird (consumer compartment j)

	Consumer compartment j																										
Prey compartment i	*Anas acuta*	*Anas penelope*	*Anas plathyrhynchos*	*Arenaria interpres*	*Branta bernicla*	*Calidris alpina*	*Calidris canutus*	*Charadrius hiaticula*	*Chroicocephalus ridibundus*	*Haematopus astralegus*	*Larus argentatus*	*Larus canus*	*Larus fuscus*	*Larus marinus*	*Limicola falcinellus*	*Limosa lapponica*	*Numenius arquata*	*Numenius phaeopus*	*Pluvialis squatarola*	*Recurvirostra avosetta*	*Somateria mollissima*	*Tadorna tadorna*	*Tringa erythropus*	*Tringa nebularia*	*Tringa totanus*
Makrophyta	0.25	0.27	0.250	-	0.500	-	-	0.001	-	-	-	-	-	-	-	-	-	-	0.019	-	-	0.030	-	-	-
Anthozoa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cerastoderma edule	-	-	-	0.280	-	-	0.517	-	0.070	0.300	0.200	0.050	0.030	-	-	-	0.150	0.150	-	-	0.210	0.030	0.040	0.040	0.040
Crassostrea gigas	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ensis directus	-	-	-	-	-	-	-	-	-	0.100	0.150	-	0.060	0.100	-	-	-	-	-	-	0.100	-	-	-	-
Fabulina fabula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Macoma balthica	0.009	-	0.019	-	-	-	0.250	0.032	0.050	0.100	0.010	-	-	-	-	0.033	0.050	0.050	0.004	-	-	0.090	0.050	0.050	0.050
Mya arenaria	0.007	-	0.008	-	-	-	-	-	0.005	-	-	0.026	-	-	-	-	-	-	-	-	-	-	-	-	-
Mytilus edulis	-	-	-	0.280	-	-	0.043	-	-	0.100	0.010	0.010	0.030	-	-	-	-	-	-	-	0.328	0.025	-	-	-
Balanidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.020	-	-	-	-
Carcinus maenas	0.005	-	0.006	0.043	-	-	-	0.020	0.020	-	0.200	0.040	-	-	-	0.015	0.200	0.200	0.003	0.100	-	0.010	0.100	0.100	0.100
Crangon crangon	-	-	0.006	-	-	-	-	-	0.100	-	-	0.080	-	-	-	0.016	0.050	0.050	-	0.010	-	-	0.030	0.030	0.030
Pygnogonum littorale	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
small crustaceans	0.010	-	0.058	0.004	-	0.143	-	0.020	0.010	-	-	0.025	-	-	0.143	-	-	-	0.003	0.010	-	0.080	0.300	0.300	0.300
Crepidula fornicata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-
Lepidochitona cinerea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Littorina littorea	-	-	-	0.120	-	-	-	0.030	-	-	-	-	-	-	-	-	-	-	0.004	-	0.155	0.095	-	-	-
Peringia ulvae	0.279	-	0.120	0.120	-	0.087	0.190	0.030	0.020	-	-	0.005	-	-	0.087	-	-	-	0.004	0.370	0.177	0.450	0.150	0.150	0.190
Retusa obtusa	-	-	-	-	-	-	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	0.050	-	-	-
Nemertea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oligochaeta	0.019	-	0.003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-	-
Arenicola marina	-	-	-	-	-	-	-	0.040	0.060	0.150	-	0.010	-	-	-	0.033	0.350	0.350	0.028	-	-	-	-	-	-
Capitella capitata	0.019	-	0. 003	-	-	-	-	0.250	-	-	-	-	-	-	-	-	-	-	0.245	-	-	-	-	-	-

Table 2: Diet matrix of the birds with references, numbers show the percentage contribution of each prey compartment i to the diet of each bird (consumer compartment j)

Eteone longa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heteromastus filiformis	0.019	-	0.003	-	-	0.050	-	0.250	0.010	-	-	0.010	-	-	0.050	-	-	-	0.245	-	-	-	-	-	-
Lanice conchilega	0.019	-	0.003	-	-	0.020	-	-	0.050	-	-	0.010	-	-	0.020	0.029	0.050	0.050	-	-	-	-	-	-	-
Lepidonotus squamatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nephthys hombergi	0.019	-	0.003	-	-	0.100	-	-	-	0.050	0.005	0.010	-	-	0.100	0.216	0.050	0.050	-	-	-	-	0.060	0.060	0.060
Nereis diversicolor	0.019	-	0.003	0.003	-	0.500	-	0.030	0.090	0.100	0.005	0.120	0.030	-	0.500	0.276	-	-	0.200	0.500	-	0.080	0.170	0.170	0.200
Phyllodoce spp.	0.019	-	0.003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pygospio elegans	0.019	-	0.003	-	-	0.050	-	-	-	-	-	-	-	-	0.050	-	-	-	-	-	-	-	-	-	-
Scoloplos armiger	0.019	-	0.003	-	-	-	-	0.250	-	0.050	-	0.010	-	-	-	0.382	-	-	0.245	-	-	-	-	-	-
small polychaetes	0.019	-	0.003	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tharyx killariensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fish/offshore prey	-	-	-	-	-	0.50	-	-	0.010	-	0.020	0.060	0.300	0.800	0.50	-	-	-	-	-	-	-	0.100	0.100	0.030
Terrestrial	0.250	0.730	0.500	0.150	0.500	-	-	0.050	0.500	0.050	0.400	0.550	0.550	0.100	-	-	0.100	0.100	-	-	-	0.060	-	-	-
Reference	Nienhuis and Groenendijk (1986), Baldwin and Lovvorn (1994), Meltofte et al. (1994)	Mathers and Montgomery (1998)	Nienhuis and Groenendijk (1986), Baldwin and Lovvorn (1994), Meltofte et al. (1994), Baird et al. (2012)	Höfmann and Hoerschelmann (1969), Harris (1979)	Mathers and Montgomery (1998)	Schwemmer et al. (2016)	Piersma et al. (1993)	Baird et al. (1985)	Kubetzki and Garthe (2003), Schwemmer (2011)	Schwemmer et al. (2012)	FTZ, unpublished data	Kubetzki and Garthe (2003), FTZ, unpublished data	Kubetzki and Garthe (2003)	FTZ, unpublished data	diet similar to *C. alpina*	Scheiffarth (2001)	Schwemmer et al. (2012)	Diet similar to *N. arquata*	Pienkowski (1980)	FTZ, unpublished data	FTZ, unpublished data	Buxton and Young (1981)	Changed after values for *T. totanus* (Goss-Custard 1977)	Changed after values for *T. totanus* (Goss-Custard 1977)	Goss-Custard (1977)

2.4 Network analysis

The methodology of Ecological Network Analysis (ENA) is based on an input-output-analysis and is detailed in Kay et al. (1989) and reviewed by Ulanowicz (2004). In this study the software package enaR for R statistics was used to conduct all the analyses (Borrett and Lau 2014, Lau et al. 2015). ENA provides several helpful tools to describe the functioning and organization of an ecosystem. One of these tools is the system attributes. A collection of various global system indices describing the developmental and organizational state (Schückel et al. 2015) but also the cycling and resilience of a system. The following indices were analyzed and described in the present study:

1) **Total System Throughput (TST):** The TST is the sum of all flows in the system and represents the system's size and activity (Wulff et al. 1989). The higher the value the bigger and more active is the system.
2) **Development Capacity (DC):** This value describes the system's potential to develop by calculating the particular set of connections and total throughflow. It is the upper limit of the system's Ascendency (Wulff et al. 1989).
3) **Ascendency (A):** It is a measurement of the activity, the size, the organization and the evenness of energy flows. High values imply complex trophodynamic relations and high system productivity (Wulff et al. 1989). Ascendency is furthermore correlated with a higher degree of specialization in the system.

   The **Relative Ascendency (A/DC)** is the ratio between A and DC and represents the system's degree of organization and the efficiency of energy flows. A high A/DC shows a well-organized and developed system that is less vulnerable to disturbances (Wulff et al. 1989, Pockberger and Asmus 2014).
4) **Overheads (OH):** The overheads characterize the free energy in a system (Wulff et al. 1989). With a high overhead the system has more capacities to react to perturbations and a larger potential of resilience. The ratio between OH and DC is described as the **Relative Overheads (OH/DC)** which is the natural counterpart of A/DC.

5) **Robustness:** It is a measurement for the system's resilience. A high value shows more stable energy flows that are less sensitive to external disturbances (Goerner 2009, Fath 2015).
6) **Gross primary production *versus* biomass (P_{GPP}/B):** This ratio is a function of the system's maturity. It is expected that biomass is accumulated when the system matures. Therefore, the value decreases with system's maturity (Christensen 1995).
7) **Flow Diversity (FD):** It is a measurement for the number of interactions and the evenness of energy flows. Comparable to the biodiversity index, a high value shows a highly diverse, well-developed and stable system (Wulff et al. 1989, Pockberger and Asmus 2014).
8) **Effective Link-Density (ELD):** It is the effective number of parallel pathways in the structure and is based on the number of flows per node (Ulanowicz et al. 2014).
9) **Average Path Length (APL):** It is a measurement of the mean number of compartments a unit of carbon passes before it leaves the system again (Wulff et al. 1989). A low APL shows that the energy is only used in few compartments and indicates an instable system. On the contrary, long path length indicate a more mature system (Christensen 1995, Pockberger and Asmus 2014).
10) **Finn Cycling Index (FCI):** This index shows the proportion of flows in a system that are recycled (Wulff et al. 1989). Higher values indicate that the system is more independent from imports.
11) **Logarithmic Trophic Efficiency (TE):** The TE shows how efficiently energy is transferred in the system (Wulff et al. 1989). For the determination of the logarithmic mean trophic efficiency of each system only trophic levels with an efficiency of ≥0.1 % were taken into account.
12) **Trophic Depth (TD):** It is the number of effective trophic levels in the system (Ulanowicz et al. 2014).

The Lindeman Trophic Aggregation Analysis is another helpful implementation that transforms the complex food web network into a linear food chain (i.e. the Lindeman spine) with integer trophic levels (Wulff et al. 1989). In this representation all primary producers and the detritus pool form the first trophic level and consumers are distributed in the following trophic levels according to their feeding behavior. The Lindeman spine shows the amount of carbon each trophic level receives from the previous one as well as energy losses due to respiration and exports. It provides a quantitative estimation of the efficiency of the energy transfer within the system. The analysis also allows a comparison of the relation between detritivory and herbivory in a system.

2.5 Uncertainty analysis

The models are based on empirical data, which can show natural variations in space (e.g. biomass variation of some species in patchy areas) or in time (e.g. seasonal variation of some species' diets or seasonal and diurnal abundance of mobile predators such as birds). Therefore, a percentage of variation can be defined for each of the standing stocks, energy budget or flows in the network. In this study, we conducted an uncertainty analysis for all six habitats in order to test the sensibility of the ENA indices to changes in the network parameters. Therefore, two additional models were created for each habitat. In the first model the standing stocks and energy budgets of all compartments were increased by 50% (maximum models). In the second model the initial values were decreased by 50% (minimum models). Flows between the compartments, inputs and outputs were then recalculated according to the new values of consumptions.

Biomass shifts of 50% represent severe changes in an ecosystem. Although it might be very unlikely that all components show minima or maxima simultaneously, we assumed that variability of the system does not exceed the range limited by these extreme situations and thus could give an appropriate overview of the respective index's variation.

3. Results

3.1 Size and activity

The six systems differed strongly in their extent of total biomass. The razor clam field had the lowest total biomass with 37,962.9 $mgC.m^{-2}$. The highest value was found in the mussel bank with 563,647.3 $mgC.m^{-2}$ followed by the cockle field with 178,227.1 $mgC.m^{-2}$.

Total system production ranged from 1,526.4 $mgC.m^{-2}.d^{-1}$ in the seagrass meadow to 5,158.4 $mgC.m^{-2}.d^{-1}$ in the mud flat. The secondary production was the lowest in the razor clam field (186.0 $mgC.m^{-2}.d^{-1}$) and the highest in the cockle field (1,019.6 $mgC.m^{-2}.d^{-1}$).

The mussel bank, the mud flat and the cockle field revealed a strong dependency on external imports with total import values of 10,091.1 $mgC.m^{-2}.d^{-1}$, 7,775.5 $mgC.m^{-2}.d^{-1}$ and 6,872.8 $mgC.m^{-2}.d^{-1}$, respectively, but showed also the highest amount of exported material among all systems (4,144.8 $mgC.m^{-2}.d^{-1}$, 4,750.4 $mgC.m^{-2}.d^{-1}$ and 5,021.5 $mgC.m^{-2}.d^{-1}$, respectively).

The mud flat had the highest P_{GPP}/B value (0.10) and mussel bank had the lowest P_{GPP}/B value (0.01).

The mussel bank was the biggest and most active system indicated by the highest TST value (29,304.2 $mgC.m^{-2}.d^{-1}$) and had the highest potential to develop as shown by the highest value of DC (138,614.2 bits). The cockle field and the mud flat were also characterized as active systems with high DC values (Table 3). The sand flat, the seagrass meadow and the razor clam field appeared to be small systems with low DC values (Table 3).

Table 3: System attributes of the six intertidal systems

System Attributes	**Cockle field**	**Razor clam field**	**Mud flat**	**Mussel bank**	**Sand flat**	**Seagrass meadow**
Number of compartments	38	29	38	48	43	45
Number of living compartments	36	27	36	46	41	43
total Biomass [mg C m^{-2}]	178,227.1	37,962.9	74,196.4	563,647.3	67,907.4	55,357.9
total Production [mg C m^{-2} d^{-1}]	3,142.3	1,802.7	5,158.4	4,097.4	2,030.8	1,526.4
secondary Production [mg C m^{-2} d^{-1}]	1,019.6	186.0	539.4	767.2	426.1	349.2
total Exports [mg C m^{-2} d^{-1}]	5,021.5	1,562.1	4,750.4	4,144.8	1,619.7	1,252.0
total Imports [mg C m^{-2} d^{-1}]	6,872.8	2,976.5	7,775.5	10,091.1	3,251.3	2,800.0
P_{GPP}/B	0.02	0.07	0.10	0.01	0.04	0.03
Total System Throughput [mg C m^{-2} d^{-1}]	23,343.7	8,095.0	21,251.5	29,304.2	10,751.6	8,996.7
Development Capacity [mg C m^{-2} d^{-1} bits]	97,450.0	32,312.3	79,397.6	138,614.2	55,260.2	49,633.0
Ascendency [mg C m^{-2} d^{-1} bits]	42,957.6	11,962.8	30,292.1	53,888.7	17,832.4	15,713.1
Overheads [mg C m^{-2} d^{-1} bits]	54,492.4	20,349.5	49,105.4	84,725.5	37,427.8	33,919.9
Relative Ascendency [%]	44.1	37.0	38.2	38.9	32.3	31.7
Relative Overheads [%]	55.9	63.0	61.9	61.1	67.7	68.3
Robustness [%]	36.1	36.8	36.8	36.7	36.5	36.4
Flow Diversity [%]	4.2	4.0	3.7	4.7	5.1	5.5
Effective Link-Density	2.3	2.4	2.2	2.7	3.3	3.7
Average Path Lenght	2.4	1.7	1.7	1.9	2.3	2.2
Finn Cycling Index [%]	2.3	5.5	2.5	1.1	7.5	6.6
Logarithmic Trophic Efficiency [%]	5.9	9.1	5.3	3.9	11.0	6.3
Trophic Depth	3.6	2.8	2.7	3.6	3.2	3.4
Detritivory:Herbivory ratio [D:H]	1 : 3.7	1 : 1.1	1 : 3.2	1 : 4.4	1 : 1.8	1 : 1.9

3.2 System structure

The structure of the six systems was described by a combination of different attributes calculated by ENA. Here, we focused on dimensionless indices describing the organization of the systems, the resilience and the ability of the system to cope with disturbances.

The system organization indicated by the relative Ascendency (A/DC) was highest in the cockle field (44.1%) and in the mussel bank (38.9%). The lowest values for A/DC were found in the sand flat and the seagrass meadow (32.3% and 31.7%, respectively). The counterpart of A/DC are the relative Overheads (OH/DC) of the system representing the part of the food web that is not yet organized and that is available as energy reserves to react to perturbations. The values for OH/DC were highest in the sand flat and the seagrass meadow (67.7% and 68.3%, respectively). The mussel bank and the cockle field showed the lowest values (61.1% and 55.9%, respectively). Analyses revealed that all six systems are equally resilient with a robustness of about 36% (Table 3).

3.3 Organization of flows

FD, the number of interactions and evenness of flows, and ELD, the effective number of parallel pathways describe the organization of flows. FD was the highest in the seagrass meadow (5.5) followed by the sand flat (5.1). The lowest value for FD was found in the mud flat (3.7).

The seagrass meadow and the sand flat had the highest number of parallel pathways with an ELD of 3.7 and 3.3 respectively. The cockle field and the mud flat showed the lowest number of parallel pathways (2.3 and 2.2, Table 3).

3.4 Recycling

The recycling magnitude of a system is described by the Finn Cycling Index (FCI) and the Average Path Length (APL). High values for FCI and APL indicate a stable system that is less dependent on external energy sources (Monaco and Ulanowicz 1986, Vasconcellos et al. 1997).

The sand flat recycled the highest amount of energy (FCI of 7.5%) followed by the seagrass meadow (6.6%). Almost no recycling occurred in the mussel bank (1.1%). The longest APL was found in the cockle field (2.4). The mud flat and the razor clam field had the shortest APL, both with 1.7.

3.5 Trophic structure

The trophic structure of a system is represented by the trophic aggregation of the Lindeman spine, the system's logarithmic Trophic Efficiency (TE) and the Trophic Depths (TD).

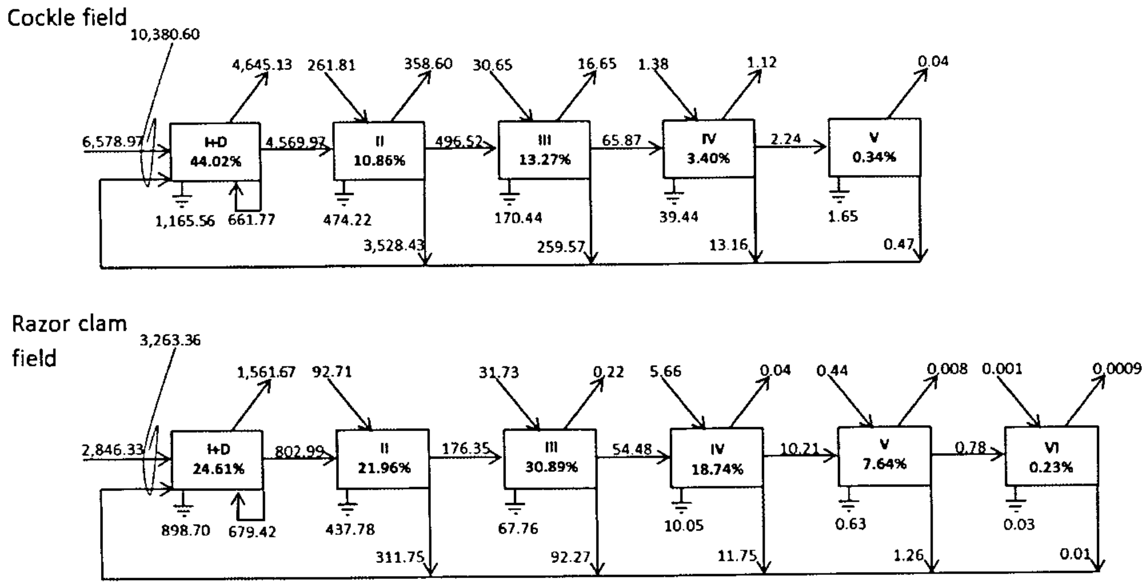
The TE ranged from 11.0 % in the sand flat to 3.9 % in the mussel bank (Table 3).

The mussel bank and the cockle field had the highest number of effective trophic levels (TD 3.6 in both systems). The mud flat had the lowest TD (2.7; Table 3).

Illustration of the Lindeman Trophic Aggregation Analysis is shown in Fig. 1. The complexity of the Lindeman spines varied from five trophic levels in the cockle field and the sand flat to six trophic levels in the razor clam field, the mud flat, the mussel bank and the seagrass meadow. In all habitats, trophic efficiencies tend to decrease from the first trophic levels towards the end of the food chain. It is noticeable that the second trophic level of the mud flat, the second trophic level of the seagrass meadow, the third trophic level of the cockle field and the third trophic level of razor clam field revealed higher efficiencies than the preceded levels.

Lindeman spines of the cockle field and the mussel bank were relatively similar: high external imports supported both systems. Trophic efficiencies were comparable in the first four trophic levels but the mussel bank showed higher trophic efficiencies in the upper trophic levels. In the sand flat and the seagrass meadow exceptional high values for trophic efficiency were noted on trophic level II with more than 40%.

Herbivory surpasses detritivory in all six systems. The difference between herbivory and detritivory was the highest in the cockle field and the mussel bank and the lowest in the razor clam field (Table 3).


Cockle field

Razor clam field

Fig. 1: Lindeman spines of the six intertidal systems. Boxes represented the distinct trophic levels, percentage values refer to trophic efficiency between the levels. Arrows indicated energy flows between trophic levels as well as im- and exports and backflows to the detritus pool. Dashed arrows show energy losses due to respiration. Values are given in mgC.m^{-2}.d^{-1}

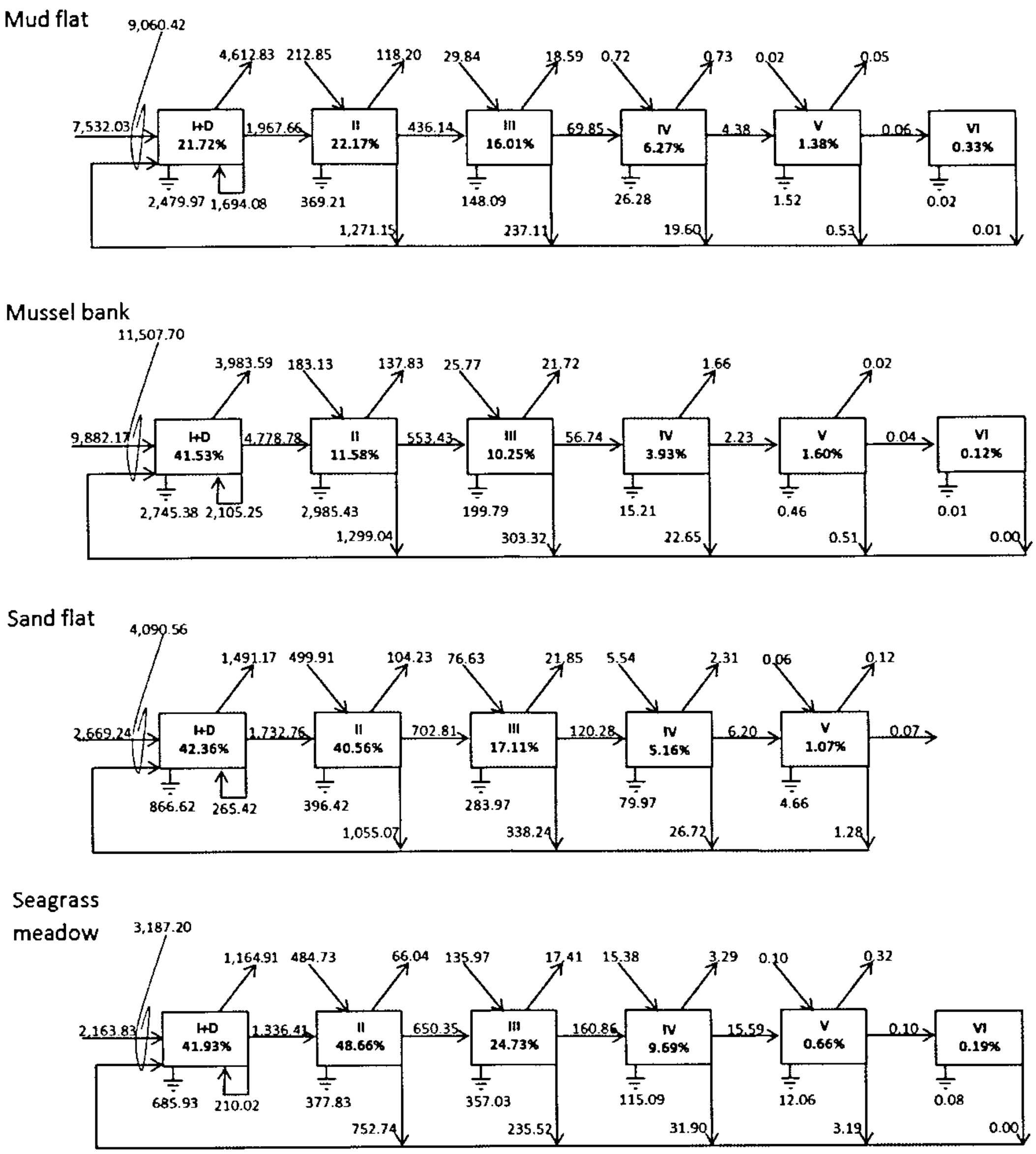


Fig. 1 (continued): Lindeman spines of the six intertidal systems. Boxes represented the distinct trophic levels, percentage values refer to trophic efficiency between the levels. Arrows indicated energy flows between trophic levels as well as im- and exports and backflows to the detritus pool. Dashed arrows show energy losses due to respiration. Values are given in mgC.m^{-2}.d^{-1}

3.6 Uncertainty analysis

The amplitude of variation differs between the habitat types (Fig. 2). The cockle field, the mud flat and the mussel bank revealed larger variations in their indices than the razor clam field, the sand flat and the seagrass meadow.

The different indices showed different sensibility to variations in the flow network as well. System attributes which were given in mgC.m^{-2}.d^{-1} (TST) or bits (ASC, OH, DC) showed a relatively high variation between the initial model and the minimum and maximum models in each habitat and were therefore sensitive to changes in the model construction. Dimensionless indices (APL, ELD, TD) and ratios (A/DC, OH/DC, robustness, TE, FCI) showed only small variations in the results of the different habitat models. These indices seem to be robust to changes in the model construction. Interpretations based on dimensionless indices and ratios were therefore considered to be more reliable compared to the other attributes.

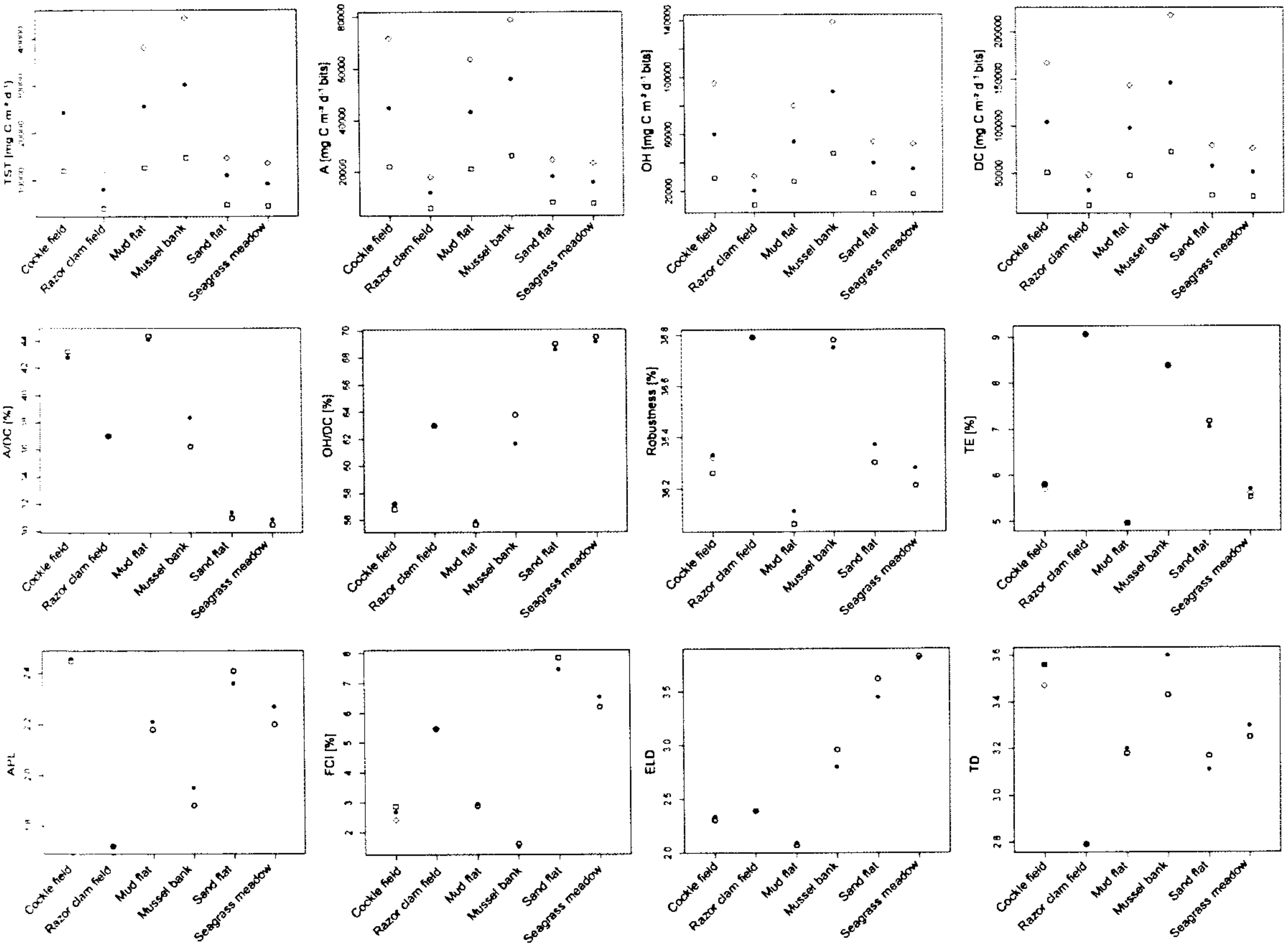


Fig. 2: Variation of the indices of each habitat with the initial model (red dot), the minimum model (black framed square) and maximum model (black framed

4. Discussion

4.1. Similarities in system structure

The structure of a system is described by two general concepts: the system's degree of organization and the ability of a system to cope with perturbations. Although the six studied systems showed differences in their degree of organization and in their diversity of flows, all of them were equally robust in front of disturbances. Fath (2015) hypothesized that an ecological system needs to attain a balance between organization and redundancy to be sustainable. Ulanowicz et al. (2009) described this optimum trade-off as the "window of vitality" in which a system would achieve an ideal balance between being efficiently organized and being resilient. Despite the differences in A/DC, the robustness index values of all six systems of this study ranged in this "window of vitality" indicating that they had a sufficient amount of both, organization and reserves of free energy to react to perturbations.

4.2. Mussel bank and cockle field: Similar roles but different features

The cockle field and the mussel bank showed similarities in their functioning. Both systems are characterized by accumulations of bivalve species which are colonized by various macrobenthic invertebrates and both provide a rich food source for foraging birds. The TST indicates both systems to be very active and productive with a high throughflow of energy and a high degree of organization. In accordance with the low recycling of matter these systems are simultaneously strongly dependent on external imports resulting in an increased sensitivity to external perturbations.

Nevertheless, the P_{GPP}/B values of both systems imply a high system's maturity, supported in the cockle field by a high FD, TD and APL and in the mussel bank by high values of FD and TD. The mussel bank appeared to be more robust than the cockle field with more parallel pathways in the system probably caused by the higher biodiversity in the mussel bank.

The trophic aggregation of the Lindeman spine revealed similar efficiencies of energy transfer in the first four levels of both systems. But at the higher trophic levels the mussel bank exceeds the efficiency of the cockle field presumably due to the higher abundance of benthic predators such as shore crabs or carnivorous polychaetes that use the lower trophic levels as food sources and being themselves eaten by top predators such as birds. The energy transfer is therefore increased in the food chain. However, on average the TE of the mussel bank is lower than the TE of the cockle field. The reasons could be diverse. The Lindeman spine of the mussel bank shows six trophic levels and is therefore longer than the spine of the cockle field indicating more complex trophic relationships with a higher influence of predators in the mussel bank. Thus, the increased length of the Lindeman spine reduces the TE on average as only little energy is transferred to the higher trophic levels.

The results of this study showed that mussel banks and habitats with similar functioning such as cockle fields are very diverse systems with a high degree in activity and organization but low cycling values and therefore a strong dependency on external imports. This is consistent with the study of Baird et al. (2007) on mussel banks in the Sylt-Rømø Bight.

Although mussel banks as well as cockle field are rather small-scaled habitats, they both appear to be very important foraging areas for birds. Their high productivity and the rich benthic fauna attract a large variety of bird species. Especially the eider duck (*Somateria mollissima*) is dependent on these habitat types as most of its prey consists of mussels and cockles (Nehls 1989). But also resident bird species (i.e. *Haematopus ostralegus*) and migrating waders (i.e. *Limosa lapponica*) use these habitats for foraging.

In conclusion the ENA of the cockle field and the mussel bank revealed both systems to be in a relatively mature and well developed status but the stability of both systems is strongly relying on the availability of phytoplankton imports to fulfill the needs of the dominating suspension feeders.

4.3 The razor clam field: Simple but efficient

The razor clam field is the third habitat dominated by a bivalve species. The American razor clam (*Ensis directus*) was introduced in the North Sea in the late 1970s (Swennen et al. 1985, Gollasch et al. 2015) and is now colonizing wide areas of the lower intertidal and subtidal in the Wadden Sea. In recent years several bird species such as the herring gull or the eider duck discovered the razor clam to be a suitable prey organism (Tulp et al. 2010). In the Wadden Sea the razor clam preferably inhabits the lower intertidal area which is characterized by harsh abiotic conditions such as intensive current velocities and high sediment mobility. The razor clam is a deep burrowing organism that is therefore able to tolerate the unfavorable conditions of moving surface sediments very well, capturing a free niche in the Wadden Sea.

However, the network analysis revealed the razor clam field to be still in an immature state. The system appeared to be very small with a low amount of available energy and a low biodiversity. Low values for ELD and APL and high values for P_{GPP}/B and FCI indicate that the system is in a stressed condition with only few and short pathways for energy transfer (Christensen 1995, Leguerrier et al. 2007a). However, the high TE implies that the energy was transferred very efficiently. The razor clam field network system is mainly characterized by a simple link between phytoplankton, razor clams and gulls as predators. The little energy that is available in the system is probably mostly and highly efficiently transferred via this three-step-link and make the system very simple and vulnerable to disturbances. Perturbations that would affect phytoplankton as the main food source or the razor clam as the dominating organisms could lead to a complete collapse of this system. The latter was already often observed during cold winters or washouts which induced a mass mortality of the razor clam (Dannheim 2012). Natural influences like this make the razor clam system short-lived and could also explain its immaturity.

4.4 Mud flats show high variability

Mud flats are known to be very productive intertidal systems which are of high importance for foraging birds (Saint-Béat et al. 2013a). Diverse studies about food web systems of mud flats exist and reveal differences in the functioning of mud flats in combination to their location and environmental circumstances such as fresh water inflow or eutrophication (Leguerrier et al. 2007a).

In the present study, the results for the mud flat habitat were difficult to interpret and led to contradicting conclusions. Indeed, the high values for TST and A/DC imply that the system is active and well organized. However, the high P_{GPP}/B value indicates an immature state and low levels of TE and ELD show that the system was neither efficient nor very robust due to a lack of parallel pathways. Furthermore, the low cycling tends to result in a strong system's dependency on external imports and the low APL shows that the energy is only used over short pathways. The mud flat therefore appears to be in a stressed and unstable condition (Monaco and Ulanowicz 1986, Leguerrier et al. 2007a, Pockberger and Asmus 2014).

The dominance of suspension feeders (e.g. *Cerastoderma edule*) and especially grazers feeding on MPB (e.g. *Peringia ulvae, Littorina littorea, Nereis diversicolor*) lead to an increased herbivory that was three times higher than detritivory. MPB was one of the major food sources in the mud flat.

Comparable results were observed in the French Brouage mud flat (Leguerrier et al. 2003). The system was characterized by a dominant influence of MPB and low values of carbon recycling. High amounts of primary production provide a rich food source for herbivores at lower trophic levels but it was noted that there was the risk of food depletion at higher predator levels. On the contrary, Baird et al. (2007) described the mud flat of the Sylt-Rømø Bight to be a system characterized by high recycling and great energy reserves to cope with perturbations.

In conclusion, the mud flat system in this study is probably not fully developed yet and might be vulnerable to perturbations due to a lack of long and parallel pathways and low internal cycling. Nevertheless, mud flats are important food sources for various bird species. Waders such as the bar-tailed godwit (*Limosa lapponica*) and the Eurasian oystercatcher (*Heamatopus ostralegus*) but also the common shellduck (*Tadorna tadorna*) and gulls (e.g. *Chroicocephalus ridibundus*) were mostly observed feeding on the mud flat. Furthermore, it was the only habitat type where pied avocets (*Recurvirostra avosetta*) were seen. This may be an effect of the feeding modes of this species which are well suited to take up comparatively small prey items in well penetrable sediments. In the Wadden Sea, the population of pied avocets showed an overall decline since 1990 although it was declared to be stable in the federal state of Schleswig-Holstein in the last years (van Roomen et al. 2012, Blew et al. 2015, Koffijberg et al. 2015). Mud flats appear to be one of the preferred foraging areas of this bird species but the present study shows that the mud flat systems might be vulnerable in front of perturbations. These results should be taken into account with respect to protection and management plans concerning the pied avocet population.

Mud flats are very dynamic systems which quickly react to changes in their environment. Therefore, it is difficult to find general characteristic system properties for this habitat type. However, a collapse of the mud flat systems might affect a wide range of bird species that preferable forage in these soft bottom habitats.

4.5 Sand flat and seagrass meadow are bird hotspots

Sand flats are the most expanded habitat type in the study site, covering about 63% of the intertidal area. They are often characterized by a high abundance of the lugworm *Arenicola marina*, a preferred food item of several bird species (Baird et al. 1985a). Seagrass meadows, on the other hand, are shallow water habitats that provide shelter for a diversity of organisms (Reise and Kohlus 2008). They are used as a nursery ground for juvenile fish and present a rich food source for herbivorous birds (Asmus and Asmus 2000a, Reise and Kohlus 2008). In contrast to the worldwide trend, the seagrass meadows in the Wadden Sea increased in terms of size during the last decades (Dolch et al. 2013) and therefore gain importance in their ecological role. Their expansion in the Wadden Sea was observed simultaneously to the decline of eutrophic nutrients in coastal waters that might have influenced the seagrass but the distinct reasons for the growing seagrass meadows are still unclear.

Although the sand flat and the seagrass meadow were very different in their biological features, we found several similarities in their functioning. Both systems are strongly exploited by a huge number of foraging birds, resulting in an increased trophic efficiency especially on the second and third trophic level.

However, both systems are relatively small with a higher degree in free energy than in organization, indicating that there is a high system's potential to react to external disturbances. Increased values of FD, ELD, APL and FCI, and a low P_{GPP}/B suggest that both systems are mature, stable and robust against perturbations and function independently of external imports (Monaco and Ulanowicz 1986, Christensen 1995, Vasconcellos et al. 1997).

Previous work on food webs of sand flats and seagrass meadows of Baird et al. (2007) already revealed comparable results for both systems in terms of high FD, high APL and a balance between detritivory and herbivory. But the degree of organization was markedly higher in the studies of Baird et al. (2007). In case of seagrass beds this might be due to the higher age of the seagrass beds in the Sylt-Rømø Bight compared to the younger and more pioneering type of meadows of the present study site. The TE was markedly higher in both systems of the present study compared to the systems of Baird et al. (2007) probably caused by a higher bird predation.

While sand flats are already known to be important feeding grounds for birds, the high abundance of foraging birds on the seagrass meadow was relatively surprising. Former observations indicated that seagrass meadows are of minor importance as a food source for non-herbivorous birds (Busch 2012) but our results indicate the contrary. Seagrasses are known to be ecosystem engineers with a strong influence on the organisms which live within this habitat, but also on the functioning of this habitat (van der Zee et al. 2016). But next to its structure the location of a seagrass meadow might influence its attraction to birds as well. Seagrass meadows often occur close to the shore in sheltered areas (Dolch et al. 2013) which can easily be disturbed by human influences such as increased tourism. In this study, the seagrass meadow was isolated and situated further away from the shore and was less influenced by human disturbances. This might explain the high abundance of birds feeding on this habitat in contrast to the formerly observed seagrass meadows in the Sylt-Rømø Bight (Busch 2012). But also the long exposure time of the seagrass meadow could play a role. Therefore, it would be interesting to include more seagrass meadows situated in diverse location (i.e. disturbed by human activities or remoted) in further studies to assess their overall importance for foraging shore birds. Furthermore, our results suggest that birds might intensively use seagrass meadows as foraging areas when they are undisturbed environments, indicating that conservation measures and management plans should focus on this particular habitat.

In conclusions the sand flat as well as the seagrass meadow seems to be mature systems in a stable status. Available energy resources are used effectively and efficiently over several parallel and long pathways with a high magnitude of recycling. The reserves of free energy indicate that the systems can cope with disturbances very well.

4.6 Birds in food web studies

Due to their high mobility birds are very difficult to include in quantitative analyses such as food web studies. Nevertheless, they are very important predators in the intertidal areas and it is strongly recommended to include birds in ecosystem models (Baird et al. 1985a). Numbers of birds but also their feeding behavior can strongly differ in correlation with the season, water level and time of low tide but also based on the location of the intertidal habitat and its exposure time (Nehls and Tiedemann 1993, Tiedemann and Nehls 1997).

It is therefore difficult to draw general conclusions on bird predation from the counts that were done in the present study as the chosen habitats but also the time of counting and the subjective error of the investigator might have biased the results. Bird predation can show high variability from one day to the other and from one sand flat to a neighbored one as birds also react to small-scaled differences (Nehls and Tiedemann 1993, Tiedemann and Nehls 1997).

In the uncertainty analysis these circumstances were taken into account. The variation of birds in the minimum and maximum models was with 50% very high to cover the natural high variability of these predators. However, results of the analysis showed rather small variations in the system attributes especially concerning the dimensionless indices and ratios. Differences were higher between the models of the six habitat types than within the three tested models of each habitat in the uncertainty analysis. It is therefore considered that the natural variability of each compartment does not severely affect the overall functioning of the different systems.

4.7 Comparison with previous studies

Comparisons between different food web studies are usually difficult as the focus of the studies and the aggregation of compartments can differ strongly. This might bias the results of the different network analyses. In the present study we focused on the link between the intertidal benthos communities and birds as top predators. Comparable intertidal models of the Sylt-Rømø Bight (Baird et al. 2004, Baird et al. 2007, 2008, 2011a, 2012) and the Brouage mud flat (Leguerrier et al. 2003, Saint-Béat et al. 2013a) are more complete with additional compartments including zooplankton and fish. The model of the Jade Bay (Schückel et al. 2015) on the other hand, does not include higher predator levels such as fish or birds but is very detailed on the macrozoobenthic level with almost each species representing one compartment.

However, there are some noticeable differences between the present models and the earlier analyzed models of the Sylt-Rømø Bight, the Brouage mud flat and the Jade Bay. The first one is the comparatively low recycling in all six habitat types of the present study. This could be either a relic of network construction because unused detritus was assumed to be exported during high tide, or a result of the difference in the location of the study area. ENA is often conducted in well-studied, enclosed bays and bights with little water exchange with the North Sea. In contrast, the present site was an open system with a direct connection to the open sea that imports regularly a high amount of food for suspension feeders presumably resulting in a less important role of recycling in this area compared to enclosed marine ecosystems.

Another notable difference to other studies is the high degree of herbivory in all systems. Intertidal areas are often characterized by a major role of detritivores in the energy transfer (Scharler and Baird 2005a, Baird et al. 2007, Schückel et al. 2015) in opposition to herbivory. However, in our six systems, herbivory always exceeded detritivory. The dominance of suspension feeders and grazers in the habitats relying on phytoplankton and MPB increased the herbivory strongly, resulting in a less important influence of detritivores in all six systems. Furthermore, the high abundance of herbivorous birds feeding on macroalgae and seagrass amplify the difference even more.

Comparisons in the food web structure of different habitat types were rarely done before. Baird et al. (2007) analyzed eight different intertidal systems in the Sylt-Rømø Bight also including mussel banks, seagrass meadows, sand flats and mud flats. Except for the already mentioned differences in cycling and the ratio between detritivory and herbivory, the results of Baird et al. (2007) for these four habitats matched the ones of the present study.

To increase the comparability of the present study it will be necessary to create a food web model of the whole study site and then analyze the system attributes and their relation to the structure of similar systems. Furthermore, it would be interesting to include compartments such as zooplankton and fish to have a more complete food web which is closer to reality. Such studies could also be used as an important background for management and protection plans in the Wadden Sea. However, habitat diversity appears to be of great importance for the Wadden Sea. Each habitat has its specific characteristics and features and plays a different role in the entire Wadden Sea ecosystem.

5. Conclusions

In this study we conducted food web analysis for six intertidal habitat types in the Wadden Sea that were known to be important forging areas for coastal bird species. The general structure of the six food webs revealed a good tradeoff between the degree of organization and the ability to cope with disturbances in all six systems. However, the systems differ in their detailed features. The cockle field and the mussel bank are mature and stable systems but with a strong reliance on external phytoplankton input. The razor clam field was shown to be a small system in an immature status and might be vulnerable to perturbations. The studied mud flat appeared to be in a stressed and unstable condition but is still used by a lot of different bird species. The sand flat and the seagrass meadow revealed several similarities in their structure and seem to be in a stable and mature status with a high importance for a large variety of foraging birds.

Our results show that every habitat has its own features and characteristics. Therefore, habitat diversity is an important trait for the function of the Wadden Sea as a whole ecosystem. Every habitat type plays a different role in the heterogeneous mosaic, but it remains unknown to what extend the different habitat types contribute to the whole system. As a next step, it would be necessary to conduct an Ecological Network Analysis of the whole study site to get insight into the complex interactions between the different habitat types and their influence on the whole system structure.

6. Acknowledgements

This study was funded by the German Federal Ministry of Education and Research in the frame of the German joint research project "STopP – From sediment to top predator" (BMBF, FKZ 03F672B). Martin Kühn assisted in counting birds on the intertidal flats. We are grateful to the team of the vessels "MS Hooge" and "FS Mya II" who enabled access to remote intertidal flats. Furthermore, we would like to thank the State Agency for Agriculture, Environment and Rural Areas of Schleswig-Holstein (LLUR) for providing the phytoplankton data, the "Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein" for eider duck numbers and Kerstin Stelzer from Brockmann Consult GmbH for the size of certain habitat types.

Many thanks as well to all the students who helped in the field and spent so much time on sorting, identifying and weighting the macrobenthos samples.

7. References

Abarca-Arenas, L. G., and R. E. Ulanowicz. 2002. The effects of taxonomic aggregation on network analysis. Ecological Modelling **149**:285-296.

Asmus, H. 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. Marine ecology progress series. Oldendorf **39**:251-266.

Asmus, H., and R. Asmus. 2000. Material exchange and food web of seagrass beds in the Sylt-Rømø Bight: how significant are community changes at the ecosystem level? Helgoland Marine Research **54**:137-150.

Asmus, R., and H. Asmus. 1998. Bedeutung der Organismengemeinschaften für den benthopelagischen Stoffaustausch im Sylt-Rømø Wattenmeer. Ökosystem Wattenmeer: Austausch-, Transport-und Stoffumwandlungsprozesse (Ch Gätje, K Reise, Hrsg) Springer, Berlin:257-302.

Baird, D., H. Asmus, and R. Asmus. 2004. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Marine Ecology Progress Series **279**:45-61.

Baird, D., H. Asmus, and R. Asmus. 2007. Trophic dynamics of eight intertidal communities of the Sylt-Rømø Bight ecosystem, northern Wadden Sea. Marine Ecology Progress Series **351**:25-41.

Baird, D., H. Asmus, and R. Asmus. 2008. Nutrient dynamics in the Sylt-Rømø Bight ecosystem, German Wadden Sea: An ecological network analysis approach. Estuarine, Coastal and Shelf Science **80**:339-356.

Baird, D., H. Asmus, and R. Asmus. 2011. Carbon, nitrogen and phosphorus dynamics in nine sub-systems of the Sylt-Rømø Bight ecosystem, German Wadden Sea. Estuarine, Coastal and Shelf Science **91**:51-68.

Baird, D., H. Asmus, and R. Asmus. 2012. Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. Marine Ecology Progress Series **462**:143-162.

Baird, D., P. Evans, H. Milne, and M. Pienkowski. 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. Oceanography and marine biology **23**:573-597.

Baird, D., B. D. Fath, R. E. Ulanowicz, H. Asmus, and R. Asmus. 2009. On the consequences of aggregation and balancing of networks on system properties derived from ecological network analysis. Ecological Modelling **220**:3465-3471.

Baird, D., J. McGlade, and R. Ulanowicz. 1991. The comparative ecology of six marine ecosystems. Philosophical Transactions of the Royal Society of London B: Biological Sciences **333**:15-29.

Baird, D., and R. Ulanowicz. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal. Marine Ecology Progress Series **99**:221-237.

Baldwin, J., and J. Lovvorn. 1994. Habitats and tidal accessibility of the marine foods of dabbling ducks and brant in Boundary Bay, British Columbia. Marine Biology **120**:627-638.

Bezzel, E. 1985. Kompendium der Vögel Mitteleuropas: Nichtsingvögel. AULA-Verlag.

Blew, J., K. Günther, B. Hälterlein, R. Kleefstra, K. Laursen, and G. Scheiffarth. 2015. Trends of Migratory and Wintering Waterbirds in the Wadden Sea 1987/1988-2011/2012.

Borrett, S., R.,, and M. Lau, L. 2014. enaR: An R package for Ecosystem Network Analysis. Methods in Ecology and Evolution **5**:1206-1213.

Busch, N. 2012. Untersuchungen zur Nutzung eulitoraler Seegraswiesen durch Wattenmeervögel während des Frühjahrszuges. Universität Kiel.

Buxton, N., and C. Young. 1981. The food of the Shelduck in north-east Scotland. Bird Study **28**:41-48.

Christensen, V. 1995. Ecosystem maturity—towards quantification. Ecological Modelling **77**:3-32.

Dannheim, J. R., H. 2012. The fate of an immigrant: *Ensis directus* in the eastern German Bight. Helgoland Marine Research **66**:307-317.

Dolch, T., C. Buschbaum, and K. Reise. 2013. Persisting intertidal seagrass beds in the northern Wadden Sea since the 1930s. Journal of Sea Research.

Edler, L. 1979. Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Publication-Baltic Marine Biologists BMB (Sweden).

Fath, B., D., Scharler, U., M., Ulanowicz, R., E., Hannon, B. 2007. Ecological network analysis: network construction. Ecological Modelling **208**:49-55.

Fath, B. D. 2015. Quantifying economic and ecological sustainability. Ocean & Coastal Management **108**:13-19.

Fath, B. D., U. M. Scharler, and D. Baird. 2013. Dependence of network metrics on model aggregation and throughflow calculations: Demonstration using the Sylt–Rømø Bight Ecosystem. Ecological Modelling **252**:214-219.

Goerner, S., J., Lietaer, B., Ulanowicz, R., E. 2009. Quantifying economic sustainability: Implications for free-enterprise theory, policy and practice. Ecological Economics **69**:76-81.

Gollasch, S., F. Kerckhof, J. Craeymeersch, P. Goulletquer, K. Jensen, A. Jelmert, and D. Minchin. 2015. Alien Species Alert: Ensis directus. Current statuts of invasions by the marine bivalve Ensis directus. ICES Cooperative Research Report:1-36.

Goss-Custard, J. 1977. The energetics of prey selection by redshank, Tringa totanus (L.), in relation to prey density. The Journal of Animal Ecology:1-19.

Heymans, J. J., M. Coll, S. Libralato, L. Morissette, and V. Christensen. 2014. Global patterns in ecological indicators of marine food webs: a modelling approach. Plos One **9**:e95845.

Höfmann, H., and H. Hoerschelmann. 1969. Nahrungsuntersuchungen bei Limikolen durch Mageninhaltsanalysen. Corax **3**:7-22.

Horn, S., and C. de la Vega. 2016. Relationships between fresh weight, dry weight, ash free dry weight, carbon and nitrogen content for selected vertebrates. Journal of Experimental Marine Biology and Ecology **481**:41-48.

Jensen, K. T. 1992. Dynamics and growth of the cockle, Cerastoderma edule, on an intertidal mud-flat in the Danish Wadden Sea: effects of submersion time and density. Netherlands Journal of Sea Research **28**:335-345.

Kabat, P., J. Bazelmans, J. van Dijk, P. M. Herman, T. van Oijen, M. Pejrup, K. Reise, H. Speelman, and W. J. Wolff. 2012. The Wadden Sea Region: Towards a science for sustainable development. Ocean & Coastal Management **68**:4-17.

Kay, J. J., L. A. Graham, and R. E. Ulanowicz. 1989. A detailed guide to network analysis. Pages 15-61 Network Analysis in Marine Ecology. Springer.

Koffijberg, K., K. Laursen, B. Hälterlein, G. Reichert, J. Frikke, and L. Soldat. 2015. Trends of Breeding Birds in the Wadden Sea 1991-2013. Wadden Sea Ecosystem.

Kubetzki, U., and S. Garthe. 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Marine Biology **143**:199-207.

Lau, M. K., S. R. Borrett, and P. Singh. 2015. Ecosystem Network Analysis with R: A guide for using enaR.

Leguerrier, D., D. Degré, and N. Niquil. 2007. Network analysis and inter-ecosystem comparison of two intertidal mudflat food webs (Brouage Mudflat and Aiguillon Cove, SW France). Estuarine, Coastal and Shelf Science **74**:403-418.

Leguerrier, D., N. Niquil, N. Boileau, J. Rzeznik, P.-G. Sauriau, O. Le Moine, and C. Bacher. 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. Marine Ecology Progress Series **246**:17-37.

Lorenzen, C. J. 1967. Determination of chlorophyll and pheo-pigments: spectrophotometric equations. Limnology and oceanography **12**:343-346.

Mann, K. H., J. G. Field, and F. Wulff. 1989. Network analysis in marine ecology: an assessment. Springer.

Mathers, R., and W. Montgomery. 1998. Behaviour of Brent geese Branta bernicla hrota and wigeon Anas penelope feeding on intertidal Zostera spp. Oceanographic Literature Review **1**:126.

Merkel, C. 2015. Ermittlung des Energiebudgets von Ensis directus im Eulitoral der Insel Sylt. Philipps-Universität Marburg, Master thesis.

Monaco, M. E., and R. E. Ulanowicz. 1986. Comparative ecosystem trophic structure of. Marine Ecology Progress Series 1:9.

Nehls, G. 1989. Occurrence and food consumption of the common eider, Somateria mollissima, in the Wadden Sea of Schleswig-Holstein. HELGOLANDER MEERESUNTERSUCHUNGEN **43**:385-393.

Nehls, G., and R. Tiedemann. 1993. What determines the densities of feeding birds on tidal flats? A case study on Dunlin, Calidris alpina, in the Wadden Sea. Netherlands Journal of Sea Research **31**:375-384.

Nienhuis, P., and A. Groenendijk. 1986. Consumption of eelgrass (Zostera marina) by birds and invertebrates: an annual budget. Marine Ecology Progress Series **29**:1-2.

Nithart, M., E. Alliot, and C. Salen-Picard. 1999. Production, respiration and ammonia excretion of two polychaete species in a north Norfolk saltmarsh. Journal of the Marine Biological Association of the UK **79**:1029-1037.

Parsons, T. R., M. Takahashi, and B. Hargrave. 1973. Biological oceanographic processes. Elsevier.

Pienkowski, M. W. 1980. Aspects of the ecology and behaviour of Ringed and Grey Plovers Charadrius hiaticula and Pluvialis squatarola. Durham University.

Piersma, T., R. Hoekstra, A. Dekinga, A. Koolhaas, P. Wolf, P. Battley, and P. Wiersma. 1993. Scale and intensity of intertidal habitat use by knots Calidris canutus in the western Wadden Sea in relation to food, friends and foes. Netherlands Journal of Sea Research **31**:331-357.

Pockberger, M., and H. Asmus. 2014. Empfehlungen zur Anwendung von Ökosystemanalysen zur Beurteilung des Nahrungsnetzes im Wattenmeer in der Meeresstrategie Rahmenrichtlinie.

Reise, K., M. Baptist, P. Burbridge, N. Dankers, L. Fischer, B. Flemming, A. Oost, and C. Smit. 2010. The Wadden Sea-a universally outstanding tidal wetland. The Wadden Sea 2010. Common Wadden Sea Secretariat (CWSS); Trilateral Monitoring and Assessment Group: Wilhelmshaven.(Wadden Sea Ecosystem; 29/editors, Harald Marencic and Jaap de Vlas) **7**.

Reise, K., and J. Kohlus. 2008. Seagrass recovery in the Northern Wadden Sea? Helgoland Marine Research **62**:77-84.

Riemann, B., P. Simonsen, and L. Stensgaard. 1989. The carbon and chlorophyll content of phytoplankton from various nutrient regimes. Journal of Plankton Research **11**:1037-1045.

Saint-Béat, B., C. Dupuy, P. Bocher, J. Chalumeau, M. De Crignis, C. Fontaine, K. Guizien, J. Lavaud, S. Lefebvre, and H. Montanié. 2013. Key Features of Intertidal Food Webs That Support Migratory Shorebirds. Plos One **8**.

Scharler, U. M., and D. Baird. 2005. A comparison of selected ecosystem attributes of three South African estuaries with different freshwater inflow regimes, using network analysis. Journal of Marine Systems **56**:283-308.

Scheiffarth, G. 2001. The diet of bar-tailed godwits *Limosa lapponica* in the Wadden Sea: Combining visual observations and faeces analyses. Ardea **89**:481-494.

Schückel, U., I. Kröncke, and D. Baird. 2015. Linking long-term changes in trophic structure and function of an intertidal macrobenthic system to eutrophication and climate change using ecological network analysis. Mar Ecol Prog Ser **536**:25-38.

Schwemmer, P., Garthe, S. 2011. Spatial and temporal patterns of habitat use by Eurasian oystercatchers (*Haematopus ostralegus*) in the eastern Wadden Sea revealed using GPS data loggers. Marine Biology **158**:541-550.

Schwemmer, P., F. Güpner, S. Adler, K. Klingbeil, and S. Garthe. 2016a. Modelling small-scale foraging habitat use in breeding Eurasian oystercatchers (Haematopus ostralegus) in relation to prey distribution and environmental predictors. Ecological Modelling **320**:322-333.

Schwemmer, P., F. Güpner, N. Guse, and S. Garthe. 2012. Nahrungswahl von Vogelarten der deutschen Nordseeküste. Vogelwarte **50**:141-154.

Schwemmer, P., C. C. Voigt, A. M. Corman, S. Adler, and S. Garthe. 2016b. Body mass change and diet switch tracked by stable isotopes indicate time spent at a stopover site during autumn migration in dunlins Calidris alpina alpina. Journal of Avian Biology.

Swennen, C., M. Leopold, and M. Stock. 1985. Notes on growth and behaviour of the American razor clam *Ensis directus* in the Wadden Sea and the predation on it by birds. Helgoländer Meeresuntersuchungen **39**:225-261.

Tiedemann, R., and G. Nehls. 1997. Saisonale und tidale Variation in der Nutzung von Wattflächen durch nahrungssuchende Vögel. Journal für Ornithologie **138**:183-198.

Tulp, I., J. Craeymeersch, M. Leopold, C. van Damme, F. Fey, and H. Verdaat. 2010. The role of the invasive bivalve *Ensis directus* as food source for fish and birds in the Dutch coastal zone. Estuarine, Coastal and Shelf Science **90**:116-128.

Ulanowicz, R. E. 2004. Quantitative methods for ecological network analysis. Computational Biology and Chemistry **28**:321-339.

Ulanowicz, R. E., S. J. Goerner, B. Lietaer, and R. Gomez. 2009. Quantifying sustainability: resilience, efficiency and the return of information theory. Ecological complexity **6**:27-36.

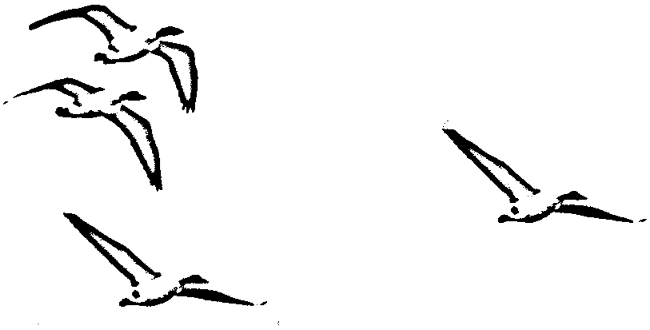
Ulanowicz, R. E., R. D. Holt, and M. Barfield. 2014. Limits on ecosystem trophic complexity: insights from ecological network analysis. Ecology letters **17**:127-136.

van der Zee, E. M., C. Angelini, L. L. Govers, M. J. Christianen, A. H. Altieri, K. J. van der Reijden, B. R. Silliman, J. van de Koppel, M. van der Geest, and J. A. van Gils. 2016. How habitat-modifying organisms structure the food web of two coastal ecosystems. Page 20152326 *in* Proc. R. Soc. B. The Royal Society.

van Roomen, M., K. Laursen, C. van Turnhout, E. van Winden, J. Blew, K. Eskildsen, K. Günther, B. Hälterlein, R. Kleefstra, and P. Potel. 2012. Signals from the Wadden sea: Population declines dominate among waterbirds depending on intertidal mudflats. Ocean & Coastal Management **68**:79-88.

Vasconcellos, M., S. Mackinson, K. Sloman, and D. Pauly. 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecological Modelling **100**:125-134.

Wulff, F., J. G. Field, and K. H. Mann. 1989. Network analysis in marine ecology: methods and applications. Springer Science & Business Media.



Chapter 4

Photo flying geese: Robert Waleczek

Impact of birds on the intertidal food web – assessed with Ecological Network Analysis

Sabine Horn[1], Camille de la Vega[1], Ragnhild Asmus[1], Philipp Schwemmer[2], Leonie Enners[2], Stefan Garthe[2], Kerstin Stelzer[3], Kirsten Binder[4], Harald Asmus[1]

Affiliation

[1] Alfred-Wegener-Institute Helmholtz Centre for Polar- and Marine Research, Wadden Sea Station Sylt Hafenstr. 43, D-25992 List/ Sylt, Germany

[2] Research and Technology Centre, University of Kiel, Hafentörn 1, 25761 Büsum, Germany

[3] Brockmann Consult GmbH, Max-Planck-Str. 2, 21502 Geesthacht, Germany

[4] State Agency for Agriculture, Environment and Rural Areas Schleswig-Holstein, Hamburger Chaussee 25, 24220 Flintbek, Germany

Corresponding author: sabine.horn@awi.de

Keywords: food web model, shorebirds, Wadden Sea, trophic impact, flow interaction

Abstract:

The Wadden Sea is one of the most important stop-over sites for breeding and migrating birds. About 10-12 million birds per year use the area for foraging and consume about 25 to 45% of the standing stock of macrozoobenthos. But little is known about the influence of birds on the entire ecosystem.

We conducted Ecological Network Analysis (ENA) in an important breeding and resting site in the north-eastern German Wadden Sea to determine the influence of birds on the food web system. The model was based on the yearly average of empirical data taken in the study site. The system appeared to be in a well-balanced status, with a relative Ascendency of 32.3% and a robustness of 36.5%. The diversity of flows was high (Flow Diversity 5.1 bits) with numerous parallel pathways

(Effective Link-Density 3.3). However, there is a strong dependency on phytoplankton imports due to the dominance of suspension feeders. A large variety of bird species uses the area for foraging and induces a negative impact on their prey items with a positive feedback reaction on the competitors and food resources of those organisms. There is also a strong negative impact among the bird compartments probably due to competition between the bird species.

Changes in the bird population could therefore affect the complexity and functioning of the whole ecosystem. It is therefore recommended to include birds in coastal food web studies which was rarely done before. The use of such holistic approaches would facilitate undertaking management measures.

1. Introduction

The Wadden Sea, stretching along the coastline of Denmark, Germany and the Netherlands, is one of the world's largest intertidal wetlands (van Roomen et al. 2012) and is therefore of outstanding importance for a variety of coastal bird species (Blew et al. 2015). Birds use the Wadden Sea for both, as a stop-over site for foraging along the East Atlantic Flyway (Scheiffarth and Nehls 1997) and as a breeding site during the spring and summer months (Schwemmer 2008, Schwemmer et al. 2016a). About 10-12 million birds per year use the intertidal flats of this ecosystem as a major food source (Koffijberg et al. 2015).

In the Wadden Sea, birds are highly protected corresponding to comprehensive regulations and conventions (e.g. EU Bird Directive, Bonn Convention and the Bern Convention, Mendel 2008). But most of the management plans are based on species abundance data which is determined in several counting programs such as ship-based and aerial transect counts, flock surveys or the waterfowl census (Mendel 2008, Markones and Garthe 2011, Blew et al. 2015, Koffijberg et al. 2015).

In some areas, birds can consume about 25 to 45% of the standing stocks of the species they prey on (Goss-Custard 1980) and may therefore have a huge influence on the intertidal ecosystem. Indeed, a model study conducted in the Brouage mud flat in the French Marennes-Olérons Bay, which is heavily used by migrating bird species during the winter months, showed that the structure and functioning of the food web varied between summer and winter in relation with the presence of the birds (Saint-Béat et al. 2013a). In winter, the food web showed specific characteristics which allowed the system to stay sustainable despite the massive increase of predation when the birds are present in the area.

Consequently, any attempts to model the dynamics of intertidal systems without including the bird species are likely to be seriously incomplete (Baird et al. 1985a). However, so far only few modeling studies examined the influence of coastal bird communities on benthic prey communities and it is rarely investigated how birds and the macrobenthic prey base influence each other.

Furthermore, birds are good bio-indicators to assess the condition of an ecosystem (Markert et al. 2003). Birds occupy various positions in the food web especially in higher trophic levels and due to their long life-span changes in the bird population generally reflect the status of the marine environment in terms of pollution, chemical contamination but also changes in fish and shellfish stocks (Markert et al. 2003).

Therefore, assessing the impact of birds on their environment, in addition to the on-going abundance monitoring programmes in the Wadden Sea (Mendel 2008, Markones and Garthe 2011, Blew et al. 2015, Koffijberg et al. 2015) would increase our knowledge about the functioning of intertidal ecosystems and improve conservation management. Food web models such as Ecological Network Analysis (ENA) are appropriate tools to assess the complex relationship between avian top predators and the ecosystem they live in. ENA methodologies allow an holistic assessment of the complex interactions within an ecosystem which are represented as flows of energy between different components (Wulff et al. 1989). ENA allows conclusions about the structural and functional properties of the system, such as organization, magnitude of cycling, trophic structure, activity, growth and development (Wulff et al. 1989, Christensen 1995, Ulanowicz and Baird 1999, Scharler and Baird 2005a, Mukherjee et al. 2015). Such outputs are of great importance for management strategies (e.g. Marine Water Framework Directives) to assess the ecological state of the Wadden Sea on ecosystem-level.

In the present study, we conducted an Ecological Network Analysis in an important foraging and breeding site for coastal birds in the north-eastern part of the German Wadden Sea. The investigated area was situated between several islands which are used by various bird species for breeding and resting while they feed mainly in the surrounding intertidal area. The aims of the study are 1) to describe the current benthic food web of the whole area including the predatory birds 2) to analyze the impact of the foraging birds on the food web components and 3) to study the sensitivity of the system to variation in the bird biomass.

2. Material and Methods

2.1. Study site

The study was conducted in the north-eastern German Wadden Sea between the islands Amrum, Föhr, Langeness and the western mainland coast of the federal state of Schleswig-Holstein (Fig. 7, General introduction, page 45). The study site had a total size of 655.4 km^2 with 286.3 km^2 of intertidal area. The area is an open system with a direct connection to the North Sea. Mean water temperature varies between 16.0 °C in summer and 5.9 °C in winter (marine environment monitoring program, State Agency for Agriculture, Environment and Rural Areas Schleswig-Holstein). The salinity ranges from 30.1 in summer and 28.5 in winter (marine environment monitoring program, State Agency for Agriculture, Environment and Rural Areas Schleswig-Holstein). Mean tidal range is 3.0 m (BSH 2016).

The area was characterized by six different habitat types (i.e. cockle field, razor clam field, mud flat, mussel bank, sand flat and seagrass meadow, Horn et. al., submitted). The size of each habitat was determined using remote sensing data (i.e. sand flat, mud flat, seagrass meadow and mussel banks) and via habitat modelling using generalized additive models (GAM) for habitat types that were not visible in satellite images (i.e. cockle field and razor clam field). The most expanded habitat type was the sand flat covering 62.7% of the intertidal area, followed by the seagrass meadows with 13.0%. Razor clam fields and mud flats covered 12.3% of and 9.3% of the studied area, respectively. The smallest habitats were cockle fields (2.4%) and mussel banks (0.2%). Detailed information about the food webs of the different habitat types is given in Horn et. al. (submitted).

2.2. Data base

Biomass samples for network construction were taken seasonally between summer 2013 and summer 2015 over one year in each habitat following a transect with five to six stations. In parallel, birds were counted seasonally in standardized areas covering the transect for benthos samples. The detailed protocol is described in Horn et. al. (submitted). A weighed average of each compartment biomass was then calculated, taking into account the size of each habitat (Table 1).

In this study, we focused on coastal birds and their interaction with the intertidal area. Therefore, the network was limited to primary producers (i.e. phytoplankton, macrophytes, microphytobenthos), sediment bacteria (BAC), meiofauna (MEI), macrozoobenthos, benthivorous birds and detritus (i.e. sediment and suspended particulate organic carbon).

2.3. Network construction

Ecological networks are based on information about the compartments' standing stocks and energy budgets as well as on the magnitude of flows between the different compartments (Fath 2007). A carbon flow model with 65 compartments was constructed (63 living and two non-living compartments, Table 1). Biomass values were given in mgC.m^{-2}. Respiration, egestion, production, consumption, imports and exports fluxes were given in mgC.m^{-2}.d^{-1}. Respiration, egestion, production and consumption values were estimated from the biomass using multiple ratios from the literature or unpublished data, which are displayed in Table 1. The diet matrix for benthic compartments was taken from Baird et al. (2004). The diet composition of birds is given in Horn et. al. (submitted). The energy budget of each compartment was balanced according to Parsons et al. (1973):

Gross primary production = Net primary production + Respiration

Consumption = Production + Respiration + Egestion

The diet of birds is often not restricted to the intertidal area as they feed also on terrestrial environments or on offshore prey items (e.g. fish, swimming crabs, Kubetzki and Garthe 2003, Schwemmer 2008, Schwemmer et al. 2012). To avoid an overestimation of predation pressure, the energy budget and corresponding consumption flows of these bird species (i. e. *Anas acuta, Anas penelope, Anas plathyrhynchas, Arenaria interpres, Branta bernicla, Charadrius hiaticula, Chroicocephalus ridibundus, Haematopus ostralegus, Larus argentatus, Larus canus, Larus fuscus, Larus marinus, Numenius arquata, Numenius phaeapus, Tadorna tadorna*) were decreased from

100% to the percentage of time they were assumed to spend feeding on intertidal areas. Detailed information about the birds' diet composition used in this study is given in Horn et. al. (submitted).

The system was considered to be in a steady-state condition. Therefore, each compartment was balanced in terms of total input and total output. As phytoplankton production within the system was not sufficient for the food demands of suspension feeders a phytoplankton-import was created assuming that additional phytoplankton was permanently entering the system from the open North Sea (Asmus and Asmus 1990). Due to the intensive bird predation, the production of some benthic compartments was not sufficient to fulfill the predators' needs. In these cases, an import was added to the prey compartment based on the assumption that this food was consumed outside of the system, and imported as "already consumed energy" via mobile predators.

Half of the unused production of macrobenthos species was assumed to be exported from the system as prey items of predators not included in this study (e.g. fish species). Half of the unused production of MPB was assumed to be re-suspended during next high tide and was therefore also exported from the system. The other half of macrobenthos and MPB production stayed in the system and was assumed to become sediment particulate organic carbon (POC). The unused production of phytoplankton and bird compartments was exported completely. Excess of suspended and sediment POC was assumed to be exported from the system by tidal currents.

Table 1: Input data for ENA; number of the compartments, compartment name, standing stocks represented by biomass in $mgC.m^{-2}$, NPP= Net primary production, GPP= Gross primary production, production, respiration, egestion and consumption of the particular compartment in $mgC.m^{-2}.d^{-1}$ and references for added biomass values and for used energy budget ratios

#	**Compartment**	**Biomass [$mgC.m^{-2}$]**	**NPP [$mgC.m^{-2}.d^{-1}$]**	**Respiration [$mgC.m^{-2}.d^{-1}$]**	**GPP [$mgC.m^{-2}.d^{-1}$]**		**Source Biomass**	**Source Energy ratios**
1	Phytoplankton	501.55	119.26	91.70	210.96		Horn et al., submitted	Baird et al. (2004)
2	Macrophyta	2,560.31	30.86	39.28	70.15		Horn et al., submitted	Baird et al. (2004)
3	Microphytobenthos	352.71	1,653.49	878.30	2531.78		Horn et al., submitted	Baird et al. (2004)
#	**Compartment**	**Biomass [$mgC.m^{-2}$]**	**Production [$mgC.m^{-2}.d^{-1}$]**	**Respiration [$mgC.m^{-2}.d^{-1}$]**	**Egestion [$mgC.m^{-2}.d^{-1}$]**	**Consumption [$mgC.m^{-2}.d^{-1}$]**		
4	Bacteria	625.00	49.24	109.00	38.15	196.39	Baird et al. (2007)	Baird et al. (2004)
5	Meiofauna	952.20	20.87	79.41	174.46	274.74	Baird et al. (2007)	Baird et al. (2004)
6	Anthozoa	17.1522	0.04	0.15	0.02	0.2115	Horn et al., submitted	Asmus (1987), Baird et al. (2004)
7	*Cerastoderma edule*	7575.28	37.74	11.83	139.15	188.73	Horn et al., submitted	Baird et al. (2004)
8	*Crassostrea gigas*	106.13	0.10	1.38	0.08	1.57	Horn et al., submitted	Baird et al. (2012)
9	*Ensis directus*	1,520.98	9.91	31.33	2.13	43.37	Horn et al., submitted	Merkel (2015)
10	*Fabulina fabula*	0.84	0.01	0.001	0.04	0.04	Horn et al., submitted	Baird et al. (2004)
11	*Macoma balthica*	1,649.22	13.59	2.53	71.76	87.88	Horn et al., submitted	Baird et al. (2004)
12	*Mya arenaria*	1,133.28	2.48	5.76	4.15	12.39	Horn et al., submitted	Baird et al. (2004)
13	*Mytilus edulis*	1,047.39	1.03	5.68	0.95	7.66	Horn et al., submitted	Baird et al. (2004)
14	*Balanidae spp.*	61.50	0.21	0.53	0.08	0.82	Horn et al., submitted	Baird et. al. (2008)
15	*Carcinus meanas*	692.90	2.93	4.40	9.64	16.97	Horn et al., submitted	Baird et al. (2004)
16	*Crangon spp.*	165.75	1.82	6.26	1.82	9.90	Horn et al., submitted	Baird et al. (2004)
17	*Pycnoganum litorale*	0.23	0.004	0.01	0.001	0.01	Horn et al., submitted	Baird et al. (2004)
18	small crustaceans	123.50	0.50	2.11	0.67	3.28	Horn et al., submitted	Baird et al. (2004)
19	*Crepidula fornicata*	0.72	0.001	0.004	0.01	0.01	Horn et al., submitted	Asmus (1987), Baird et al. (2012)
20	*Lepidochitona cinerea*	0.71	0.004	0.004	0.01	0.02	Horn et al., submitted	Asmus (1987), Baird et al. (2004)

Table 1 (continued): Input data for ENA; number of the compartments, compartment name, standing stocks represented by biomass in mgC.m^{-2}, NPP= Net primary production, GPP= Gross primary production, production, respiration, egestion and consumption of the particular compartment in mgC.m^{-2}.d^{-1} and references for added biomass values and for used energy budget ratios

21	*Littorina littorea*	1,059.71	2.17	6.56	13.10	21.83	Horn et al., submitted	Baird et al. (2004)
22	*Peringia ulvae*	14,406.20	259.71	86.70	419.64	766.05	Horn et al., submitted	Asmus (1987), Baird et al. (2004)
23	*Retusa obtusa*	712.91	2.78	4.29	20.77	27.84	Horn et al., submitted	Baird et al. (2004)
24	Nemertea	110.29	0.71	1.16	4.19	6.06	Horn et al., submitted	Asmus (1987), Baird et al. (2004)
25	Oligochaeta	661.96	1.81	17.67	8.93	28.41	Horn et al., submitted	Baird et al. (2004)
26	*Arenicola marina*	3334.82	23.90	22.23	113.17	159.30	Horn et al., submitted	Baird et al. (2004)
27	*Capitella capitata*	44.46	0.24	1.03	2.52	3.79	Horn et al., submitted	Baird et al. (2004)
28	*Eteone spp.*	39.49	0.19	0.03	0.33	0.55	Horn et al., submitted	Baird et al. (2004)
29	*Heteromastus filiformis*	0.13	0.001	0.001	0.01	0.01	Horn et al., submitted	Baird et al. (2004)
30	*Lanice conchilega*	16.23	0.08	0.16	0.07	0.32	Horn et al., submitted	Baird et al. (2004)
31	*Lepidonotus squamatus*	0.94	0.003	0.01	0.04	0.05	Horn et al., submitted	Asmus (1987), Baird et al. (2004)
32	*Nephtys spp.*	126.66	1.40	1.33	4.81	7.53	Horn et al., submitted	Baird et al. (2004)
33	*Nereis spp.*	1,234.72	5.92	14.50	37.84	58.27	Horn et al., submitted	Nithart et al. (1999), Baird et al. (2004)
34	*Phyllodoce spp.*	449.27	1.23	13.28	1.75	16.26	Horn et al., submitted	Baird et al. (2004)
35	*Pygospio elegans*	31.38	0.12	0.53	0.23	0.88	Horn et al., submitted	Baird et al. (2004)
36	*Scoloplos armiger*	1,797.19	7.83	13.05	34.03	54.91	Horn et al., submitted	Nithart et al. (1999), Baird et al. (2004)
37	small polychaetes	46.68	0.21	0.68	0.39	1.29	Horn et al., submitted	Baird et al. (2004)
38	*Tharyx killariensis*	21.29	0.12	0.22	0.24	0.57	Horn et al., submitted	Baird et al. (2004)
39	*Anas acuta*	29.14	0.08	1.77	1.01	2.86	Horn et al., submitted	Baird et al. (2004)
40	*Anas penelope*	2,274.43	1.29	40.72	23.76	65.77	Horn et al., submitted	Baird et al. (2004)
41	*Anas platyrhynchos*	208.19	0.12	4.38	2.60	7.10	Horn et al., submitted	Baird et al. (2004)
42	*Arenaria interpres*	4.48	0.01	0.48	0.12	0.61	Horn et al., submitted	Baird et al. (2004)
43	*Branta bernicla*	336.19	0.34	8.40	4.71	13.45	Horn et al., submitted	Baird et al. (2004)
44	*Calidris alpina*	81.13	0.17	9.72	2.51	12.40	Horn et al., submitted	Baird et al. (2004)

Table 1 (continued): Input data for ENA; number of the compartments, compartment name, standing stocks represented by biomass in mgC.m^{-2}, NPP= Net primary production, GPP= Gross primary production, production, respiration, egestion and consumption of the particular compartment in mgC.m^{-2}.d^{-1} and references for added biomass values and for used energy budget ratios

45	*Calidris canutus*	139.24	0.52	27.33	7.22	35.07	Horn et al., submitted	Baird et al. (2004)
46	*Charadrius hiaticula*	3.34	0.01	0.40	0.10	0.51	Horn et al., submitted	Baird et al. (2004)
47	*Chroicocephalus ridibundus*	50.82	0.12	2.73	0.71	3.56	Horn et al., submitted	Baird et al. (2004)
48	*Haematopus ostralegus*	366.10	1.66	38.09	9.94	49.69	Horn et al., submitted	Baird et al. (2004)
49	*Larus agentatus*	112.32	0.17	5.08	1.35	6.60	Horn et al., submitted	Baird et al. (2004)
50	*Larus conus*	41.42	0.07	1.62	0.44	2.13	Horn et al., submitted	Baird et al. (2004)
51	*Larus fuscus*	3.48	0.001	0.04	0.01	0.05	Horn et al., submitted	Baird et al. (2004)
52	*Larus marinus*	2.41	0.001	0.001	0.02	0.02	Horn et al., submitted	Baird et al. (2004)
53	*Limicola falcinellus*	0.23	0.001	0.03	0.01	0.04	Horn et al., submitted	Baird et al. (2004)
54	*Limosa lapponica*	631.40	2.34	100.56	25.72	128.62	Horn et al., submitted	Baird et al. (2004)
55	*Numenius arquata*	114.72	0.21	6.32	1.69	8.22	Horn et al., submitted	Baird et al. (2004)
56	*Numenius phaeapus*	4.37	0.01	0.24	0.06	0.31	Horn et al., submitted	Baird et al. (2004)
57	*Pluvialis squatarola*	54.31	0.17	4.75	1.19	6.11	Horn et al., submitted	Baird et al. (2004)
58	*Recurvirostra avasetta*	3.71	0.04	0.62	0.16	0.82	Horn et al., submitted	Baird et al. (2004)
59	*Somateria mollissima*	10.66	0.03	1.13	0.29	1.45	Horn et al., submitted	Baird et al. (2004)
60	*Todorna tadorna*	212.47	0.50	17.19	5.12	22.81	Horn et al., submitted	Baird et al. (2004)
61	*Tringa erythropus*	5.47	0.02	1.04	0.28	1.34	Horn et al., submitted	Baird et al. (2004)
62	*Tringa nebularia*	9.11	0.03	1.61	0.43	2.06	Horn et al., submitted	Baird et al. (2004)
63	*Tringa totanus*	66.79	0.24	12.72	3.36	16.32	Horn et al., submitted	Baird et al. (2004)
64	sediment POC	19,000.00					Baird et al. (2007)	
65	suspended POC	167.44					Baird et al. (2007)	

2.4. Network analysis

Ecological Network Analysis (ENA) is based on the concept of input-output analysis and provides a set of tools useful to describe the status of a network at different levels: whole system level, environ level (i.e. group of nods), nod level. The methodology is described in detail by Kay et al. (1989) and in the review of Ulanowicz (2004). We used the software package enaR for R statistics for all the analyses (Borrett and Lau 2014, Lau et al. 2015).

2.4.1 System attributes

The system attributes are global information indices that describe the current situation of the system. These indices include information about the organization and development of the system, its magnitude of cycling, its ability to cope with perturbations but also about the health status and the system's maturity (Mann et al. 1989, Wulff et al. 1989, Baird and Ulanowicz 1993, Christensen 1995, Scharler and Baird 2005a, Mukherjee et al. 2015). The indices analyzed and determined in the present study are given in Table 2.

Table 2: List of analyzed system attributes. Name of the index, abbreviation used in the text, unit of the index and description of the index

Index	Abbreviation	Unit	Description
Total System Throughput	TST	$mgC.m^{-2}.d^{-1}$	The TST is the sum of all flows and represents the size and activity of the system (Wulff et al. 1989). The higher the value the bigger and more active is the system.
Development Capacity	DC	$mgC.m^{-2}.d^{-1}$ bits	The system's potential to develop by calculating the particular set of connections and total throughflow. It's the upper limit of the system's Ascendency (Wulff et al. 1989).
Ascendency	A	$mgC.m^{-2}.d^{-1}$ bits	It is a measurement of the activity, the size, the organization and the evenness of energy flows. High values imply complex trophodynamic relations and high system productivity (Wulff et al. 1989). Ascendency is furthermore correlated with a higher degree of specialization in the system.

Table 2 (continued): List of analyzed system attributes. Name of the index, abbreviation used in the text, unit of the index and description of the index

Relative Ascendency	A/DC	%	The ratio between A and DC represents the system's degree of organization and the efficiency of energy flows. A high A/DC shows a well-organized and developed system that is less vulnerable to disturbances (Wulff et al. 1989, Pockberger and Asmus 2014).
Overheads	OH	$mgC.m^{-2}.d^{-1}$ bits	The overheads characterize the free energy in a system (Wulff et al. 1989). With a high overhead the system has more capacities to react to perturbations and a larger potential of resilience
Relative Overheads	OH/DC	%	The ratio between OH and DC is the natural counterpart of A/DC.
Robustness		%	A balanced trade-off between the efficiency and redundancy that describes the system's sustainability (Fath 2015).
Flow Diversity	FD	bits	The number of interactions and the evenness of energy flows. Comparable to the biodiversity index, a high value shows a highly diverse, well-developed and stable system (Wulff et al. 1989, Pockberger and Asmus 2014).
Effective Link-Density	ELD		The effective number of parallel pathways and is based on the number of flows per node (Ulanowicz et al. 2014).
Average Path Length	APL		The mean number of compartments a unit of carbon passes before it leaves the system again (Wulff et al. 1989). A low APL shows that the energy is only used in few compartments and indicates an instable system. On the contrary, long path lengths indicate a more mature system (Christensen 1995, Pockberger and Asmus 2014).
Finn Cycling Index	FCI	%	It is the proportion of flows in a system that are recycled (Wulff et al. 1989). Higher values indicate that the system is more independent from imports
Logarithmic Trophic Efficiency	TE	%	Shows how energy is efficiently transferred in the system (Wulff et al. 1989). For the determination of the logarithmic mean trophic efficiency of each system only trophic levels with an efficiency of ≥0.1 % were taken into account.
Trophic Depth	TD		The number of effective trophic levels in the system (Ulanowicz et al. 2014).

2.4.2 Lindeman spine

The Lindeman spine is a simplified representation of the food web calculated using the Lindeman Trophic Aggregation Analysis. This implementation transforms the complex network into a linear food chain with integer trophic levels (Wulff et al. 1989). Primary producers and the detritus pool form the first trophic level; the following trophic levels are then built by the consumers according to their trophic position within the food web. Carbon flows within the system as well as imports to the system and energy losses due to respiration and exports are computed. Furthermore, the efficiency of energy transfer is quantified within the Lindeman spine. The amount of detritivory and herbivory was calculated and therefore the relation of the feeding types could be determined.

2.4.3 Mixed Trophic Impact analysis

The input-output analysis of ENA provides information on the magnitude of direct and indirect effects that an interaction between two compartments might have on other compartments in the network (Scharler and Baird 2005a). These effects can be computed using the Mixed Trophic Impact (MTI) analysis which is based on the concept that in an ecological network, all components are linked to, and therefore influence each other (Ulanowicz and Puccia 1990). A matrix of dependency coefficients is calculated and shows the fraction of energy leaving compartment i that is eventually entering compartment j (Baird et al. 2004). The MTI analysis therefore represents the impact of biomass change of one compartment on the biomass of other compartments (Pockberger et al. 2014) taking into account direct connections (e.g. predator-prey relationships) and indirect connections (e.g. top-down or bottom-up effects, competition).

In order to determine the impact of the birds on the whole system, a Mixed Trophic Impact analysis (MTI) was conducted with all combined bird compartments.

2.4.4 Bird uncertainty analysis

The Wadden Sea undergoes large seasonal changes in abundance, biomass and species composition of multiple components of its food web. Due to migration patterns, the bird abundance and species composition particularly vary across seasons (Blew et al. 2013). Furthermore, since the 1980s, positive or negative trends are observed for some bird species in the Wadden Sea (van Roomen et al. 2012, Blew et al. 2015, Koffijberg et al. 2015). These variations might influence the system functioning. To assess the sensitivity of the ENA indices to these natural variation, 10 additional models with a gradual increase (+10%, +20%, +30%, + 40% and +50%) and gradual decrease (-10%, -20%, -30%, -40% and -50%) of the birds' biomass were constructed. In addition, one model with a negligible biomass of 0.001 mgC.m^{-2} in each bird compartment was created (no birds) in order to estimate the magnitude of the impact of birds on the system. In total, twelve models were analyzed using ENA, including the initial model and the models with changed biomass.

3 Results

3.1 System description

3.1.1 Production and size

The otal production and the secondary production in the system were 2,260.7 mgC.m^{-2}.d^{-1} and 457.0 mgC.m^{-2}.d^{-1}, respectively. In total 44.6% of the consumer fluxes was based on primary production (i. e. 11.0% Phytoplankton, 3.6% Macrophytes and 30.0% MPB), 31.2% was due to predation on benthic organisms and only 24.2% of the total consumption in the system was based on detritivory. Herbivory was therefore 1.84 times higher than detritivory.

The Total System Throughput (TST), reflecting the size and activity of the system, was 11,437.1 mgC.m^{-2}.d^{-1}. The Development Capacity (DC) of the system was 57,940.9 bits.

3.1.2 System organization and flow structure

The relative Ascendency (A/DC), relative Overheads (OH/DC) and the robustness reflect the organization and the structure of the system. The values of A/DC (32.3%) and the robustness (36.5%) were in the window of vitality defined by Fath et al. (2015) and Ulanowicz et al. (2009). This therefore showed a good trade-off between organization and redundancy in the system. The relatively high OH/DC value (67.8%) suggested high energy reserves within the system.

The relative high values of Flow Diversity (5.1 bits) and Effective Link-Density (3.3) suggested a high number of parallel pathways in the system. The Average Path Length (2.1) indicated that a unit of carbon passes on average 2.1 compartments, before it leaves the system again. 6.0% of the TST in the system was recycled, as indicated by the Finn Cycling Index (FCI) value.

The trophic structure of the system is represented by the Trophic Depth (TD), the logarithmic mean Trophic Efficiency (TE) and the Lindeman Trophic Aggregation Analysis. The system had a TD of 3.1 and a TE of 3.8%. The results of the trophic aggregation of the system were displayed as the food chain of the Lindeman spine and included eight trophic levels (Fig. 1). Despite this extensive food chain the highest trophic position was only 3.6 (*Larus canus*, Table 3). Energy transfer decreased within the Lindeman spine from the first trophic level towards higher trophic levels. It is remarkable that the first and the second trophic level of the Lindeman spine showed similar trophic efficiencies (36.8% and 35.8%, respectively). Only little energy was obtained from trophic level IV and higher.

Table 3: Compartment number (#), name of compartment and trophic position of the compartment determined by Lindeman Trophic Aggregation Analysis

#	**Compartment**	**Trophic position**
1	Phytoplankton	1.00
2	Macrophyta	1.00
3	MPB	1.00
4	BAC	2.00
5	MEI	2.29
6	*Anthozoa*	2.00
7	*Cerastoderma edule*	2.00
8	*Crassostrea gigas*	2.00
9	*Ensis directus*	2.00
10	*Fabulina fabula*	2.13
11	*Macoma balthica*	2.13
12	*Mya arenaria*	2.00
13	*Mytilus edulis*	2.00
14	*Balanidae spp.*	2.00
15	*Carcinus+Hemigrapsus*	3.22
16	*Crangon spp.*	3.03
17	*Pycnogonum litorale*	3.00
18	small crustaceans	2.13
19	*Crepidula fornicata*	2.00
20	*Lepidochitona cinerea*	2.00
21	*Littarina littorea*	2.00
22	*Peringia ulvae*	2.13
23	*Retusa obtusa*	3.13
24	*Nemertea*	3.27
25	*Oligachaeta*	2.50
26	*Arenicola marina*	2.45
27	*Capitella capitata*	2.50
28	*Eteone spp.*	3.26
29	*Heteromastus filiformis*	2.50
30	*Lanice conchilega*	2.00
31	*Lepidonotus squamatus*	3.29
32	*Nephtys spp.*	3.29
33	*Nereis spp.*	2.71
34	*Phylladoce spp.*	3.27
35	*Pygospio elegons*	2.00
36	*Scoloplas armiger*	2.45
37	small polychaetes	2.06
38	*Tharyx killariensis*	2.50
39	*Anas acuta*	2.86
40	*Anas penelape*	2.00
41	*Anas platyrhynchos*	2.61
42	*Arenaria interpres*	3.08
43	*Branta bernicla*	2.00
44	*Calidris alpina*	3.57
45	*Calidris canutus*	3.06
46	*Charadrius hiaticula*	3.46
47	*Chroicocephalus ridibundus*	3.49
48	*Haematopus ostralegus*	3.25
49	*Larus agentatus*	3.44
50	*Larus canus*	3.63
51	*Larus fuscus*	3.14
52	*Larus marinus*	3.00
53	*Limicola falcinellus*	3.57
54	*Limasa lapponica*	3.70
55	*Numenius arquata*	3.58
56	*Numenius phaeopus*	3.58
57	*Pluvialis squatarola*	3.50
58	*Recurvirostra avasetta*	3.54
59	*Samateria mollissima*	3.02
60	*Tadorna tadorna*	3.18
61	*Tringa erythropus*	3.45
62	*Tringa nebularia*	3.46
63	*Tringa totanus*	3.45

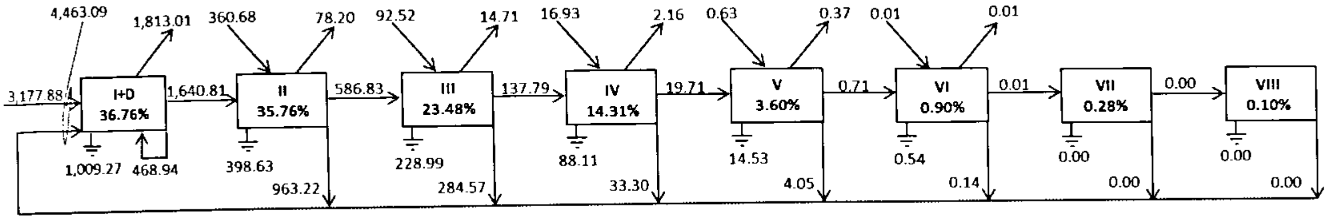


Fig. 1: Lindeman spine of the studied intertidal system. Boxes represent the integer trophic levels, percentage values refer to trophic efficiency between the levels. Arrows indicate energy flows between trophic levels as well as import and exports and backflows to the detritus pool. Dashed arrows show energy losses due to respiration. Values are given in $mgC.m^{-2}.d^{-1}$

3.2 Impact analysis

The impact analysis revealed positive and negative influences of the birds on the system (Fig. 2). The prey items of the birds (e.g. small crustaceans, *Heteromastus filiformis*, *Lanice conchilega*, *Mytilus edulis*), benthic carnivores (e.g. *Lepidonotus squamatus*) and the bird compartments themselves were negatively impacted by the activity of the birds. On the contrary, the competitors of the birds' prey items that are not or only rarely eaten by birds (e. g. *Crassostrea gigas*, *Tharyx killariensis*), and the food sources of the birds' prey items (e.g. phytoplankton and detritus) were positively impacted by the presence of the birds.

Overall, the negative influences were more pronounced than the positive influences of the birds.

Fig. 2: Mixed trophic impact of the birds as combined impacting compartments on the system

3.3 Bird uncertainty analysis

In comparison to the present state of the food web (Paragraph 3.1.1 and 3.1.2) the system varied with changes in the bird biomass. The system attributes showed different sensitivities to variations in the bird compartments (Fig. 3). The TST, OH/DC, APL, ELD, TD and FD, and in less extent A, OH and DC, decreased with decreasing bird biomass. The A/DC and robustness increased and FCI slightly increased with decreasing bird biomass. The Trophic Efficiency was not sensitive to changes in the bird biomass but sharply decreased when all birds were removed from the system. Same trends were observed for OH/DC, APL, FD, ELD and TD which sharply decreased when birds were totally absent of the system.

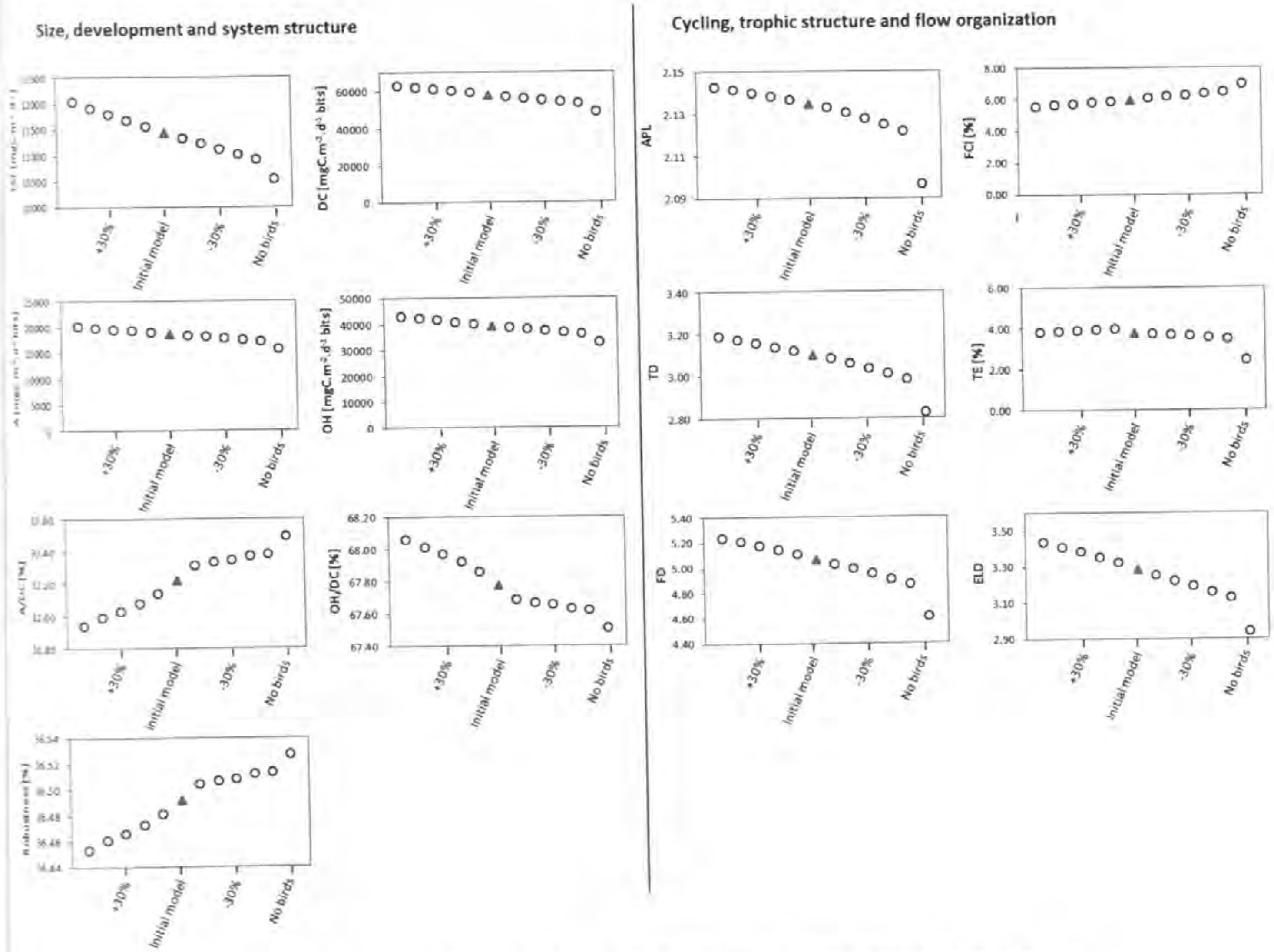


Fig. 3: Sensitivity of system attributes to changes in bird biomass, initial model = red triangle

4 Discussion

4.1 System description

There are only few tools for ecologists to examine the structure and function of whole ecosystems despite the general tendency towards approaches of environmental problems at ecosystem-level (Scharler and Baird 2005a). Ecological Network Analysis is one of the methodologies allowing a holistic representation of a whole ecosystem based on trophic interactions.

The study site shows a good trade-off between organization and redundancy and can therefore be described as stable and sustainable (Fath 2015, Mukherjee et al. 2015). Indeed, Mukherjee et al. (2015) postulated that a healthy system can develop an efficient diversity of components and exchange pathways while maintain some overhead as insurance to deal with stress and perturbations. Coastal ecosystems such as the studied area are often subjected to various perturbations directly connected to anthropogenic activities (Wolff et al. 2010). Therefore, it is important to assess the health and stability of coastal ecosystems.

The high values of Flow Diversity and Effective Link-Density support the description of the system as stable and sustainable. Indeed, the high diversity of flows and the increased level of complexity (high FD) suggest that the system is stable and mature (Christensen 1995, Pockberger and Asmus 2014). The numerous parallel pathways (high ELD) indicate a high redundancy which suggests a high resistance of the system to external perturbations (Ulanowicz et al. 2014). The high APL also shows that the system already reached a high level of maturity (Christensen 1995). On the contrary, the recycling is relatively low (FCI of 6.0%) indicating that the system is strongly dependent on external sources (Pockberger and Asmus 2014). Indeed, detritivory which increases the cycling, was of minor importance reflecting only 24.2% of the consumption fluxes. The system is dominated by huge standing stocks of grazers (e.g. *Peringia ulvae*) feeding on microphytobenthos and suspension feeders (e.g. *Mytilus edulis, Cerastoderma edule, Crassostrea gigas*) which rely on regular phytoplankton import.

Larus canus occupies the highest trophic position in the modeled food web (3.6), although it is known to be an opportunistic gull species, feeding on a large variety of prey items (Kubetzki and Garthe 2003). This result might be caused by the exclusion of fish in the present study. Fish also maintain high trophic levels in a food web and are the main prey of larger gull species such as *L. fuscus* and *L. marinus*. An inclusion of fish might therefore increase the trophic position of these species

Our results are comparable to the very well-studied Sylt-Rømø Bight (Baird et al. 2004, Baird et al. 2007, 2008, 2012), but in contrast to the Sylt-Rømø Bight we found a higher degree of herbivory probably caused by the predominance of grazers and suspension feeders (Horn et. al, submitted). Furthermore, the present system appears to be bigger and more active than the Sylt-Rømø Bight with a higher importance for coastal birds.

4.2 Impact analysis

The Mixed Trophic Impact (MTI) analysis revealed a relatively strong impact of coastal birds on the system they live in. Especially prey organisms that are limited in their availability (e. g. small crustaceans or *Mytilus edulis*) were directly negatively impacted by the intensive predation pressure of foraging birds. On the other hand, the food sources of these prey organisms (e.g. Phytoplankton, sediment POC) and also their competitors (e.g. *Crassostrea gigas*) were indirectly positively impacted. This feedback reaction indicates a top-down cascade effect of the birds on the benthic habitats they use for feeding.

We also found a strong negative influence among the different bird compartments. This suggests high competition for food between bird species on the intertidal flats. Indeed, studies about foraging behavior of birds in intertidal flats showed that several wading bird species defend their feeding territories (Ens et al. 1992, Colwell 2000, Schwemmer 2011). Each intertidal area has a capacity to support a certain amount of foraging birds in a particular time of the year (Goss-Custard et al. 2002) and this capacity can vary due to changes in the availability of benthic prey items (Goss-

Custard 1980). Because of the large number of bird individuals in foraging areas, density-dependent interactions such as interference, competition, or kleptoparasitism are often observed (Goss-Custard 1980, Galbraith et al. 2002). The negative influence among the bird compartments observed in this study support these inter-individual and inter-species interactions on the tidal flats.

4.3 Influence of birds on system attributes

The ENA system attributes stayed relatively constant despite the large biomass variations of birds tested on the system. Only the total removal of birds from the system induced a sharp change. However, with decreasing bird biomass there was an increase in the degree of organization (A/DC) and a decrease in free energy reserves (OH/DC). This implies that a system with a small amount of birds would be less complex and more organized. This might be explained by the high mobility of birds which export energy by foraging and then leaving the system. Therefore, they do not participate in recycling material in the detritus pool and are not included in the system´s cycles. A decrease in birds then tends to increase the Finn Cycling Index and the degree of organization (A/DC) because less energy is removed from the system.

On the contrary, a decline in birds induces a decrease of Average Paths Length (APL), Flow Diversity (FD), Effective Link-Density (ELD) and Trophic Depth (TD). As top predators, birds are at high trophic positions within the intertidal food web and therefore transport the energy over longer pathways than benthic predators. A decrease of birds in the system will then lead to a decline of APL and TD.

The connectivity of the system appears to decrease with decreasing bird biomass. This might be a consequence of the decrease of parallel pathways (ELD) when birds are removed. Indeed, there are a lot of different bird species in the system which generate redundant flows in the higher trophic levels. Predation by birds therefore appears to be important to stabilize the flows in the higher trophic levels of the system.

The complexity and diversity of flows in the system also decrease with decreasing bird biomass. Because of the use of logarithmic transformation in the calculation of FD index, small changes in FD can indicate large differences in reality (Monaco and Ulanowicz 1986).

Because they reflect the connectivity and the redundancy in the system, high values of FD and ELD generally indicate a stable system resistant to perturbations (Christensen 1995, Baird et al. 2007). A decrease in the bird biomass would therefore lead to a system less stable and more vulnerable to external perturbations. Birds are therefore important factors for the systems diversity and complexity.

4.4 Birds in the Wadden Sea

There are only few network studies about coastal systems which include birds as top predators (Baird et al. 2004, Scharler and Baird 2005a, Saint-Béat et al. 2013a), although birds induce a high predation pressure on benthic organisms and are therefore important components of the intertidal food web. There are clear trends that birds increase the size and activity of the system (TST), the diversity and structure of flows (FD and ELD) and the length of trophic pathways (APL and TD). Birds are therefore important drivers for the complexity and functioning of intertidal food webs and changes in the bird community could affect the whole intertidal ecosystem.

In the Wadden Sea, there was a strong decline in a majority of coastal bird populations in the last decades (van Roomen et al. 2012, Blew et al. 2015, Koffijberg et al. 2015). Reasons for these trends are diverse and probably interconnected. Habitat destruction and the loss of breeding sites due to sea-level rise, and mammalian predation are important drivers for the population changes (van de Pol 2010, van Roomen et al. 2012, Koffijberg et al. 2015). In addition, the decrease in food supply may play a role (Koffijberg et al. 2014) as there is a strong interaction between birds and their foraging areas.

Including ecosystem-based studies in the decisions about bird management, in addition to the on-going population monitoring, would improve considerably the conservation strategies. ENA is an efficient tool to have a holistic approach of ecosystem functioning and would help to assess how a further decline of the bird population would affect the whole intertidal system.

5 Conclusion

The Wadden Sea is a very important breeding and resting site for a huge number of birds which use the intertidal flats as a major food source. With Ecological Network Analysis (ENA) we showed that the system is in a good trade-off between its degree of organization and its ability to cope with disturbances. It is furthermore characterized by a high diversity and complexity of flows with relatively long pathways.

Birds have a strong negative impact on their prey items which induces a top-down cascade effect on the competitors and the food sources of these organisms. But the birds also influence themselves negatively due to density-dependent interactions on the intertidal flats such as interference or competition for food. Furthermore, scenarios of variations in the birds biomass showed that an increase of bird biomass tend to increase the activity and the degree of interactions within the food web. Birds are therefore an important factor for the functioning of the food web.

Scenarios taking into account changes in some specific bird species reflecting the observed trends in the Wadden Sea might give more detailed results about how birds interact with each other in their foraging area. The use of such holistic studies in management decisions are the basis for assessing the current ecological state of an ecosystem and could improve the conservation measures.

6 Acknowledgements

This study was funded by the German Federal Ministry of Education and Research in the frame of the German joint research project "STopP – From sediment to top predator" (BMBF, FKZ 03F672B). We are grateful to all the people who helped creating the dataset for the model; the teams of the vessels “MS Hooge” and “FS Mya II” who brought us safely to mussel banks, cockle fields and razor clam field, Martin Kühn and the team of the FTZ Büsum for counting the birds on the areas, Birgit Hussel for analyzing the microphytobenthos and all the students and internships who worked on the macrozoobenthos samples.

7 References

Asmus, H. 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. Marine ecology progress series. Oldendorf **39**:251-266.

Asmus, H., and R. Asmus, M. 1990. Trophic relationships in tidal flat areas: to what extend are tidal flats dependant on imported food? Netherlands Journal of Sea Research **27**:93-99.

Baird, D., H. Asmus, and R. Asmus. 2004. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Marine Ecology Progress Series **279**:45-61.

Baird, D., H. Asmus, and R. Asmus. 2007. Trophic dynamics of eight intertidal communities of the Sylt-Rømø Bight ecosystem, northern Wadden Sea. Marine Ecology Progress Series **351**:25-41.

Baird, D., H. Asmus, and R. Asmus. 2008. Nutrient dynamics in the Sylt-Rømø Bight ecosystem, German Wadden Sea: An ecological network analysis approach. Estuarine, Coastal and Shelf Science **80**:339-356.

Baird, D., H. Asmus, and R. Asmus. 2012. Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. Marine Ecology Progress Series **462**:143-162.

Baird, D., P. Evans, H. Milne, and M. Pienkowski. 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. Oceanography and marine biology **23**:573-597.

Baird, D., and R. Ulanowicz. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal. Marine Ecology Progress Series **99**:221-237.

Blew, J., K. Günther, B. Hälterlein, R. Kleefstra, K. Laursen, and G. Scheiffarth. 2015. Trends of Migratory and Wintering Waterbirds in the Wadden Sea 1987/1988-2011/2012.

Borrett, S., R.,, and M. Lau, L. 2014. enaR: An R package for Ecosystem Network Analysis. Methods in Ecology and Evolution **5**:1206-1213.

BSH. 2016. Gezeitenkalender 2016. Hoch- und Niedrigwasserzeiten für die Deutsche Bucht und deren Flussgebiete. Federal Maritime and Hydrographic Agency.

Christensen, V. 1995. Ecosystem maturity—towards quantification. Ecological Modelling **77**:3-32.

Colwell, M. A. 2000. A review of territoriality in non-breeding shorebirds (Charadrii). BULLETIN-WADER STUDY GROUP **93**:58-66.

Ens, B. J., M. Kersten, A. Brenninkmeijer, and J. B. Hulscher. 1992. Territory quality, parental effort and reproductive success of oystercatchers (Haematopus ostralegus). Journal of Animal Ecology:703-715.

Fath, B. D. 2015. Quantifying economic and ecological sustainability. Ocean & Coastal Management **108**:13-19.

Galbraith, H., R. Jones, R. Park, J. Clough, S. Herrod-Julius, B. Harrington, and G. Page. 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. Waterbirds **25**:173-183.

Goss-Custard, J. 1980. Competition for food and interference among waders. Ardea **68**:31-52.

Goss-Custard, J., R. Stillman, A. West, R. Caldow, and S. McGrorty. 2002. Carrying capacity in overwintering migratory birds. Biological Conservation **105**:27-41.

Koffijberg, K., K. Laursen, B. Hälterlein, G. Reichert, J. Frikke, and L. Soldat. 2015. Trends of Breeding Birds in the Wadden Sea 1991-2013. Wadden Sea Ecosystem.

Kubetzki, U., and S. Garthe. 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Marine Biology **143**:199-207.

Lau, M. K., S. R. Borrett, and P. Singh. 2015. Ecosystem Network Analysis with R: A guide for using enaR.

Mann, K. H., J. G. Field, and F. Wulff. 1989. Network analysis in marine ecology: an assessment. Springer.

Markert, B., A. Breure, and H. Zechmeister. 2003. Biomonitoring with birds. Bioindicators & Biomonitors:677.

Markones, N., and P. D. S. Garthe. 2011. Marine Säugetiere und Seevögel in der deut-schen AWZ von Nord-und Ostsee-Teilbericht Seevögel.

Mendel, B. 2008. Profiles of seabirds and waterbirds of the German North and Baltic Seas: distribution, ecology and sensitivities to human activities within the marine environment. Bundesamt f. Naturschutz.

Merkel, C. 2015. Ermittlung des Energiebudgets von Ensis directus im Eulitoral der Insel Sylt. Philipps-Universität Marburg, Master thesis.

Monaco, M. E., and R. E. Ulanowicz. 1986. Comparative ecosystem trophic structure of. Marine Ecology Progress Series **1**:9.

Mukherjee, J., U. M. Scharler, B. D. Fath, and S. Ray. 2015. Measuring sensitivity of robustness and network indices for an estuarine food web model under perturbations. Ecological Modelling **306**:160-173.

Nithart, M., E. Alliot, and C. Salen-Picard. 1999. Production, respiration and ammonia excretion of two polychaete species in a north Norfolk saltmarsh. Journal of the Marine Biological Association of the UK **79**:1029-1037.

Parsons, T. R., M. Takahashi, and B. Hargrave. 1973. Biological oceanographic processes. Elsevier.

Pockberger, M., and H. Asmus. 2014. Empfehlungen zur Anwendung von Ökosystemanalysen zur Beurteilung des Nahrungsnetzes im Wattenmeer in der Meeresstrategie Rahmenrichtlinie.

Pockberger, M., F. Kellnreitner, H. Ahnelt, R. Asmus, and H. Asmus. 2014. An abundant small sized fish as keystone species? The effect of Pomatoschistus microps on food webs and its trophic role in two intertidal benthic communities: A modeling approach. Journal of Sea Research **86**:86-96.

Saint-Béat, B., C. Dupuy, P. Bocher, J. Chalumeau, M. De Crignis, C. Fontaine, K. Guizien, J. Lavaud, S. Lefebvre, and H. Montanié. 2013. Key Features of Intertidal Food Webs That Support Migratory Shorebirds. Plos One **8**.

Scharler, U. M., and D. Baird. 2005. A comparison of selected ecosystem attributes of three South African estuaries with different freshwater inflow regimes, using network analysis. Journal of Marine Systems **56**:283-308.

Scheiffarth, G., and G. Nehls. 1997. Consumption of benthic fauna by carnivorous birds in the Wadden Sea. HELGOLANDER MEERESUNTERSUCHUNGEN **51**:373-387.

Schwemmer, P., Garthe, S. 2008. Regular habitat switch as an important feeding strategy of an opportunistic seabird species at the interface between land and sea. Estuarine, Coastal and Shelf Science **77**:12-22.

Schwemmer, P., Garthe, S. 2011. Spatial and temporal patterns of habitat use by Eurasian oystercatchers (*Haematopus ostralegus*) in the eastern Wadden Sea revealed using GPS data loggers. Marine Biology **158**:541-550.

Schwemmer, P., F. Güpner, S. Adler, K. Klingbeil, and S. Garthe. 2016. Modelling small-scale foraging habitat use in breeding Eurasian oystercatchers (Haematopus ostralegus) in relation to prey distribution and environmental predictors. Ecological Modelling **320**:322-333.

Schwemmer, P., F. Güpner, N. Guse, and S. Garthe. 2012. Nahrungswahl von Vogelarten der deutschen Nordseeküste. Vogelwarte **50**:141-154.

Ulanowicz, R., and C. Puccia. 1990. Mixed trophic impacts in ecosystems. Coenoses **5**:7-16.

Ulanowicz, R. E., and D. Baird. 1999. Nutrient controls on ecosystem dynamics: the Chesapeake mesohaline community. Journal of Marine Systems **19**:159-172.

Ulanowicz, R. E., S. J. Goerner, B. Lietaer, and R. Gomez. 2009. Quantifying sustainability: resilience, efficiency and the return of information theory. Ecological complexity **6**:27-36.

Ulanowicz, R. E., R. D. Holt, and M. Barfield. 2014. Limits on ecosystem trophic complexity: insights from ecological network analysis. Ecology letters **17**:127-136.

van Roomen, M., K. Laursen, C. van Turnhout, E. van Winden, J. Blew, K. Eskildsen, K. Günther, B. Hälterlein, R. Kleefstra, and P. Potel. 2012. Signals from the Wadden sea: Population declines dominate among waterbirds depending on intertidal mudflats. Ocean & Coastal Management **68**:79-88.

Wolff, W. J., J. P. Bakker, K. Laursen, and K. Reise. 2010. The Wadden Sea Quality Status Report-Synthesis Report 2010. The Wadden Sea 2010. Common Wadden Sea Secretariat (CWSS); Trilateral Monitoring and Assessment Group: Wilhelmshaven.(Wadden Sea Ecosystem; 29/editors, Harald Marencic and Jaap de Vlas) **25**.

Wulff, F., J. G. Field, and K. H. Mann. 1989. Network analysis in marine ecology: methods and applications. Springer Science & Business Media.

General discussion

General Discussion

1. The food web of the Wadden Sea

1.1. The influence of different habitat types on the whole ecosystem

Our study revealed similarities as well as differences in the functioning of different intertidal habitat types. Each of the habitats showed specific traits and features. Cockle fields and mussel banks were very active and complex systems but were simultaneously highly dependent on external imports. The direct connection to the open North Sea might therefore be very important for these systems. Phytoplankton is regularly imported from the North Sea due to tidal currents (Asmus and Asmus 1990) and it is a required food source for the highly abundant suspension-feeders in the study site. Systems such as cockle fields or mussel banks can only persist due to the connection to the North Sea. However, both systems appear to be of high importance for the functioning of the whole ecosystem. A high amount of energy is stored in these systems and with their rich biodiversity they increase the complexity and flow diversity of the entire system.

In contrast, razor clam fields were very small and simple systems, dominated by short pathways. The lower intertidal area, where this habitat type occurs, is a harsh environment and only few species are able to settle here. However, *Ensis directus* captured a free niche in the Wadden Sea when it was introduced in the late 1970s (Tulp et al. 2010, Dannheim 2012) and therefore the razor clam field is a rather young habitat type increasing the productivity of the whole area.

The mud flat was a very active system with a high throughput of energy. But it was dominated by simple and short pathways and a low recycling. Therefore, it might be vulnerable to perturbations and can be described as a fragile system. It was also the system with the highest primary production due to the dominance of microphytobenthos. Although, the vulnerability of the mud flat might decrease the overall stability of the whole area, the large extent of primary production which is probably partly exported into other sub-systems is important for the functioning of the entire study site on ecosystem-level.

The sand flat and the seagrass meadow were the most extended habitat types in the area. At first sight, both systems differ a lot as sand flats appear to be bare sediments while seagrass meadows are macrophyte-dominated habitats. Nevertheless, both systems revealed several similarities in their ecological role. Both habitats were intensively exploited by foraging birds. The highest numbers and the highest biodiversity of birds were observed in these two habitats. Furthermore, they were similar in their system attributes. Both systems had a complex flow structure with long and redundant pathways. These habitats might therefore increase the overall stability and redundancy of the whole study site. In comparison to the other systems, the recycling of the sand flat and the seagrass meadow was also high. The large extension of these two habitats might therefore increase the independence of the study site on external resources (Pockberger and Asmus 2014).

The difference in the system attributes indicates that each habitat has its specific role in the whole ecosystem and changes in the habitat heterogeneity might therefore induce severe alterations in the system functioning. The Dutch Wadden Sea already suffers from a loss of habitat diversity. Seagrass meadows declined since the 1970s and are almost vanished nowadays (van Katwijk et al. 2009). Additionally, there was a harsh decline in mussel banks and cockle fields due to over-exploitation in combination with severe winters and low spatfall (Imeson and Van Den Bergh 2006). It is not known how these changes affect the ecosystem of the Dutch Wadden Sea on the food web level but results from our study imply that the loss of habitats could be a severe drawback for the system functioning.

Yearly average values were used to construct these models. However, we observed seasonal variations in the biomass of microphytobenthos and macrozoobenthos and in the abundance of foraging shorebirds in all six habitats. Seasonal variations in the functioning of the food webs are therefore likely. In a recent study about the Sylt-Rømø Bight in the northern Wadden Sea seasonal fluctuations in the food web structure were observed (de la Vega, personal communication). The system appeared to be more redundant in spring and summer when a lot of opportunistic predators (i.e. fish, harbor seals) were abundant. However, the differences were not significant and the fluctuations during the seasons probably stabilize the food web system of the Bight in the course of the year (de la Vega, personal communication). Regarding the seasonal biomass and abundance differences in the present study it is likely that the food web would show a seasonal fluctuation similar to the Sylt-Rømø Bight. However, the study site is more visited by birds and especially during the migrating periods in spring and autumn changes in the food web might be more pronounced than in the Sylt-Rømø Bight.

1.2. Sustainability of the systems

The sustainability of a system can be described as the system's capacity to endure disturbances while maintaining its vital functions (Fath 2015). For being sustainable, a system requires organized flows to efficiently use the energy resources (organization) but also a reserve of free energy to cope with perturbations (redundancy, Ulanowicz 2004, Fath 2015). This trade-off between organization and redundancy can be displayed in an optimum curve (Fig. 1) between the indices of relative Ascendency (A/DC) and robustness (Fath 2015). Theoretically, a system can be located at any point of the curve. On the left side of the curve, the system would be overly redundant. On the right side, the system would be highly organized and might be bristle and vulnerable to perturbation because every compartment of the system has its specific role. The curve peaks in an optimal trade-off between organization and redundancy, the "window of vitality" (Ulanowicz 2004), indicating high efficiency and sufficient redundancy.

The six analyzed habitat systems as well as the system of the whole study site are located in the window of vitality implying that they are all well-balanced between their degree of order and their redundancy (Fig. 1). Therefore, the six habitats and also the entire study site appear to be sustainable systems, which are already well-adapted to the large natural fluctuations (e.g. temperature, wind, tidal range) in the Wadden Sea.

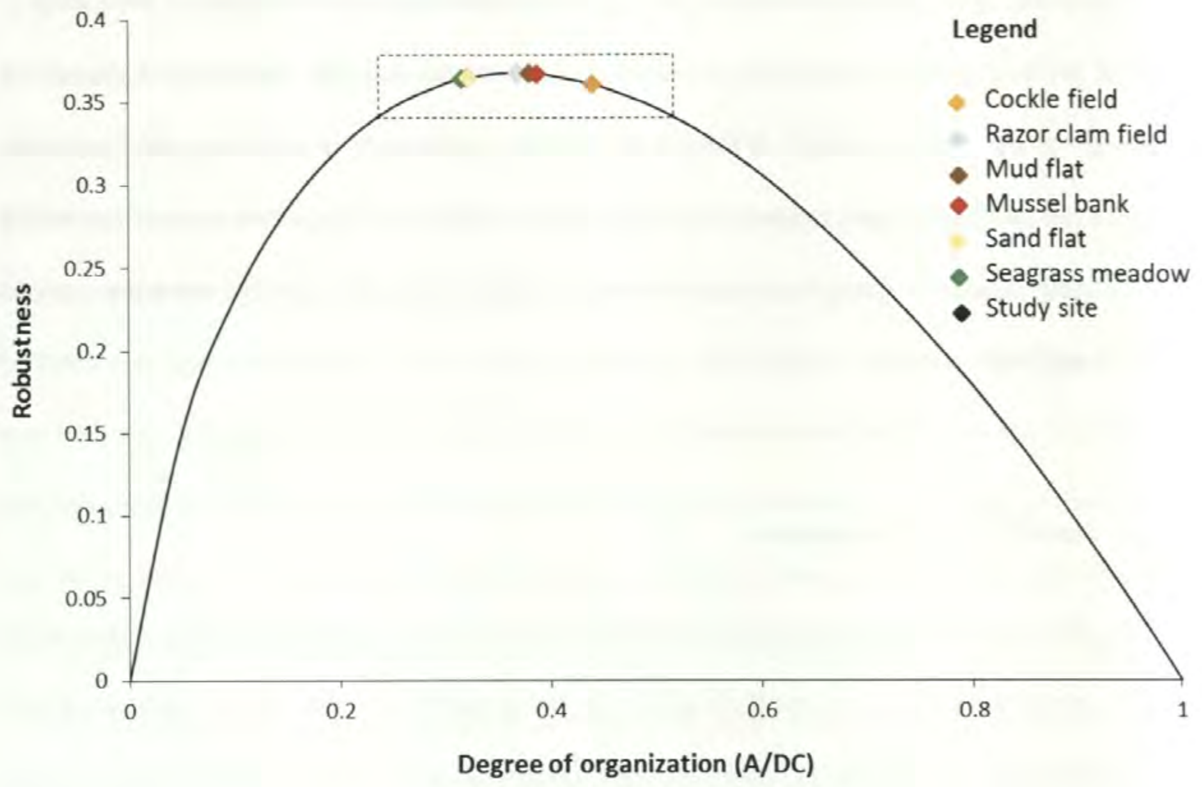


Fig. 1: Relationship between the degree of organization and the robustness of the analyzed systems, the dashed rectangle delimits the "window of vitality"

1.3. How healthy is the Wadden Sea food web?

The Wadden Sea is confronted to a diversity of different stressors. Nutrient input, invading species, fisheries and changes in climatic conditions are severe anthropogenic impacts. One of the major questions is therefore: How healthy is this unique ecosystem in its current state?

Eutrophication was one of the major problems for the Wadden Sea ecosystem in 1980s (Wolff et al. 2010). The enrichment of nutrients induced changes in the trophic structure resulting in a different functioning of the marine food web (Schückel et al. 2015). The reduction of nutrient input was therefore necessary to maintain the functioning of the Wadden Sea ecosystem. Drastic controlling and management strategies resulted in a strong decline in nutrient input and therefore in a decrease of eutrophication. In the Jade Bay, the recovery of the food web from the severe eutrophication in the 1980s was studied in a modeling approach (Schückel et al. 2015). The system showed an increase in Flow Diversity but decreases in Finn Cycling Index, Trophic Efficiency and Average Path Length during the period of eutrophication. The attributes changed again after the system recovered from the extraordinary high nutrient load. In our study, we only have a snap-shot of the present food web and therefore it is difficult to conclude if the ecosystem is affected by eutrophication. A long-term monitoring in the study site for all system components would be required to assess fluctuations in the system attributes with increasing and decreasing nutrient availability. However, general nutrient input into the Wadden Sea gradually decreased since the 1980s although the system is still not free of eutrophication yet (Wolff et al. 2010).

Another ongoing challenge for the Wadden Sea are alien species which immigrate to the area due to changing climatic conditions or by human-induced imports (Wolff et al. 2010). Once in the system, it is almost impossible to remove the introduced species again and they establish in the native species community. Some of them, such as *Ensis directus*, quickly become part of the food web. We could show that intertidal razor clam fields are heavily used by different gull species, especially during their breeding period. Other species remain "dead ends" in the native food web such as *Crassostrea gigas* due to a lack of specialized predators (Baird et al. 2012). The vulnerability of a system towards invading species can be shown by the connectivity of a system. The more connected a system is, the harder invaders can find a free niche (Smith-Ramesh et al. 2016). Even though the food web of the study site appears to be well-connected (e.g. Effective Link-Density: 3.3), there are still free niches in the marine environment and climatic changes trigger the immigration of temperate species which are better adapted to the warmer environment. Invading species will therefore be an ongoing challenge for the Wadden Sea ecosystem.

Fishing in the Wadden Sea is mainly represented by shrimp and shellfish fisheries (Imeson and Van Den Bergh 2006, Wolff et al. 2010). In the present study, we focused on the benthic food web, not including the pelagial. Thus, it is difficult to assess the impact of shrimp fisheries on the study site. Shrimps are one of the main food sources for different fish species (Kellnreitner 2012) which can play a key role in the food web functioning (Pockberger et al. 2014). It is therefore likely, that shrimp fisheries have a large impact on the entire food web. Including compartments about the pelagial (e.g. zooplankton, shrimps, fish) in the studied food web model could give more insight into the influence of fisheries on the ecosystem.

Shellfish fisheries are forbidden in the Danish and German Wadden Sea (Wolff et al. 2010). In the Dutch Wadden Sea only manual cockle fishery is still allowed (Wolff et al. 2010). The mechanical cockle dredging was banned in 2004 after a population collapse of cockles due to over-exploitation (Imeson and Van Den Bergh 2006). Instead of fishing wild shellfish, the economic use mainly focuses on the cultivation of mussels and oysters in the Wadden Sea. However, seed mussels for cultivation are still collected from wild mussel banks (Imeson and Van Den Bergh 2006, Wolff et al. 2010). There are regulations to prevent overfishing (Imeson and Van Den Bergh 2006, Wolff et al. 2010) but determining the impact of seed mussel collection of the mussel bank habitats would be a helpful approach to assess the influence on the whole ecosystem. Mussel banks and cockle fields appear to be important habitats for the whole ecosystem due to the rich biodiversity, the high amount of stored energy and the complex flow structure. Preserving these habitats is therefore of great importance for the whole ecosystem.

There are more anthropogenic influences affecting the Wadden Sea and it is poorly understood how the use of the Wadden Sea's resources impacts the natural ecosystem. Ecological Network Analysis could give insight into the system changes over time and an evitable decreasing health status. In the current state, results of the present study site are comparable with those of the well-studied Sylt-Rømø Bight (de la Vega, personal communication, Baird et al. 2004, 2007) and the Jade Bay (Schückel et al. 2015). Even though there are slight differences in the network construction these similarities indicate that at least the German Wadden Sea is in a consistent state. The attributes of the food web analyses reveal characteristics of sustainability and resistance in front of perturbations. However, nothing is known about the food web condition of the Dutch and the Danish Wadden Sea and about areas where large rivers discharge. These gaps should be filled to assess the health condition of the whole World Heritage Site.

In general, the Wadden Sea always was a changing ecosystem and in terms of geomorphology it still is relatively young. For organisms living in the intertidal, abiotic conditions are harsh and only few species can survive. However, these species are robust and adapted to drastic changes in temperature, salinity, currents and sediment mobility. It is therefore reasonable that also the food web of the Wadden Sea is robust in front of natural perturbations. Storm events or severe winters might induce local damages but the ecosystem itself is relatively resistant and stable. Anthropogenic impacts are more likely to cause irreversible disturbances. Management strategies should therefore focus on the reduction of human influences.

2. The importance of birds for the Wadden Sea food web

2.1. Challenges to include birds in food web studies

Birds are important top predators in the Wadden Sea food web but it is very difficult to include bird data appropriately into quantitative analyzes due to their high mobility. Birds occupy high trophic positions in the food web and feed on a large spatial scale. In contrast, their prey items (e.g. polychaetes and clams) are mostly restricted to a small spatial area. Birds therefore couple different habitats and ecosystems with each other by feeding at different locations (McCann and Rooney 2009). In our studies, we could show that birds have a large impact on the intertidal food web and that changes in the bird population induce shifts in the whole network. An intertidal trophic study without birds is therefore likely to be seriously incomplete (Baird et al. 1985a). Including birds in intertidal network studies is therefore strongly recommended and the tools to incorporate birds need to be improved.

In addition to their mobility, lacking weight-to-weight conversion factors were a serious problem for the inclusion of birds in food web studies. Bird data are traditionally determined in abundance (Mendel 2008, Markones and Garthe 2011, Blew et al. 2015, Koffijberg et al. 2015) which can be transformed in fresh weight using mean biomass values for each bird species. On the other hand, food web studies are based on standardized biomass units such as carbon or nitrogen (Ulanowicz

2004). Conversion of biomass of bird data was therefore always underlying large approximations. With the determination of conversion factors of birds from fresh weight to standardized biomass units (i.e. dry weight, ash free dry weight, carbon, nitrogen) we filled an important gap in food web research. Indeed, previous studies including birds often over- or underestimated the biomass of birds in the system and therefore probably also the avian influence (Baird et al. 2004, Leguerrier et al. 2007a, Saint-Béat et al. 2013a).

The food composition of birds is another challenge for their inclusion in food web studies. Birds feed on a variety of prey items on the intertidal area. General information about the diet of different species is available in the literature. However, food web studies require more precise information about what the birds feed and in which proportion (Ulanowicz 2004, Fath 2007). The diet matrix, used in this thesis, was set up according to all available information, including unpublished data about faeces analyzes or stomach dissections (FTZ, unpublished data). But the food composition of certain bird species can vary from one intertidal area to the next (Kubetzki and Garthe 2003, Schwemmer and Garthe 2008). Indeed, we found differences in the avian prey composition from this study site compared to the one used in the food web model of the Sylt-Rømø Bight (de la Vega, personal communication). The diet of birds therefore still underlies large uncertainties even though we used several information sources to be as precise as possible. Trophic markers could help to assess the birds' diet more detailed and could also reveal seasonal variations in the prey composition. Schwemmer et al. (2016b) used trophic markers to determine a diet shift in *Calidris alpina* from terrestrial prey in their breeding sites to marine prey in the Wadden Sea. Seasonal diet variations are also known from geese (Mathers and Montgomery 1998) and *Limosa lapponica* (Scheiffarth 2001) and might alter the structure of the entire food web.

2.2. Habitat choice of foraging birds

The community of birds feeding on the intertidal flats differs between the six habitat types. While some bird species were very opportunistic in their habitat choice, there are also species which rely on a special habitat type. For example, *Recurvirostra avosetta* depends on mud flats to forage. This soft-bottom habitat is easy to penetrate with long beaks and provides a rich diversity of benthic fauna. On the other hand, *Somateria mollissima* mainly forages on mussel banks and cockle fields (Nehls 1989). The accumulation of these bivalve species provides sufficient food even for large flocks of *S. mollissima*. Herbivorous birds (e.g. *Anas penelope, Branta bernicla*) rely on seagrass meadows and green algae as intertidal food sources (Mathers and Montgomery 1998, Wolff et al. 2010). The diversity of different habitats in the Wadden Sea is therefore an important trait for foraging birds. A decrease in a single habitat type could severely affect the whole population of certain bird species. This was shown in the Dutch Wadden Sea in the 1990s (Imeson and Van Den Bergh 2006). *Cerastoderma edule* and *Mytilus edulis* simultaneously declined sharply due to high mortality during harsh winter conditions and an overexploitation by shellfish fisheries (Beukema and Cadée 1996, Smit et al. 1998, Imeson and Van Den Bergh 2006). The remaining population of bivalves was not sufficient to support the large numbers of *Somateria mollissima* and *Heamatopus ostralegus* and lots of the birds starved to death (Beukema and Cadée 1996). Habitat heterogeneity is therefore needed to provide foraging areas for the large diversity of breeding and migrating birds.

Sand flats and seagrass meadows seem to be especially important as feeding areas. The highest numbers and the highest diversity of foraging birds were found in these two habitat types. However, we could only investigate few locations of the habitats, although we tried to choose representative areas. Food density and the distance to roosting places influence the attractiveness of an area for foraging birds (Wolff 1983). The location of a certain habitat type might therefore be crucial for birds. For example, a mussel bank close to the roosting site could be a preferred foraging area for *Haematopus ostralegus* while a remote one would be too energy demanding to go there for foraging. The same principle could be observed in our seagrass meadow, which was heavily used by birds, while the seagrass meadows in the Sylt-Rømø Bight appeared to be of less importance for birds (Busch 2012) probably due to increased levels of perturbations such as tourism. The identification of preferred avian foraging sites is thus very important to develop effective protection strategies.

Telemetric studies could give necessary information about the dispersal of the birds on the intertidal flats to define foraging habitats (Schwemmer et al. 2016a) which could then be analyzed in more detail.

2.3. The influence of birds on the intertidal food web

Birds occupy various trophic positions in the intertidal food web and induce an intense predation pressure on their benthic prey (Markert et al. 2003). Their inclusion in intertidal food web studies is therefore a necessary requirement to get a realistic representation of the natural ecosystem structure.

The negative influence of birds on their prey items causes a top-down cascade effect on food sources and competitors of the birds' prey. Furthermore, birds impact each other negatively due to interference and competition for food on the intertidal flats. The indirect effects of birds in the food web seem to be more pronounced than the direct effects of predation. The different bird species feed on a wide spectrum of prey items and a decline in the population impacts a variety of organisms in the intertidal flats. It is therefore very difficult to predict how the present changes in the avian population structure affect the whole intertidal ecosystem.

Our model approach indicates that a decline in birds decreases the complexity and connectivity of the food web structure. But also the length of pathways and the redundancy of flows are affected by the decrease. A decline in birds therefore decreases the stability and resistance of the system and causes an increased vulnerability in front of perturbations. Indeed, opportunistic top predators seem to be very important for food webs to maintain sustainable. They occupy high trophic positions while feeding on a variety of different prey items and therefore increase the path length (Average Path Length) and connectivity (Effective Link-Density) resulting in a more stable and resistant system (Baird et al. 2007, Saint-Béat et al. 2013a). The ongoing decline of various bird species is therefore alarming and might affect all parts of the food web due to top-down cascade effects.

The Wadden Sea is a core area on the East Atlantic Flyway (Blew et al. 2015, Koffijberg et al. 2015). Migrating birds induce a large-scale connection of the Wadden Sea with breeding and wintering sites in the Arctic and Africa, respectively. Although the birds are confronted to a variety of threats in the Wadden Sea (e.g. habitat loss, disturbances, pollution) the decrease of the population could also be caused by changes in their breeding and wintering sites. However, birds are important components of the intertidal food web and keeping the Wadden Sea itself in a good ecological state is essential to counteract the avian population decline even if additional factors might affect the bird population at other locations of the East Atlantic Flyway.

3. Including ENA in ecosystem-based management

3.1. Advantage of studies on ecosystem-level

Scientists are strongly encouraged to provide investigation on ecosystem-level which can be included in decisions about protection and management strategies (Scharler and Baird 2005a, Levin 2009, Saint-Béat 2015). ENA is a useful tool to assess the ecological status of ecosystems (Scharler and Baird 2005a, Saint-Béat 2015). ENA outputs can be used to describe systems in terms of growth and development, organization and robustness in front of perturbations (Wulff et al. 1989).

In this thesis, we got insight into the complexity of ENA results. The structure of different sub-systems (e.g. habitats) can strongly differ and each system has its characteristic traits and features. The system of the entire study site showed influences from all habitat types. Habitat heterogeneity therefore appears to be of great importance. The current system appeared to be relatively stable and robust in front of perturbations with a good balance of organization and redundancy.

Furthermore, ENA revealed the importance of indirect relationships in the study site. Natural food webs are networks in which all components are somehow linked to each other (Ulanowicz and Puccia 1990). Changes in one part of the network (e.g. decline in bird population) can therefore affect the whole ecosystem. We could show that a decrease in the bird population causes changes in the food web structure. With declining bird biomass, the system loses complexity and redundancy resulting in an increased vulnerability to perturbations. Furthermore, birds induce large direct and indirect impacts on the other compartments of the food web. A decline in birds will therefore cause further changes in the Wadden Sea ecosystem.

Especially these indirect and cascading effects, which are very common in nature, are not assessable in studies on single species or populations. Studies on ecosystem-level such as ENA are therefore needed as a basis for management to determine future changes in the Wadden Sea. Additionally, human influences (e.g. fisheries) could also be included as compartments in ENA to assess the impact on the ecosystem (de la Vega, personal communication). Other anthropogenic changes (e.g. eutrophication) and their effects on the ecosystem could be determined by creating artificial models following a scenario. Indeed, it was already shown that increasing fisheries or additional riverine impact would severely affect the estuarine ecosystems in South Africa (Mukherjee et al. 2015). Scenarios like these could give fundamental insight into the functioning and the health state of the Wadden Sea and how future changes might influence the ecosystem.

However, ENA just provides a snap-shot of the current system's status and it is rarely known how natural or anthropogenic impacts affect the system attributes. To include ENA results in ecosystem-based management a regular monitoring of all system components is necessary. Several monitoring programs are already established in different parts in the Wadden Sea (e.g. mussel bank monitoring in the intertidal area of Schleswig-Holstein, fish monitoring in the Sylt-Rømø Bight, phytoplankton monitoring of the Federal Agency of Agriculture and Rural Areas). Up to now, these valuable data are only partly analyzed and could be the basis for further ENA studies. However, there are still gaps to be filled such as a bacteria or meiofauna monitoring and even long-term benthos data is rare for some habitat types. Only a long-term monitoring covering all ENA components in all habitats would reveal trends such as decreases in flow diversity or organization. These results could give information about an increasing stress level or disturbance of the system and therefore about the ecosystem health.

3.2. ENA as a management tool

ENA results are complex and provide comprehensive information about the ecosystem. But interpretation of ENA is often based on multiple indices which are difficult to interpret. The diversity of indices reflects the complexity of a natural ecosystem and changes in the indices can have different meaning. For example, an increased Finn Cycling Index (FCI) may indicate that the system is under stress (Baird and Ulanowicz 1993). On the other hand, enhanced cycling also implies increased system's maturity and independence from external sources (Pockberger and Asmus 2014). To clarify the interpretation of FCI an additional index is needed, for example Average Path Length (APL). High values for FCI and APL indicate that the system is stable and independent (Monaco and Ulanowicz 1986, Vasconcellos et al. 1997, Pockberger and Asmus 2014), whereas a high FCI with a low APL could imply a stressed condition (Leguerrier et al. 2007a, Baird et al. 2012). One single index is therefore not sufficient to describe the system's status. A combination of indices is needed to support an interpretation.

It is obvious that it is impossible to include all the diverse system attributes and indices in a concept for ecosystem-based management. The interpretation would be not feasible to support political decisions. A combination of chosen indices combined would be probably more manageable. Future research about ENA should therefore focus on developing such a management tool to finally include ENA results in conservation management (e.g. Marine Water Framework Directives).

Scientific output about ENA results such as the present thesis but also studies from the Sylt-Rømø Bight (de la Vega, personal communication, Baird et al. 2004, 2007) and the Jade Bay (Schückel et al. 2015) could then be the basis for political decision about management strategies to preserve the unique ecosystem of the Wadden Sea.

In this thesis, the functioning of different intertidal habitats and the impact of foraging birds were studied using Ecological Network Analysis. Habitat diversity appears to be of major importance for the entire intertidal food web ecosystem. Each habitat has a specific role and contributes in a certain way to the functioning of the entire Wadden Sea ecosystem. Furthermore, the habitats are used in different intensities by foraging birds which have a large influence on the intertidal food web. Birds increase the complexity and connectivity in the food web and are therefore important stabilizers. Insights gained in this study could be the basis for management and conservation strategies to preserve the habitat heterogeneity of the Wadden Sea and its key role for migrating birds.

4. Conclusion

The Wadden Sea is a unique ecosystem of outstanding importance for millions of breeding and migrating birds on the East Atlantic Flyway. Nevertheless, the area is confronted to increasing anthropogenic challenges and an ongoing decline of various bird species that might result in unknown consequences for the functioning of the ecosystem. Ecological Network Analysis could give insight into the complex intertidal food web structure assessing the problems on ecosystem-level.

The studied system consisted of six different habitat types, each of them with a distinct role for the functioning of the whole ecosystem. Cockle fields and mussel banks have a complex and diverse flow structure but are simultaneously very dependent on external imports due to the low recycling. Razor clam fields are small but efficient systems in the lower intertidal area. Mud flats appear to be very active with a high primary production, but dominated by short and simple pathways and might therefore be vulnerable to perturbations. Sand flats and seagrass meadows are stable and resistant systems with a high recycling.

The habitats are used in different intensities by foraging birds. Habitat heterogeneity is therefore an important trait for avian predators which might be specialized to a certain environment. Birds are an important component of the intertidal food web. They occupy high trophic positions and increase the path length in the food web and the number and redundancy of flows. Furthermore, birds influence the whole intertidal food web via direct or indirect connection. A decline in bird population might therefore affect the whole Wadden Sea ecosystem.

Up to now, the whole system appears to be in a sustainable condition but management strategies should focus on a decrease of anthropogenic influences. A good ecological state of the Wadden Sea could also help the declining bird populations to recover.

5. References

Abarca-Arenas, L. G., and R. E. Ulanowicz. 2002. The effects of taxonomic aggregation on network analysis. Ecological Modelling **149**:285-296.

Asmus, H. 1982. Field measurements on respiration and secondary production of a benthic community in the northern Wadden Sea. Netherlands Journal of Sea Research **16**:403-413.

Asmus, H. 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. Marine ecology progress series. Oldendorf **39**:251-266.

Asmus, H., and R. Asmus. 1985. The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. HELGOLANDER MEERESUNTERSUCHUNGEN **39**:273-301.

Asmus, H., and R. Asmus. 2000a. Material exchange and food web of seagrass beds in the Sylt-Rømø Bight: how significant are community changes at the ecosystem level? Helgoland Marine Research **54**:137-150.

Asmus, H., and R. Asmus. 2000b. Material exchange and food web of seagrass beds in the Sylt-Rømø Bight: how significant are community changes at the ecosystem level? Helgoland Marine Research **54**:137-150.

Asmus, H., and R. Asmus, M. 1990. Trophic relationships in tidal flat areas: to what extend are tidal flats dependant on imported food? Netherlands Journal of Sea Research **27**:93-99.

Asmus, R., and H. Asmus. 1998. Bedeutung der Organismengemeinschaften für den benthopelagischen Stoffaustausch im Sylt-Rømø Wattenmeer. Ökosystem Wattenmeer: Austausch-, Transport-und Stoffumwandlungsprozesse (Ch Gätje, K Reise, Hrsg) Springer, Berlin:257-302.

Asmus, R., M., , and E. Bauerfeind. 1994. The microphytobenthos of Königshafen - spatial and seasonal distribution on a sandy tidal flat. HELGOLANDER MEERESUNTERSUCHUNGEN **48**:257-276.

Atkinson, S. 1997. Reproductive biology of seals. Reviews of Reproduction **2**:175-194.

Baird, D., H. Asmus, and R. Asmus. 2004. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Marine Ecology Progress Series **279**:45-61.

Baird, D., H. Asmus, and R. Asmus. 2007. Trophic dynamics of eight intertidal communities of the Sylt-Rømø Bight ecosystem, northern Wadden Sea. Marine Ecology Progress Series **351**:25-41.

Baird, D., H. Asmus, and R. Asmus. 2008. Nutrient dynamics in the Sylt-Rømø Bight ecosystem, German Wadden Sea: An ecological network analysis approach. Estuarine, Coastal and Shelf Science **80**:339-356.

Baird, D., H. Asmus, and R. Asmus. 2011a. Carbon, nitrogen and phosphorus dynamics in nine sub-systems of the Sylt-Rømø Bight ecosystem, German Wadden Sea. Estuarine, Coastal and Shelf Science **91**:51-68.

Baird, D., H. Asmus, and R. Asmus. 2011b. Carbon, nitrogen and phosphorus dynamics in nine sub-systems of the Sylt-Rømø Bight ecosystem, German Wadden Sea. Estuarine, Coastal and Shelf Science **91**:51-68.

Baird, D., H. Asmus, and R. Asmus. 2012. Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. Marine Ecology Progress Series **462**:143-162.

Baird, D., P. Evans, H. Milne, and M. Pienkowski. 1985a. Utilization by shorebirds of benthic invertebrate production in intertidal areas. Oceanography and marine biology **23**:573-597.

Baird, D., P. R. Evans, H. Milne, and P. M. W. 1985b. Utilization by shorebirds of benthic invertabrate production in intertidal areas. Oceanogr. Mar. Biol. Ann. Rev. **23**:573-597.

Baird, D., B. D. Fath, R. E. Ulanowicz, H. Asmus, and R. Asmus. 2009. On the consequences of aggregation and balancing of networks on system properties derived from ecological network analysis. Ecological Modelling **220**:3465-3471.

Baird, D., J. McGlade, and R. Ulanowicz. 1991. The comparative ecology of six marine ecosystems. Philosophical Transactions of the Royal Society of London B: Biological Sciences **333**:15-29.

Baird, D., and R. Ulanowicz. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal. Marine Ecology Progress Series **99**:221-237.

Baldwin, J., and J. Lovvorn. 1994. Habitats and tidal accessibility of the marine foods of dabbling ducks and brant in Boundary Bay, British Columbia. Marine Biology **120**:627-638.

Benke, H., U. Siebert, R. Lick, B. Bandomir, and R. Weiss. 1998. The current status of harbour porpoises (*Phocoena phocoena*) in German waters. Arch. Fish. Mar. Res. **46**:97–123.

Beukema, J. 1974. Seasonal changes in the biomass of the macro-benthos of a tidal flat area in the Dutch Wadden Sea. Netherlands Journal of Sea Research **8**:94-107.

Beukema, J., and G. Cadée. 1996. Consequences of the sudden removal of nearly all mussels and cockles from the Dutch Wadden Sea. Marine Ecology **17**:279-289.

Beukema, J., J. 1976. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. Netherlands Journal of Sea Research **10**:236-261.

Bezzel, E. 1985. Kompendium der Vögel Mitteleuropas: Nichtsingvögel. AULA-Verlag.

Blew, J., K. Günther, B. Hälterlein, R. Kleefstra, K. Laursen, and G. Scheiffarth. 2013. Trends of Migratory and Wintering Waterbirds in the Wadden Sea 1987/1988 - 2010/2011. Wadden Sea Ecosystem No.31. Common Wadden Sea Secretariat, Joint Monitoring Group of Migratory Birds in the Wadden Sea, Wilhelmshaven, Germany.

Blew, J., K. Günther, B. Hälterlein, R. Kleefstra, K. Laursen, and G. Scheiffarth. 2015. Trends of Migratory and Wintering Waterbirds in the Wadden Sea 1987/1988-2011/2012.

Block, W. 2003. Water or ice?–the challenge for invertebrate cold survival. Science Progress **86**:77-101.

Borrett, S., R.,, and M. Lau, L. 2014. enaR: An R package for Ecosystem Network Analysis. Methods in Ecology and Evolution **5**:1206-1213.

Bossart, G. D. 2011. Marine Mammals as Sentinel Species for Oceans and Human Health. Veterinary Pathology Online **48**:676-690.

Bowen, W. D. 1997. Role of marine mammals in aquatic ecosystems. Marine Ecology Progress Series **158**:267-274.

Bowen, W. D., O. T. Oftedal, and D. Boness, J. 1992. Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). Physiological Zoology **65**:844-866.

Bradford-Grieve, J. M., P. K. Probert, S. D. Nodder, D. Thompson, J. Hall, S. Hanchet, P. Boyd, J. Zeldis, A. N. Baker, H. A. Best, N. Broekhuizen, S. Childerhouse, M. Clark, M. Hadfield, K. Safi, and I. Wilkinson. 2003. Pilot trophic model for subantarctic water over the Southern Plateau, New Zealand: a low biomass, high transfer efficiency system. Journal of Experimental Marine Biology and Ecology **289**:223-262.

Brasseur, S., B. Diederichs, R. Czeck, L. F. Jensen, A. Galatius, S. Ramdohr, U. Siebert, J. Teilmann, P. Körber, and S. Klöpper. 2013. Aerial surveys of Harbour Seals in the Wadden Sea in 2013 - Is the population growth rate slowing down?

BSH. 2016. Gezeitenkalender 2016. Hoch- und Niedrigwasserzeiten für die Deutsche Bucht und deren Flussgebiete. Federal Maritime and Hydrographic Agency.

Busch, N. 2012. Untersuchungen zur Nutzung eulitoraler Seegraswiesen durch Wattenmeervögel während des Frühjahrszuges. Universität Kiel.

Cauffopé, G., and S. J. Heymans. 2005a. Energy contents and conversion factors for sea lion's prey. Fish. Cent. Res. Rep. **13**:225-237.

Cauffopé, G., and S. J. Heymans. 2005b. Energy contents and conversion factors for sea lion's prey. . Fish. Cent. Res. Rep. **13**:225-237.

Chapman, G. 1958. The hydrostatic skeleton in the invertebrates Biological Reviews **33**:338-371.

Christensen, V. 1995. Ecosystem maturity—towards quantification. Ecological Modelling **77**:3-32.

Colijn, F., and K. S. Dijkema. 1981. Species composition of benthic diatoms and distribution of chlorophyll a on an intertidal flat in the Dutch Wadden Sea. Marine Ecology Progress Series **4**:9-21.

Colwell, M. A. 2000. A review of territoriality in non-breeding shorebirds (Charadrii). BULLETIN-WADER STUDY GROUP **93**:58-66.

Dannheim, J. R., H. 2012. The fate of an immigrant: *Ensis directus* in the eastern German Bight. Helgoland Marine Research **66**:307-317.

Dekker, R. 1989. The macrozoobenthos of the subtidal western Dutch Wadden Sea. I. Biomass and species richness. Netherlands Journal of Sea Research **23**:57-68.

Dolch, T., C. Buschbaum, and K. Reise. 2013. Persisting intertidal seagrass beds in the northern Wadden Sea since the 1930s. Journal of Sea Research.

Doney, S., Ruckelshaus, M, Duffy, JE, Barry, JP, Chan, F, English, CA, Galindo, HM, Grebmeier, JM, Hollowed, AB, Knowlton, N, Polovina, J, Rabalais, NN, Sydeman, WJ, Talley, LD. 2012. Climate Change Impacts on Marine Ecosystems. Annual Reviews **4**:11-37.

Dumont, H. J., I. Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia **19**:75-97.

Dunajski, E. 1980. Texture of fish muscle Journal of Texture Studies **10**:301-318.

Edler, L. 1979. Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Publication-Baltic Marine Biologists BMB (Sweden).

Ens, B. J., M. Kersten, A. Brenninkmeijer, and J. B. Hulscher. 1992. Territory quality, parental effort and reproductive success of oystercatchers (Haematopus ostralegus). Journal of Animal Ecology:703-715.

Fath, B., D., Scharler, U., M., Ulanowicz, R., E., Hannon, B. 2007. Ecological network analysis: network construction. Ecological Modelling **208**:49-55.

Fath, B. D. 2015. Quantifying economic and ecological sustainability. Ocean & Coastal Management **108**:13-19.

Fath, B. D., U. M. Scharler, and D. Baird. 2013. Dependence of network metrics on model aggregation and throughflow calculations: Demonstration using the Sylt–Rømø Bight Ecosystem. Ecological Modelling **252**:214-219.

Fath, B. D., U. M. Scharler, R. E. Ulanowicz, and B. Hannon. 2007. Ecological network analysis: network construction. Ecological Modelling **208**:49-55.

Flach, E. C. 1996. The influence of the cockle, Cerastoderma edule, on the macrozoobenthic community of tidal flats in the Wadden Sea. Marine Ecology **17**:87-98.

Friedrich, C., and W. Hagen. 1994. Lipid contents of five species of notothenioid fish from high-Antarctic waters and ecological implications. Polar Biology **14**:359-369.

Furness, R. W., and K. Camphuysen. 1997. Seabirds as monitors of the marine environment. ICES Journal of Marine Science: Journal du Conseil **54**:726-737.

Galatius, A., S. Brasseur, R. Czeck, B. Diederichs, L. F. Jensen, P. Körber, U. Siebert, J. Teilmann, and S. Klöpper. 2014. Aerial surveys of Harbour Seals in the Wadden Sea in 2014 - The highest pup count recorded yet.

Galbraith, H., R. Jones, R. Park, J. Clough, S. Herrod-Julius, B. Harrington, and G. Page. 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. Waterbirds **25**:173-183.

Gätje, C., and K. Reise. 1998a. Ökosystem Wattenmeer: Austausch-, Transport-und Stoffumwandlungsprozesse. Springer, Berlin.

Gätje, C., and K. Reise. 1998b. Ökosystem Wattenmeer: Austausch-, Transport-und Stoffumwandlungsprozesse. Springer, Berlin.

Goerner, S., J., Lietaer, B., Ulanowicz, R., E. 2009. Quantifying economic sustainability: Implications for free-enterprise theory, policy and practice. Ecological Economics **69**:76-81.

Gollasch, S., F. Kerckhof, J. Craeymeersch, P. Goulletquer, K. Jensen, A. Jelmert, and D. Minchin. 2015. Alien Species Alert: Ensis directus. Current statuts of invasions by the marine bivalve Ensis directus. ICES Cooperative Research Report:1-36.

Goss-Custard, J. 1980. Competition for food and interference among waders. Ardea **68**:31-52.

Goss-Custard, J., R. Stillman, A. West, R. Caldow, and S. McGrorty. 2002. Carrying capacity in overwintering migratory birds. Biological Conservation **105**:27-41.

Greenstreet, S. P. R., A. D. Bryant, N. Broekhuizen, S. J. Hall, and M. R. Heath. 1997. Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. ICES Journal of Marine Science: Journal du Conseil **54**:243-266.

Hannon, B. 1973. The structure of ecosystems. Journal of theoretical biology **41**:535-546.

Heath, M. R. 2007. The consumption of zooplankton by early life stages of fish in the North Sea. ICES Journal of Marine Science: Journal du Conseil **64**:1650-1663.

Henderson, R. J., N. Kalogeropoulos, and M. N. Alexis. 1994. The lipid composition of selected tissues from a Mediterranean monk seal, *Monachus monachus*. Lipids **29**:577-582.

Heymans, J. J., M. Coll, S. Libralato, L. Morissette, and V. Christensen. 2014. Global patterns in ecological indicators of marine food webs: a modelling approach. Plos One **9**:e95845.

Höfmann, H., and H. Hoerschelmann. 1969. Nahrungsuntersuchungen bei Limikolen durch Mageninhaltsanalysen. Corax **3**:7-22.

Horn, S., and C. de la Vega. 2016. Relationships between fresh weight, dry weight, ash free dry weight, carbon and nitrogen content for selected vertebrates. Journal of Experimental Marine Biology and Ecology **481**:41-48.

Imeson, R., and J. Van Den Bergh. 2006. Policy failure and stakeholder dissatisfaction in complex ecosystem management: the case of the Dutch Wadden Sea shellfishery. Ecological Economics **56**:488-507.

Ings, T. C., J. M. Montoya, J. Bascompte, N. Blüthgen, L. Brown, C. F. Dormann, F. Edwards, D. Figueroa, U. Jacob, and J. I. Jones. 2009. Review: Ecological networks–beyond food webs. Journal of Animal Ecology **78**:253-269.

Iverson, S. J. 2009. Tracing aquatic food webs using fatty acids: from qualitative indicators to quantitative determination. Pages 281-308 Lipids in Aquatic Ecosystems. Springer.

Jensen, K. T. 1992. Dynamics and growth of the cockle, Cerastoderma edule, on an intertidal mud-flat in the Danish Wadden Sea: effects of submersion time and density. Netherlands Journal of Sea Research **28**:335-345.

Jørgensen, S. E., L. Xu, and R. Costanza. 2010. Handbook of ecological indicators for assessment of ecosystem health. CRC press.

Kabat, P., J. Bazelmans, J. van Dijk, P. M. Herman, T. van Oijen, M. Pejrup, K. Reise, H. Speelman, and W. J. Wolff. 2012. The Wadden Sea Region: Towards a science for sustainable development. Ocean & Coastal Management **68**:4-17.

Käkelä, R., R. Ackman, and H. Hyvärinen. 1995. Very long chain polyunsaturated fatty acids in the blubber of ringed seals (*Phoca hispida sp.*) from Lake Saimaa, Lake Ladoga, the Baltic Sea, and Spitsbergen. Lipids **30**:725-731.

Kay, J. J., L. A. Graham, and R. E. Ulanowicz. 1989. A detailed guide to network analysis. Pages 15-61 Network Analysis in Marine Ecology. Springer.

Kellnreitner, F. 2012. The trophic structure of a Wadden Sea fish community and its feeding interactions with alien species. Universitätsbibliothek Kiel.

Koffijberg, K., K. Laursen, B. Hälterlein, G. Reichert, and J. Frikke. 2013. Trends of Breeding Birds in the Wadden Sea 1991-2009.

Koffijberg, K., K. Laursen, B. Hälterlein, G. Reichert, J. Frikke, and L. Soldat. 2015. Trends of Breeding Birds in the Wadden Sea 1991-2013. Wadden Sea Ecosystem.

Kubetzki, U., and S. Garthe. 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Marine Biology **143**:199-207.

Lau, M. K., S. R. Borrett, and P. Singh. 2015. Ecosystem Network Analysis with R: A guide for using enaR.

Leguerrier, D., D. Degré, and N. Niquil. 2007a. Network analysis and inter-ecosystem comparison of two intertidal mudflat food webs (Brouage Mudflat and Aiguillon Cove, SW France). Estuarine, Coastal and Shelf Science **74**:403-418.

Leguerrier, D., D. Degré, and N. Niquil. 2007b. Network analysis and inter-ecosystem comparison of two intertidal mudflat food webs (Brouage Mudflat and Aiguillon Cove, SW France). Estuarine, Coastal and Shelf Science **74**:403-418.

Leguerrier, D., N. Niquil, N. Boileau, J. Rzeznik, P.-G. Sauriau, O. Le Moine, and C. Bacher. 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. Marine Ecology Progress Series **246**:17-37.

Leontief, W. W. 1951. Input-output economics. Sci Am **185**:15-21.

Levin, P., Fogarty, MJ, Murawski, SA, Fluharty, D. 2009. Integrated Ecosystem Assessments: Developing the Scientific Basis for Ecosystem-Based Management of the Ocean. PLoS Biology **7**:23-28.

Lorenzen, C. J. 1967. Determination of chlorophyll and pheo-pigments: spectrophotometric equations. Limnology and oceanography **12**:343-346.

Lozán, J. L., E. Rachor, K. Reise, H. Von Westernhagen, and W. Lenz. 1994. Warnsignale aus dem Wattenmeer: wissenschaftliche Fakten. Blackwell Wissenschafts-Verlag.

Mandema, F. S., J. M. Tinbergen, B. J. Ens, K. Koffijberg, K. S. Dijkema, and J. P. Bakker. 2015. Moderate livestock grazing of salt, and brackish marshes benefits breeding birds along the mainland coast of the Wadden Sea. The Wilson Journal of Ornithology **127**:467-476.

Mann, K. H., J. G. Field, and F. Wulff. 1989. Network analysis in marine ecology: an assessment. Springer.

Markert, A., W. Esser, D. Frank, A. Wehrmann, and K.-M. Exo. 2013. Habitat change by the formation of alien Crassostrea-reefs in the Wadden Sea and its role as feeding sites for waterbirds. Estuarine, Coastal and Shelf Science **131**:41-51.

Markert, B., A. Breure, and H. Zechmeister. 2003. Biomonitoring with birds. Bioindicators & Biomonitors:677.

Markones, N., and P. D. S. Garthe. 2011. Marine Säugetiere und Seevögel in der deut-schen AWZ von Nord-und Ostsee-Teilbericht Seevögel.

Mathers, R., and W. Montgomery. 1998. Behaviour of Brent geese Branta bernicla hrota and wigeon Anas penelope feeding on intertidal Zostera spp. Oceanographic Literature Review **1**:126.

Mc Mahon, K. W., L. L. Hamady, and S. R. Thorrold. 2013. Ocean Ecogeochemistry: A review. Pages 327-374 *in* R. N. Hughes, D. J. Hugues, and I. P. Smith, editors. Oceanography and Marine Biology: an annual review. Taylor and Francis Group.

McCann, K. S., and N. Rooney. 2009. The more food webs change, the more they stay the same. Philosophical Transactions of the Royal Society of London B: Biological Sciences **364**:1789-1801.

McLusky, D. 1989. The Estuarine Environment. Page 215 The Estuarine Ecosystem. Glasgow and London: Blackie and Son Ltd, New York: Chapman & Hall 1989.

Meeresumwelt, G. d. 2012. Umsetzung der Meeresstrategie-Rahmenrichtlinie. Bund- Länder Messprogramm.

Mendel, B. 2008. Profiles of seabirds and waterbirds of the German North and Baltic Seas: distribution, ecology and sensitivities to human activities within the marine environment. Bundesamt f. Naturschutz.

Merkel, C. 2015. Ermittlung des Energiebudgets von Ensis directus im Eulitoral der Insel Sylt. Philipps-Universität Marburg, Master thesis.

Monaco, M. E., and R. E. Ulanowicz. 1986. Comparative ecosystem trophic structure of. Marine Ecology Progress Series **1**:9.

Moreira, F. 1997. The importance of shorebirds to energy fluxes in a food web of a south European estuary. Estuarine, Coastal and Shelf Science **44**:67-78.

Mukherjee, J., U. M. Scharler, B. D. Fath, and S. Ray. 2015. Measuring sensitivity of robustness and network indices for an estuarine food web model under perturbations. Ecological Modelling **306**:160-173.

Nehls, G. 1989. Occurrence and food consumption of the common eider, Somateria mollissima, in the Wadden Sea of Schleswig-Holstein. HELGOLANDER MEERESUNTERSUCHUNGEN **43**:385-393.

Nehls, G., I. Hertzler, and G. Scheiffarth. 1997. Stable musselMytilus edulis beds in the Wadden Sea—They're just for the birds. HELGOLANDER MEERESUNTERSUCHUNGEN **51**:361-372.

Nehls, G., and R. Tiedemann. 1993. What determines the densities of feeding birds on tidal flats? A case study on Dunlin, Calidris alpina, in the Wadden Sea. Netherlands Journal of Sea Research **31**:375-384.

Nienhuis, P., and A. Groenendijk. 1986. Consumption of eelgrass (Zostera marina) by birds and invertebrates: an annual budget. Marine Ecology Progress Series **29**:1-2.

Nithart, M., E. Alliot, and C. Salen-Picard. 1999. Production, respiration and ammonia excretion of two polychaete species in a north Norfolk saltmarsh. Journal of the Marine Biological Association of the UK **79**:1029-1037.

Pace, N., and E. N. Rathbun. 1945. Studies on body composition. 3. The body water and chemically combined nitrogen content in relation to fat content. Journal of Biological Chemistry **158**:685-691.

Parsons, T. R., M. Takahashi, and B. Hargrave. 1973. Biological oceanographic processes. Elsevier.

Pearson, L. E. 2015. Blubber and Beyond: The Role od Lipids in Thermoregulation and Energy Reserves of Phocid Seals. Alaska Fairbanks.

Piersma, T., R. Hoekstra, A. Dekinga, A. Koolhaas, P. Wolf, P. Battley, and P. Wiersma. 1993. Scale and intensity of intertidal habitat use by knots Calidris canutus in the western Wadden Sea in relation to food, friends and foes. Netherlands Journal of Sea Research **31**:331-357.

Pinkerton, M., and J. Bradford-Grieve. 2008. Seals: Trophic modelling of the Ross Sea.

Pinkerton, M., J. Bradford-Grieve, and S. Hanchet. 2010. A balanced model of the food web of the Ross Sea, Antarctica. CCAMLR Science **17**:1-31.

Pockberger, M., and H. Asmus. 2014. Empfehlungen zur Anwendung von Ökosystemanalysen zur Beurteilung des Nahrungsnetzes im Wattenmeer in der Meeresstrategie Rahmenrichtlinie.

Pockberger, M., F. Kellnreitner, H. Ahnelt, R. Asmus, and H. Asmus. 2014. An abundant small sized fish as keystone species? The effect of Pomatoschistus microps on food webs and its trophic role in two intertidal benthic communities: A modeling approach. Journal of Sea Research **86**:86-96.

Reddy, L., L. A. Dierauf, and F. M. Gulland. 2001. Marine mammals as sentinels of ocean health. CRC handbook of marine mammal medicine: Health, disease and rehabilitation:3-13.

Reijnders, P. J. H., S. M. J. M. Brasseur, T. Borchardt, K. Camphuysen, R. Czeck, A. Gilles, L. F. Jensen, M. Leopold, K. Lucke, S. Ramdohr, M. Scheidat, U. Siebert, and J. Teilmann. 2009. Marine mammals. Thematic Report N°20. In: Marencic, H. and Vlas, J. de, editors. Quality status report 2009. Wadden Sea Ecosystem N°25. Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.

Reijnders, P. J. H., E. H. Ries, S. Tougaard, N. Nørgaard, G. Heidemann, J. Schwarz, E. Vareschi, and I. M. Traut. 1997. Population development of harbour seals *Phoca vitulina* in the Wadden Sea after the 1988 virus epizootic. Journal of Sea Research **38**:161-168.

Reise, K., M. Baptist, P. Burbridge, N. Dankers, L. Fischer, B. Flemming, A. Oost, and C. Smit. 2010. The Wadden Sea-a universally outstanding tidal wetland. The Wadden Sea 2010. Common Wadden Sea Secretariat (CWSS); Trilateral Monitoring and Assessment Group: Wilhelmshaven.(Wadden Sea Ecosystem; 29/editors, Harald Marencic and Jaap de Vlas) **7**.

Reise, K., and J. Kohlus. 2008. Seagrass recovery in the Northern Wadden Sea? Helgoland Marine Research **62**:77-84.

Ricciardi, A., and E. Bourget. 1998a. Weight-to-weight conversion factors for marine benthic macroinvertebrates. Marine Ecology Progress Series.

Ricciardi, A., and E. Bourget. 1998b. Weight-to-weight conversion factors for marine benthic macroinvertebrates. Marine Ecology Progress Series **163**:245-251.

Riemann, B., P. Simonsen, and L. Stensgaard. 1989. The carbon and chlorophyll content of phytoplankton from various nutrient regimes. Journal of Plankton Research **11**:1037-1045.

Rumohr, H., T. Brey, and S. Ankar. 1987. A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. Institut für Meereskunde.

Rumohr, H., Brey, T, Ankar, S. 1987. A Compilation of Biometric Conversion Factors for Benthic Invertebrates of the Baltic Sea. The Baltic Marine Biologists Publication **9**:1-56.

Ryg, M., C. Lydersen, N. H. Markussen, T. G. Smith, and N. A. Øritsland. 1990. Estimating the blubber content of phocid seals. Canadian Journal of Fisheries and Aquatic Sciences **47**:1223-1227.

Saint-Béat, B., Baird, D., Asmus, H., Asmus, R., Bacherd, C., Pacellaa, S., R., Johnsona,G., A., Davida, V., Vézinaf, A., F., Niquila, N. 2015. Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review. Ecological indicators **52**:458-471.

Saint-Béat, B., C. Dupuy, P. Bocher, J. Chalumeau, M. De Crignis, C. Fontaine, K. Guizien, J. Lavaud, S. Lefebvre, and H. Montanié. 2013a. Key Features of Intertidal Food Webs That Support Migratory Shorebirds. Plos One **8**.

Saint-Béat, B., C. Dupuy, P. Bocher, J. Chalumeau, M. De Crignis, C. Fontaine, K. Guizien, J. Lavaud, S. Lefebvre, and H. Montanié. 2013b. Key features of intertidal food webs that support migratory shorebirds.

Samhouri, J., F., Levin, P., S., Harvey, C., J. 2009. Quantitative Evaluation of Marine Ecosystem Indicator Performance Using Food Web Models. Ecosystems **12**:1283-1298.

Samhouri, J., P. Levin, and C. Harvey. 2009. Quantitative Evaluation of Marine Ecosystem Indicator Performance Using Food Web Models. Ecosystems **12**:1283-1298.

Scharler, U. M., and D. Baird. 2005a. A comparison of selected ecosystem attributes of three South African estuaries with different freshwater inflow regimes, using network analysis. Journal of Marine Systems **56**:283-308.

Scharler, U. M., and D. Baird. 2005b. A comparison of selected ecosystem attributes of three South African estuaries with different freshwater inflow regimes, using network analysis. Journal of Marine Systems **56**:283-308.

Scheiffarth, G. 2001. The diet of bar-tailed godwits *Limosa lapponica* in the Wadden Sea: Combining visual observations and faeces analyses. Ardea **89**:481-494.

Scheiffarth, G., and G. Nehls. 1997. Consumption of benthic fauna by carnivorous birds in the Wadden Sea. HELGOLANDER MEERESUNTERSUCHUNGEN **51**:373-387.

Schückel, U., I. Kröncke, and D. Baird. 2015. Linking long-term changes in trophic structure and function of an intertidal macrobenthic system to eutrophication and climate change using ecological network analysis. Mar Ecol Prog Ser **536**:25-38.

Schwemmer, P., Garthe, S. 2008. Regular habitat switch as an important feeding strategy of an opportunistic seabird species at the interface between land and sea. Estuarine, Coastal and Shelf Science **77**:12-22.

Schwemmer, P., Garthe, S. 2011. Spatial and temporal patterns of habitat use by Eurasian oystercatchers (*Haematopus ostralegus*) in the eastern Wadden Sea revealed using GPS data loggers. Marine Biology **158**:541-550.

Schwemmer, P., F. Güpner, S. Adler, K. Klingbeil, and S. Garthe. 2016a. Modelling small-scale foraging habitat use in breeding Eurasian oystercatchers (Haematopus ostralegus) in relation to prey distribution and environmental predictors. Ecological Modelling **320**:322-333.

Schwemmer, P., F. Güpner, N. Guse, and S. Garthe. 2012. Nahrungswahl von Vogelarten der deutschen Nordseeküste. Vogelwarte **50**:141-154.

Schwemmer, P., C. C. Voigt, A. M. Corman, S. Adler, and S. Garthe. 2016b. Body mass change and diet switch tracked by stable isotopes indicate time spent at a stopover site during autumn migration in dunlins Calidris alpina alpina. Journal of Avian Biology.

Siebert, U., A. Gilles, K. Lucke, M. Ludwig, H. Benke, K.-H. Kock, and M. Scheidat. 2006. A decade of harbour porpoise occurrence in German waters—Analyses of aerial surveys, incidental sightings and strandings. Journal of Sea Research **56**:65-80.

Siebert, U., P. Wohlsein, K. Lehnert, and W. Baumgärtner. 2007. Pathological Findings in Harbour Seals (*Phoca vitulina*): 1996–2005. Journal of Comparative Pathology **137**:47-58.

Smardon, R. 2009. The Wadden Sea Wetlands: A Multi-jurisdictional Challenge. Pages 21-56 Sustaining the World's Wetlands. Springer.

Smit, C. J., N. Dankers, B. J. Ens, and A. Meijboom. 1998. Birds, mussels, cockles and shellfish fishery in the Dutch Wadden Sea: how to deal with low food stocks for eiders and oystercatchers? Senckenbergiana maritima **29**:141-153.

Smith-Ramesh, L. M., A. C. Moore, and O. J. Schmitz. 2016. Global synthesis suggests that food web connectance correlates to invasion resistance. Global Change Biology.

Swennen, C., M. Leopold, and M. Stock. 1985. Notes on growth and behaviour of the American razor clam *Ensis directus* in the Wadden Sea and the predation on it by birds. Helgoländer Meeresuntersuchungen **39**:225-261.

Taylor, A. M., R. H. C. Bonser, and J. W. Farrent. 2004. The influence of hydration on the tensile and compressive properties of avian keratinous tissues. Journal of Materials Science **39**:939-942.

Tiedemann, R., and G. Nehls. 1997. Saisonale und tidale Variation in der Nutzung von Wattflächen durch nahrungssuchende Vögel. Journal für Ornithologie **138**:183-198.

Tulp, I., J. Craeymeersch, M. Leopold, C. van Damme, F. Fey, and H. Verdaat. 2010. The role of the invasive bivalve *Ensis directus* as food source for fish and birds in the Dutch coastal zone. Estuarine, Coastal and Shelf Science **90**:116-128.

Ulanowicz, R., and C. Puccia. 1990. Mixed trophic impacts in ecosystems. Coenoses **5**:7-16.

Ulanowicz, R. E. 2004. Quantitative methods for ecological network analysis. Computational Biology and Chemistry **28**:321-339.

Ulanowicz, R. E., and D. Baird. 1999. Nutrient controls on ecosystem dynamics: the Chesapeake mesohaline community. Journal of Marine Systems **19**:159-172.

Ulanowicz, R. E., S. J. Goerner, B. Lietaer, and R. Gomez. 2009. Quantifying sustainability: resilience, efficiency and the return of information theory. Ecological complexity **6**:27-36.

Ulanowicz, R. E., R. D. Holt, and M. Barfield. 2014. Limits on ecosystem trophic complexity: insights from ecological network analysis. Ecology letters **17**:127-136.

van de Kam, J. 2004. Shorebirds: an illustrated behavioural ecology. KNNV.

van de Pol, M., Ens, B., J., Heg, D., Brouwer, L., Krol, J., Maier, M., Exo, K., Oosterbeek, K., Lok, T.,Eising, C., M., Koffijberg, K. 2010. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? Journal of Applied Ecology **47**:720-730.

van der Zee, E. M., C. Angelini, L. L. Govers, M. J. Christianen, A. H. Altieri, K. J. van der Reijden, B. R. Silliman, J. van de Koppel, M. van der Geest, and J. A. van Gils. 2016. How habitat-modifying organisms structure the food web of two coastal ecosystems. Page 20152326 *in* Proc. R. Soc. B. The Royal Society.

van Katwijk, M. M., A. R. Bos, V. N. de Jonge, L. S. A. M. Hanssen, D. C. R. Hermus, and D. J. de Jong. 2009. Guidelines for seagrass restoration: Importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Marine Pollution Bulletin **58**:179-188.

van Roomen, M., K. Laursen, C. van Turnhout, E. van Winden, J. Blew, K. Eskildsen, K. Günther, B. Hälterlein, R. Kleefstra, and P. Potel. 2012. Signals from the Wadden sea: Population declines dominate among waterbirds depending on intertidal mudflats. Ocean & Coastal Management **68**:79-88.

Vasconcellos, M., S. Mackinson, K. Sloman, and D. Pauly. 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecological Modelling **100**:125-134.

Vitousek, P., and R. Howarth. 1991. Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry **13**:87-115.

Volkenborn, N., S. Hedtkamp, J. Van Beusekom, and K. Reise. 2007. Effects of bioturbation and bioirrigation by lugworms (Arenicola marina) on physical and chemical sediment properties and implications for intertidal habitat succession. Estuarine, Coastal and Shelf Science **74**:331-343.

Wolff, W. 1983. Ecology of the Wadden Sea. v. 2: Fishes and fisheries, birds, marine mammals, pollution.

Wolff, W. J., J. P. Bakker, K. Laursen, and K. Reise. 2010. The Wadden Sea Quality Status Report-Synthesis Report 2010. The Wadden Sea 2010. Common Wadden Sea Secretariat (CWSS); Trilateral Monitoring and Assessment Group: Wilhelmshaven.(Wadden Sea Ecosystem; 29/editors, Harald Marencic and Jaap de Vlas) **25**.

Wulff, F., J. G. Field, and K. H. Mann. 1989. Network analysis in marine ecology: methods and applications. Springer Science & Business Media.

Appendix

App. 1: Energy flow table of the cockle field; biomass in $mgC.m^{-2}$; production (P), consumption, respiration, egestion (E), imports, exports and flows in $mgC.m^{-2}.d^{-1}$

Comp #i	Compartment	Biomass	Consumption	Imports	Exports	Produktion	Production - Cosumtion	Comp #j	flow from #i to #j	Sum	Egestion	Sum of Excess P+E	Respiration
1	Phytoplankton	605.8309		3096.5616		144.0538	-2841.7980	6	2773.5996				110.7622
1								7	156.5458				
1								8	3.8361				
1								9	1.2571				
1								20	1.5334				
1								22	46.8671				
1								24	1.1043				
1								26	1.1083	2985.8518			
2	Makrophyta	428.0207		11.7266	1.4806	5.1597	2.9612	12	0.8757			1.4806	6.5669
2								29	1.3228	2.1985			
2								36	1.4806				
3	Microphytobenthos	420.9488		3021.6481	620.2651	1973.4163	1240.5302	5	72.1322			620.2651	1048.2325
3								7	91.0150				
3								12	1.5674				
3								13	20.4044				
3								14	446.1144				
3								17	7.7562				
3								22	93.7343				
3								25	0.1183				
3								26	0.0440	732.8861			
3								36	620.2651				
4	Bacteria	625.0000	196.3920	234.5519		49.2410	-234.5519	5	72.1322		38.1500	38.1500	109.0010
4								7	45.5075				
4								11	3.3901				
4								12	0.3319				
4								14	74.3524				
4								16	0.7290				
4								17	34.9028				
4								18	4.6222				
4								22	46.8671				
4								25	0.5325				
4								26	0.0866				
4								27	0.3387	283.7929			
4								36	38.1500				
5	Meiofauna	1000.0000	288.5289	72.1233		21.9180	-72.1233	5	36.0661		183.2139	183.2139	83.3969
5								10	1.6900				
5								11	4.5201				
5								19	0.1957				
5								22	46.8671				
5								23	4.7023	94.0414			
5								36	183.2139				
6	*Cerastoderma edule*	129451.1887	3225.1158		236.1278	645.0061	472.2555	10	5.6555		2377.9200	2614.0477	202.1898
6								11	9.4538				
6								12	0.1272				
6								19	0.6549				
6								21	47.5876				
6								22	78.4184				
6								23	3.9340				
6								28	20.5259				
6								29	1.3228				
6								30	0.9651				
6								31	0.2689				
6								33	1.8749				
6								34	1.7791				
6								35	0.1823	172.7506			
6								36	2614.0477				
7	*Macoma balthica*	6832.1618	364.0599		17.9687	56.2995	35.9375	10	0.2983		297.2680	315.2367	10.4925
7								11	0.4990				
7								12	0.0068				
7								19	0.0345				
7								21	2.5142				
7								22	4.1388				
7								23	0.2078				
7								28	5.1193				
7								29	3.9685				
7								30	0.3217				
7								31	0.1673				
7								32	0.6578				
7								33	2.3780				
7								34	0.0502	20.3620			
7								36	315.2367				
8	*Mya arenaria*	408.1242	4.4606		0.1934	0.8919	0.3868	10	0.0177		1.4935	1.6869	2.0752

App. 1 (continued): Energy flow table of the cockle field; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

8								11	0.0298				
8								12	0.0004				
8								19	0.0021				
8								21	0.1479				
8								22	0.2472				
8								23	0.0122				
8								31	0.0164				
8								35	0.0314	0.5051			
8								36	1.6869				
9	*Mytilus edulis*	199.7880	1.4618	6.3447		0.1971	-6.3447	10	0.0084		0.1810	0.1810	1.0838
9								11	0.0146				
9								12	0.0002				
9								19	0.0010				
9								21	0.0739				
9								22	0.1210				
9								23	0.0056				
9								28	5.1193				
9								29	1.1161				
9								34	0.0502				
9								35	0.0314	6.5418			
9								36	0.1810				
10	*Carcinus meanas*	345.1000	8.4499	6.8764		1.4595	-6.8764	10	0.0152		4.7998	4.7998	2.1906
10								11	0.0252				
10								12	0.0004				
10								19	0.0018				
10								21	0.1251				
10								22	0.2091				
10								23	0.0103				
10								29	0.4547				
10								30	1.2753				
10								31	0.0672				
10								32	0.2990				
10								33	4.7102				
10								34	1.0179				
10								35	0.1244	8.3359			
10								36	4.7998				
11	*Crangon spp.*	378.3340	22.6005		0.5447	4.1536	1.0894	10	0.0169		4.1536	4.6983	14.2933
11								11	0.0276				
11								12	0.0004				
11								19	0.0020				
11								21	0.1365				
11								22	0.2292				
11								23	0.0113				
11								30	0.3217				
11								31	0.3345				
11								32	0.3189				
11								33	1.4176				
11								35	0.2475	3.0642			
11								36	4.6983				
12	small crustaceans	150.7807	3.9985	17.3172		0.6090	-17.3172	10	0.0068		0.8150	0.8150	2.5744
12								11	0.0110				
12								12	0.0001				
12								19	0.0008				
12								21	0.0569				
12								22	0.0913				
12								23	0.0047				
12								29	3.5137				
12								31	0.0328				
12								33	14.1307				
12								35	0.0773	17.9262			
12								36	0.8150				
13	*Littorina littorea*	990.6400	20.4044	3.2666		2.0240	-3.2666	10	0.0431		12.2506	12.2506	6.1297
13								11	0.0723				
13								12	0.0008				
13								19	0.0050				
13								21	0.3640				
13								22	0.6001				
13								23	0.0301				
13								29	4.1752	5.2906			
13								36	12.2506				
14	*Peringia ulvae*	11186.0896	594.8192		79.4576	201.6561	158.9153	10	0.4884		325.8387	405.2963	67.3244
14								11	0.8169				
14								12	0.0108				
14								15	1.2927				
14								19	0.0566				
14								21	4.1126				

App. 1 (continued): Energy flow table of the cockle field; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

14								22	6.7763				
14								23	0.3395				
14								29	19.8010				
14								31	0.0672				
14								33	8.9632				
14								35	0.0157	42.7408			
14								36	405.2963				
15	*Retusa obtusa*	33.1004	1.2927	2.1147		0.1293	-2.1147	10	0.0017		0.9642	0.9642	0.1992
15								11	0.0024				
15								12	0.0000				
15								19	0.0002				
15								21	0.0114				
15								22	0.0201				
15								23	0.0009				
15								29	2.1909				
15								31	0.0164	2.2440			
15								36	0.9642				
16	Oligochaeta	33.9742	1.4580		0.0279	0.0931	0.0558	10	0.0017		0.4582	0.4861	0.9067
16								11	0.0025				
16								12	0.0000				
16								19	0.0002				
16								21	0.0114				
16								22	0.0206				
16								23	0.0009	0.0373			
16								36	0.4861				
17	*Arenicola marina*	1623.6520	77.5618	1.0046		11.6345	-1.0046	10	0.0710		55.1022	55.1022	10.8251
17								11	0.1186				
17								12	0.0016				
17								19	0.0082				
17								21	0.5973				
17								22	0.9836				
17								23	0.0489				
17								28	7.7033				
17								30	2.2175				
17								31	0.2001				
17								32	0.6578				
17								35	0.0314	12.6391			
17								36	55.1022				
18	*Capitella capitata*	108.5683	9.2443		0.2307	0.5845	0.4615	10	0.0051		6.1551	6.3859	2.5047
18								11	0.0079				
18								12	0.0001				
18								19	0.0006				
18								21	0.0398				
18								22	0.0658				
18								23	0.0038	0.1230			
18								36	6.3859				
19	*Eteone spp.*	70.6392	0.9785		0.1293	0.3408	0.2587	10	0.0034		0.5908	0.7201	0.0469
19								11	0.0052				
19								12	0.0001				
19								19	0.0004				
19								21	0.0284				
19								22	0.0428				
19								23	0.0019	0.0821			
19								36	0.7201				
20	*Lanice conchilega*	90.1900	1.7830	0.7335		0.4678	-0.7335	10	0.0042		0.4122	0.4122	0.9029
20								11	0.0066				
20								12	0.0001				
20								19	0.0005				
20								21	0.0341				
20								22	0.0546				
20								23	0.0028				
20								30	0.3217				
20								31	0.1673				
20								32	0.5781				
20								35	0.0314	1.2014			
20								36	0.4122				
21	*Nephtys spp.*	956.3910	56.8822	0.6372		10.5453	-0.6372	10	0.0414		36.3177	36.3177	10.0192
21								11	0.0698				
21								12	0.0008				
21								19	0.0048				
21								21	0.3527				
21								22	0.5794				
21								23	0.0292				
21								28	2.5840				
21								30	0.3217				
21								32	4.3055				

App. 1 (continued): Energy flow table of the cockle field; biomass in $mgC.m^{-2}$; production (P), consumption, respiration, egestion (E), imports, exports and flows in $mgC.m^{-2}.d^{-1}$

21								33	2.8353				
21								34	0.0266				
21								35	0.0314	11.1825			
21								36	36.3177				
22	*Nereis spp.*	1450.8804	468.6713	18.9349		6.9563	-18.9349	10	0.0634		444.6725	444.6725	17.0425
22								11	0.1060				
22								12	0.0016				
22								19	0.0073				
22								21	0.5347				
22								22	0.8789				
22								23	0.0442				
22								28	5.1193				
22								29	3.5137				
22								31	0.3017				
22								32	5.5015				
22								33	9.4205				
22								34	0.0266				
22								35	0.3719	25.8912			
22								36	444.6725				
23	*Phyllodoce spp.*	259.8421	9.4047		0.2093	0.7119	0.4186	10	0.0110		1.0124	1.2217	7.6804
23								11	0.0190				
23								12	0.0004				
23								19	0.0013				
23								21	0.0967				
23								22	0.1574				
23								23	0.0075	0.2933			
23								36	1.2217				
24	*Pygospio elegans*	45.7985	1.2840		0.0595	0.1700	0.1189	10	0.0017		0.3335	0.3930	0.7805
24								11	0.0033				
24								12	0.0000				
24								19	0.0002				
24								21	0.0171				
24								22	0.0277				
24								23	0.0009	0.0510			
24								36	0.3930				
25	*Scoloplos ormiger*	38.7295	1.1834	10.1073		0.1687	-10.1073	10	0.0017		0.7334	0.7334	0.2812
25								11	0.0028				
25								12	0.0000				
25								19	0.0002				
25								21	0.0171				
25								22	0.0235				
25								23	0.0009				
25								28	2.5840				
25								32	7.6143				
25								35	0.0314	10.2760			
25								36	0.7334				
26	small polychaetes	55.1580	1.5185		0.0929	0.2508	0.1859	10	0.0025		0.4613	0.5542	0.8064
26								11	0.0040				
26								12	0.0000				
26								19	0.0003				
26								21	0.0228				
26								22	0.0334				
26								23	0.0019	0.0649			
26								36	0.5542				
27	*Tharyx killariensis*	25.1498	0.6774		0.0537	0.1378	0.1075	10	0.0008		0.2782	0.3319	0.2614
27								11	0.0018				
27								12	0.0000				
27								19	0.0001				
27								21	0.0114				
27								22	0.0152				
27								23	0.0009	0.0304			
27								36	0.3319				
28	*Haematopus ostralegus*	359.2475	48.7550		1.6252	1.6252		36	9.7510		9.7510	9.7510	37.3789
29	*Tadorna tadorna*	384.9898	41.3382		0.9106	0.9106		36	9.2714		9.2714	9.2714	31.1562
30	*Numenius arquata*	80.1968	5.7447		0.1473	0.1473		36	1.1784		1.1784	1.1784	4.4190
31	*Chroicocephalus ridibundus*	23.4266	1.6399		0.0547	0.0547		36	0.3280		0.3280	0.3280	1.2572
32	*Limosa lapponica*	97.8520	19.9328		0.3624	0.3624		36	3.9866		3.9866	3.9866	15.5838
33	*Tringa tatanus*	187.1926	45.7305		0.6725	0.6725		36	9.4151		9.4151	9.4151	35.6429
34	*Larus agentatus*	50.2174	2.9504		0.0757	0.0757		36	0.6052		0.6052	0.6052	2.2696
35	*Larus canus*	23.4872	1.2075		0.0416	0.0416		36	0.2498		0.2498	0.2498	0.9160
36	sediment POC	19000.0000			4245.1303		18459.9275	4	196.3920				
36								5	108.1983				
36								7	45.5075				
36								11	3.3901				
36								12	0.7197				

App. 1 (continued): Energy flow table of the cockle field; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

36								14	74.3524				
36								16	0.7290				
36								17	34.9028				
36								18	4.6222				
36								22	70.3007				
36								25	0.5325				
36								26	0.0866				
36								27	0.3387	540.0725			
37	Suspended POC	167.4370		549.0857			-381.6487	6	451.5162				
37								7	25.4842				
37								8	0.6245				
37								9	0.2047				
37								12	0.3439				
37								20	0.2496				
37								22	70.3007				
37								24	0.1798				
37								26	0.1822	549.0857			

App. 2: Energy flow table of the razor clam field; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

Comp #i	Compartment	Biomass	Consumption	Imports	Exports	Produktion	Production - Cosumtion	Comp #j	flow from #i to #j	Sum	Egestion	Sum of Excess P+E	Respiration
1	Phytoplankton	706.8027		460.5618		168.0627	-163.3376	5	303.0153			0.0000	129.2226
1								6	0.1564				
1								7	27.1440				
1								16	0.3983				
1								18	0.6864	331.4004			
2	Microphytobenthos	309.0100		2218.1313	679.3745	1448.6453	1358.7491	4	72.1322			679.3745	769.4865
2								6	0.0909				
2								7	15.7814				
2								9	1.2493				
2								10	0.0324				
2								17	0.5847				
2								18	0.0254	89.8962			
2								28	679.3745				
3	Bacteria	625.0000	196.3920	45.3357		49.2410	-45.3357	4	72.1322		38.1500	38.1500	109.0010
3								6	0.0455				
3								7	7.8907				
3								8	10.9659				
3								9	0.2645				
3								10	0.0054				
3								12	0.1846				
3								13	0.4032				
3								17	2.6312				
3								18	0.0536	94.5767			
3								28	38.1500				
4	Meiofauna	1000.0000	288.5289	28.7902		21.9180	-28.7902	4	36.0661		183.2139	183.2139	83.3969
4								8	14.6212				
4								14	0.0209	50.7082			
4								28	183.2139				
5	*Ensis directus*	12355.6200	352.3434			80.5198	73.1195	19	0.7518		17.2979	90.4173	254.5258
5								20	0.7616				
5								22	0.2172				
5								23	0.0281				
5								24	0.1692				
5								26	5.4421				
5								27	0.0303	7.4003			
5								28	90.4173				
6	*Fabulina fabula*	6.8247	0.3637	0.1037		0.0562	-0.1037	8	0.0658		0.2969	0.2969	0.0105
6								9	0.0003				
6								14	0.0002				
6								15	0.0936	0.1599			
6								28	0.2969				
7	*Macoma balthica*	1184.6500	63.1255	18.8398		9.7619	-18.8398	8	11.9163		51.5442	51.5442	1.8193
7								9	0.0395				
7								14	0.0272				
7								15	16.0588				
7								19	0.1000				
7								21	0.0487				
7								23	0.0556				
7								25	0.2606				
7								26	0.0950	28.6018			
7								28	51.5442				
8	*Crangon spp.*	1223.8000	73.1061	15.9669		13.4357	-15.9669	8	12.3038		13.4357	13.4357	46.2347
8								9	0.0408				
8								14	0.0281				
8								15	16.5910				
8								21	0.0487				
8								23	0.0832				
8								25	0.2241				
8								27	0.0831	29.4027			
8								28	13.4357				
9	*small crustaceans*	120.1760	3.1869	2.4390		0.4854	-2.4390	8	1.2063		0.6496	0.6496	2.0519
9								9	0.0041				
9								14	0.0028				
9								15	1.6310				
9								23	0.0335				
9								27	0.0468	2.9244			
9								28	0.6496				
10	*Peringia ulvae*	0.8120	0.0432	0.3320		0.0146	-0.3320	8	0.0073		0.0237	0.0237	0.0049
10								9	0.0000				
10								11	0.0929				
10								14	0.0000				
10								15	0.0099				

App. 2 (continued): Energy flow table of the razor clam field; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

10								20	0.1638				
10								23	0.0391				
10								27	0.0337	0.3467			
10								28	0.0237				
11	*Retusa obtusa*	2.3780	0.0929	0.0780		0.0093	-0.0780	8	0.0219		0.0693	0.0693	0.0143
11								9	0.0001				
11								14	0.0001				
11								15	0.0345				
11								23	0.0308	0.0873			
11								28	0.0693				
12	Oligochaeta	8.6006	0.3691	0.1829		0.0236	-0.1829	8	0.0877		0.1160	0.1160	0.2295
12								9	0.0003				
12								14	0.0002				
12								15	0.1183	0.2065			
12								28	0.1160				
13	*Capitella capitata*	9.4716	0.8065	0.1727		0.0510	-0.1727	8	0.0950		0.5370	0.5370	0.2185
13								9	0.0003				
13								14	0.0002				
13								15	0.1281	0.2237			
13								28	0.5370				
14	*Eteone spp.*	7.5400	0.1044	0.1407		0.0364	-0.1407	8	0.0731		0.0631	0.0631	0.0050
14								9	0.0003				
14								14	0.0002				
14								15	0.1035	0.1771			
14								28	0.0631				
15	*Nephtys spp.*	828.4913	49.2753	11.3160		9.1351	-11.3160	8	8.3341		31.4609	31.4609	8.6793
15								9	0.0277				
15								14	0.0190				
15								15	11.2298				
15								19	0.0505				
15								21	0.0487				
15								25	0.6539				
15								26	0.0503				
15								27	0.0370	20.4510			
15								28	31.4609				
16	*Pygospio elegans*	16.5177	0.4631	0.3296		0.0613	-0.3296	8	0.1681		0.1203	0.1203	0.2815
16								9	0.0006				
16								14	0.0004				
16								15	0.2217	0.3909			
16								28	0.1203				
17	*Scoloplos armiger*	191.3607	5.8470	4.7899		0.8336	-4.7899	8	1.9227		3.6239	3.6239	1.3895
17								9	0.0064				
17								14	0.0044				
17								15	2.5919				
17								19	0.0505				
17								25	1.0107				
17								27	0.0370	5.6235			
17								28	3.6239				
18	*small polychaetes*	34.1620	0.9405			0.1553	-0.6535	8	0.3436		0.2857	0.2857	0.4994
18								9	0.0013				
18								14	0.0008				
18								15	0.4632	0.8088			
18								28	0.2857				
19	*Haematopus ostralegus*	7.0206	0.9528		0.0318	0.0318		28	0.1906		0.1906	0.1906	0.7305
20	*Somateria mollissima*	6.8127	0.9254		0.0185	0.0185		28	0.1845		0.1845	0.1845	0.7224
21	*Numenius arquata*	6.8127	0.1460		0.0037	0.0037		28	0.0299		0.0299	0.0299	0.1123
22	*Larus fuscus*	14.2944	0.2172		0.0056	0.0056		28	0.0446		0.0446	0.0446	0.1671
23	*Chroicocephalus ridibundus*	3.8614	0.2703		0.0090	0.0090		28	0.0541		0.0541	0.0541	0.2072
24	*Larus marinus*	19.5973	0.1692		0.0114	0.0114		28	0.1527		0.1527	0.1527	0.0051
25	*Limosa lapponica*	10.5509	2.1493		0.0391	0.0391		28	0.4299		0.4299	0.4299	1.6803
26	*Larus agentatus*	95.0998	5.5874		0.1433	0.1433		28	1.1461		1.1461	1.1461	4.2980
27	*Larus canus*	5.0084	0.2575		0.0089	0.0089		28	0.0533		0.0533	0.0533	0.1953
28	sediment POC	19000.0000			768.3109		18672.6433	3	196.3920				
28								4	108.1983				
28								6	0.0455				
28								7	7.8907				
28								8	10.9659				
28								9	0.5864				
28								10	0.0054				
28								12	0.1846				
28								13	0.4032				
28								17	2.6312				
28								18	0.0536	327.3567			

App. 2 (continued): Energy flow table of the razor clam field; biomass in $mgC.m^{-2}$; production (P), consumption, respiration, egestion (E), imports, exports and flows in $mgC.m^{-2}.d^{-1}$

29	Suspended POC	167.4370		167.4370	113.2129		113.2129	5	49.3281				
29								6	0.0255				
29								7	4.4188				
29								9	0.2741				
29								16	0.0648				
29								18	0.1129	54.2241			

App. 3: Energy flow table of the mud flat; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

Comp #i	Compartment	Biomass	Consumption	Imports	Exports	Produktion	Production - Cosumtion	Comp #j	flow from #i to #j	Sum	Egestion	Sum of Excess P+E	Respiration
1	Phytoplankton	468.5092		539.1943		111.4016	-342.1772	5	336.5906				85.6561
1								6	26.0058				
1								16	0.0473				
1								17	89.5798				
1								18	0.5849				
1								20	0.7704	453.5788			
2	Microphytobenthos	961.5090		6901.8898	623.1686	4507.5738	1246.3373	4	36.0661			623.1686	2394.3176
2								6	15.1196				
2								9	0.2202				
2								10	13.5973				
2								11	687.8921				
2								17	2508.2347				
2								19	0.0759				
2								20	0.0306	3261.2366			
2								37	623.1686				
3	Bacteria	625.0000	196.3920	211.5715		49.2410	-211.5715	4	36.0661		38.1500	38.1500	109.0010
3								6	7.5598				
3								8	0.5262				
3								9	0.0299				
3								11	114.6487				
3								13	8.9709				
3								14	1.9419				
3								17	89.5798				
3								19	0.3417				
3								20	0.0602				
3								21	1.0872	260.8125			
3								37	38.1500				
4	Meiofauna	500.0000	144.2644	131.1187		10.9590	-131.1187	4	18.0331		91.6069	91.6069	41.6985
4								7	33.7429				
4								8	0.7016				
4								15	0.0204				
4								17	89.5798	142.0777			
4								37	91.6069				
5	*Cerastoderma edule*	15709.5685	391.3844		7.1852	78.2748	14.3704	7	41.0651		288.5728	295.7580	24.5368
5								8	0.5336				
5								9	0.0042				
5								15	0.0248				
5								17	9.0842				
5								23	4.5164				
5								24	0.4042				
5								25	4.4196				
5								26	0.5163				
5								27	0.0494				
5								28	0.1405				
5								30	1.0554				
5								32	0.9924				
5								34	0.9623				
5								36	0.1361	63.9044			
5								37	295.7580				
6	*Macoma balthica*	1134.9754	60.4785	3.1673		9.3526	-3.1673	7	2.9694		49.3829	49.3829	1.7430
6								8	0.0386				
6								9	0.0003				
6								15	0.0018				
6								17	0.6563				
6								23	2.2542				
6								24	1.0633				
6								26	0.2921				
6								27	0.0605				
6								29	0.0484				
6								30	0.7850				
6								31	2.8401				
6								32	1.2113				
6								34	0.2036				
6								35	0.0951	12.5199			
6								37	49.3829				
7	*Carcinus maenas*	6890.4000	168.7143	0.8531		29.1413	-0.8531	7	18.0018		95.8355	95.8355	43.7374
7								8	0.2340				
7								9	0.0018				
7								15	0.0109				
7								17	3.9844				
7								24	0.1879				
7								26	0.6274				

App. 3 (continued): Energy flow table of the mud flat; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

7								27	0.1112				
7								29	0.0472				
7								30	0.3826				
7								31	2.1539				
7								32	2.2264				
7								33	0.8849				
7								34	0.9623				
7								35	0.0651				
7								36	0.1124	29.9944			
7								37	95.8355				
8	*Crangon spp.*	58.7250	3.5081	4.6803		0.6447	-4.6803	7	0.1518		0.6447	0.6447	2.2186
8								8	0.0021				
8								9	0.0000				
8								15	0.0001				
8								17	0.0340				
8								26	0.2921				
8								27	0.0393				
8								30	1.4578				
8								31	2.1920				
8								32	0.7933				
8								33	0.0885				
8								35	6.5102E-02				
8								36	2.0889E-01	5.3250			
8								37	0.6447				
9	small crustaceans	13.5913	0.3604	8.6619		0.0549	-8.6619	7	0.0337		0.0735	0.0735	0.2321
9								8	0.0004				
9								9	3.6049E-06				
9								15	0.0000				
9								17	0.0079				
9								22	0.4418				
9								24	0.9500				
9								27	0.3159				
9								29	0.0472				
9								30	0.2441				
9								32	6.3266				
9								33	0.0885				
9								35	0.1851				
9								36	0.0755	8.7168			
9								37	0.0735				
10	*Littorina littorea*	660.1560	13.5973	5.6901		1.3488	-5.6901	7	1.7209		8.1637	8.1637	4.0848
10								8	0.0225				
10								9	0.0002				
10								15	0.0010				
10								17	0.3817				
10								24	1.1148				
10								25	3.7493				
10								29	0.0484	7.0388			
10								37	8.1637				
11	*Peringia ulvae*	17248.5425	917.1895		118.1213	310.9463	236.2426	7	45.0805		502.4314	620.5527	103.8117
11								8	0.5858				
11								9	0.0046				
11								12	1.4066				
11								15	0.0273				
11								17	9.9741				
11								22	0.2989				
11								24	5.0076				
11								25	4.0174				
11								27	0.1628				
11								29	0.0484				
11								30	0.3826				
11								32	4.0775				
11								33	3.2741				
11								35	0.3282				
11								36	0.0273	74.7037			
11								37	620.5527				
12	*Retusa obtusa*	36.0180	1.4066	0.7811		0.1407	-0.7811	7	0.1012		1.0492	1.0492	0.2168
12								8	0.0011				
12								9	0.0000				
12								15	0.0001				
12								17	0.0208				
12								24	0.6205				
12								30	0.1781	0.9218			
12								37	1.0492				
13	Oligochaeta	418.0689	17.9419	0.3556		1.1454	-0.3556	7	1.0966		5.6388	5.6388	11.1577

App. 3 (continued): Energy flow table of the mud flat; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

13								8	0.0140				
13								9	0.0001				
13								15	0.0007				
13								17	0.2418				
13								33	0.0885				
13								35	0.0593	1.5010			
13								37	5.6388				
14	*Capitella capitata*	45.6129	3.8838	0.2962		0.2456	-0.2962	7	0.1181		2.5860	2.5860	1.0523
14								8	0.0014				
14								9	0.0000				
14								15	0.0001				
14								17	0.0264				
14								29	0.3365				
14								35	0.0593	0.5418			
14								37	2.5860				
15	*Eteone spp.*	7.3660	0.1020		0.0070	0.0355	0.0140	7	0.0169		0.0616	0.0686	0.0049
15								8	0.0004				
15								9	0.0000				
15								15	0.0000				
15								17	0.0043	0.0215			
15								37	0.0686				
16	*Lanice conchilega*	2.7840	0.0550	3.9851		0.0144	-3.9851	7	0.0073		0.0127	0.0127	0.0279
16								8	0.0001				
16								9	0.0000				
16								15	0.0000				
16								17	0.0016				
16								22	0.1269				
16								26	0.2921				
16								30	0.7850				
16								31	2.6876				
16								35	0.0593				
16								36	0.0396	3.9996			
16								37	0.0127				
17	*Nereis spp.*	9243.8337	2985.9936	13.3585		44.3198	-13.3585	7	24.1599		2833.0927	2833.0927	108.5812
17								8	0.3140				
17								9	0.0025				
17								15	0.0146				
17								17	5.3453				
17								22	1.3501				
17								23	2.2542				
17								24	0.9500				
17								27	0.1831				
17								28	0.1405				
17								29	0.2827				
17								30	1.3259				
17								31	12.1039				
17								32	4.2765				
17								33	4.4245				
17								34	0.1851				
17								35	0.0593				
17								36	0.3063	57.6783			
17								37	2833.0927				
18	*Pygospio elegans*	24.2585	0.6801	0.2560		0.0900	-0.2560	7	0.0675		0.1767	0.1767	0.4134
18								8	0.0007				
18								9	0.0000				
18								15	0.0000				
18								17	0.0140				
18								22	0.2044				
18								35	0.0593	0.3460			
18								37	0.1767				
19	*Scoloplos armiger*	24.8530	0.7594	18.2513		0.1083	-18.2513	7	0.0675		0.4707	0.4707	0.1805
19								8	0.0007				
19								9	0.0000				
19								15	0.0000				
19								17	0.0144				
19								23	1.6967				
19								29	0.3365				
19								31	16.1449				
19								35	0.0593				
19								36	0.0396	18.3596			
19								37	0.4707				
20	small polychaetes	38.3380	1.0554	0.0099		0.1743	-0.0099	7	0.1012		0.3206	0.3206	0.5605
20								8	0.0014				
20								9	0.0000				

App. 3 (continued): Energy flow table of the mud flat; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

20								15	0.0001				
20								17	0.0222				
20								35	0.0593	0.1842			
20								37	0.3206				
21	*Tharyx killariensis*	80.7336	2.1744		0.0867	0.4424	0.1734	7	0.2193		0.8930	0.9797	0.8390
21								8	0.0028				
21								9	0.0000				
21								15	0.0001				
21								17	0.0467	0.2690			
21								37	0.9797				
22	*Calidris alpina*	15.8491	2.4222		0.0327	0.0327		37	0.4910		0.4910	0.4910	1.8985
23	*Haematopus ostralegus*	79.0000	10.7214		0.3574	0.3574		37	2.1443		2.1443	2.1443	8.2198
24	*Tadorna tadorna*	95.9109	10.2984		0.2268	0.2268		37	2.3097		2.3097	2.3097	7.7618
25	*Somateria mollissima*	89.7155	12.1864		0.2430	0.2430		37	2.4298		2.4298	2.4298	9.5136
26	*Numenius arquata*	28.2003	2.0201		0.0518	0.0518		37	0.4144		0.4144	0.4144	1.5539
27	*Tringa nebularia*	4.0684	0.9222		0.0136	0.0136		37	0.1899		0.1899	0.1899	0.7188
28	*Larus fuscus*	18.4879	0.2809		0.0072	0.0072		37	0.0576		0.0576	0.0576	0.2161
29	*Pluvialis squatarola*	10.6250	1.1953		0.0332	0.0332		37	0.2324		0.2324	0.2324	0.9297
30	*Chroicocephalus ridibundus*	94.2338	6.5964		0.2199	0.2199		37	1.3193		1.3193	1.3193	5.0572
31	*Limosa lapponica*	187.1472	38.1226		0.6931	0.6931		37	7.6245		7.6245	7.6245	29.8049
32	*Tringa totanus*	81.4750	19.9040		0.2927	0.2927		37	4.0979		4.0979	4.0979	15.5134
33	*Recurvirostra avosetta*	39.8203	8.8489		0.4424	0.4424		37	1.7698		1.7698	1.7698	6.6367
34	*Larus agentatus*	39.3736	2.3133		0.0593	0.0593		37	0.4745		0.4745	0.4745	1.7795
35	*Anas platyrhynchos*	33.8491	1.1539		0.0192	0.0192		37	0.4231		0.4231	0.4231	0.7116
36	*Larus canus*	18.3960	0.9457		0.0326	0.0326		37	0.1957		0.1957	0.1957	0.7174
37	sediment POC	19000.0000			4216.6322		18524.7261	3	196.3920				
37								4	54.0992				
37								6	7.5598				
37								8	0.5262				
37								9	0.0663				
37								11	114.6487				
37								13	8.9709				
37								14	1.9419				
37								17	89.5798				
37								19	0.3417				
37								20	0.0602				
37								21	1.0872	475.2739			
38	Suspended POC	167.4370		167.4370	18.5693		18.5693	5	54.7938				
38								6	4.2335				
38								9	0.0310				
38								16	0.0077				
38								17	89.5798				
38								18	0.0952				
38								20	0.1267	148.8677			

App. 4: Energy flow table of the mussel bank; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

Comp #i	Compartment	Biomass	Consumption	Imports	Exports	Produktion	Production - Cosumtion	Comp #j	flow from #i to #j	Sum	Egestion	Sum of Excess P+E	Respiration
1	Phytoplankton	605.8309		254.7636		144.0538	-3303.2227	6	84.5862				110.7622
1				3303.2227				7	279.7413				
1								8	539.7334				
1								9	0.1482				
1								10	1841.9921				
1								11	322.4473				
1								16	4.8090				
1								26	93.5531				
1								29	6.1070				
1								31	0.1063				
1								33	274.0525	3447.2765			
2	Makrophyta	105400.2100		2887.6770	634.8507	1270.5779	1269.7015	15	0.7448			634.8507	1617.0991
2								39	0.0025				
2								45	0.1291	0.8764			
2							634.8507	47	634.8507				
3	Micrphytobenthos	408.6154		2933.1167		1915.5971	1470.3986	5	36.0661			1470.3986	1017.5203
3								9	0.0862				
3								15	1.3332				
3								17	6.6736				
3								18	373.1178				
3								19	1.1832				
3								22	3.5464				
3								29	12.2140				
3								32	0.1944				
3								33	10.7836	445.1985			
3								47	1470.3986				
4	Bacteria	625.0000	196.3920	114.9739		49.2410	-114.9739	5	36.0661		38.1500	38.1500	109.0010
4								9	0.0431				
4								13	1.3138				
4								15	0.2823				
4								19	0.1972				
4								21	65.7155				
4								22	15.9590				
4								23	14.1284				
4								25	2.2441				
4								29	6.1070				
4								32	0.8750				
4								33	21.1954				
4								34	0.0880	164.2149			
4								47	38.1500				
5	Meiofauna	500.0000	144.2644	86.3113		10.9590	-86.3113	5	18.0331		91.6069	91.6069	41.6985
5								12	60.3938				
5								13	1.7518				
5								24	0.1027				
5								29	6.1070				
5								30	10.8821	97.2704			
5								47	91.6069				
6	Anthozoa	6860.8783	84.5862		3.5714	15.9774	7.1428	12	4.2043		9.1476	12.7190	59.4612
6								14	4.6303	8.8346			
6								47	12.7190				
7	*Cerastoderma edule*	13056.2640	325.2806		18.3521	65.0544	36.7041	12	8.0008		239.8336	258.1857	20.3926
7								13	0.8118				
7								15	0.0240				
7								20	1.8523				
7								24	0.0761				
7								27	3.6068				
7								28	2.1880				
7								29	2.2639				
7								30	2.0171				
7								35	0.7242				
7								36	6.3593				
7								37	0.0917				
7								38	0.0055				
7								40	0.0166				
7								42	0.0439				
7								43	0.1749				
7								44	0.0503				
7								46	0.0432	28.3503			
7								47	258.1857				
8	*Crassostrea gigas*	42450.4660	627.5970			41.8969	41.8969	47	75.7410		33.8441	75.7410	551.8561
9	*Macoma balthica*	6.4670	0.3446	0.4342		0.0533	-0.4342	12	0.0040		0.2814	0.2814	0.0099
9								13	0.0004				
9								15	0.0000				

App. 4 (continued): Energy flow table of the mussel bank; biomass in $mgC.m^{-2}$; production (P), consumption, respiration, egestion (E), imports, exports and flows in $mgC.m^{-2}.d^{-1}$

9								20	0.0009				
9								24	0.0000				
9								27	0.0018				
9								28	0.0011				
9								29	0.0011				
9								30	0.0010				
9								35	0.2625				
9								37	0.0307				
9								38	0.0070				
9								39	0.0005				
9								40	0.0119				
9								41	0.0717				
9								42	0.0556				
9								43	0.0270				
9								45	0.0100	0.4875			
9								47	0.2814				
10	*Mytilus edulis*	292734.1965	2141.8512		49.6608	288.7267	99.3215	12	179.3861		265.1557	314.8165	1587.9688
10								35	0.2625				
10								36	9.6698				
10								43	0.0270				
10								44	0.0503				
10								46	0.0093	189.4051			
10								47	314.8165				
11	*Balanidae spp.*	24184.1543	322.4473		32.3786	80.6058	64.7571	12	14.8199		32.2447	64.6233	209.5968
11								36	1.0287	15.8486			
11								47	64.6233				
12	*Carcinus maenas*	12332.6003	301.9688		15.9842	52.1578	31.9685	12	7.5574		171.5287	187.5129	78.2823
12								13	0.7668				
12								15	0.0226				
12								20	1.7496				
12								24	0.0719				
12								27	3.4069				
12								28	2.0668				
12								29	2.1385				
12								30	1.9053				
12								37	0.1208				
12								38	0.0139				
12								39	0.0004				
12								40	0.0049				
12								41	0.0326				
12								42	0.1102				
12								43	0.1749				
12								44	0.0078				
12								45	0.0033				
12								46	0.0349	20.1893			
12								47	187.5129				
13	*Crangon spp.*	146.6240	8.7589		0.5886	1.6097	1.1773	12	0.0899		1.6097	2.1984	5.5394
13								13	0.0091				
13								15	0.0003				
13								20	0.0208				
13								24	0.0009				
13								27	0.0405				
13								28	0.0246				
13								29	0.0254				
13								30	0.0227				
13								37	0.0307				
13								38	0.0041				
13								40	0.0236				
13								41	0.0348				
13								42	0.0332				
13								45	0.0033				
13								46	0.0688	0.4325			
13								47	2.1984				
14	*Pycnoganum littorale*	90.4800	4.6303		0.7881	1.7207	1.5762	12	0.0554		0.4891	1.2772	2.4206
14								13	0.0056				
14								15	0.0002				
14								20	0.0128				
14								24	0.0005				
14								27	0.0250				
14								28	0.0152				
14								29	0.0157				
14								30	0.0140	0.1444			
14								47	1.2772				
15	small crustaceans	128.2461	3.4009	0.1149		0.5180	-0.1149	12	0.0786		0.6932	0.6932	2.1897
15								13	0.0080				

App. 4 (continued): Energy flow table of the mussel bank; biomass in $mgC.m^{-2}$; production (P), consumption, respiration, egestion (E), imports, exports and flows in $mgC.m^{-2}.d^{-1}$

15								15	0.0002				
15								20	0.0182				
15								24	0.0007				
15								27	0.0354				
15								28	0.0215				
15								29	0.0222				
15								30	0.0198				
15								38	0.0418				
15								39	0.0004				
15								40	0.0025				
15								42	0.3306				
15								44	0.0008				
15								45	0.0302				
15								46	0.0219	0.6329			
15								47	0.6932				
16	*Crepidula fornicata*	287.3801	5.5919	0.9471		0.2598	-0.9471	12	0.1761		3.5538	3.5538	1.7782
16								13	0.0179				
16								15	0.0005				
16								20	0.0408				
16								24	0.0017				
16								27	0.0794				
16								28	0.0482				
16								29	0.0498				
16								30	0.0444				
16								36	0.7481	1.2069			
16								47	3.5538				
17	*Lepidochitona cinerea*	283.4971	6.6736		0.4805	1.4136	0.9611	12	0.1737		3.5058	3.9864	1.7542
17								13	0.0176				
17								15	0.0005				
17								20	0.0402				
17								24	0.0017				
17								27	0.0783				
17								28	0.0475				
17								29	0.0492				
17								30	0.0438	0.4525			
17								47	3.9864				
18	*Littorina littorea*	18115.0278	373.1178		1.6287	37.0114	3.2574	12	11.1008		224.0171	225.6458	112.0893
18								13	1.1263				
18								15	0.0332				
18								20	2.5700				
18								24	0.1056				
18								27	5.0043				
18								28	3.0358				
18								29	3.1411				
18								30	2.7986				
18								36	4.8162				
18								39	0.0005				
18								44	0.0216	33.7540			
18								47	225.6458				
19	*Peringia ulvae*	29.6670	1.5775	5.2708		0.5348	-5.2708	12	0.0182		0.8642	0.8642	0.1786
19								13	0.0018				
19								15	0.0001				
19								20	0.0042				
19								24	0.0002				
19								27	0.0082				
19								28	0.0050				
19								29	0.0051				
19								30	0.0046				
19								36	5.4334				
19								38	0.0210				
19								39	0.0005				
19								40	0.0049				
19								42	0.2097				
19								44	0.0216				
19								45	0.0622				
19								46	0.0050	5.8056			
19								47	0.8642				
20	Nemertea	181.9750	9.9932		0.4431	1.1766	0.8861	12	0.1115		6.9103	7.3533	1.9064
20								13	0.0113				
20								15	0.0003				
20								20	0.0258				
20								24	0.0011				
20								27	0.0503				
20								28	0.0305				
20								29	0.0316				

App. 4 (continued): Energy flow table of the mussel bank; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

20								30	0.0281	0.2905			
20								47	7.3533				
21	Oligochaeta	3062.5088	131.4310		1.7500	8.3904	3.5000	12	1.8767		41.3063	43.0562	81.7343
21								13	0.1904				
21								15	0.0056				
21								20	0.4345				
21								24	0.0179				
21								27	0.8460				
21								28	0.5132				
21								29	0.5310				
21								30	0.4731				
21								45	0.0020	4.8905			
21								47	43.0562				
22	*Arenicola marina*	742.4000	35.4644		1.7219	5.3198	3.4439	12	0.4549		25.1950	26.9169	4.9497
22								13	0.0462				
22								15	0.0014				
22								20	0.1053				
22								24	0.0043				
22								27	0.2051				
22								28	0.1244				
22								29	0.1287				
22								30	0.1147				
22								35	0.3785				
22								37	0.2135				
22								39	0.0036				
22								40	0.0142				
22								41	0.0717				
22								46	0.0093	1.8759			
22								47	26.9169				
23	*Capitella capitata*	331.8567	28.2568		0.6116	1.7866	1.2232	12	0.2034		18.8142	19.4258	7.6560
23								13	0.0206				
23								15	0.0006				
23								20	0.0471				
23								24	0.0019				
23								27	0.0917				
23								28	0.0556				
23								29	0.0575				
23								30	0.0513				
23								39	0.0317				
23								45	0.0020	0.5634			
23								47	19.4258				
24	*Eteone spp.*	37.0620	0.5134		0.0598	0.1788	0.1197	12	0.0227		0.3100	0.3698	0.0246
24								13	0.0023				
24								15	0.0001				
24								20	0.0053				
24								24	0.0002				
24								27	0.0102				
24								28	0.0062				
24								29	0.0064				
24								30	0.0057	0.0592			
24								47	0.3698				
25	*Heteromastus filiformis*	52.2105	4.4882		0.0786	0.2861	0.1572	12	0.0320		3.6569	3.7355	0.5453
25								13	0.0032				
25								15	0.0001				
25								20	0.0074				
25								24	0.0003				
25								27	0.0144				
25								28	0.0087				
25								29	0.0091				
25								30	0.0081				
25								39	0.0317				
25								40	0.0025				
25								45	0.0020				
25								46	0.0093	0.1289			
25								47	3.7355				
26	*Lanice conchilego*	5502.6746	108.7827		9.8217	28.5439	19.6434	12	3.3720		25.1494	34.9711	55.0894
26								13	0.3421				
26								15	0.0101				
26								20	0.7807				
26								24	0.0321				
26								27	1.5201				
26								28	0.9222				
26								29	0.9542				
26								30	0.8501				
26								37	0.0307				

App. 4 (continued): Energy flow table of the mussel bank; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

26								40	0.0119				
26								41	0.0630				
26								45	0.0020				
26								46	0.0093	8.9005			
26								47	34.9711				
27	*Lepidonotus squamatus*	376.3040	19.4587		0.3131	1.2269	0.6262	12	0.2306		14.2897	14.6028	3.9422
27								13	0.0234				
27								15	0.0007				
27								20	0.0534				
27								24	0.0022				
27								27	0.1040				
27								28	0.0631				
27								29	0.0653				
27								30	0.0581	0.6007			
27								47	14.6028				
28	*Nephtys spp.*	198.4760	11.8045		0.5566	2.1884	1.1132	12	0.1216		7.5369	8.0935	2.0792
28								13	0.0123				
28								15	0.0004				
28								20	0.0282				
28								24	0.0012				
28								27	0.0548				
28								28	0.0333				
28								29	0.0344				
28								30	0.0307				
28								35	0.1488				
28								37	0.0307				
28								38	0.0084				
28								41	0.4694				
28								42	0.0663				
28								43	0.0234				
28								45	0.0020				
28								46	0.0093	1.0752			
28								47	8.0935				
29	*Nereis spp.*	1294.1540	61.0702		1.4282	6.2048	2.8564	12	0.7931		39.6638	41.0920	15.2016
29								13	0.0805				
29								15	0.0024				
29								20	0.1836				
29								24	0.0075				
29								27	0.3575				
29								28	0.2169				
29								29	0.2244				
29								30	0.1999				
29								35	0.2625				
29								38	0.0237				
29								39	0.0259				
29								40	0.0213				
29								41	0.5998				
29								42	0.2204				
29								43	0.0234				
29								44	0.0006				
29								45	0.0020				
29								46	0.1030	3.3484			
29								47	41.0920				
30	*Phyllodoce spp.*	601.3208	21.7641		0.3428	1.6475	0.6856	12	0.3685		2.3429	2.6857	17.7738
30								13	0.0374				
30								15	0.0011				
30								20	0.0853				
30								24	0.0035				
30								27	0.1661				
30								28	0.1008				
30								29	0.1043				
30								30	0.0929				
30								45	0.0020	0.9619			
30								47	2.6857				
31	*Pygospio elegans*	4.4080	0.1236		0.0037	0.0164	0.0073	12	0.0027		0.0321	0.0358	0.0751
31								13	0.0003				
31								15	0.0000				
31								20	0.0006				
31								24	0.0000				
31								27	0.0012				
31								28	0.0007				
31								29	0.0008				
31								30	0.0007				
31								45	0.0020	0.0091			
31								47	0.0358				

App. 4 (continued): Energy flow table of the mussel bank; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

32	*Scoloplos ormiger*	63.6357	1.9444	0.8463		0.2772	-0.8463	12	0.0390		1.2051	1.2051	0.4621
32								13	0.0040				
32								15	0.0001				
32								20	0.0090				
32								24	0.0004				
32								27	0.0176				
32								28	0.0107				
32								29	0.0110				
32								30	0.0098				
32								35	0.1488				
32								39	0.0317				
32								41	0.8301				
32								45	0.0020				
32								46	0.0093	1.1235			
32								47	1.2051				
33	small polychaetes	13507.1944	371.8488		19.9249	61.4123	39.8497	12	8.2771		112.9617	132.8866	197.4748
33								13	0.8398				
33								15	0.0248				
33								20	1.9163				
33								24	0.0788				
33								27	3.7313				
33								28	2.2636				
33								29	2.3421				
33								30	2.0867				
33								45	0.0020	21.5626			
33								47	132.8866				
34	*Tharyx killariensis*	6.5347	0.1760		0.0127	0.0358	0.0254	12	0.0040		0.0723	0.0850	0.0679
34								13	0.0004				
34								15	0.0000				
34								20	0.0009				
34								24	0.0000				
34								27	0.0018				
34								28	0.0011				
34								29	0.0011				
34								30	0.0010	0.0104			
34								47	0.0850				
35	*Haematopus ostralegus*	16.1212	2.1879		0.0729	0.0729		47	0.4376		0.4376	0.4376	1.6774
36	*Somateria mollissima*	206.5443	28.0556		0.5594	0.5594		47	5.5939		5.5939	5.5939	21.9023
37	*Numenius arquata*	7.6634	0.5489		0.0141	0.0141		47	0.1126		0.1126	0.1126	0.4223
38	*Tringa nebularia*	0.5542	0.1256		0.0018	0.0018		47	0.0259		0.0259	0.0259	0.0979
39	*Pluvialis squatarola*	1.1507	0.1294		0.0036	0.0036		47	0.0252		0.0252	0.0252	0.1007
40	*Chroicocephalus ridibundus*	1.6326	0.1143		0.0038	0.0038		47	0.0229		0.0229	0.0229	0.0876
41	*Limosa lapponica*	10.6682	2.1732		0.0395	0.0395		47	0.4346		0.4346	0.4346	1.6990
42	*Tringa totanus*	4.3794	1.0699		0.0157	0.0157		47	0.2203		0.2203	0.2203	0.8339
43	*Larus agentatus*	7.6718	0.4507		0.0116	0.0116		47	0.0925		0.0925	0.0925	0.3467
44	*Arenoria interpres*	1.1186	0.1530		0.0021	0.0021		47	0.0310		0.0310	0.0310	0.1199
45	*Anas platyrhynchos*	7.5753	0.2582		0.0043	0.0043		47	0.0947		0.0947	0.0947	0.1593
46	*Larus canus*	6.4640	0.3323		0.0115	0.0115		47	0.0688		0.0688	0.0688	0.2521
47	sediment POC	19000.0000			3348.7429		18617.9631	4	196.3920				
47								5	54.0992				
47								9	0.0431				
47								13	1.3138				
47								15	0.6258				
47								19	0.1972				
47								21	65.7155				
47								22	15.9590				
47								23	14.1284				
47								25	2.2441				
47								29	9.1605				
47								32	0.8750				
47								33	21.1954				
47								34	0.0880	382.0369			
48	Suspended POC	167.4370		167.4370 335.9538			-335.9538	7	45.5393				
48								8	87.8636				
48								9	0.0241				
48								10	299.8592				
48								15	0.2925				
48								16	0.7829				
48								26	15.2296				
48								29	9.1605				
48								31	0.0173				
48								33	44.6219	503.3908			

App. 5: Energy flow table of the sand flat; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

Comp #i	Compartment	Biomass	Consumption	Imports	Exports	Produktion	Production - Cosumtion	Comp #j	flow from #i to #j	Sum	Egestion	Sum of Excess P+E	Respiration
1	Phytoplankton	468.5092		197.0171		111.4016	-50.0899	6	84.4795				85.6561
1				50.0899				7	41.5132				
1								8	16.8500				
1								9	3.1197				
1								19	14.7180				
1								21	0.7110				
1								23	0.1002	161.4914			
2	Makrophyta	2855.1964		78.2246		34.4188	-64.0477	10	0.0318				43.8058
2				64.0477				27	0.9967				
2								30	0.1349				
2								33	83.3788				
2								35	9.5800				
2								37	0.0008				
2								40	4.3434	98.4665			
3	Microphytobenthos	296.0296		2124.9552	252.8537	1387.7927	505.7073	5	72.1322			252.8537	737.1630
3								7	24.1356				
3								10	0.0570				
3								11	26.2772				
3								12	698.5166				
3								16	23.0880				
3								19	29.4359				
3								22	8.4391				
3								23	0.0039	882.0854			
3								42	252.8537				
4	Bacteria	625.0000	196.3920	331.0720		49.2410	-331.0720	5	72.1322		38.1500	38.1500	109.0010
4								7	12.0678				
4								10	0.0121				
4								12	116.4194				
4								15	20.7340				
4								16	103.8959				
4								17	2.3251				
4								19	14.7180				
4								22	37.9758				
4								23	0.0077				
4								24	0.0250	380.3130			
4								42	38.1500				
5	Meiofauna	1000.0000	288.5289	41.7366		21.9180	-41.7366	5	36.0661		183.2139	183.2139	83.3969
5								18	0.1223				
5								19	14.7180				
5								20	12.7483	63.6546			
5								42	183.2139				
6	*Cerastoderma edule*	3942.8814	98.2320	25.1451		19.6459	-25.1451	10	0.0006		72.4277	72.4277	6.1584
6								14	1.0117				
6								18	0.0514				
6								19	3.0950				
6								20	1.3411				
6								26	17.0295				
6								27	1.0356				
6								28	2.0928				
6								29	0.1436				
6								31	13.0169				
6								32	0.4102				
6								36	1.1380				
6								38	3.6397				
6								39	0.2763				
6								41	0.5086	44.7910			
6								42	72.4277				
7	*Macoma balthica*	1811.7678	96.5422	27.3779		14.9296	-27.3779	10	0.0003		78.8302	78.8302	2.7824
7								14	0.4649				
7								18	0.0237				
7								19	1.4222				
7								20	0.6170				
7								26	6.5332				
7								27	3.0290				
7								28	1.3089				
7								29	0.1636				
7								30	0.2486				
7								31	6.2944				
7								32	0.3212				
7								34	18.9000				
7								36	1.2941				
7								37	0.0815				

App. 5 (continued): Energy flow table of the sand flat; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

7								38	1.2425				
7								40	0.3625	42.3075			
7								42	78.8302				
8	*Mya arenaria*	1792.6640	19.5930			3.9177	0.9108	10	0.0003		6.5602	7.4710	9.1152
8								14	0.4601				
8								18	0.0234				
8								19	1.4072				
8								20	0.6094				
8								32	0.1215				
8								40	0.1714				
8								41	0.2136	3.0068			
8								42	7.4710				
9	*Mytilus edulis*	495.7840	3.6275	9.7391		0.4890	-9.7391	26	6.5332		0.4491	0.4491	2.6894
9								27	0.8799				
9								31	1.0826				
9								38	1.2425				
9								39	0.2763				
9								41	0.2136	10.2281			
9								42	0.4491				
10	small crustaceans	5.4810	0.1453	10.2409		0.0221	-10.2409	10	0.0000		0.0296	0.0296	0.0936
10								14	0.0010				
10								18	0.0001				
10								19	0.0043				
10								20	0.0025				
10								25	0.1710				
10								27	2.6864				
10								29	0.6251				
10								30	0.2415				
10								32	0.1433				
10								36	4.9407				
10								37	0.0726				
10								39	0.0111				
10								40	1.0400				
10								41	0.3235	10.2630			
10								42	0.0296				
11	*Littorina littorea*	1275.7680	26.2772	2.8096		2.6066	-2.8096	10	0.0002		15.7766	15.7766	7.8940
11								14	0.3273				
11								18	0.0166				
11								19	1.0014				
11								20	0.4334				
11								27	3.1848				
11								30	0.2486				
11								37	0.0815				
11								39	0.1224	5.4162			
11								42	15.7766				
12	*Peringia ulvae*	17514.9459	931.3554		110.4587	315.7489	220.9173	10	0.0026		510.1915	620.6501	105.4151
12								13	43.9202				
12								14	4.4963				
12								18	0.2284				
12								19	13.7486				
12								20	5.9535				
12								25	0.1196				
12								27	14.9583				
12								29	0.3485				
12								30	0.2486				
12								31	4.7838				
12								32	0.1888				
12								36	3.3373				
12								37	0.0815				
12								39	0.1224				
12								40	2.1172				
12								41	0.1760	94.8316			
12								42	620.6501				
13	*Retusa obtusa*	1124.6200	43.9202		0.5063	4.3927	1.0125	10	0.0002		32.7590	33.2652	6.7686
13								14	0.2888				
13								18	0.0147				
13								19	0.8828				
13								20	0.3824				
13								27	1.6897				
13								32	0.1215	3.3801			
13								42	33.2652				
14	Nemertea	175.2857	9.6259		0.4448	1.1334	0.8896	10	0.0000		6.6563	7.1010	1.8363
14								14	0.0452				
14								18	0.0023				

App. 5 (continued): Energy flow table of the sand flat; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

14								19	0.1376				
14								20	0.0586	0.2438			
14								42	7.1010				
15	Oligochaeta	966.2581	41.4680		0.6028	2.6473	1.2056	10	0.0001		13.0326	13.6354	25.7881
15								14	0.2483				
15								18	0.0126				
15								19	0.7585				
15								20	0.3289				
15								40	0.0932	1.4417			
15								42	13.6354				
16	*Arenicola marina*	4833.1559	230.8797	4.9249		34.6327	-4.9249	10	0.0007		164.0239	164.0239	32.2232
16								14	1.2408				
16								18	0.0630				
16								19	3.7938				
16								20	1.6420				
16								26	9.1697				
16								28	3.6606				
16								30	0.4190				
16								32	0.3646				
16								34	18.9000				
16								37	0.0897				
16								41	0.2136	39.5576			
16								42	164.0239				
17	*Capitella capitata*	54.6134	4.6502	1.8351		0.2940	-1.8351	10	0.0000		3.0962	3.0962	1.2599
17								14	0.0144				
17								18	0.0007				
17								19	0.0429				
17								20	0.0178				
17								30	1.9600				
17								40	0.0932	2.1291			
17								42	3.0962				
18	*Eteone spp.*	44.1303	0.6113		0.0754	0.2129	0.1509	10	0.0000		0.3691	0.4445	0.0293
18								14	0.0116				
18								18	0.0006				
18								19	0.0346				
18								20	0.0153	0.0620			
18								42	0.4445				
19	*Nereis spp.*	455.6287	147.1797	80.4982		2.1845	-80.4982	10	0.0001		139.6432	139.6432	5.3520
19								14	0.1174				
19								18	0.0059				
19								19	0.3577				
19								20	0.1555				
19								25	0.4978				
19								26	6.5332				
19								27	2.6864				
19								29	0.3852				
19								30	1.6404				
19								32	0.4992				
19								34	63.9265				
19								36	3.4792				
19								37	0.0815				
19								38	1.1840				
19								39	0.0102				
19								40	0.0932				
19								41	1.0291	82.6828			
19								42	139.6432				
20	*Phyllodace spp.*	704.4448	25.4966		0.4270	1.9300	0.8539	10	0.0001		2.7447	3.1716	20.8220
20								14	0.1810				
20								18	0.0092				
20								19	0.5530				
20								20	0.2397				
20								40	0.0932	1.0761			
20								42	3.1716				
21	*Pygospio elegans*	29.4877	0.8267	0.1082		0.1094	-0.1082	10	0.0000		0.2147	0.2147	0.5026
21								14	0.0077				
21								18	0.0004				
21								19	0.0231				
21								20	0.0102				
21								25	0.0830				
21								40	0.0932	0.2176			
21								42	0.2147				
22	*Scoloplos armiger*	2761.9365	84.3906	81.8713		12.0314	-81.8713	10	0.0004		52.3040	52.3040	20.0552
22								14	0.7094				
22								18	0.0360				

App. 5 (continued): Energy flow table of the sand flat; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

22								19	2.1680				
22								20	0.9383				
22								26	3.9465				
22								30	1.9600				
22								34	83.5677				
22								37	0.2696				
22								40	0.0932				
22								41	0.2136	93.9027			
22								42	52.3040				
23	small polychaetes	4.9300	0.1357	0.0782		0.0224	-0.0782	10	0.0000		0.0412	0.0412	0.0721
23								14	0.0010				
23								18	0.0001				
23								19	0.0039				
23								20	0.0025				
23								40	0.0932	0.1006			
23								42	0.0412				
24	*Tharyx killariensis*	1.8560	0.0500		0.0038	0.0102	0.0076	10	0.0000		0.0205	0.0243	0.0193
24								14	0.0005				
24								18	0.0000				
24								19	0.0015				
24								20	0.0006	0.0026			
24								42	0.0243				
25	*Calidris alpina*	5.7020	0.8714		0.0118	0.0118		42	0.1766		0.1766	0.1766	0.6830
26	*Haematopus ostralegus*	366.5448	49.7454		1.6582	1.6582		42	9.9491		9.9491	9.9491	38.1381
27	*Tadorna tadarna*	290.0762	31.1469		0.6861	0.6861		42	6.9857		6.9857	6.9857	23.4751
28	*Numenius arquata*	98.5890	7.0622		0.1811	0.1811		42	1.4487		1.4487	1.4487	5.4325
29	*Tringa nebulario*	7.3504	1.6661		0.0245	0.0245		42	0.3430		0.3430	0.3430	1.2986
30	*Pluvialis squatarola*	63.1243	7.1015		0.1973	0.1973		42	1.3808		1.3808	1.3808	5.5234
31	*Calidris canutus*	99.9702	25.1777		0.3703	0.3703		42	5.1836		5.1836	5.1836	19.6238
32	*Chroicocephalus ridibundus*	31.0072	2.1705		0.0724	0.0724		42	0.4341		0.4341	0.4341	1.6641
33	*Anas penelope*	2883.2410	83.3788		1.6389	1.6389		42	30.1147		30.1147	30.1147	51.6252
34	*Limasa lapponica*	909.6266	185.2943		3.3690	3.3690		42	37.0589		37.0589	37.0589	144.8665
35	*Branta bernicla*	239.5005	9.5800		0.2395	0.2395		42	3.3530		3.3530	3.3530	5.9875
36	*Tringa totanus*	58.0825	14.1893		0.2087	0.2087		42	2.9213		2.9213	2.9213	11.0593
37	*Charadrius hiaticula*	5.3271	0.8141		0.0110	0.0110		42	0.1650		0.1650	0.1650	0.6381
38	*Larus agentatus*	124.3948	7.3086		0.1874	0.1874		42	1.4992		1.4992	1.4992	5.6220
39	*Arenaria interpres*	5.9867	0.8186		0.0111	0.0111		42	0.1659		0.1659	0.1659	0.6416
40	*Anas platyrhynchos*	254.8134	8.6868		0.1448	0.1448		42	3.1852		3.1852	3.1852	5.3569
41	*Larus canus*	56.2524	2.8919		0.0997	0.0997		42	0.5983		0.5983	0.5983	2.1938
42	sediment POC	19000.0000			1171.6358		18379.8553	4	196.3920				
42								5	108.1983				
42								7	12.0678				
42								10	0.0267				
42								12	116.4194				
42								15	20.7340				
42								16	103.8959				
42								17	2.3251				
42								19	22.0769				
42								22	37.9758				
42								23	0.0077				
42								24	0.0250	620.1447			
43	Suspended POC	167.4370		167.4370	121.4542		121.4542	6	13.7525				
43								7	6.7580				
43								8	2.7430				
43								9	0.5079				
43								10	0.0125				
43								19	22.0769				
43								21	0.1157				
43								23	0.0163	45.9828			

App. 6: Energy flow table of the seagrass meadow; biomass in $mgC.m^{-2}$; production (P), consumption, respiration, egestion (E), imports, exports and flows in $mgC.m^{-2}.d^{-1}$

Comp #i	Compartment	Biomass	Consumption	Imports	Exports	Produktion	Production - Cosumtion	Comp #j	flow from #i to #j	Sum	Egestion	Sum of Excess P+E	Respiration
1	Phytoplankton	468.5092		197.0171	8.6454	111.4016	8.6454	6	72.0641				85.6561
1								7	16.7290				
1								8	0.1059				
1								19	12.3641				
1								20	1.3847				
1								22	0.1084	102.7562			
1								45	0.0000				
2	Makrophyta	3819.1381		237.9315		46.0389	-133.2975	10	4.4600				58.5950
2								26	0.3257				
2								30	0.2260				
2								33	103.8994				
2								36	57.1792				
2								39	7.3088				
2								41	5.9374	179.3365			
2								44	0.0000				
3	Microphytobenthos	217.5264		1561.4447	199.4691	1019.7682	398.9382	5	72.1322			199.4691	541.6769
3								7	9.7262				
3								10	7.9832				
3								11	20.4533				
3								12	475.1609				
3								15	9.7128				
3								19	24.7282				
3								21	0.9289				
3								22	0.0043	620.8300			
3								44	199.4691				
4	Bacteria	625.0000	196.3920	171.8995		49.2410	-171.8995	5	72.1322		38.1500	38.1500	109.0010
4								7	4.8631				
4								10	1.6903				
4								12	79.1935				
4								14	1.3244				
4								15	43.7077				
4								16	0.4382				
4								19	12.3641				
4								21	4.1800				
4								22	0.0084				
4								23	1.2386	221.1405			
4								44	38.1500				
5	Meiofauna	1000.0000	288.5289	27.1466		21.9180	-27.1466	5	36.0661		183.2139	183.2139	83.3969
5								9	0.4557				
5								17	0.1787				
5								19	12.3641	49.0646			
5								44	183.2139				
6	*Cerostoderma edule*	3363.4200	83.7954	124.2403		16.7586	-124.2403	9	0.2930		61.7835	61.7835	5.2533
6								10	0.1242				
6								17	0.1150				
6								18	0.0549				
6								19	3.9780				
6								25	43.6728				
6								26	0.3588				
6								27	0.4660				
6								28	4.9999				
6								29	0.3495				
6								31	78.7249				
6								32	2.1458				
6								35	0.4544				
6								37	1.5525				
6								38	3.2043				
6								40	0.2912				
6								42	0.2136	140.9989			
6								44	61.7835				
7	*Macoma balthica*	730.1069	38.9046	63.8837		6.0163	-63.8837	9	0.0636		31.7670	31.7670	1.1213
7								10	0.0265				
7								17	0.0249				
7								18	0.0119				
7								19	0.8635				
7								25	17.4194				
7								26	1.0102				
7								27	0.5789				
7								28	2.0634				
7								29	0.4356				
7								30	0.3715				
7								31	39.1649				
7								32	1.6706				
7								34	2.5521				
7								35	0.1875				

App. 6 (continued): Energy flow table of the seagrass meadow; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

7								37	1.9284				
7								38	0.5768				
7								39	0.4390				
7								41	0.5115	69.9001			
7								44	31.7670				
8	*Balanidae spp.*	7.9460	0.1059		0.0129	0.0265	0.0258	9	0.0007	0.0007	0.0106	0.0235	0.0689
8								44	0.0235				
9	*Carcinus maenas*	93.0610	2.2786	19.1343		0.3936	-19.1343	9	0.0082		1.2943	1.2943	0.5907
9								10	0.0041				
9								17	0.0032				
9								18	0.0015				
9								19	0.1101				
9								26	0.1450				
9								27	1.1020				
9								28	6.4549				
9								29	0.8302				
9								30	0.3596				
9								32	0.9635				
9								34	1.4178				
9								35	0.5866				
9								37	3.6713				
9								38	3.2043				
9								39	0.3292				
9								40	0.0803				
9								41	0.0745				
9								42	0.1815	19.5279			
9								44	1.2943				
10	small crustaceans	767.9650	20.3653	33.1774		3.1018	-33.1774	9	0.0670		4.1512	4.1512	13.1122
10								10	0.0285				
10								17	0.0263				
10								18	0.0125				
10								19	0.9083				
10								24	14.7884				
10								26	0.8982				
10								27	3.2152				
10								29	2.4230				
10								30	0.3596				
10								32	0.7201				
10								37	10.7113				
10								39	0.4609				
10								40	0.0454				
10								41	1.4377				
10								42	0.1314				
10								43	0.0455	36.2792			
10								44	4.1512				
11	*Littorina littorea*	993.0180	20.4533	0.9001		2.0289	-0.9001	9	0.0866		12.2800	12.2800	6.1444
11								10	0.0367				
11								17	0.0339				
11								18	0.0162				
11								19	1.1745				
11								26	1.0611				
11								30	0.3715				
11								40	0.1486	2.9290			
11								44	12.2800				
12	*Peringia ulvae*	11914.4161	633.5479		64.9061	214.7859	129.8122	9	1.0384		347.0541	411.9602	71.7079
12								10	0.4419				
12								13	1.1303				
12								17	0.4072				
12								18	0.1946				
12								19	14.0914				
12								24	9.5196				
12								26	4.9085				
12								27	2.0560				
12								29	1.2320				
12								30	0.3715				
12								31	30.2750				
12								32	0.9635				
12								37	6.8495				
12								39	8.3403				
12								40	0.1486				
12								41	2.9102				
12								42	0.0658				
12								43	0.0293	84.9737			
12								44	411.9602				
13	*Retusa obtusa*	28.9420	1.1303	1.1039		0.1130	-1.1039	9	0.0025		0.8430	0.8430	0.1742

App. 6 (continued): Energy flow table of the seagrass meadow; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

13								10	0.0020				
13								17	0.0010				
13								18	0.0005				
13								19	0.0342				
13								26	0.5725				
13								32	0.6042	1.2170			
13								44	0.8430				
14	*Oligochaeta*	61.7227	2.6489	0.7822		0.1691	-0.7822	9	0.0055		0.8325	0.8325	1.6473
14								10	0.0020				
14								17	0.0021				
14								18	0.0010				
14								19	0.0730				
14								39	0.7243				
14								41	0.1434	0.9513			
14								44	0.8325				
15	*Arenicola marina*	2033.2480	97.1282	29.2593		14.5695	-29.2593	9	0.1773		69.0028	69.0028	13.5559
15								10	0.0754				
15								17	0.0695				
15								18	0.0332				
15								19	2.4048				
15								25	24.0138				
15								28	10.8728				
15								30	0.6570				
15								32	1.9024				
15								34	2.5521				
15								35	0.9881				
15								42	0.0825	43.8288			
15								44	69.0028				
16	*Capitella capitata*	10.2924	0.8764	4.0649		0.0554	-4.0649	9	0.0009		0.5835	0.5835	0.2374
16								10	0.0004				
16								17	0.0004				
16								18	0.0002				
16								19	0.0122				
16								30	3.2387				
16								39	0.7243				
16								41	0.1434	4.1203			
16								44	0.5835				
17	*Eteone spp.*	64.4880	0.8933		0.1119	0.3111	0.2238	9	0.0057		0.5393	0.6512	0.0428
17								10	0.0020				
17								17	0.0022				
17								18	0.0011				
17								19	0.0763	0.0873			
17								44	0.6512				
18	*Nephtys spp.*	5.7420	0.3415	42.8708		0.0633	-42.8708	9	0.0005		0.2180	0.2180	0.0602
18								10	0.0002				
18								17	0.0002				
18								18	0.0001				
18								19	0.0068				
18								24	10.6805				
18								25	10.9493				
18								27	0.6814				
18								28	2.0634				
18								29	0.5145				
18								34	14.0837				
18								35	0.1875				
18								37	2.2702				
18								38	0.5127				
18								39	0.7243				
18								41	0.1434				
18								42	0.0825				
18								43	0.0329	42.9341			
18								44	0.2180				
19	*Nereis spp.*	382.7594	123.6410	101.2256		1.8351	-101.2256	9	0.0333		117.3099	117.3099	4.4960
19								10	0.0143				
19								17	0.0130				
19								18	0.0062				
19								19	0.4527				
19								24	48.2766				
19								25	17.4194				
19								26	0.8982				
19								27	2.1586				
19								29	1.3899				
19								30	2.7033				
19								32	2.6211				

App. 6 (continued): Energy flow table of the seagrass meadow; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

19								34	17.8646				
19								37	7.1913				
19								38	0.5127				
19								39	0.7243				
19								40	0.0446				
19								41	0.1434				
19								42	0.4448				
19								43	0.1486	103.0608			
19								44	117.3099				
20	*Pygospio elegans*	57.4281	1.6101	6.8296		0.2131	-6.8296	9	0.0062		0.4182	0.4182	0.9788
20								10	0.0448				
20								17	0.0001				
20								18	0.0008				
20								19	0.0679				
20								24	6.0368				
20								39	0.7243				
20								41	0.1434				
20								43	0.0186	7.0428			
20								44	0.4182				
21	*Scoloplos armiger*	304.0052	9.2888	38.7715		1.3243	-38.7715	9	0.0264		5.7571	5.7571	2.2075
21								10	0.0122				
21								17	0.0104				
21								18	0.0050				
21								19	0.3596				
21								25	10.9493				
21								30	3.2387				
21								34	24.5441				
21								39	0.7243				
21								41	0.1434				
21								42	0.0825	40.0958			
21								44	5.7571				
22	small polychaetes	5.3360	0.1469	0.8506		0.0243	-0.8506	9	0.0005		0.0446	0.0446	0.0780
22								10	0.0002				
22								17	0.0002				
22								18	0.0001				
22								19	0.0063				
22								39	0.7243				
22								41	0.1434	0.8749			
22								44	0.0446				
23	*Tharyx killoriensis*	91.9783	2.4772		0.1893	0.5040	0.3785	9	0.0080		1.0174	1.2067	0.9559
23								10	0.0041				
23								17	0.0031				
23								18	0.0015				
23								19	0.1088	0.1255			
23								44	1.2067				
24	*Calidris alpina*	584.3368	89.3019		1.2068	1.2068		44	18.1017		18.1017	18.1017	69.9934
25	*Haematopus ostralegus*	916.8087	124.4240		4.1475	4.1475		44	24.8848		24.8848	24.8848	95.3918
26	*Tadorna tadorna*	94.7927	10.1784		0.2242	0.2242		44	2.2828		2.2828	2.2828	7.6713
27	*Tringa erythropus*	41.9905	10.2581		0.1509	0.1509		44	2.1120		2.1120	2.1120	7.9953
28	*Numenius arquata*	369.3063	26.4544		0.6783	0.6783		44	5.4265		5.4265	5.4265	20.3495
29	*Tringa nebularia*	31.6533	7.1747		0.1055	0.1055		44	1.4772		1.4772	1.4772	5.5921
30	*Pluvialis squatarola*	105.7521	11.8971		0.3305	0.3305		44	2.3133		2.3133	2.3133	9.2533
31	*Calidris conutus*	588.3014	148.1648		2.1789	2.1789		44	30.5045		30.5045	30.5045	115.4814
32	*Chroicocephalus ridibundus*	165.5897	11.5913		0.3864	0.3864		44	2.3183		2.3183	2.3183	8.8866
33	*Anas penelope*	3592.8443	103.8994		2.0422	2.0422		44	37.5263		37.5263	37.5263	64.3308
34	*Limosa lapponica*	309.3431	63.0143		1.1457	1.1457		44	12.6029		12.6029	12.6029	49.2658
35	*Numenius phaeopus*	33.5623	2.4042		0.0616	0.0616		44	0.4932		0.4932	0.4932	1.8494
36	*Branta bernicla*	1429.4796	57.1792		1.4295	1.4295		44	20.0127		20.0127	20.0127	35.7370
37	*Tringa totanus*	139.8895	34.1745		0.5026	0.5026		44	7.0359		7.0359	7.0359	26.6360
38	*Larus agentatus*	136.3464	8.0108		0.2054	0.2054		44	1.6432		1.6432	1.6432	6.1621
39	*Anas acuta*	223.7856	21.9482		0.6455	0.6455		44	7.7464		7.7464	7.7464	13.5562
40	*Arenaria interpres*	5.5486	0.7587		0.0103	0.0103		44	0.1538		0.1538	0.1538	0.5947
41	*Anas platyrhynchos*	348.3276	11.8748		0.1979	0.1979		44	4.3541		4.3541	4.3541	7.3228
42	*Larus canus*	24.9899	1.2847		0.0443	0.0443		44	0.2658		0.2658	0.2658	0.9746
43	*Limicola falcinellus*	1.7982	0.2748		0.0037	0.0037		44	0.0557		0.0557	0.0557	0.2154
44	sediment POC	19000.0000			860.4339		18538.1624	4	196.3920				
44								5	108.1983				
44								7	4.8631				
44								10	3.7472				
44								12	79.1935				
44								14	1.3244				
44								15	43.7077				

App. 6 (continued): Energy flow table of the seagrass meadow; biomass in $mgC.m^{-2}$; production (P), consumption, respiration, egestion (E), imports, exports and flows in $mgC.m^{-2}.d^{-1}$

44								16	0.4382				
44								19	18.5462				
44								21	4.1800				
44								22	0.0084				
44								23	1.2386	461.8376			
45	Suspended POC	167.4370		167.4370	132.4417		132.4417	6	11.7314				
45								7	2.7233				
45								10	1.7514				
45								19	18.5462				
45								20	0.2254				
45								22	0.0176	34.9953			

App. 7: Energy flow table of the entire project area; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

Comp #i	Compartment	Biomass	Consumption	Imports	Exports	Produktion	Production - Cosumtion	Comp #j	flow from #i to #j	Sum	Egestion	Sum of Excess P+E	Respiration
1	Phytoplankton	501.5511		354.0063		119.2583	-143.0510	6	0.2115				91.6971
1								7	160.4194				
1								8	1.3336				
1								9	36.8675				
1								10	0.0192				
1								11	37.7886				
1								12	10.5283				
1								13	6.5139				
1								14	0.8199				
1								19	0.0119				
1								30	0.2726				
1								33	5.8265				
1								35	0.7479				
1								37	0.9484	262.3092			
2	Macrophyta	2560.3074		124.5659		30.8640	-54.4205	18	0.7172				39.2814
2								39	0.9516				
2								40	65.7728				
2								41	3.5486				
2								43	13.4476				
2								46	0.0005				
2								57	0.1161				
2								60	0.7300	85.2845			
3	Microphytobenthos	352.7053		2531.7848	468.9376	1653.4898	937.8752	5	68.6843			468.9376	878.2950
3								10	0.0112				
3								11	21.9701				
3								18	1.2838				
3								20	0.0167				
3								21	21.8270				
3								22	574.5360				
3								26	15.9304				
3								33	5.8265				
3								36	5.4913				
3								37	0.0373	715.6146			
3								64	468.9376				
4	Bacteria	625.0000	196.3920	246.6342		49.2410	-246.6342	5	68.6843		38.1500	38.1500	109.0010
4								10	0.0056				
4								11	10.9851				
4								16	1.4852				
4								18	0.2718				
4								22	95.7560				
4								25	14.2045				
4								26	71.6870				
4								27	1.8928				
4								29	0.0056				
4								33	5.8265				
4								36	24.7108				
4								37	0.0732				
4								38	0.2867	295.8752			
4								64	38.1500				
5	Meiofauna	952.2000	274.7372	32.9117		20.8704	-32.9117	5	34.3421		174.4563	174.4563	79.4106
5								15	3.3932				
5								16	1.9803				
5								28	0.1094				
5								33	5.8265				
5								34	8.1304	53.7820			
5								64	174.4563				
6	Anthozoa	17.1522	0.2115		0.0110	0.0399	0.0220	15	0.0064		0.0229	0.0339	0.1487
6								17	0.0116	0.0179			
6								64	0.0339				
7	*Cerastoderma edule*	7575.2817	188.7287	5.4411		37.7447	-5.4411	15	2.8121		139.1522	139.1522	11.8318
7								42	0.2015				
7								45	18.1298				
7								47	0.5087				
7								48	15.7006				
7								49	2.2767				
7								50	0.2726				
7								51	0.0106				
7								55	1.3724				
7								56	0.0523				
7								59	0.3041				
7								60	0.7300				
7								61	0.0548				

App. 7 (continued): Energy flow table of the entire project area; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

7								62	0.0908				
7								63	0.6690	43.1858			
7								64	139.1522				
8	*Crassostrea gigas*	106.1262	1.5690		0.0524	0.1047	0.1047	64	0.1370		0.0846	0.1370	1.3796
9	*Ensis directus*	1520.9768	43.3735		1.4089	9.9120	2.8178	48	5.2170		2.1294	3.5383	31.3321
9								49	1.7091				
9								51	0.0212				
9								52	0.0021				
9								59	0.1448	7.0942			
9								64	3.5383				
10	*Fabulina fabula*	0.8395	0.0447		0.0033	0.0069	0.0066	15	0.0003	0.0003	0.0365	0.0398	0.0013
10								64	0.0398				
11	*Macoma balthica*	1649.2166	87.8805	9.7486		13.5901	-9.7486	15	0.6122		71.7576	71.7576	2.5328
11								39	0.0343				
11								41	0.2697				
11								45	8.7668				
11								46	0.0163				
11								47	0.3628				
11								48	5.2170				
11								49	0.1122				
11								54	4.2444				
11								55	0.4602				
11								56	0.0175				
11								57	0.0244				
11								60	2.1673				
11								61	0.0695				
11								62	0.1156				
11								63	0.8484	23.3387			
11								64	71.7576				
12	*Mya arenaria*	1133.2797	12.3862		0.9129	2.4767	1.8258	15	0.4207		4.1472	5.0601	5.7624
12								39	0.0257				
12								41	0.1136				
12								47	0.0356				
12								50	0.0554	0.6509			
12								64	5.0601				
13	*Mytilus edulis*	1047.3861	7.6634	7.5512		1.0330	-7.5512	15	0.3888		0.9487	0.9487	5.6817
13								42	0.2015				
13								45	1.5079				
13								48	5.2170				
13								49	0.1122				
13								50	0.0554				
13								51	0.0106				
13								59	0.4750				
13								60	0.6160	8.5843			
13								64	0.9487				
14	*Balanidae spp.*	61.4955	0.8199		0.0766	0.2050	0.1532	15	0.0228		0.0820	0.1586	0.5330
14								59	0.0290	0.0518			
14								64	0.1586				
15	*Carcinus maenas*	692.8991	16.9659	6.3377		2.9305	-6.3377	15	0.2572		9.6372	9.6372	4.3982
15								39	0.0200				
15								41	0.0852				
15								42	0.0312				
15								46	0.0107				
15								47	0.1458				
15								49	2.2767				
15								50	0.2193				
15								54	1.9293				
15								55	1.8243				
15								56	0.0695				
15								57	0.0183				
15								58	0.0824				
15								60	0.2510				
15								61	0.1376				
15								62	0.2291				
15								63	1.6806	9.2682			
15								64	9.6372				
16	*Crangon spp.*	165.7532	9.9016	3.0078		1.8198	-3.0078	15	0.0615		1.8198	1.8198	6.2621
16								16	0.0352				
16								18	0.0009				
16								24	0.0430				
16								28	0.0031				
16								31	0.0003				
16								32	0.0535				
16								33	0.1656				
16								34	0.0578				

App. 7 (continued): Energy flow table of the entire project area; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

16								41	0.0852				
16								47	0.7257				
16								50	0.4365				
16								54	2.0579				
16								55	0.4602				
16								56	0.0175				
16								58	0.0082				
16								61	0.0414				
16								62	0.0681				
16								63	0.5058	4.8276			
16								64	1.8198				
17	*Pycnogonum litorale*	0.2262	0.0116		0.0021	0.0043	0.0042	15	0.0001	0.0001	0.0012	0.0033	0.0061
17								64	0.0033				
18	small crustaceans	123.4976	3.2750	10.8816		0.4988	-10.8816	15	0.0458		0.6676	0.6676	2.1086
18								16	0.0262				
18								18	0.0007				
18								24	0.0321				
18								28	0.0023				
18								31	0.0003				
18								32	0.0399				
18								33	0.1234				
18								34	0.0430				
18								39	0.0372				
18								41	0.8233				
18								42	0.0031				
18								44	1.8722				
18								46	0.0107				
18								47	0.0711				
18								50	0.1363				
18								53	0.0054				
18								57	0.0183				
18								58	0.0082				
18								60	1.9392				
18								61	0.4127				
18								62	0.6874				
18								63	5.0417	11.3804			
18								64	0.6676				
19	*Crepidula fornicata*	0.7185	0.0140	0.0141		0.0006	-0.0141	15	0.0003		0.0089	0.0089	0.0044
19								59	0.0145	0.0147			
19								64	0.0089				
20	*Lepidochitona cinerea*	0.7088	0.0167		0.0016	0.0035	0.0033	15	0.0003	0.0003	0.0088	0.0104	0.0044
20								64	0.0104				
21	*Littorina littorea*	1059.7078	21.8270	0.8840		2.1651	-0.8840	15	0.3934		13.1047	13.1047	6.5571
21								42	0.0864				
21								46	0.0163				
21								57	0.0244				
21								59	0.2245				
21								60	2.3042	3.0492			
21								64	13.1047				
22	*Peringia ulvae*	14406.1973	766.0481		84.5517	259.7062	169.1034	15	5.3478		419.6370	504.1887	86.7049
22								16	3.0579				
22								18	0.0769				
22								23	27.8416				
22								24	3.7410				
22								28	0.2703				
22								31	0.0300				
22								32	4.6530				
22								33	14.3953				
22								34	5.0218				
22								39	1.0631				
22								41	1.7033				
22								42	0.0864				
22								44	1.1407				
22								45	6.6628				
22								46	0.0163				
22								47	0.1458				
22								50	0.0277				
22								53	0.0033				
22								57	0.0244				
22								58	0.3048				
22								59	0.2563				
22								60	10.9277				
22								61	0.2618				
22								62	0.3447				

App. 7 (continued): Energy flow table of the entire project area; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

22								63	3.1980	90.6029			
22								64	504.1887				
23	*Retusa obtusa*	712.9123	27.8416	0.2710		2.7846	-0.2710	15	0.2646		20.7664	20.7664	4.2907
23								16	0.1513				
23								18	0.0038				
23								24	0.1851				
23								28	0.0134				
23								31	0.0015				
23								32	0.2303				
23								33	0.7124				
23								34	0.2485				
23								47	0.0356				
23								60	1.2091	3.0556			
23								64	20.7664				
24	Nemertea	110.2917	6.0567		0.2165	0.7131	0.4330	15	0.0409		4.1882	4.4047	1.1554
24								16	0.0234				
24								18	0.0006				
24								24	0.0286				
24								28	0.0021				
24								31	0.0002				
24								32	0.0356				
24								33	0.1102				
24								34	0.0384	0.2802			
24								64	4.4047				
25	Oligochaeta	661.9640	28.4089		0.0014	1.8136	0.0027	15	0.2457		8.9284	8.9298	17.6669
25								16	0.1405				
25								18	0.0035				
25								24	0.1719				
25								28	0.0124				
25								31	0.0014				
25								32	0.2138				
25								33	0.6615				
25								34	0.2308				
25								39	0.0714				
25								41	0.0497				
25								58	0.0082	1.8109			
25								64	8.9298				
26	*Arenicola marina*	3334.8226	159.3044	0.6699		23.8961	-0.6699	15	1.2379		113.1746	113.1746	22.2336
26								16	0.7079				
26								18	0.0178				
26								24	0.8660				
26								28	0.0626				
26								31	0.0070				
26								32	1.0771				
26								33	3.3323				
26								34	1.1625				
26								46	0.0214				
26								47	0.4340				
26								48	7.8503				
26								50	0.0554				
26								54	4.2444				
26								55	3.1967				
26								56	0.1218				
26								57	0.1711	24.5660			
26								64	113.1746				
27	*Capitella capitata*	44.4600	3.7857	1.6259		0.2394	-1.6259	15	0.0165		2.5206	2.5206	1.0257
27								16	0.0094				
27								18	0.0002				
27								24	0.0115				
27								28	0.0008				
27								31	0.0001				
27								32	0.0144				
27								33	0.0444				
27								34	0.0155				
27								39	0.0714				
27								41	0.0497				
27								46	0.1342				
27								57	1.4970	1.8652			
27								64	2.5206				
28	*Eteone spp.*	39.4861	0.5470		0.0451	0.1905	0.0902	15	0.0147		0.3302	0.3753	0.0262
28								16	0.0084				
28								18	0.0002				
28								24	0.0103				
28								28	0.0007				
28								31	0.0001				

App. 7 (continued): Energy flow table of the entire project area; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

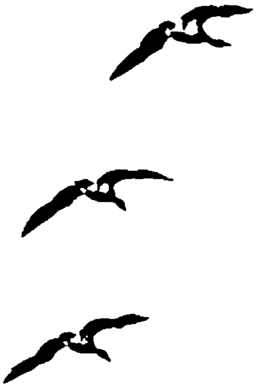
28								32	0.0128				
28								33	0.0395				
28								34	0.0138	0.1003			
28								64	0.3753				
29	*Heteromastus filiformis*	0.1305	0.0112	2.5375		0.0007	-2.5375	15	0.0000		0.0091	0.0091	0.0014
29								16	0.0000				
29								18	0.0000				
29								24	0.0000				
29								28	0.0000				
29								31	0.0000				
29								32	0.0000				
29								33	0.0001				
29								34	0.0000				
29								39	0.0714				
29								41	0.0497				
29								44	0.6571				
29								46	0.1342				
29								47	0.0711				
29								50	0.0554				
29								53	0.0019				
29								57	1.4970	2.5382			
29								64	0.0091				
30	*Lanice conchilego*	16.2251	0.3208	4.9651		0.0842	-4.9651	15	0.0060		0.0742	0.0742	0.1624
30								16	0.0034				
30								18	0.0001				
30								24	0.0042				
30								28	0.0003				
30								31	0.0000				
30								32	0.0052				
30								33	0.0162				
30								34	0.0057				
30								39	0.0714				
30								41	0.0497				
30								44	0.2604				
30								47	0.3628				
30								50	0.0554				
30								53	0.0008				
30								54	3.7299				
30								55	0.4602				
30								56	0.0175	5.0493			
30								64	0.0742				
31	*Lepidonotus squamatus*	0.9408	0.0486		0.0003	0.0031	0.0007	15	0.0003		0.0357	0.0361	0.0099
31								16	0.0002				
31								18	0.0000				
31								24	0.0002				
31								28	0.0000				
31								31	0.0000				
31								32	0.0003				
31								33	0.0009				
31								34	0.0003	0.0024			
31								64	0.0361				
32	*Nephtys spp.*	126.6622	7.5333	32.5918		1.3966	-32.5918	15	0.0470		4.8098	4.8098	1.3269
32								16	0.0269				
32								18	0.0007				
32								24	0.0329				
32								28	0.0024				
32								31	0.0003				
32								32	0.0409				
32								33	0.1266				
32								34	0.0442				
32								39	0.0714				
32								41	0.0497				
32								44	1.3018				
32								48	2.6333				
32								49	0.0594				
32								50	0.0554				
32								53	0.0038				
32								54	27.7815				
32								55	0.4602				
32								56	0.0175				
32								61	0.0828				
32								62	0.1383				
32								63	1.0116	33.9884			
32								64	4.8098				
33	*Nereis spp.*	1234.7156	58.2654	53.5922		5.9199	-53.5922	15	0.4583		37.8421	37.8421	14.5034

App. 7 (continued): Energy flow table of the entire project area; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

33								16	0.2621				
33								18	0.0066				
33								24	0.3206				
33								28	0.0232				
33								31	0.0026				
33								32	0.3988				
33								33	1.2338				
33								34	0.4304				
33								39	0.0714				
33								41	0.0497				
33								42	0.0024				
33								44	6.5216				
33								46	0.0163				
33								47	0.6545				
33								48	5.2170				
33								49	0.0594				
33								50	0.6559				
33								51	0.0106				
33								53	0.0188				
33								54	35.4985				
33								57	1.2220				
33								58	0.4119				
33								60	1.9392				
33								61	0.2751				
33								62	0.3901				
33								63	3.3611	59.5121			
33								64	37.8421				
34	*Phyllodoce spp.*	449.2715	16.2609	0.0315		1.2309	-0.0315	15	0.1668		1.7504	1.7504	13.2795
34								16	0.0954				
34								18	0.0024				
34								24	0.1167				
34								28	0.0084				
34								31	0.0009				
34								32	0.1451				
34								33	0.4489				
34								34	0.1566				
34								39	0.0714				
34								41	0.0497	1.2623			
34								64	1.7504				
35	*Pygospio elegans*	31.3812	0.8798	0.7434		0.1165	-0.7434	15	0.0116		0.2285	0.2285	0.5348
35								16	0.0067				
35								18	0.0002				
35								24	0.0081				
35								28	0.0006				
35								31	0.0001				
35								32	0.0101				
35								33	0.0314				
35								34	0.0109				
35								39	0.0714				
35								41	0.0497				
35								44	0.6571				
35								53	0.0019	0.8599			
35								64	0.2285				
36	*Scoloplos armiger*	1797.1916	54.9130	50.3093		7.8289	-50.3093	15	0.6671		34.0342	34.0342	13.0499
36								16	0.3815				
36								18	0.0096				
36								24	0.4667				
36								28	0.0337				
36								31	0.0037				
36								32	0.5805				
36								33	1.7958				
36								34	0.6265				
36								39	0.0714				
36								41	0.0497				
36								46	0.1342				
36								48	2.6333				
36								50	0.0554				
36								54	49.1320				
36								57	1.4970	58.1382			
36								64	34.0342				
37	small polychaetes	46.6784	1.2850	0.0275		0.2122	-0.0275	15	0.0173		0.3904	0.3904	0.6824
37								16	0.0099				
37								18	0.0002				
37								24	0.0121				
37								28	0.0009				

App. 7 (continued): Energy flow table of the entire project area; biomass in mgC.m^{-2}; production (P), consumption, respiration, egestion (E), imports, exports and flows in mgC.m^{-2}.d^{-1}

37								31	0.0001				
37								32	0.0151				
37								33	0.0466				
37								34	0.0163				
37								39	0.0714				
37								41	0.0497	0.2397			
37								64	0.3904				
38	*Tharyx killariensis*	21.2897	0.5734		0.0313	0.1167	0.0626	15	0.0079		0.2355	0.2668	0.2212
38								16	0.0045				
38								18	0.0001				
38								24	0.0055				
38								28	0.0004				
38								31	0.0000				
38								32	0.0069				
38								33	0.0213				
38								34	0.0074	0.0541			
38								64	0.2668				
39	*Anas acuta*	29.1375	2.8577		0.0841	0.0841		64	1.0086		1.0086	1.0086	1.7651
40	*Anas penelope*	2274.4260	65.7728		1.2928	1.2928		64	23.7558		23.7558	23.7558	40.7242
41	*Anas platyrhynchos*	208.1869	7.0973		0.1183	0.1183		64	2.6023		2.6023	2.6023	4.3767
42	*Arenaria interpres*	4.4787	0.6124		0.0083	0.0083		64	0.1241		0.1241	0.1241	0.4800
43	*Branta bernicla*	336.1890	13.4476		0.3362	0.3362		64	4.7066		4.7066	4.7066	8.4047
44	*Calidris alpina*	81.1283	12.3985		0.1675	0.1675		64	2.5132		2.5132	2.5132	9.7178
45	*Calidris canutus*	139.2379	35.0673		0.5157	0.5157		64	7.2197		7.2197	7.2197	27.3319
46	*Charadrius hiaticula*	3.3398	0.5104		0.0069	0.0069		64	0.1035		0.1035	0.1035	0.4000
47	*Chroicocephalus ridibundus*	50.8168	3.5572		0.1186	0.1186		64	0.7114		0.7114	0.7114	2.7272
48	*Haematopus ostralegus*	366.1036	49.6855		1.6562	1.6562		64	9.9371		9.9371	9.9371	38.0922
49	*Larus agentatus*	112.3173	6.5990		0.1692	0.1692		64	1.3536		1.3536	1.3536	5.0762
50	*Larus canus*	41.4214	2.1294		0.0734	0.0734		64	0.4406		0.4406	0.4406	1.6154
51	*Larus fuscus*	3.4805	0.0529		0.0014	0.0014		64	0.0108		0.0108	0.0108	0.0407
52	*Larus marinus*	2.4128	0.0208		0.0014	0.0014		64	0.0188		0.0188	0.0188	0.0006
53	*Limicola falcinellus*	0.2344	0.0358		0.0005	0.0005		64	0.0073		0.0073	0.0073	0.0281
54	*Limosa lapponica*	631.3966	128.6178		2.3385	2.3385		64	25.7236		25.7236	25.7236	100.5558
55	*Numenius arquata*	114.7213	8.2178		0.2107	0.2107		64	1.6857		1.6857	1.6857	6.3214
56	*Numenius phaeopus*	4.3695	0.3130		0.0080	0.0080		64	0.0642		0.0642	0.0642	0.2408
57	*Pluvialis squatarola*	54.3112	6.1100		0.1697	0.1697		64	1.1881		1.1881	1.1881	4.7522
58	*Recurvirostra avasetta*	3.7072	0.8238		0.0412	0.0412		64	0.1648		0.1648	0.1648	0.6179
59	*Somateria mollissima*	10.6618	1.4482		0.0289	0.0289		64	0.2888		0.2888	0.2888	1.1306
60	*Tadorna tadorna*	212.4673	22.8136		0.5025	0.5025		64	5.1167		5.1167	5.1167	17.1944
61	*Tringa erythropus*	5.4671	1.3356		0.0196	0.0196		64	0.2750		0.2750	0.2750	1.0410
62	*Tringa nebularia*	9.1066	2.0642		0.0304	0.0304		64	0.4250		0.4250	0.4250	1.6088
63	*Tringa totanus*	66.7886	16.3162		0.2399	0.2399		64	3.3592		3.3592	3.3592	12.7170
64	sediment POC	19000.0000			1227.2878			4	196.3920				
64								5	103.0264				
64								10	0.0056				
64								11	10.9851				
64								16	1.4852				
64								18	0.6026				
64								22	95.7560				
64								25	14.2045				
64								26	71.6870				
64								27	1.8928				
64								29	0.0056				
64								33	5.8265				
64								36	24.7108				
64								37	0.0732				
64								38	0.2867	526.9401			
65	suspended POC	167.4400		167.4400	116.7825		116.7825	7	28.3093				
65								8	0.2353				
65								9	6.5060				
65								10	0.0031				
65								11	6.1516				
65								12	1.8579				
65								13	1.1495				
65								18	0.2816				
65								19	0.0021				
65								30	0.0481				
65								33	5.8265				
65								35	0.1320				
65								37	0.1542	50.6575			



Acknowledgements

Photo flying geese: Robert Waleczek

This work wouldn't have been possible without the direct and indirect connection to a complex network of people.

My thesis was part of the project "STopP – From sediment to top predator" and therefore I'd like to thank first the German Federal Ministry of Education and Research for funding the project and the Alfred-Wegener-Institute Helmholtz Centre for Polar and Marine Research for hosting it.

I'm grateful to my supervisors Harald and Ragnhild Asmus. Thank you for introducing me into the wonderful world of Wadden Sea research. Thanks for all the fruitful discussion, for your advice and for your trust in me. You were always open to my ideas and I learned a lot during my time as your PhD student.

I'd also like to thank Stefanie Ismar for agreeing on being my second reviewer.

Many thanks to my working group "Ecosystem analysis" and to the whole team of the Wadden Sea station Sylt.

Camille, I'm so glad we ended up as partners. We constructed our models together, we answered the question which is the best way to homogenize a bird and we spent a lot of time organizing institute events. Thank you for ordering my thoughts, when there was only chaos in my head. I think without you I would have got lost somewhere between Ascendency and Uncertainty analysis.

Thank you, Petra for your help, whenever it was needed. Thanks for all the nice conversations and for guiding me through the labyrinth of AWI bureaucracy. Birgit, thank you for your support. Without your help I would still work on the microphytobenthos samples.

Thanks to my fellow PhD students Camille, Marieke, Martin, Andreas and Jonas. I think we organized the best PhD days in the history of the AWI! The suckling pig was awesome! Our theme song "Under the sea" will be my catchy song for life. It even followed us to London! Marieke, thanks for all the nice baking sessions, creative nights and for taking me to Judo! You guys made Sylt a home! Benni, Tim and Fabiola, thank you for the great frist time on Sylt.

I'm grateful to my master student Cosima Merkel. I think there was a point when we both really hated the razor clams for being so complicated but I always enjoyed the work with you and your creative ideas how to set up the experiments. Thank you for your help to include the inveraders in my food web.

I'd also like to thank the team of the "FS Mya II", Alfred Resch and Kai von Böhlen. The journey to Amrum was far and I always brought bad weather but I enjoyed each of our trips!

Thanks to the team of the Naturgewalten for providing so many nice pictures for my work!

And I'd also like to thank all the students and interships who spent so many days on sorting, identifying and weighting my smples. Without your help, science would not be possible!

I'm grateful to my STopP family! It was a pleasure to work with such a nice project team!

Many thanks to the ornithology group of the FTZ Büsum. Without your help the implementation of the birds in the model wouldn't have been possible. Thank you, Stefan Garthe and Philipp Schwemmer, for your advices and the discussions about my work. Whenever I had questions about birds you were there to give an answer. Stefan, I'd like to thank you for being part of my PhD committee and for joining my defense jury. Philipp, thanks for all the help you offered during the last years. Without your cooperation my work wouldn't have been the same.

Thank you Leonie! You taught me that not every bird in the intertidal area is a "gull". I learned a lot about bird identification and about being fascinated by birds. Thank you for the great field trips which always ended in a new story. I can still taste the "Strandhafer" we drank on Amrum and feel the "roller coaster" ship trip. Thank you for your positive nature and for your organization talent. I'm already looking forward to our future field trips!

I'd like to thank Kirsten Binder for your data support and for the nice field trips to Föhr and Langeness which we organized together. Thank you, Kerstin Stelzer for providing the remote sensing data for the size of my habitats and to Heike Büttger who shared her experience and data about mussel banks with me.

During every STopP meeting I got more insight into geology. Thank you, Klaus Ricklefs, Maria Stage, Klaus Schwarzer and Kerstin Wittbrodt.

Thank you, Jörn Kohlus, for showing me "my" seagrass meadow. Many thanks go also to the STopP coordination team, Kai Eskildsen and Alexandra Ruales, and to Christian Reimers.

I'd also like to thank Ulrike Schückel. Every time we talk about food webs I learn something new.

I'm grateful to my family for your support during the last years. Thank you, mom and dad, you gave your children wings to fly their own way, but you are always there if we need a rest. My siblings, Março, Annika, Heike and Kathrin, maybe one day I can answer all your "You are a biologist…"-questions (but most likely not). Thanks to Sylvie, Markus and Sebastian and to my newest family members Marlon, Nico and Weda (one of you should definetly become a scientist).

Furthermore, I'd like to thank my friends for all the nice events during the last years where I could refuel my energy reserves on my migration along the PhD thesis. Thank you, Kathi, for visiting me so often on my lonely island and for encouraging me to hang on! You are always there when I need someone to talk and I'm very grateful for your help and your friendship. Thanks to Janina, Nadine, Daniel, Dennis, Kai, and Torben who also showed me that Sylt is not too far away to visit a friend (either planned or as a surprise). Nadine, thank you for all the encouraging conversations and for sharing the challenges of being a PhD student with me. Maybe, one day, we can work on a food web including soil crusts together.

Thanks to all of you for creating my personal "stop-over site"!

And thank you Til. Thank you for being by my side the whole long journey of my PhD. Thank you, for encouraging me to go my own way and for joining it. I couldn't have done this without your support, your patience and your love. You cheered me up, when I was down, you listened to my problems, when I thought there was no way out and you believed in me when I did not. Thank you for motivating me. You never lost the interest in my work and I'm so happy that I could practice my talks in front of you and share my experiences with you (I still think you were more enthusiastic about collecting the razor clams than I was). Thank you for being you. I love you.

Lebenslauf

Sabine Horn
Listlandstraße 18 B
25992 List/Sylt
sabine.horn87@gmx.de

Persönliche Daten

Geburtsdatum	17.11.1987
Geburtsort	Achim
Familienstand	Ledig, keine Kinder
Staatsangehörigkeit	Deutsch

Beruflicher Werdegang

Seit Mai 2013	**Promotion** in Biologie *Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Sylt* Thema der Arbeit: Feed and fly – a model study about the relationship between coastal birds and intertidal food webs

Studium

Oktober 2010 – November 2012	**Master of Science** in Biologie *Carl von Ossietzky Universität, Oldenburg* Thema der Abschlussarbeit: Temporal variability of infauna communities in the eastern North Sea
Oktober 2007 – Oktober 2010	**Bachelor of Science** in Biologie *Carl von Ossietzky Universität, Oldenburg* Thema der Abschlussarbeit: Visual kin recognition in juvenile zebrafish (*Danio rerio*)

Schulische Ausbildung

2004 – 2007	**Allgemeine Hochschulreife** *Gymnasium Osterholz-Scharmbeck*
2000 – 2004	*Realschule Osterholz-Scharmbeck*
1998 – 2000	*Orientierungsstufe Osterholz-Scharmbeck*
1994 – 1998	*Menckeschule Osterholz-Scharmbeck*

Hilfswissenschaftliche Tätigkeiten

5. - 22. März 2013	Praktikum auf dem Forschungsschiff *Heincke* zur Beprobung der Epi- und Infauna in der Deutschen Bucht *Senckenberg Institut für Meeresbiologie, Wilhelmshaven*
Oktober – Dezember 2011	Auswertung von Infauna Proben des Jade-Weser-Ports

	Senckenberg Institut für Meeresbiologie, Wilhelmshaven
August 2008 – Oktober 2012	Versorgung und Aufzucht von Zebrabärblingen *Carls von Ossietzky Universität, Oldenburg*

Publikationen

Horn, Sabine, and Camille de la Vega. "Relationships between fresh weight, dry weight, ash free dry weight, carbon and nitrogen content for selected vertebrates." Journal of Experimental Marine Biology and Ecology 481 (2016): 41-48.

Vorträge

6.-9.9.2015	The impact of birds on the Wadden Sea food web *ECSA 55 Unbounded boundaries and shifting baselines: Estuaries and coastal seas in a rapidly changing world, London*
21.-25.9.2015	Top-down or bottom-up The role of birds in the Wadden Sea food web *50th European Marine Biology Symposium, Helgoland*
10.-11.2.2016	Die ökologische Netzwerkanalyse – Das Wattenmeer als Nahrungsnetz *STopP Statusseminar, Büsum*
4.-7.9.2016	Food web characteristics of six intertidal habitat types of the Wadden Sea *ECSA 56 Coastal systems in transition: From a 'natural' to an 'anthropogenically-modified' state, Bremen*

Eidesstattliche Erklärung

Hiermit versichere ich, dass ich die vorliegende Doktorarbeit

„Feed and fly – A model study about the relationship between coastal birds and intertidal food webs"

Mit Unterstützung meiner Betreuer, Co-Autoren und Praktikanten und nur unter Zuhilfenahme der angegeben Hilfsmittel und Quellen angefertigt habe. Die Arbeit wurde bisher in keinem Prüfungs- und Promotionsverfahren vorgelegt. Teile der Arbeit wurden in wissenschaftlichen Zeitschriften veröffentlicht oder zur Veröffentlichung eingereicht.

Die Arbeit wurde unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft verfasst.

Ich habe bis zum heutigem Tage weder an der Christian Albrechts Universität zu Kiel noch an einer anderen Hochschule ein Promotionsverfahren endgültig nicht bestanden, noch befinde ich mich in einem entsprechenden Verfahren.

19.1.17,

Datum, Unterschrift

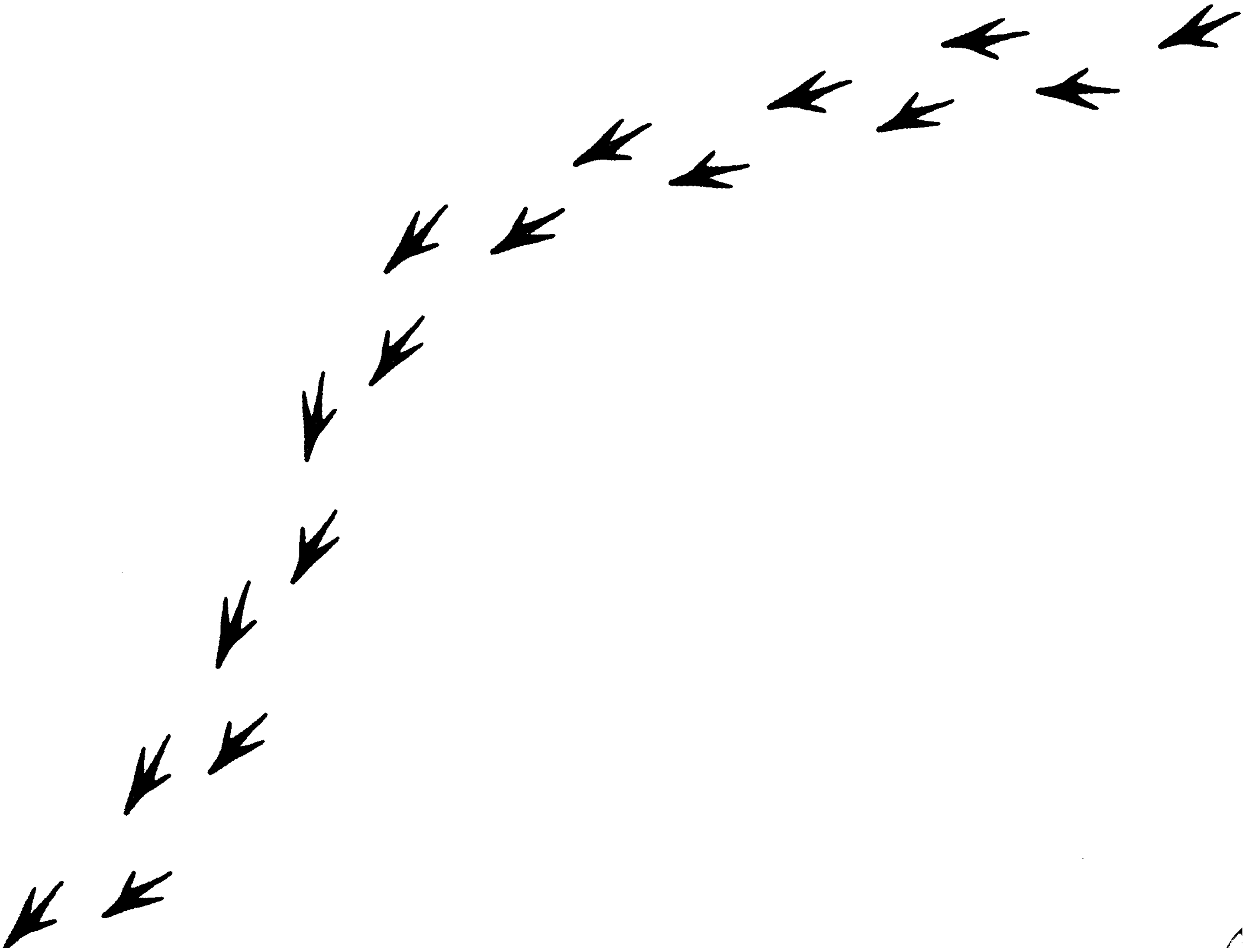


Photo walking oystercatcher: Mike Kuschereitz