ABSCHLUSSBERICHT

Zuwendungsempfänger:

PD. Dr. Harald Asmus, als Projektkoordinator

Alfred-Wegener Institut für Polar-und Meeresforschung, Wattenmeerstation Sylt, Hafenstrasse 43.

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Vorhabenbezeichnung:

Der Einfluss von eingeschleppten Arten auf das Nahrungsnetz des Wattenmeeres

The impact of biological invasions on the food web of the Wadden Sea

INFOWEB

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Autoren:

Koordination: PD Dr. Harald Asmus

Teilprojektleitung: Dr. Henk van der Veer, PD Dr. Ingrid Kröncke, PD Dr. Harald Asmus

INHALTSVERZEICHNIS

1.1 Aufgabenstellung

The aim of the project was constructing a food web model for the Wadden Sea considering the new communities such as Pacific oyster beds, *Sargassum muticum*- forests, and American razor clam beds. We also included new species such as *Caprella mutica,* their probable place in the food web and their role as predators and prey. For the established communities we considered alterations in species composition and in energy flow rates due to altered seasonal temperatures.

Using an already existing model as a background established the food web of the Sylt-Rømø Bight as a reference food web for the Northern German and Danish part of the Wadden Sea. We initiated an adaptation of this idea to the Trilateral strategy of the Wadden Sea, by installing two additional areas for research, the Jade Bay and an additional one that is situated in the Western part of the Wadden Sea to cover the total area. As it is not indicated in the proposal we also delivered a food web model of the heavily impacted Ems estuary.

These food webs were compared and delivered scenarios of the changing environment of the Wadden Sea, especially due to temperature and biotic invasions. They are helpful tools for the management of the area and in detecting indirect effects between components and trophic cascades of the area. Especially the future trends in the development of populations of invertebrates, fishes, birds and mammals are currently proven from a trophic perspective and the influence of mussel, shrimp as well as flatfish fishery will then be evaluated by an ecosystem based management concept, that is still under construction.

The project was related to multiple political and strategic aims of the federal government of Germany. It contributes to the **scientific-technological cooperation in Europe** by creating scientific basic information for the **Integrated Coastal Zone Management** and the use of valuable marine resources.

The main focus lies on the contribution to the **Marine Research Programme**:

- The project performs a contribution to the field of **Marine Environmental Research** by the analysis of structure and function, cycling and perturbations of threatened marine ecosystems.
- By its focus on the changes in food webs due to invasive species, whose establishment is mainly promoted by the global climate change, the project contributes to the **Marine Climate Research**, making a contribution to the description of impacts of climate fluctuations. This has an important share in preventive and protection measures and in the prognosis of future developments

By means of the expected results related to the resilience of coastal food webs against anthropogenic perturbations the research of our project supports the aim of the framework programme "**Research for sustainable development (FoNa)**" formulated 2004 by the Federal government of Research and Education. Thus the research is related mainly to the **sustainable use concepts for regions** (especially **sensitive regions**) and **concept for the monitoring of biodiversity**.

The present project is in accordance to the comprehensive IGBP and IHDP programme *Land Ocean Interaction in the Coastal Zone* (LOICZ). The objectives of the INFOWEB project are in line with those

of LOICZ. By the analysis of anthropogenic impacts to coastal systems INFOWEB contributes to the research of the link between social and ecological systems in the coastal zone, as one of the 3 priorities formulated by the Scientific Steering Comitee of LOICZ in June 2006.

Investigations of the ecosystem function by analysing the food webs of its community constituents has been practiced for the Wadden Sea only in certain areas such as the Sylt- Rømø Bight (Baird et al. 2007). This allows evaluating the relative importance of community functions for the total system and assessing the significance of communities for the energy flow. The community aspect is often poorly represented in energy flow studies. Including community aspects shows the influence of the habitat structure and habitat diversity on ecosystem functioning.

The investigation of the food webs focussed on two main parts, stable isotope analysis and network analysis. Stable isotope measurements on the dominant food web components gave insight into the trophic position of the particular components and helped to identify the food spectrum of the heterotrophic compartments

Ecological network analysis has been used as a suitable tool for elucidating the relation of trophic ecosystem function as well as exchange processes to both habitat and species diversity. For the Sylt-Rømø Bight a first synopsis has been presented corresponding to a snapshot of the system which is representative for a time frame of the mid nineties of the last century. Thus it complies with a quantitative picture of the food web of a part of the Wadden Sea before the major system alterations that occur presently, i.e. the invasion of neophytes and invasive animals (Markert et al. 2010, Philippart & Epping 2010, Van Walraven et al. 2011) have been observed.

The above mentioned alterations have been accommodated in this early model by including new parameters and modifications of the food web components. In this way a new model of the Sylt-Rømø Bight was constructed. Comparisons between the systems by network analysis gave results on trophic efficiency and on the recycling potential (indicated by Finn cycling index), the mutual exclusive system attributes such as ascendency and redundancy as well as the connectance indices. The consequences for the total system, stability characteristics and the susceptibility to perturbations have been assessed and theories on the future of the Wadden Sea were developed (e.g. Baird et al 2007).

It was expected that invasions have altered the system in many parts. The meanwhile established Pacific oyster (*Crassostrea gigas*) beds have expanded in 2003-2009 and are probably reduced by the hard winters 2009/2010 and 2010/2011. The control of oyster larvae due to warm and colder summers is reported, however, a biological control of oyster larvae of the species *Crassostrea virginica* by the jellyfish *Mnemiopsi leydii* is reported for the American East Coast and can be also assumed to occur in the Wadden Sea on *C. gigas*, since *M. leydii* has invaded here recently.

The introduced razor clam (*Ensis americanus*) is also established in the Wadden Sea where it can attain large biomass values similar to that of intertidal mussel beds. The role of razor clam beds for the food web of the Wadden Sea has not been assessed. In contrast to Pacific oysters and slipper limpets this species has been reported as food for birds, especially the common scoter (*Melanitta nigra*) perhaps substituting the original prey (*Spisola* spec.) which decrease in some regions.

Whether native species declined in the same time period when invasive species increased in population density depends on the region. In the Sylt Rømø Bight mussel beds suffer from mild winters showing low recruitment, while spawning of Pacific oysters is promoted by warm summers. These species show thus an antidromic trend of population development due to the climate regime. However, both species occur together and a net increase of large suspension feeders could be

observed. Therefore the hypothesis that secondary production may have increased because these filter-feeders directly filter primary producers and thereby short-circuit the pelagic food web could be confirmed. Hence, food web efficiency from primary production to secondary production has increased. Because invading species are not predated with the same efficiency the hypothesis could also been confirmed that food web efficiency from secondary producers to higher trophic levels has decreased Invasive seaweeds also contribute to the Wadden Sea food web in our days. *Sargassum muticum* beds has occupied large areas in the Sylt Rømø Bight. This new community attracts many fish species. They feed upon the alien *Caprella mutica*, a dominant epibenthic species in this community, which was also recently found in the Jade Bay. Most of these fish species were absent for the Wadden Sea since the subtidal *Zostera marina* beds have been wiped out in the 1930ies. The *Sargassum muticum* community is undoubtly a new community element that was investigated with respect to its food web and the importance for the total system of the particular Wadden Sea tidal basin.

In addition to these examples of alien plants and animals, introduced into the Wadden Sea system by man, there has been observed a subtle immigration of species with a southern distribution centre and an emigration or increased mortality (Markert et al. 2010) of northern species due to increasing winter and summer temperatures, especially among mobile organisms such as fish. These species are also expected to change dominance and interactions with the food web on a community as well as ecosystem level.

The relation of food web dynamics to exchange processes forms a link between the system and the material import thereby considering the system response by feedback mechanisms. This allows an action-oriented consideration of impacts of human activities, such as eutrophication or pollution on the food web.

Data on food web structure and function are converted by network analysis into a standardized form, such as the Lindeman spine, facilitating the comparison between food webs and ecosystems with different ecological backgrounds. The consideration of the community level allows the selection of comparable scales within systems of different sizes and helps to exclude scaling artefacts when comparing different systems and scenarios.

The existing food web models are mainly focused on the intertidal area of the Wadden Sea and thus should be expanded to include also the subtidal part, especially because the shallow subtidal area is the hot spot of the invasive settlement and community forming.

To represent the food web of the whole Wadden Sea region, we have to consider the different regional peculiarities of the system. The micro-tidal regions of the Northern and Southern Wadden Sea are different with respect to benthic communities compared to the macro-tidal Central Wadden Sea, which is strongly influenced by the large estuaries. Also the degree of establishment of invasive species and the human impact shows differences due to the geographical region. Thus food web models are needed that represent the Southern as well as the Central part, and have a background in long term data of the different food web components from bacteria to the fish, birds and mammals. We therefore investigated three areas (a =Balgzand area; b= the Jade Bay and c= the Sylt Rømø Bay (see Fig. 1) and included a fourth one (d= Ems estuary)

1.2 Planung und Ablauf des Vorhabens

The work plan of the theme required a close cooperation between Dutch, German and Danish partners. Because Danish partners have not been funded in that frame, they are mentioned as associates of this project.

Most of the work has been spent into the compilation of data for the four food web models and the integrated subsystems. Data used for the food web modelling will currently be stored in a project data bank that is installed by the project partners into their institutional data bank (e.g. Pangaea) where they are available freely after the project has finished. Two models have been established for the Southern Wadden Sea. The Dutch partners compiled the data material from existing monitoring and long term series collected in the Balgzand area around Texel (Table 1) and from the Ems- Dollard Estuary. For the estuarine part of the Central Wadden Sea a second model has been constructed which covers the area of the Jade Bay and adjoining areas, for which a lot of suitable long term data series exist collected by Senckenberg am Meer, Wilhelmshaven, and the University of Oldenburg (Table 1). The third food web model represents the Northern part of the Wadden Sea at the German-Danish border. Here a food web model already exists for the Sylt-Rømø Bight that represents currently a time frame before invasions of alien species increased. This model will be a kind of prototype for the other two models still to construct, which should be formed in a similar way to allow comparisons of regional characteristics. This model will be updated to include the recent ecosystem changes that occurred in the region. For updating this model German and Danish scientists will closely work together. The food web models will also consider the impact of man by including human activities in the prospected regions as far as they influence material pools (e.g. eutrophication) or biomasses of living organisms or extracting and adding them (e.g. fisheries and aquaculture).

Table 1: Long term series in the Northern, Central and Southern Wadden Sea, and the long term series in the adjoining coastal North Sea measured on Helgoland.

Long term series	
Sylt	**since**
Hydrography, Nutrients	1984
Phytoplankton	1984
Zooplankton	1984
Meroplankton	1996
Makrozoobenthos	1992
Makroalgae, Seagrass	1991
Helgoland	
Hydrography, Nutrients	1962
Phytoplankton	1962
Zooplankton	1962
Meroplankton	1974
Macrozoobenthos	1999
Macroalgae, Seagrass	2002
Jade Bay	
Hydrography, Salinity	1980
Macrozoobenthos (decadal scale)	1930
Epifauna	1970

Spiekeroog tidal inlet	
Hydrography	2003
Nutrients	2006
Chlorophyll fluorescence	2006
Suspended matter	2006
Spectral daylight and reflectance	2004
Balgzand	
Hydrography, Nutrients	1970
Phytoplankton	1970
Zooplankton, Meroplankton	2009
Macrozoobenthos	1974
Fish and epibenthic predators	1975

1.3 STAND VON WISSENSCHAFT UND TECHNIK

1.3.1 STAND VON WISSENSCHAFT UND TECHNIK

The Wadden Sea ecosystem is seldom considered from a holistic point of view, but some approaches to do so have been developed as well as in comparable systems worldwide. The first fundamental investigation of the Wadden Sea in this direction was already carried out at 1877 by Karl Möbius, who gave the first community concept using the example of an oyster bed of the Sylt-Rømø Bight. He stated that the system´s immanent mechanisms of self regulation guarantee the preservation and survival of this community. For an oyster bed this concept could not be further sustained (Reise 1990), although the biocoenosis or community as a scientific term has been defined at first time and this gave an important impulse for the further development of ecology as a scientific discipline. This scientific discipline subsequently developed rapidly through investigations in terrestrial, limnic and marine systems (e.g. Warming 1909; Elton 1927; Allee 1932; Allee et al. 1949). Only at a very much later stage ecology turned to intertidal systems (e.g. Connell 1961; Paine 1966; 1974). Odum & Hoskin (1958) analysed estuarine habitats at the American coast and used the holistic approach for ecosystems which was formulated some years earlier (Clements 1905; Gleason 1926) and has been debated controversially but found later large agreement in ecological concepts (e.g. Simberloff 1980;

Wilson 1988; Liu et al. 2007). Subsequently in Europe scientists initiated investigations at the ecosystem level in different marine systems based upon the concepts of energy and material flow (e.g. Hughes 1970; van Es 1982; Warwick & Price 1975). In shallow water areas of the Baltic Sea many communities have been investigated, with the aim to assess the energy budget of the various subsystems of the Baltic (e.g. Jansson & Wulff 1977). In the North Sea in the late 70's and early 80's an energy budget has been developed for the Balgzand area in the Dutch Wadden Sea (Wolff & de Wolf 1977; Wilde de 1980; Kuipers et al. 1981). Influenced by the rapid economic and industrial development in coastal areas and the assessment of consequences for the marine ecosystem, especially eutrophication, investigations of material flow gained importance, but focussed mainly on smaller sub-systems or sections thereof (e.g. Witte & Zijlstra 1984; Veldhuis et al. 1988; van der Veer 1989).

Only few analyses of whole ecosystems have been carried out in the German Wadden Sea. Between the two World Wars ecological research in the Sylt-Rømø Bight has been applied to aspects such as identifying and mapping coastal communities and their habitat requirements (e.g. sediments and tidal exposure) (Nienburg 1927). It was the aim to prove whether the Wadden Sea was a useful area for commercial fishing, especially shellfish (Hagmeier & Kändler 1927; Hagmeier 1941) and for land reclamation (Wohlenberg 1933; 1934; 1937). At the late 70ies to the beginning of the early 80ies research at the ecosystem level did start in earnest in the Wadden Sea. Following the paradigm of the American research (e.g. Paine 1966; 1974) exclusion/inclusion experiments of certain organisms have been used to investigate their interaction with adjacent communities (Reise 1978; 1981). Investigations of the energy flow following a holistic approach such as those used in North America (e.g. Teal 1962; Pamatmat 1968; Hargrave 1969; Pomeroy & Wiegert 1981; Dame 1996) and Sweden (Jansson & Wulff 1977) have been transferred to the Wadden Sea ecosystem (Asmus H 1982; Asmus R 1982; Asmus & Asmus 1985). In the Sylt-Rømø Bight ecological research has been carried out in one defined spatial area using both the organism approach (e.g. Reise 1998; Beusekom & Reise 2008; Reise & Beusekom 2008; Reise et al. 2008) and the material and energy flow approach (e.g. Asmus et al. 1998a,b,c; Asmus & Asmus 2000; Baird, Asmus, Asmus 2004; 2007; 2008; Baird et al. 2009) for a long period of time since 1978.

In the 90's extended ecosystem analyses have been conducted, with results forming the base of a fundamental inventory of organism resources as well as of material and energy flow (Leuschner & Scherer 1989; Lindeboom et al. 1989). In the Sylt-Rømø Bight these investigations were limited to the intertidal area, but considered also for the first time fish, birds and marine mammals of the area (for summary see Gätje & Reise 1998). The outcome of these analyses was the development of nature conservation concepts, which has been scientifically. While the knowledge on Wadden Sea ecosystems was further complimented by this research, a total and common view on the interlinked dynamics of the material flow and the organisms was yet to be done. Even two dimensional hydrodynamic and numerical models that have been described during this period remained widely limited on abiotic processes such as currents and material transport (Stanev et al. 2003; Kohlmeyer & Ebenhöh 2009).

In the middle of the nineties research on biodiversity became a dominant discipline against the background of a drastic decrease in species numbers in various ecosystems of the world, apparently through anthropogenic activities (Chadwick & Furman 1992; Tilman 1999). Concepts attempting to describe the relationship between biodiversity and ecosystem functioning were at the time rather elementary and rudimentary although many promising aspects have been published (Forster et al. 2006; Waldbusser & Marinelli 2006; Stachowicz & Byrnes 2006; Naeem 2006; Bulling et al. 2006; Duffy & Stachowicz 2006; Ruesink et al. 2006; Duffy 2006; Ieno et al. 2006; Raffaelli 2006; Heip et al. 2009).

During the last hundred years ecosystem research has developed along two routes. On one hand there is an approach that describes a community as the sum of its traits. Here spatial and temporal variabilities of abundances of species come to the fore, which are defined by their population dynamics (e.g. Turchin 2003; Geritz & Kisdi 2004) and their species diversity (Rosenzweig 1995) as well as the number of interactions between the organisms. This research focuses on ecosystem stability and resilience (e.g. Hughes 2003), on the occupation of niches by organisms, as well as the various effects that the organisms exert on each other (e.g. Bruno et al. 2003); these ideas were considered to impact on the development and structure of the community. Thus the community in an ecosystem is determined by the interplay between immigration and emigration, drift, recruitment, mortality as well as predator-prey interactions. By incorporating various community information an ecosystem model emerges which not only gives a qualitative image, but also quantitative information on the system as a whole. Within this quantitative ecosystem approach we are able to explain and describe the population dynamics of single species.

To characterise the function of an ecosystem a further approach is necessary which describes the material or energy budget of an ecosystem. Trophic dynamics and relationships are of prime importance in this context. The dynamics are defined by gross and net primary production for plants, while secondary production, consumption, as well as energy loss by respiration typifies that of an heterotroph (see Crisp 1984). Imports from outside the system and exports of material and energy from the system are some of the main controllers of the ecosystem behaviour and dynamics.

The cross-linking of organisms in a food web describes an ecosystem through the availability of its resources and their efficient use from primary producer to top consumer. The mathematical formulation in form of vectors and matrices describe the interactions between donor and recipient within a food web and thus enables us to analyse not only single components but also imports, exports, recycling of material and common transformation tracks which are used by different ecological components. From this model system an array of indices can be derived which provides information on system characteristics which is greater than the information content of the sum of ecosystem parts. This approach describes the dynamics of ecosystem processes as well as the functioning of an ecosystem. For the Wadden Sea this approach was only applied on the food web of the Sylt-Rømø Bight describing the carbon, nitrogen and phosphorus flow through the food web of the total bight (Baird et al 2004, 2008) and on the basis of dominant communities (Baird et al. 2007; 2011)

Both approaches indicate different directions. The population dynamic model illuminates primarily the qualitative changes within a system in the course of time, whereas the material and energy flow model illustrates a state description of the potential of an ecosystem on its sustainability, stability, maturity and the degree of development. To describe an ecosystem close to reality we have to consider the ability of change as well as the state of single and multiple functions. It is of special importance to note that certain key species can be able to influence the structure and dynamics of a system and are able to control material and energy flow in the system (e.g. Eriksson et al. 2010).

1.3.2 ANGABE BEKANNTER KONSTRUKTIONEN, VERFAHREN UND SCHUTZRECHTE, DIE FÜR DIE DURCHFÜHRUNG DES VORHABENS BENUTZT WURDEN

Es wurden keine Verfahren genutzt, bei denen Schutzrechte zu berücksichtigen waren.

1.3.3 ANGABE DER VERWENDETEN FACHLITERATUR

Allee WC (1932) Animal life and social growth. The Williams & Wilkins Company and Associates, Baltimore, 159 pp

Allee WC, Emerson A, Park O, Park T, Schmidt K (1949) Principles of animal ecology. WB Saunders Company, Philadelphia, 837 pp

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. Helgoländer Meeresuntersuchungen 39: 273-301

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

Asmus H, Lackschewitz D, Asmus R, Scheiffarth G, Nehls G, Herrmann J-P (1998)a Transporte im Nahrungsnetz eulitoraler Wattflächen des Sylt-Rømø Wattenmeeres. In: Gätje C, Reise K (eds) Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, 393-420

Asmus R (1982) Field measurements on seasonal variation of the activity of primary producers on a sandy tidal flat in the northern Wadden Sea. Netherlands Journal of Sea Research 16: 389-402

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

Asmus RM, Jensen MH, Jensen KM, Kristensen E, Asmus H, Wille A (1998)b The role of water movement and spatial scaling for measurement of dissolved inorganic nitrogen fluxes in intertidal sediments. Estuarine, Coastal and Shelf Science 46: 221-232

Asmus R, Jensen MH, Murphy D, Doerffer R (1998)c Primärproduktion von Mikrophytobenthos, Phytoplankton und jährlicher Biomasseertrag des Makrophytobenthos im Sylt-Rømø Wattenmeer. In: Gätje C, Reise K (eds) Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, 367-392

Baird D, Asmus H, Asmus R (2004) <u>Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight</u>. Marine Ecology Progress Series 279: 45-61

Baird D, Asmus H, Asmus R (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, Asmus H, Asmus R (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, Fath BD, Ulanowicz RE, Asmus H, Asmus R (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, Asmus H, Asmus R (2011) Carbon nitrogen and phosphorus dynamics in nine subsystems of the Sylt-Rømø Bight ecosystem, Northern Wadden Sea. Estuarine, Coastal and Shelf Science, 91: 51-60

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18: 119-125

Bulling MT, White PCL, Raffaelli D, Pierce GJ (2006) Using model systems to address the biodiversity–ecosystem functioning process. Marine Ecology Progress Series 311: 295–309

Chadwick-Furman NE (1992) <u>Reef coral diversity and global change</u>. Global Change Biology 2 (6): 559-568

Clements FE (1905) Research Methods in Ecology. Lincoln Nebraska University Publication

Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42: 710-723

Crisp DJ (1984) Energy flow measurements. In: Holme NA, McIntyre AD (eds) Methods for the study of marine benthos. Blackwell, Oxford, 284-372

Dame RF (1996) Ecology of marine bivalves: an ecosystem approach. Boca Raton Fla. CRC, 254 pp

Duffy JE (2006) Biodiversity and seagrass ecosystem function. Marine Ecology Progress Series 311: 233–250

Duffy JE, Stachowic JJ (2006) Why biodiversity is important to oceanography. Marine Ecology Progress Series 311: 179–189

Elton CS (1927) Animal Ecology – 1st edn, Sidgwick and Jackson, London. Reprinted several times, e.g. 2001 by The University of Chicago Press, 211 pp

Eriksson BK, van der Heide T, van de Koppel J, Piersma T, van der Veer H, Olff H (2010) Major changes in the ecology of the Wadden Sea: Human impacts, ecosystem engineering and sediment dynamics. Ecosystems 13: 752-764

Es FB van (1982) Community metabolism of intertidal flats in the Ems-Dollard estuary. Marine Biology 66(1): 95-108

Forster RM, Créach V, Sabbe K, Vyverman W, Stal LJ (2006) Biodiversity–ecosystem function relationship in microphytobenthic diatoms of the Westerschelde estuary. Marine Ecology Progress Series 311: 191–201

Gätje C, Reise K (eds.)(1998) Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer Berlin, 570 pp

Geritz SA, Kisdi E (2004) On the mechanistic underpinning of discrete-time population models with complex dynamics. Journal of Theoretical Biology 228(2): 261-269

Gleason HA (1926) The individualistic concept of plant association. Bulletin of the Torrey Botanical club 53(1): 7-26

Hagmeier A (1941) Die intensive Nutzung des nordfriesischen Wattenmeeres durch Austern- und Muschelkultur. Zeitschrift für Fischerei und deren Hilfswissenschaften 39(2): 105-165

Hagmeier A, Kändler R (1927) Neue Untersuchungen im nordfriesischen Wattenmeer und auf den fiskalischen Austernbänken. Helgoländer wissenschaftliche Meeresuntersuchungen 16(6): 5-89

Heip C, Hummel H, van Avesaath P, Appeltans W, Arvanitidis C, Aspden R, Austen M, Boero F, Bouma TJ, Boxshall G, Buchholz F, Crowe T, Delaney A, Deprez T, Emblow C, Feral JP, Gasol JM, Gooday A, Harder J, Ianora A, Kraberg A, Mackenzie B, Ojaveer H, Paterson D, Rumohr H, Schiedek D, Sokolowski A, Somerfield P, Sousa Pinto I, Vincx M, Węsławski JM, Nash R (2009) Marine Biodiversity and Ecosystem Functioning. Printbase, Dublin, Ireland, 92 pp

Hughes RN (1970) An energy budget for a tidal flat population of the bivalve *Scrobicularia plana* (Da Costa). Journal of Animal Ecology 39: 357-370

Hughes TP (2003) Climate change, human Impacts, and the resilience of coral reefs. Science 301: 929-933

Ieno EN, Solan M, Batty P, Pierce GJ (2006). How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. Marine Ecology Progress Series 311: 263–271

Jansson BO, Wulff F(1977) Ecosystem analysis of a shallow sound in the northern Baltic- a joint study by the Askö group- Contribution of the Askö Laboratory 18, 160pp

Kohlmeyer C, Ebenhöh W (2009) Modelling the biogeochemistry of a tidal flat ecosystem. Ocean Dynamics 59: 393-415

Kuipers BR, de Wilde PAWJ, Creutzberg F (1981) Energy flow in a tidal flat ecosystem. Marine Ecology Progress Series 5: 215-221

Leuschner C, Scherer B (1989) Fundamentals of an applied ecosystem research project in the Wadden Sea of Schleswig Holstein. Helgoländer Meeresuntersuchungen 43 (3-4): 565-574

Lindeboom HJ, Van Raaphorst W, Ridderinkhof H, Vanderveer HW (1989) Ecosystem model of the Western Wadden Sea – a bridge between Science and Management . Helgoländer Meeresuntersuchungen 43(3-4): 549-564

Liu J, Dietz T, Carpenter S, Folke C, Alberti M, Redman C, Schneider S, Ostrom E, Pell A, Lubchenco J, Taylor W, Ouyang Z, Deadman P, Kratz T, Provencher W (2007) Coupled human and natural systems. *Ambio* 36(8): 639-649

Naeem S (2006) Expanding scales in biodiversity-based research: challenges and solutions for marine systems. Marine Ecology Progress Series 311: 273–283

Nienburg W (1927) Zur Oekologie der Flora des Wattenmeeres. I. Der Königshafen bei List auf Sylt. Wissenschaftliche Meeresuntersuchungen, Kiel, 20:146-196

Paine RT (1966) Food web complexity and species diversity. American Naturalist 100: 65-75

Paine, RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15: 93-120

Pamatmat MM (1968) Ecology and metabolism of a benthic community on an intertidal sand flat. Internationale Revue der gesamten Hydrobiologie 53: 211-298

Pomeroy LR, Wiegert RG (eds) (1981) The ecology of a salt marsh. Springer New York, 271 pp

Raffaelli D (2006) Biodiversity and ecosystem functioning. Marine Ecology Progress Series 311: 285–294

Reise (1978) Experiments on epibenthic predation in the Wadden Sea. Helgoländer wissenschaftliche Meeresuntersuchungen 31: 55-101

Reise K (1981) Wissenschaftliches Programm I. Tierökologische Probleme in Küstengewässern. Ökologische Experimente zur Dynamik und Vielfalt der Bodenfauna in den Nordseewatten. Verhandlungen deutsche zoologische Gesellschaft 1981: 1-15

Reise K (1990) August Möbius dredging the first community concept from the bottom of the sea. Deutsche Hydrographische Zeitschrift Erg.-H.B. 22: 149-152

Reise K (1998) Coastal change in a tidal backbarrier basin of the Northern Wadden Sea. Are tidal flats fading away? Senckenbergiana maritima 29: 121-127

Reise K, Beusekom J van (2008) Interactive effects of global and regional change on a coastal ecosystem. Helgoland Marine Research, 62(1): 85-91

Reise K, Herre E, Sturm M (2008) Mudflat biota since the 1930s: change beyond return? Helgoland Marine Research 62(1): 13-22

Rosenzweig M (1995) Species diversity in space and time. Cambridge University Press, 436 pp

Ruesink JL, Feist BE, Harvey CJ, Hong JS, Trimble AC, Wisehart LM (2006) Introduced species and transformation of a 'pristine' estuary. Marine Ecology Progress Series 311: 203–215

Simberloff D (1980) A succession in ecology: Essentialism to materialism and probalism. Synthese 43: 3-39

Stachowicz JJ, Byrnes JE (2006). Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. Marine Ecology Progress Series 311: 251–262

Stanev EV, Wolff J-O, Burchhard H, Bolding K, Flöser G (2003) On the circulation in the East Frisian Wadden Sea: Numerical modelling and data analysis. Ocean Dynamics 53: 27-51

Teal JM (1962) Energy flow in a salt marsh ecosystem of Georgia. Ecology 43: 614-624

Tilman D (1999) The ecological consequences of changes in biodiversity: A search for general principles. Ecology 80(5): 1455-1474

Turchin P (2003) Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press, 450 pp

Veer HW van der (1989) Eutrophication and mussel culture in the Western Dutch Wadden Sea – Impact on the benthic ecosystem – a hypothesis. Helgoländer Meeresuntersuchungen 43(3-4): 517-527

Veldhuis MJW, Colijn F, Venekamp LAH, Villerius L (1988) Phytoplankton primary production and biomass in the western Wadden Sea (the Netherlands) – a comparison with an ecosystem model. Netherlands Journal of Sea Research 22(1): 37-49

Waldbusser GG, Marinelli RL (2006) Macrofaunal modification of porewater advection: role of species function, species interaction, and kinetics. Marine Ecology Progress Series 311: 217–231

Warming E (1909) Plantesamfund- Grundtræk af den økologiske plantegeografi. Philipsens PG Forlag, Copenhagen, 335 pp

Warwick RM, Price R (1975) Macrofauna production in an estuarine mudflat. Journal of Marine Biological Association UK 55: 1-18

Wilde PAWJ de (1980) Dynamics and metabolism of the benthos of the Wadden Sea. Hydrobiological Bulletin 14: 216-218

Wilson DS (1988) Holism and reductionism in evolutionary ecology. Oikos 53(2): 269-273

Witte JI, Zijlstra JJ (1984) The meiofauna of a tidal flat in the western part of the Wadden Sea and its role in the benthic ecosystem. Marine Ecology Progress Series 14(2-3): 129-138

Wohlenberg E (1933) Ueber die tatsächliche Leistung von *Salicornia herbacea* L. im Haushalt der Watten. Wissenschaftliche Meeresuntersuchungen Helgoland 19,3: 1-20

Wohlenberg E (1934) Biologische Landgewinnungsarbeiten im Wattenmeer. Der Biologe 7: 182-183

Wohlenberg E (1937) Die Wattenmeergemeinschaften im Königshafen von Sylt. Helgoländer wissenschaftliche Meeresuntersuchungen 1: 1-92

Wolff WJ, de Wolf L (1977) Biomass and production of zoobenthos in the Grevelingen Estuary, the Netherlands. Estuarine and Coastal Marine Science 5: 1-24

1.4 ZUSAMMENARBEIT MIT ANDEREN STELLEN

The aim of the present project is to describe the food web of three representative regions in the Wadden Sea and to assess the influence of invasive species on the whole system.

The project established a trophodynamic model based on the different communities for well investigated parts of the Wadden Sea as an integrative tool to assess the ecological status of the area and its possible future development. This end product could be used by the coastal zone management, the national park authorities and other authorities dealing with environmental and spatial planning in the coastal area. It will be also used by the fishery organisations for environmental risk assessment.

2 AUSFÜHRLICHE DARSTELLUNG DER PROJEKTERGEBNISSE

2.1. VERWENDUNG DER ZUWENDUNG UND DES ERZIELTEN ERGEBNISSES

2.1.1 PROJEKTMANAGEMENT

This task encompassed a consolidation of a variety of ecological data from bacteria to mammals including humans, but this has to be accomplished by a relatively low budget, particularly for personnel. Constructing food webs with only few specialists bears the risk of weighting those food web components that are well known and neglecting those that are less well investigated. To avoid this we chosed three PhD students with a broader interest each

focussing on a cluster of several groups of organisms and each being responsible for the food web of one of the proposed sites (see Fig.1). Together the PhD students compiled the data on mans activity, such as data and statistics on fishery and eutrophication and to integrate this into the different models being generated.
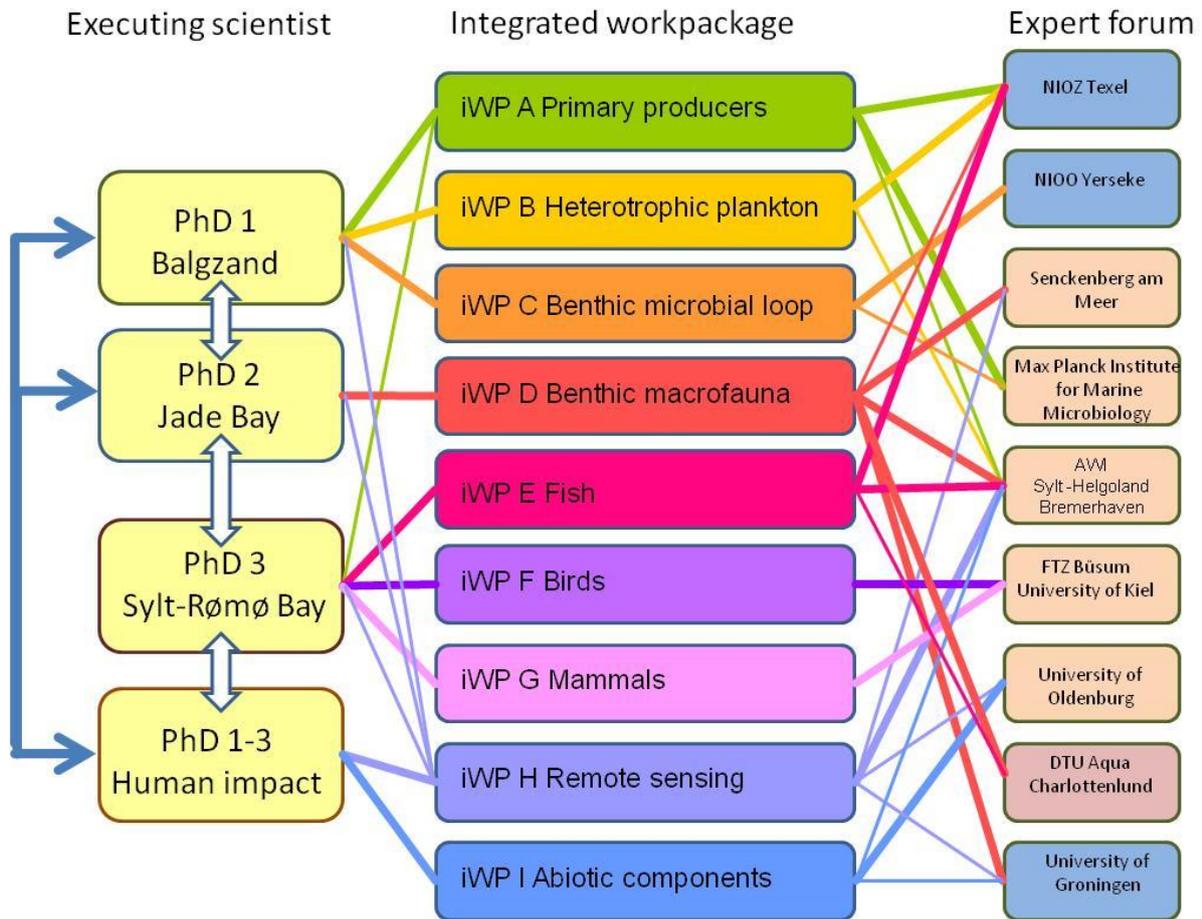

Fig.1. Co-operation and communication plan between executing scientists (PhD students) and expert forum organized in nine integrated work packages A-I and supported by 9 scientific institutions (blue = The Netherlands, beige = Germany; rose = Denmark).

In the course of the project we associated additional expertise of groups from outside that made valuable contributions and delivered products such as a food web model for an additional tidal basin. We integrated the expertise of Victor de Jonge who made together with the Senckenberg group an additional food web for the Ems estuary using data material from Dutch coastal authorities. We also integrated Diana Giebels from the University of Rotterdam/The Netherlands who investigated the science –politics interface of the project analysing possible pathways from the natural sciences and the food web modelling to the further use of these tools by different stakeholders and decision makers.

The management of the different tasks of the project is shown in Fig. 1.

Food web model by ecological network analysis (ENA) for a Southern Wadden Sea ecosystem, the Balgzand area

The main aim was the description of a food web model for the Balgzand area in the western Dutch Wadden Sea to analyse the impact of invasive species. Selection of the Balgzand area was based on the fact that it represents the western Wadden Sea and that over the years the area has been investigated intensively, resulting in long-term data sets going back to the late 1970-ties.

Between the late 1970-ties and present, not only invasive species have impacted the area. Also species have disappeared but on top, the whole systems has passed through a period of serious eutrophication in the late 1970-ties – early 1980-ties. Furthermore, the area has gone thought various regime shifts (Weijerman et al., 2005). Therefore, there will not be such a thing as the Balgzand food web, but a series of food webs representing and characterizing the various time periods. To be able the compare the Balgzand food web with other areas in a correct way not only for all the distinct time period food webs need to be constructed but also the long term trends over time need to be analysed.

The PhD project intended to analyse the long-term trends in abiotic and biotic conditions for the Balgzand area, identifying the various periods based on the time of establishing of the various invasive species and the observed regime shifts and construct food webs (ENA's, ecological network analysis) for these periods. Reconstructing the various monitoring series took more effort and time than expected and consequently only a basic Balgzand food web for one of the time periods could be constructed. However, the present information allows also a construction of food webs for the other time periods. Below the main results of WP1 are summarized:

Long term trends in Balgzand

Royal NIOZ is responsible for a number of time series that are still ongoing. In addition, the Dutch government is responsible for and carrying out various monitoring programmes. Most programmes did start around 1970 or later, therefore the present analysis is restricted to the period after 1960.

Wadden Sea temperature and salinity

Daily measurements of sea surface temperature and salinity started already in 1860 from the sea dyke in Den Helder; an initiative for scientific support of the fisheries in the Netherlands. With the transfer of NIOZ from Den Helder in the 1960-ties and the establishment of the NIOZ jetty for seawater inflow, these measurements were performed from the NIOZ jetty. This allowed monitoring the variation of the sea water temperature and salinity. The monthly averages of these data until 1982 were described by Van der Hoeven (1982) and the long-term trends in water temperature and salinity until 2005 were analysed by Van Aken (2008a,b).
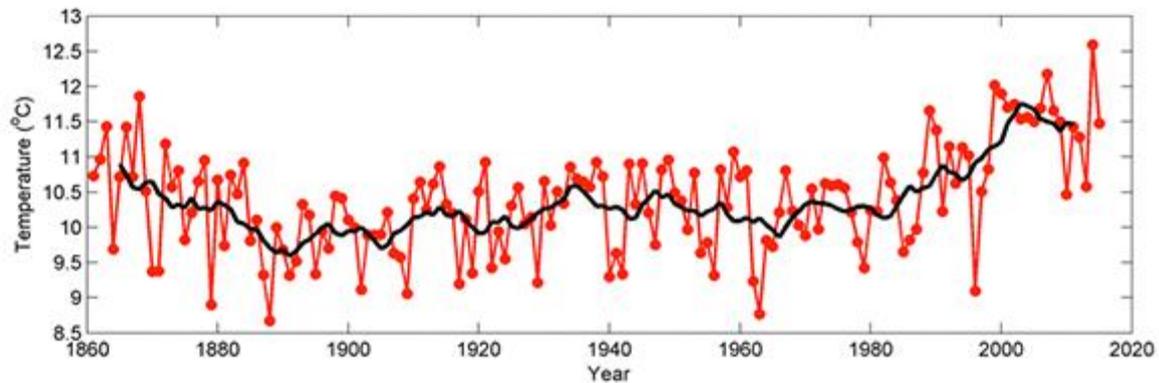
Fig. 2: Mean monthly (red) and mean annual (black) sea water temperature in the western Dutch Wadden Sea. Data: NIOZ (unpubl.)

Mean monthly water temperature shows a clear seasonal pattern but also trends over time (Fig. 2). Mean annual temperature dropped until about 1890 and varied until about 1980. During the last decades, mean annual temperature showed a strong increase. Based on mean annual temperature, at least the following time period can be distinguished:
-period 1960 – 1980
-period around 1990
-period around 2000
-period 2005 – present.
Data are available from the NIOZ database (open access)

Wadden Sea nutrients

Nutrients are main drivers behind local primary production. Long-term field observations mainly collected by the Dutch government were used to construct nutrient budgets for nitrogen and phosphorus for the western Dutch Wadden Sea between 1976 and 2012. For phosphorus, the previous period from 1950 – 1980 was already analysed by van Raaphorst & van der Veer (1990).

The Balgzand area and the western part of the Dutch Wadden Sea are under the influence of both river runoff and exchange with the coastal zone of the North Sea. The data show that, as many other estuarine ecosystems in the world, the western Wadden Sea became eutrophic with highest concentrations in phosphorus and nitrogen in the mid-1980s. Improved phosphorus removal at waste water treatment plants, management of fertilization in agriculture and removal of phosphates from detergents led to reduced riverine nutrient inputs and, consequently, reduced nutrient concentrations in the Wadden Sea.

The budgets (Fig. 3) suggest that the period of the initial net gain of phosphorus and nitrogen switched to a net loss in the areas in 1981 for nitrogen and in 1992 for phosphorus. Such different behaviour in nutrients during nutrient increase and reduction may be the result of net import of P and N from the North Sea (being more rich in nutrients than the Wadden Sea at the start of the study period) in combination with a strong sediment import, followed by long-term storage of P in the sediment, and subsequent delayed release of P and enhanced denitrification during the period of maximum eutrophication in the mid-1980s. From 1992 onwards, budgets of P and N were closed by net loss, most probably because P stores were then depleted and denitrification continued.

Under present conditions (less sediment import, depletion of P stores), nutrient concentrations in this area are expected to be more strongly influenced by variations in winddriven exchange with the North Sea and precipitation-driven discharge from Lake IJssel, e.g. as the result of climate change, then during the 1970s and 1980s.
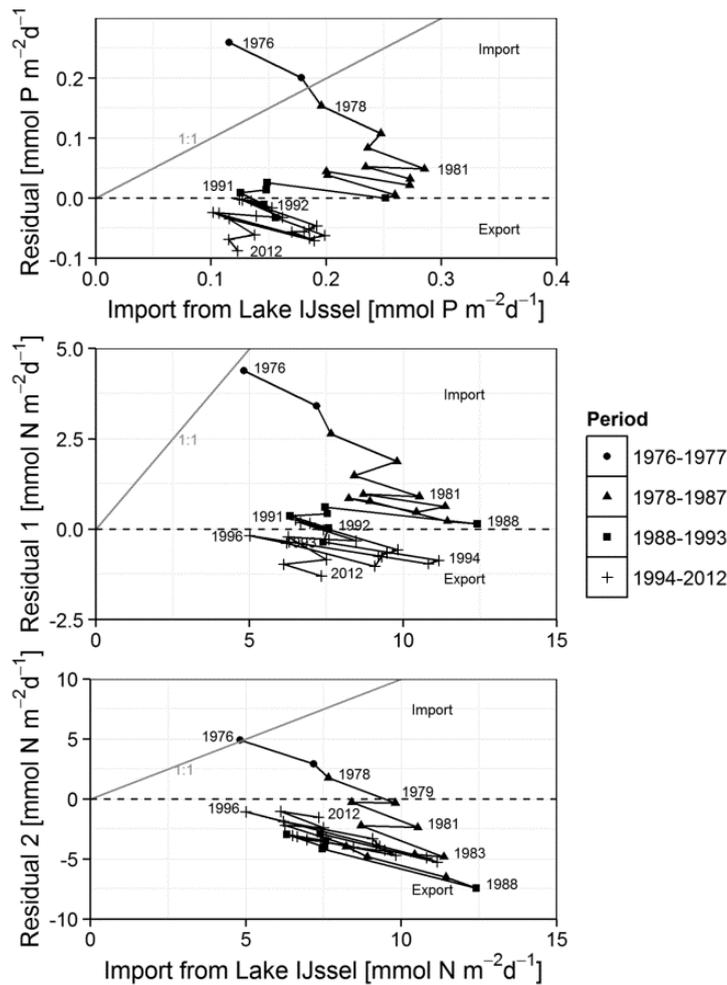
Fig. 3: Closing residuals for the Wadden Sea nutrient budgets versus import from Lake IJssel. Residual of Phosphorous vs import of P from Lake IJssel (A). Residual 1 of nitrogen (B) and Residual 2 of nitrogen (C) vs import of N from Lake IJssel in different periods; grey line represents the 1:1 line, note the difference in the scale of the axes (Jung et al., under review).

This implies that based on the nutrient budgets, at least the following time period can be distinguished:
-period 1960 - 1977
-period 1978 - 1991
-period 1992 - 2012.
The analysed data have been compiled in a manuscript:
Jung AS, Brinkman AG, Folmer EO, Herman PMJ, van der Veer HW, Philippart CJM (2017). Long-term trends in nutrient budgets of the western Dutch Wadden Sea (1976 - 2012). J. Sea Res (under review).

Wadden Sea plankton

In the early 1970s research cruise observations started in the Wadden Sea under the International Biological Programme (IBP) revealed variations in the timing of the phytoplankton spring bloom. It was realised that in order to gain a more precise overview of Wadden Sea primary production and to ensure peaks in the seasonal dynamics were not missed, more regular sampling throughout the year was necessary and hence the phytoplankton observation programme was initiated. Since 1974, bucket water samples have been collected at the NIOZ-Texel sampling jetty, located at the northern side of the Marsdiep tidal inlet between the North Sea and the Wadden Sea (53°00'06"N, 4°47'21"E)

with a sampling resolution of an average 40 times per annum. The first parameters measured were phytoplankton species densities, Secchi disc depth, suspended particulate matter, dissolved nutrients, chlorophyll a, and primary production. The NIOZ Jetty was chosen as sampling location for logistical reasons including ease of access (no boat necessary) and close vicinity to the NIOZ buildings.

Chlorophyll-a

Chlorophyll-a concentration is an indirect index for the phytoplankton biomass (Fig. 4). Mean annual values show low values before the eutrophication event in the late 1970-ties and values at a higher level even since.
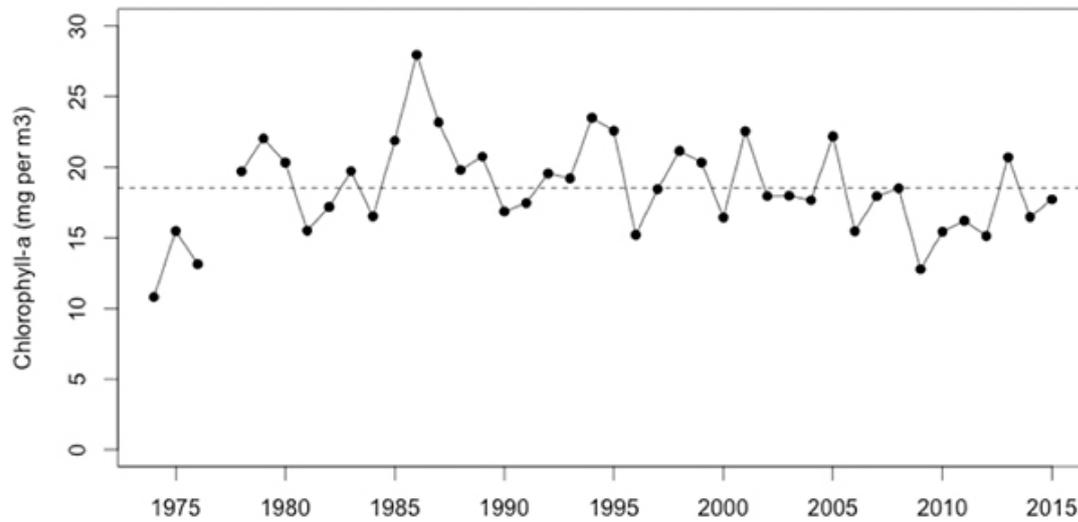

Fig. 4: Mean chlorophyll-a values in the Marsdiep inlet. (NIOZ jetty). Data: NIOZ (unpubl.)

Based on chlorophyll-a concentrations, two different periods can be distinguished:
-period until 1977
-period 1977 to present.
These periods overlapped with those in primary productivity as far as the measurements were consistent, i.e. from 1974 to 2003 (Philippart et al. 2009).

Phytoplankton species composition

Previously to this PhD thesis, three different periods were distinguished with regard to phytoplankton species composition in the western Wadden Sea (Philippart et al. 2000):
-period 1974-1976
-period 1978-1987
-period 1988-1994

In addition, the long-time series of phytoplankton richness has been applied to quantify the exchange of particulate matter between coastal and open waters, being an important and still unresolved issue. With phytoplankton order richness as an innovative marine tracer we tried to identify the geographic position of a coastal exchange zone in the SE North Sea, including its variability in time and space. Previous observations on the dynamics of suspended particulate matter accumulation already resulted in a hypothesized boundary between coastal waters (including the Wadden Sea) and open North Sea waters, the so-called 'line-of-no-return' (Postma, 1984). Along two transects (Terschelling, Noordwijk) in the Dutch coastal zone phytoplankton richness was analysed. Seasonality patterns both for diatoms and flagellates were observed (Fig. 5).

The coastal Wadden Sea was found to be clearly different from the open North Sea, implying that seasonality in Wadden Sea phytoplankton is at least partly driven by local environmental conditions. Seasonality in flagellates was found to be more uniform than seasonality in diatoms. Stations in the coastal North Sea to a distance of 10 km (Terschelling) to 20 km (Noordwijk) from the shore appeared to be at the inside of the 'line-of-no-return'. No long-term trends could be found.
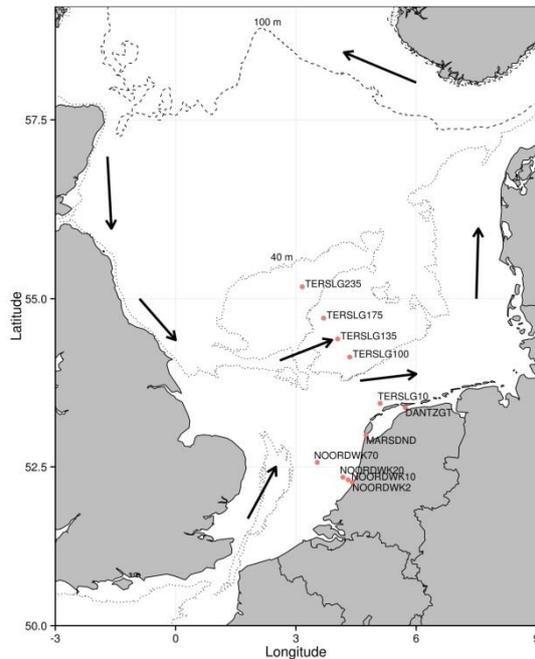

Fig. 5:   Map of study area with stations (points) and basic currents (black arrows) (Jung et al. 2017, in press)

These findings indicate that this approach is a useful aid in exploring mixing of particulate matter between coastal and open waters and to study the responses of phytoplankton communities to environmental drivers.

This implies that based on the phytoplankton species richness no periods could be distinguished.

The analysed data have been compiled in a manuscript:

Jung AS, Bijkerk R, van der Veer HW, Philippart CJM (2017). Spatial and temporal trends in order richness of marine phytoplankton as a tracer for the exchange zone between coastal and open waters. J. mar. biol. Ass UK (in press) Published online: 20 October 2016. DOI: https://doi.org/10.1017/S0025315416001326.

Gelmesozooplankton

Research on zooplankton in the western Dutch Wadden Sea is restricted at NIOZ. There are some zooplankton data for the 1980-ties, and some more extensive time series about gelmesozooplankton

A 50-year high-resolution time series of daily kom-fyke catches, including scyphomedusae showed that species composition and general pattern of appearance has remained the same (Fig. 6): the first species that occurred in spring was *Aurelia aurita*, followed by *Cyanea lamarckii/C. capillata*. *Chrysaora hysoscella* and *Rhizostoma octopus* occurred from June to July onwards. All species appeared earlier in recent decades and first appearance and peak occurrence of *A. aurita* was in part inversely related to previous winter seawater temperature.
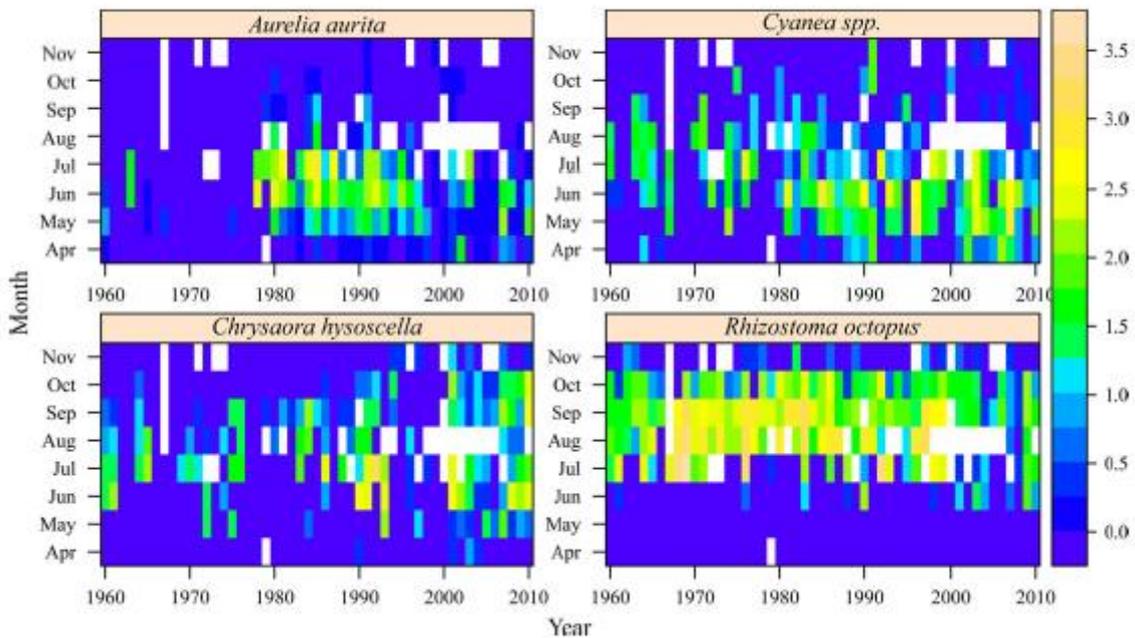
Fig. 6:   Contour plot of base 10 log (n + 1) values of mean daily catch (n day^{-1}), averaged per month for each year. Months in which there was no fishing are white. Data after van Walraven et al. (2015)

The ctenophore *Mnemiopsis leidyi* is one of the successful invaders in the area with a first observation in the western Dutch Wadden Sea in 2006, but maybe already an earlier date of invasion. The impact of *M. leidyi* on the gelatinous zooplankton community in the western Dutch Wadden Sea could be studied by comparing data from before and after its introduction; the periods 1980-1983 and 2009-2012.

Results indicate that gelatinous zooplankton species composition in the western Wadden Sea was largely the same between both periods (Fig. 7). Only the hydromedusa *Eutonina indicans* was absent in recent years and *Cosmetira pilosella* and *Margelopsis haeckelii* were rare species observed only in 2009{2012. *M. leidyi* was present every year since 2006, with high densities in summer and autumn.

Predation pressure by scyphomedusae, ctenophores and hydromedusae on fish larvae and zooplankton in 1980-1983 was low, because of low densities and a temporal mismatch between gelatinous zooplankton and their prey. Despite the decrease in abundance of scyphomedusae in recent decades, the introduction of *M. leidyi* and its large annual blooms has increased the overall importance of gelatinous zooplankton as predators in the western Wadden Sea, whereby *M. leidyi* is responsible for most of the grazing pressure on mesozooplankton in the area.

Rather than outcompeting local species, *M. leidyi* appeared to fill in a previously unoccupied niche in the pelagic western Wadden Sea in late summer and autumn.

This implies that based on the gelmesozooplankton data only two periods could be distinguished
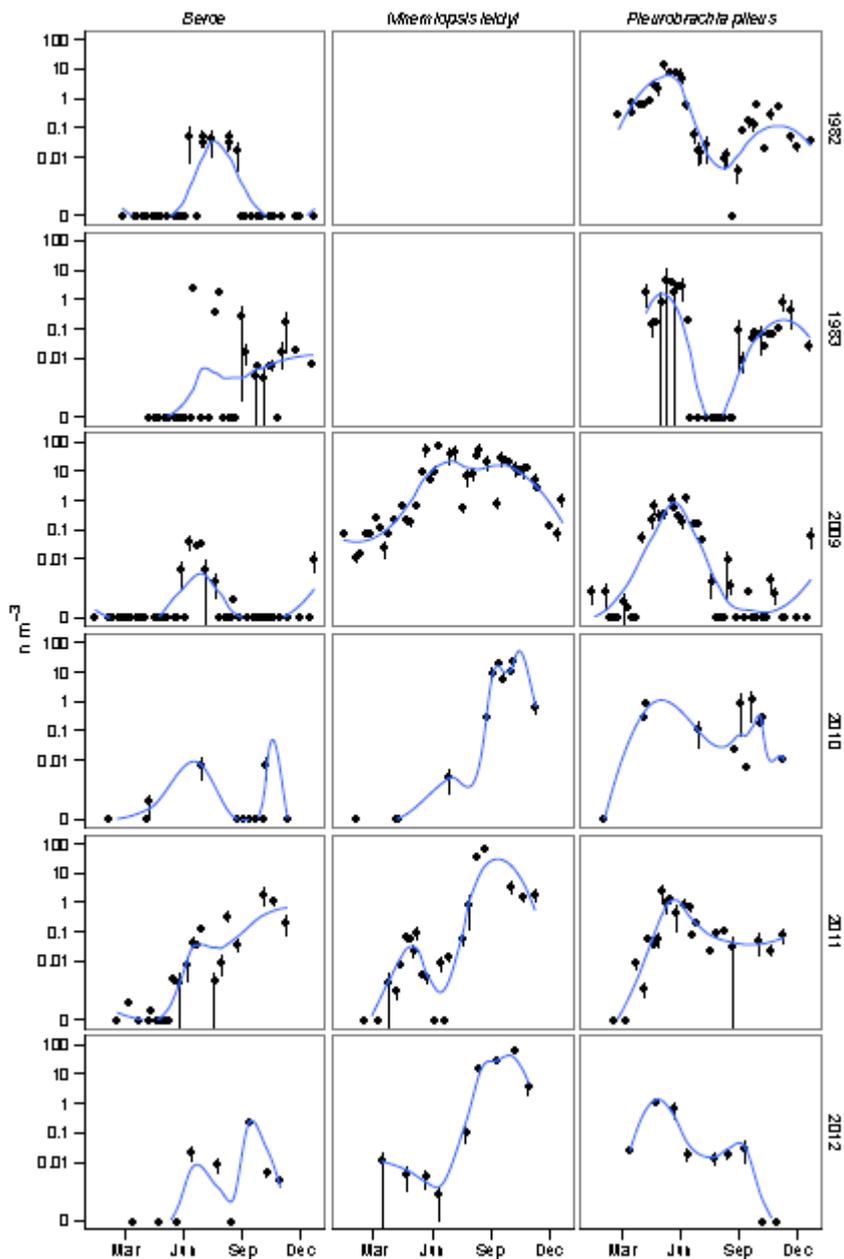-period before 2006
-period after 2006.

Fig. 7:   Mean weekly densities (n m^{-3} + 1e^{-4}) with standard errors for *Pleurobrachia pileus*, *Mnemiopsis leidyi* and *Beroe* spp. in the western Dutch Wadden Sea. A LOESS smoother (span=0.6) is added for interpretation. Data after: van Walraven et al. 2017a

Wadden Sea benthos and higher trophic levels

The higher trophic levels and their interactions were analysed in three different ways: firstly by following coinciding changes in both the macrozoobenthic and the epibenthic community at Balgzand in the western Wadden Sea; secondly by analysing the food web with stable isotopes and thirdly by long term changes in the fish fauna in the western Wadden Sea

Long-term trends in macrozoobenthic and the epibenthic community

Trends in macrozoobenthos and in epibenthic predators were analysed in 24 years over the period from 1975 to 2014 and the potential food intake of epibenthic fish and crustaceans was quantified

23

together with the availability of macrozoobenthic bivalves and polychaetes as a food source. Historical and more recent invasions into the macrozoobenthic community resulted in an increase of relatively large and long-lived bivalves (*Mya arenaria*, *Ensis directus* (2002), *Crassostrea gigas* around 1995) that outgrow their epibenthic predators as well as a polychaete (*Marenzelleria viridis*) that probably became an important food source during the early 2000s.

Whilst bivalves dominated the total biomass of macrozoobenthos, the food availability for epibenthic predators was mainly determined by polychaetes. Predation pressure by epibenthic crustaceans, in particular that of brown shrimp (*Crangon crangon*), on macrozoobenthos almost doubled from 5 to 10 g AFDM m^{-2} y^{-1} during the past decades (Fig. 8).
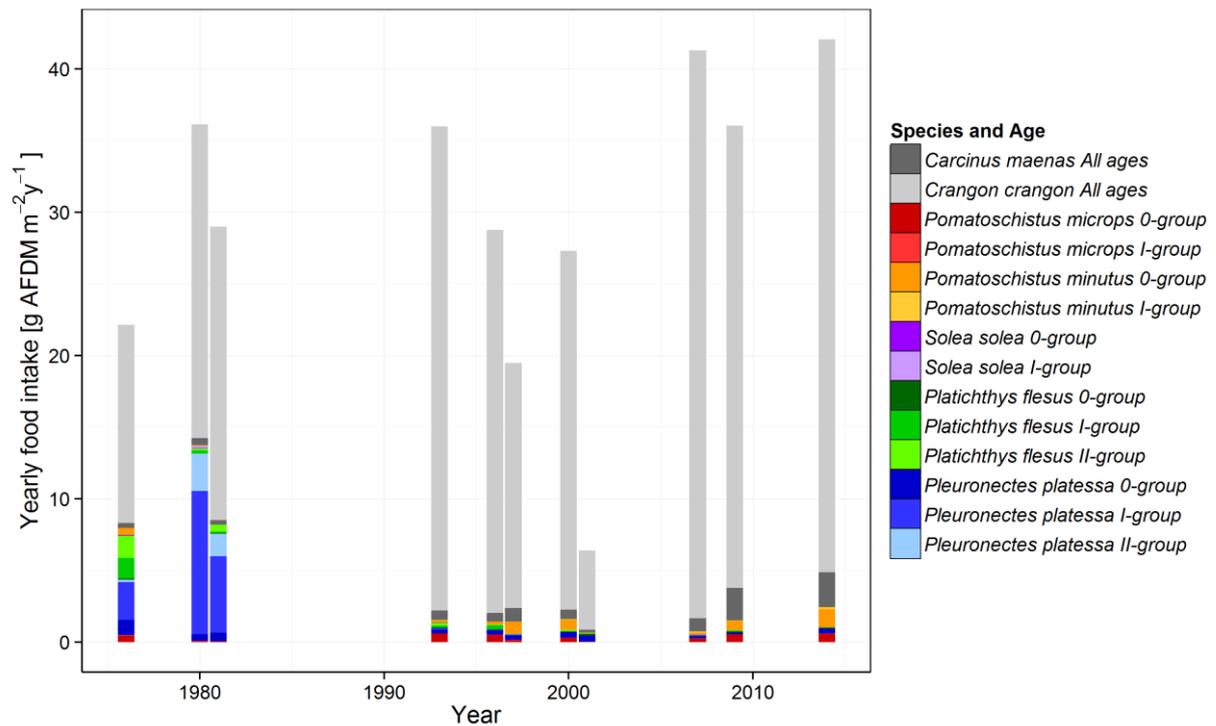

Fig. 8: Yearly food intake of different epibenthic species at the Balgzand intertidal (Jung et al. submitted).

During the same period, the predation pressure by epibenthic fish decreased by more than 80%, mainly due to the disappearance of juvenile plaice (*Pleuronectes platessa*) from the area. Whilst the overall food requirements of the epibenthic predators stayed more or less constant during the study period, the edible fraction of the macrozoobenthic biomass increased from 5 to 20 g AFDM m^{-2} until the 2000s and decreased to 10 g AFDM m^{-2} hereafter. This trend was the result of an increase in *Nereis diversicolor* and *Heteromastus filiformis* in the 1980s followed by the wax and wane of *Marenzelleria viridis*. These findings illustrate that coinciding species-specific changes and interactions of both predators and prey should be taken into account to determine the impacts of invasions on food web structure and functioning of coastal systems.

This implies that based on the long term trends and food consumption estimates, at least the following time period can be distinguished:
-period until 1982
-period after 1991

The analysed data have been compiled in a manuscript:
Jung AS, Dekker R, Germain M, Philippart CJM, Witte JIJ, van der Veer HW (2017). Decadal shifts in intertidal predator and prey communities in the Wadden Sea and consequences for food requirements and supply. Mar. Ecol. Prog. Ser. (submitted)
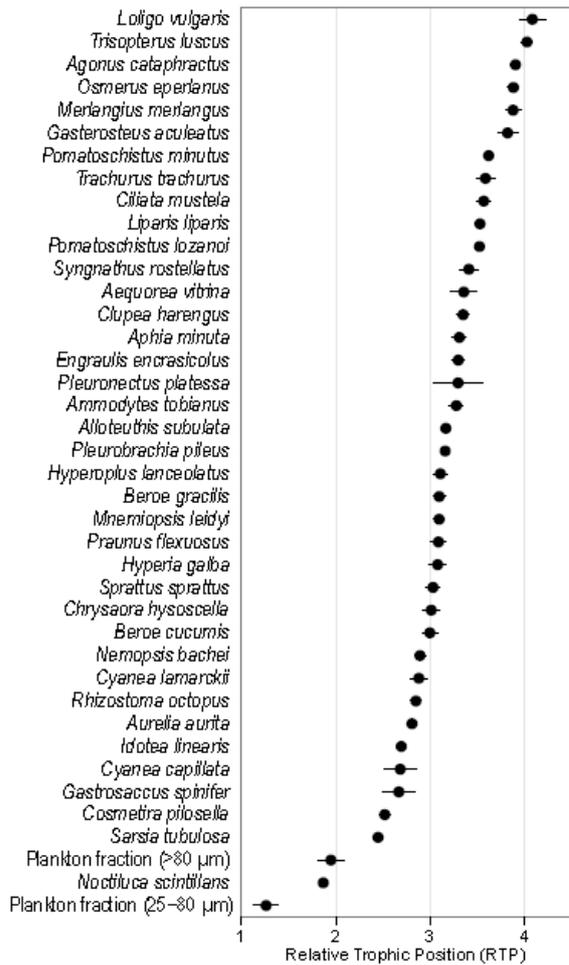
Food web structure

Fig. 9:   Mean Relative Trophic Position (RTP) per species in the western Wadden Sea 2011, ordered highest to lowest. Data van Walraven & Jung (in prep).

The food web structure was determined by analysing stable carbon and nitrogen isotope signatures of fish, scyphozoa, hydromedusa, ctenophores, crustaceans and cephalopods were determined. In addition, the diet of macroplankton and nekton of species in the western Wadden Sea was determined from monthly samples in March-August, 2011 in the Marsdiep area and adjacent tidal gullies. A cluster analysis showed that average 13C and 15N ratios of the invasive *Mnemiopsis leidyi* were similar to those of most other gelatinous zooplankton species and fish species of intermediate trophic level.

Estimation and comparison of isotopic niches for each species in each month showed that the isotopic niche of *M. leidyi* overlaps with that of fish species such as the glass goby *Aphia minuta*, the herring *Clupea harengus* and the horse mackerel *Trachurus trachurus* as well as with that of gelatinous zooplankton species such as the compass jellyfish *Chrysaora hysoscella*, the sea gooseberry *Pleurobrachia pileus* and the hydroid *Nemopsis bachei* in the spring and early summer period, when *M. leidyi* densities are low.

15N of *M. leidyi* was positively related to ctenophore size, suggesting that small ctenophores occupy a lower trophic level than large ones. At the beginning of the bloom period in August when almost the entire population consisted of larvae and juveniles there was no overlap in isotopic niche of *M.*

25

leidyi with that of any other pelagic zooplanktivore. The period of high diet overlap with other consumers is also the period in which *M. leidyi* is least abundant. This suggests that at present, *M. leidyi* is not a significant competitor for other gelatinous zooplankton and fish species. During the bloom period of *M. leidyi* the abundance of competing species is low, suggesting that *M. leidyi* is using an unoccupied niche.

The analysed data have been compiled in a manuscript
van Walraven L, van Looijengoed W, Jung AS, Langenberg VT, van der Veer HW (2017).Trophic
     overlap of the invasive ctenophore *Mnemiopsis leidyi* with other zooplanktivores in the
     western Dutch Wadden Sea. (in prep).

Long term changes in the fish fauna

An ongoing daily sampling programme of the fish fauna in the Dutch Wadden Sea using fixed gear was analysed for the years 1960-2011. Spring sampling caught immigrating fish from the coastal zone and autumn samples reflected emigration of young-of-the-year. In total 82 fish species were caught with no clear trend in biodiversity. In both spring and autumn total daily catch fluctuated and peaked in the late 1970s. From 1980 to the present catches of both pelagic and demersal species showed a 10-fold decrease in total biomass (Fig. 10).
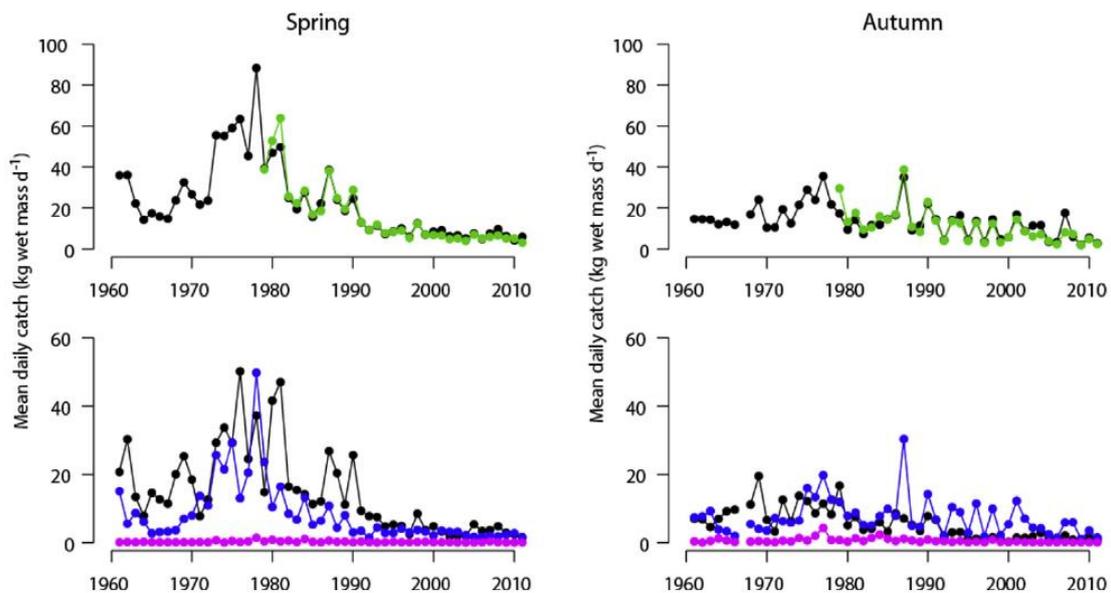

Fig. 10: Trends in total daily catch (kg d^{-1}) in wet mass in spring (left column) and autumn (right column). Top panel: Total daily catch based on direct measurements of fish size (green line) and based on reconstructed size, i.e. fixed ratio (black line); Bottom panel: Daily catch of demersal (black line), pelagic (blue line) and benthopelagic (pink line) fish species (van der Veer et al. 2015).

Mean individual biomass decreased in spring between 1980 and the present from about 150 to 20 g wet weight. No trend was found in autumn mean individual biomass, which fluctuated around 20 g wet weight. The trophic structure remained constant for both the demersal and benthopelagic fish fauna from 1980 to 2011, whilst the trophic position of pelagic fish in spring fell from about 3.9 to 3.1.

Min/max auto-correlation factor analysis showed similar trends in spring and autumn species biomass time series: the first axis represented a decrease from the 1960s followed by stabilization from the mid-1990s. The second trend showed an increase with a maximum around 1980 followed by a steady decrease in spring and a decrease and stabilization from 2000 in autumn. It is argued that

the most likely explanatory variables are a combination of external factors: increased water temperature, habitat destruction in the coastal zone (sand dredging and beach nourishment, fishing) and increased predation by top predators for the first trend, and large-scale hydrodynamic circulation for the second trend. We conclude that both the trophic structure of the coastal zone fauna and the nursery function of the Wadden Sea have been reduced since the 1980s. Our findings corroborate that ecological change in coastal ecosystems has not only occurred in the past but still continues.

This implies that based on the fish fauna four periods could be distinguished
-period 1960 - 1980
-period 1980 - 1990
-period 1990 - 2000
-period after 2000.

The analysed data have been compiled in a manuscript
van der Veer HW, Dapper R, Henderson PA, Jung AS, Philippart CJM, Witte JIJ, Henderson PA (2015). Long–term changes of the marine fish fauna in the temperate western Dutch Wadden: degradation of trophic structure and nursery function. Est Coastal Shelf Sci 155, 156-166

INVASIVE SPECIES IN THE WESTERN WADDEN SEA

It is expected that invasions in the western Dutch Wadden Sea have altered the system in many parts. Since 1960, a variety of species have invaded the Wadden Sea (Wolff, 2005), however only a few species could be ranked as successful and permanent having reached high numbers and biomass values:

The introduced razor clam (*Ensis americanus*) is also established in the Wadden Sea where it can attain large biomass values similar to that of intertidal mussel beds. The role of razor clam beds for the food web of the Wadden Sea has not been assessed. In contrast to Pacific oysters and slipper limpets this species has been reported as food for birds, especially the common scoter (*Melanitta nigra*), perhaps substituting the original prey (*Spisula* spec.) that decreases in some regions.

The recently established Pacific oyster (*Crassostrea gigas*) beds have expanded in 2003-2009 and are probably reduced to an unknown extent by the hard winters 2009/2010 and 2010/2011. The trophodynamic function of this new community is still unknown, although it can be expected that it may increase the filtration potential of the intertidal area but may on the other hand lower the prey potential for foraging mollusc eating birds such as eiders and oyster catchers. Although a quantitative comparison between the trophodynamic function of a native mussel bed and an alien oyster bed is still missing, predation pressure in mussel beds is to a large extent directed to the associated fauna, and this could be also expected for intertidal oyster beds. The control of oyster larvae due to warm and colder summers is reported, however, a biological control of oyster larvae of the species *Crassostrea virginica* by the jellyfish *Mnemiopsi leydii* is reported for the American East Coast and can be also assumed to occur in the Wadden Sea on *C. gigas*, since *M. leydii* has invaded here recently.

An additional strengthening of the filtration potential can be expected due to the recently noticed expansion of the slipper limpet *Crepidula fornicata*. This species tends to form large aggregations in subtidal parts of the Wadden Sea, which were not included in food web descriptions until now. The trophodynamic function of these aggregations is thus still unknown.

The first publications dealing with *Mnemiopsis leidyi* occurrence in the Wadden Sea date from 2006, when reports were published of M. leidyi sightings in coastal waters of Sweden, Germany and The Netherlands. Soon after, reports of *M. leidyi* occurrence in other areas appeared. Even though its occurrence in North-western European waters was only confirmed

in 2006 *Mnemiopsis leidyi* was most likely present there earlier, mistakenly identified as *Bolinopsis infundibulum*. In Dutch waters *M. leidyi* was probably present much earlier than 2006.

During the same period as several of the invasions in the macrozoobenthic community in the Wadden Sea took place, also changes in epibenthic predators were observed whereby actually an inverse invasion took place. Juvenile flatfish, mainly plaice (*Pleuronectes platessa*), declined in the western Wadden Sea between the 1970s and late 1980s). Large brown shrimp (*Crangon crangon*) appears to have increased since the 1990s. Because these predators feed on different food items at different rates, the changes in the epibenthic community must have had consequences for the predation pressure on the macrozoobenthic community.

ENA periods

The various time series all indicate different time period with respect the various trophic levels, however the suggested breaks in the various time periods do not match completely (Fig. 11).
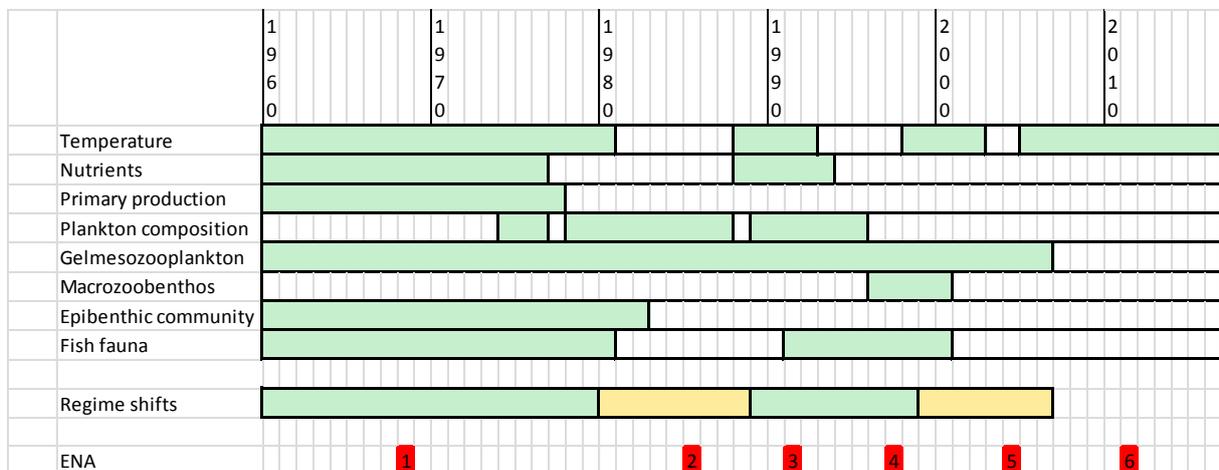

Fig. 11: Time periods (alternately in green and white) for the various trophic levels together with observed regime shifts in the western Wadden Sea (according to Weijerman et al., 2005) and proposed years for different ENS's for Balgzand

The analysis of regime shifts in the Wadden Sea by Weijermans et al. (2005) suggests that at least four different periods can be distinguished with regime shifts in 1979, 1987 and 1999 (Fig. 9), which partly overlap with the shifts between trophic periods in 1979 and 1987 as derived from nutrients and phytoplankton species composition (Philippart et al. 2000, 2007). However, the various time series indicate that four time periods would miss the impact of important invasions. Therefore, for the Balgzand ENA, years are identified covering the most important events (regime shifts and invasive species) (Fig. 11).

PhD results

The PhD project has ended meanwhile and the candidate (AS Jung) is finalizing her thesis with expected date of defence at Utrecht University in mid -2017 (Promotor: prof. dr. Henk Brinkhuis; co-promotors dr. ir. Katja (C.) M. J. Philippart and dr. ir. Henk W. van der Veer
Preliminary content of the thesis is listed below:
Title: Impacts of major invasions in the western Wadden Sea food-web structure since the 1970's
Outline:
Chapter 1: Introduction
Chapter 2: Nutrient budgets of the Marsdiep tidal basin, western Dutch Wadden Sea for 1976 to
          2012

Chapter 3: Spatial and temporal trends in marine phytoplankton richness as a tracer for mixing
    between Wadden Sea and North Sea waters
Chapter 4: Trophic interactions among epibenthic species in the Wadden Sea intertidal: did the
    disappearance of a top predator create an open niche or are other species taking over?
Chapter 5: Possible causes for growth variability and summer growth reduction in juvenile plaice
    Pleuronectes platessa L. in the western Dutch Wadden Sea
Chapter 6: Trophic interactions within the Balgzand food-web as interpreted from stable isotopes
Chapter 7: INFOWEB: Carbon budget/network analysis Balgzand
Chapter 8: Final Discussion and Conclusion

References used in this chapter:
References referring to publications of the entire INFOWEB group are listed Chapter 2.6

Postma H (1984) Introduction to the symposium on organic matter in the Wadden Sea. Neth. Inst.
    Sea Res. Publ. Ser. 10, 15–22.
van Aken HM (2008a). Variability of the salinity in the western Wadden Sea on tidal to centennial
    time scales. J. Sea Res. 59, 121-132.
van Aken HM (2008b). Variability of the water temperature in the western Wadden Sea on tidal to
    centennial time scales. J. Sea Res. 60, 227-234.
van der Hoeven PCT (1982). Observations of surface water temperature and salinity, State Office of
    Fishery Research (RIVO): 1860–1981. KNMI Scientific Report W.R., vol. 82–2, p. 118.
van Raaphorst W, van der Veer HW (1990). The phosphorus budget of the Marsdiep tidal inlet (Dutch
    Wadden Sea) in the period 1950 - 1985: importance of the exchange with the North Sea.
    Hydrobiologia 195, 21-38.
Weijerman M, Lindeboom H, Zuur AF (2005). Regime shifts in marine ecosystems of the North Sea
    and Wadden Sea. Mer. Ecol. Prog. Ser. 298, 21-39.
Wolff WJ (2005). Non-indigenous marine and estuarine species in the Netherlands. Zool. Med. 79,1-
    116.

2.1.3. WP 2: NAHRUNGSNETZMODELL JADEBUSEN

Das Teilprojekt 2 hatte den Aufbau eines Nahrungsnetzmodells mit Hilfe der Ökologischen Netzwerkanalyse (ENA) im Jadebusen zum Ziel. Um ein Nahrungsnetzmodell zu erstellen, benötigt man die Biomasse aller lebenden und nicht-lebenden Kompartimente sowie Informationen zu Stoffflüssen, Atmung und dem Nahrungsspektrum der Arten. Im Ergebnis liefern Nahrungsnetzmodelle detaillierte Informationen zu den Energie- und Stoffflüssen im System, den Interaktionen zwischen den Arten sowie verschiedene Indizes, die zur Bewertung des ökologischen Zustandes und zum Vergleich mit anderen Systemen genutzt werden können.

Datengrundlage bildeten hierbei verschiedene LTER Langzeitdaten von Senckenberg   (z. B. Makrozoobenthos im Eulitoral und Sublitoral, Epifauna, demersale Fischbestände). In Zusammenarbeit mit PD Dr. Holger Freund (Institut für Chemie und Biologie des Meeres (ICBM) wurden weitere Daten zur räumlichen Verbreitung und Biomasse benthischer Diatomeen aufgenommen. Die Nationalparkverwaltung Niedersächsisches Wattenmeer (NPV) stellte Vogeldaten zur Verfügung. In interdisziplinären Feldkampagnen wurden stabile Isotope sowie

Mageninhaltsanalysen verschiedener Benthos- und Fischarten gesammelt, sowie Informationen über Zooplankton und dem Gehalt an organischem Material in der Wassersäule und dem Sediment.

Diese Daten bildeten die Datengrundlage zur Erstellung i) eines Gesamt-Nahrungsnetz-modells, ii) eines Langzeitvergleichs dreier benthischer Nahrungsnetze, die den Zustand aus den 1930er Jahren, den 1970er Jahren sowie 2009 repräsentieren, iii) von fünf benthischen Nahrungsnetzen in verschiedenen Habitaten, um Unterschiede und Gemeinsamkeiten in Struktur und Funktion festzustellen.
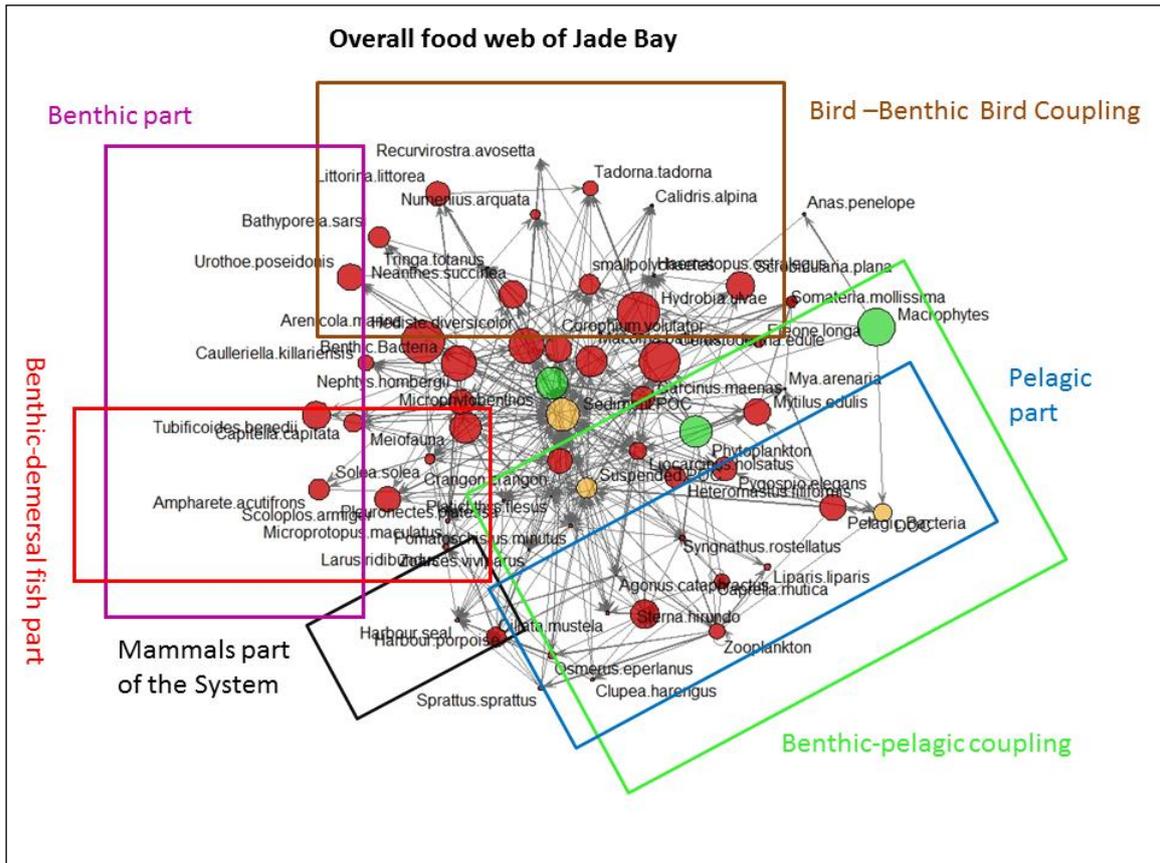
Fig. 12. Das Nahrungsnetz des Jadebusens mit 62 Kompartimenten. Die Kreise repräsentieren die Biomasse. Grün: Primärproduzenten, Gelb: nicht lebende Bestandteile (Detritus); Rot: Arten. Graue Pfeile: Stoffflüsse.

Das Nahrungsnetzmodell des Jadebusens (Fig. 12) mit 62 Kompartimenten besteht aus Primärproduzenten, Bakterien, Zooplankton, Meiofauna, Makro- und Epifauna, Fische, Vögel sowie drei abiotischen Bestandteilen.

Die Größe und Aktivität des Jadebusensystems (Summe aller Energieflüsse durch die Kompartimente) beträgt 3561 mg C m² d^{-1}. Die Energieflüsse werden dominiert von Detritus, Primärproduzenten, Bakterien, Meiofauna sowie *Arenicola marina, Peringia ulvae* und *Cerastoderma edule*. Die Dominanz

an Detritus- sowie Mikrophytobenthos fressenden Arten spiegelt sich zudem in der „Detritivory/Herbivory ratio" mit 1.37:1 wieder.

Der nicht-heimische Gespensterkrebs *Caprella mutica* spielt aufgrund der geringen Biomasse (bezogen auf das Gesamtsystem) keine Rolle im Nahrungsnetz und wird lediglich von Hering (*Clupea harengus*) und der Kleinen Seenadel (*Syngnathus rostellatus*), sowie der eigenen Art als Beute genutzt.

Die Strandkrabbe *Carcins maenas* und die Schwimmkrabbe *Liocarcinus holsatus* gehören mit zu den bedeutensten Räubern im Jadebusen. Die Ergebnisse zeigen einen starken Prädationsdruck auf ihre Beuteorganismen (Fig. 13). Zudem sind sie direkte Konkurrenten. Gleichzeitig haben sie einen positiven Einfluss auf z. B. tiefgrabene Borstenwürmer sowie auf die Phytoplanktonbiomasse, da sie Muscheln dezimieren, die sich wiederum von Phytoplankton ernähren.
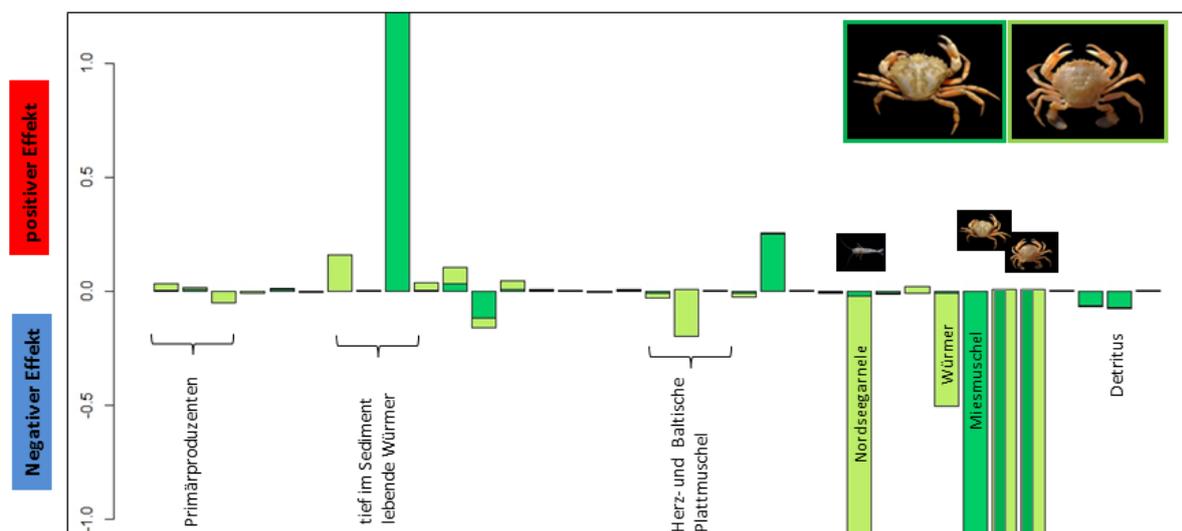
Fig 13. Einfluss von Strandkrabbe (*Carcinus maenas*) und Schwimmkrabbe (*Liocarcinus holsatus*) auf Primärproduzenten und Benthosarten im Nahrungsnetz des Jadebusens.

Seit 2014 arbeitet Dr. Ulrike Schückel mit Prof. Dr. Victor de Jonge (Institute of Estuarine and Coastal Studies, Hull, United Kingdom) und Prof. Dr. Dan Baird (University of Stellenbosch, South Africa) außerdem intensiv an verschiedenen Nahrungsnetzmodellen in der Ems.

Das Gesamt-Nahrungsnetzmodell der Ems besteht aus 57 Kompartimenten und weist eine größere Aktivität von 5286 mg C m² d^{-1} auf, was auf die größere Fläche des Ems-Systems im Vergleich zum Jadebusen zurückzuführen ist. Benthische Bakterien und organisches Material tragen zum größten Anteil an der Gesamtaktivität des Nahrungsnetzes bei, gefolgt von den Primärproduzenten, Meiofauna sowie *Scrobicularia plana, Hediste diversicolor* und *Lemicola (Macoma) balthica.* Die nicht-heimische Wollhandkrabbe (*Eriocheir sinensis*) wird neben der Strand-und Schwimmkrabbe von verschiedenen Fischarten als Beute genutzt.

Die für einen Vergleich von verschiedenen Systemen geeigneten normalisierten Indizes (Finn Cycling Index, Flow Diversity) und die relative Ascendency weisen darauf hin, dass in der Ems mehr Material bzw. Energie vom System wiederverwendet und zurückgehalten wird, während sich der Jadebusen durch eine größere Anzahl von Interaktionen im Nahrungsnetz auszeichnet. Auffällig zwischen beiden Systemen ist der drastische Unterschied in der „Detritivory/Herbivory ratio", die sich in der Ems deutlich mit 8.42:1 im Vergleich zum Jadebusen unterscheidet (Tabelle 2).

Tabelle 2: Vergleich verschiedener Systemattribute und ENA Indizes zwischen Jadebusen und Ems.

	Jade Bay	Ems
number of compartments	62	57
total system throughput (mg C m² d^{-1})	3561	5286
Finn cycling index (FCI, %)	26	33
Flow Diversity	5.28	4.46
Relative Ascendency	0.38	0.45
Detritivory/Herbivory ratio	1.37:1	8.42:1

In Zusammenarbeit mit Prof. Dr. Dan Baird (University of Stellenbosch, South Africa) wurden für den Jadebusen drei benthische Nahrungsnetzmodelle erstellt, die den Zustand in den 1930er Jahren, den 1970er Jahren sowie 2009 repräsentieren (Schückel et al. 2015). Es konnte gezeigt werden, dass Auswirkungen von kalten Wintern, klimatischen Veränderungen (Temperaturanstieg) und anthropogenen Einflüssen (Eutrophierung) nachweisbare Effekte auf die benthischen Nahrungsnetze haben. Im Zuge lokaler Nährstoffanreicherungen im Jadebusen stieg die benthische Biomasse zwischen den 1930er und 1970er Jahren an. Vor allem die filtrierende heimischen Muschelpopulationen, darunter die Miesmuschel (*Mytilus edulis*), Herzmuschel (*Cerastoderma edule*) und Baltische Plattmuschel (*Macoma balthica*), und opportunistische Arten profitierten davon. Auf Grund der Eutrophierung in den 1970er Jahren und dem damit einhergehenden Anstieg der Primärproduktion herrschten kurze Wege innerhalb des Nahrungsnetzes vor, und es wurde nur wenig Energie im Nahrungsnetz wiederverwertet. In der Bewertung sind dies deutliche Hinweise auf ein gestresstes System. Im Gegensatz dazu zeichnete sich die Periode zwischen den 1970er Jahren bis 2009 durch milde Winter, Einwanderung invasiver Arten und geringe Eutrophierung aus. Die seit 1997 vorherrschenden milden Winter führten zu einem starken Rückgang der heimischen Muschelpopulationen aufgrund von ausbleibenden Rekrutierungserfolgen, bei gleichzeitiger

Zunahme von Arten, die sich von benthischen Diatomeen und organischem Material im Meeresboden ernähren (Fig 14).

Fig 14: Zeitliche Veränderung dominierender Kompartimente (dargestellt mittels „throughflow centrality") in den Nahrungsnetzen aus den 1930er Jahren, den 1970er Jahren und 2009.

Unterschiede in Struktur und Funktion weisen auch die Ergebnisse der fünf benthischen Nahrungsnetze in verschiedenen Habitaten auf. Im Rahmen dieser Analyse wurden 4 eulitorale und 1 sublitorales Habitat-Nahrungsnetzmodell untersucht.

Die räumliche Variabilität der Nahrungsnetz-Indizes ist höher in den eulitoralen schlickigen Bereichen im Vergleich zu Sandwatt und dem Sublitoral.

Schlickwatt und Seegras weisen eine hohe Biomasse sowie Primär- und Sekundärproduktion auf. Die benthischen Nahrungsnetze dieser beiden Habitate zeigen die größte Aktivität (Summe aller Energieflüsse, Fig. 15: total system throughput).
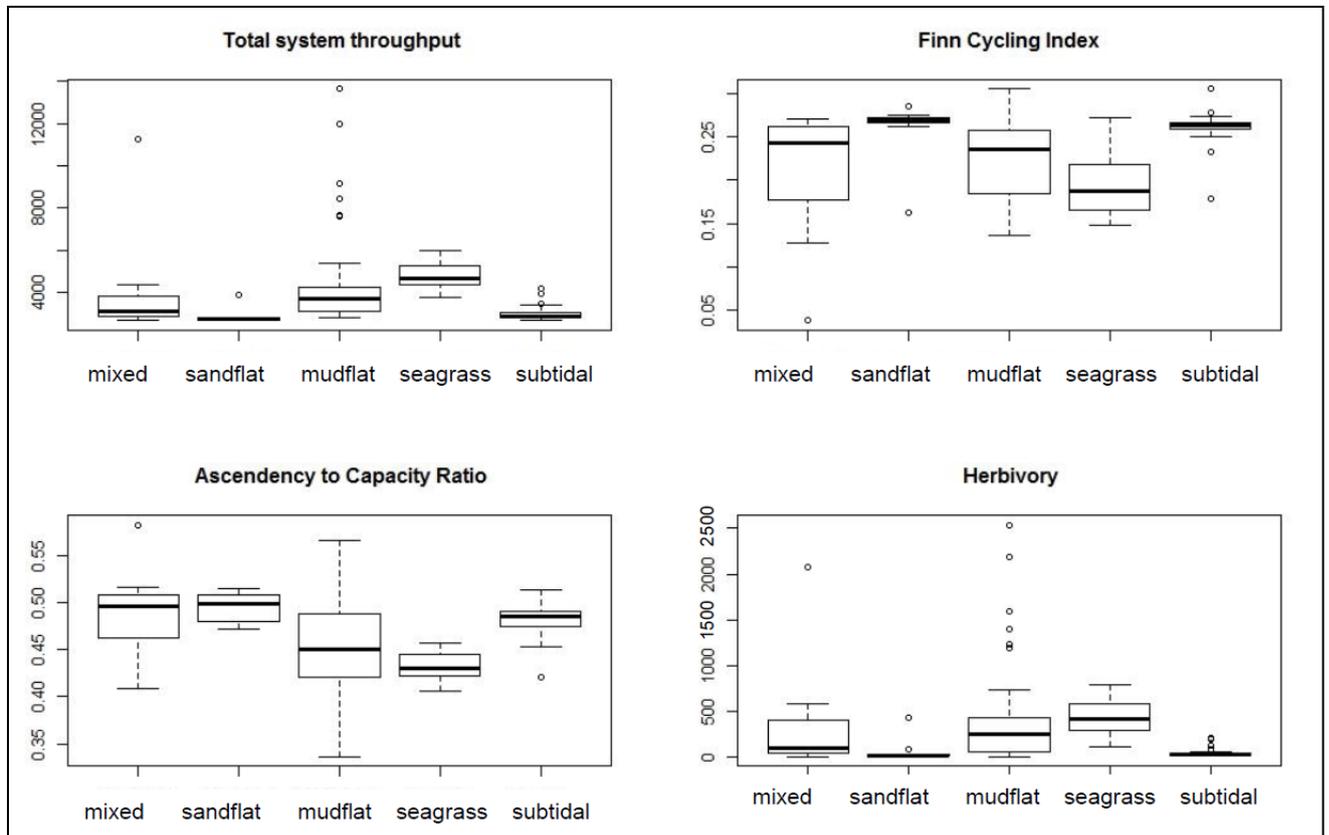

Fig. 15: Räumliche Variabilität verschiedener ENA Indizes aus fünf benthischen Nahrungsnetzen verschiedener Habitate im Jadebusen

Der Finn Cycling Index weist mit 26% in dem exponierten Sandwatt und den sublitoralen Bereichen den höchsten Wert auf, was darauf schließen lässt, dass viel Material vom Benthos wiederverwendet wird.

Einen signifikanten Einfluss auf den „Herbivory Flow" (Fig. 14) und damit auf die trophische Effizienz der trophischen Stufe 1 (Fig 16.) hat die räumliche Verbreitung der Wattschnecke (*Peringia ulvae*). Die Wattschnecke verdriftet bei Hochwasser und kann in den schwach exponierten, schlickigen oder mit Seegras-bewachsenen Bereichen Individuendichten von   >300.000 Ind./m² erreichen. Als „grazer" von benthischen Diatomeen beeinflusst die Wattschnecke maßgeblich die Konsumption der benthischen Primärproduktion und führte zu trophischen Effizienzen von 75% in den Schlickwatten.

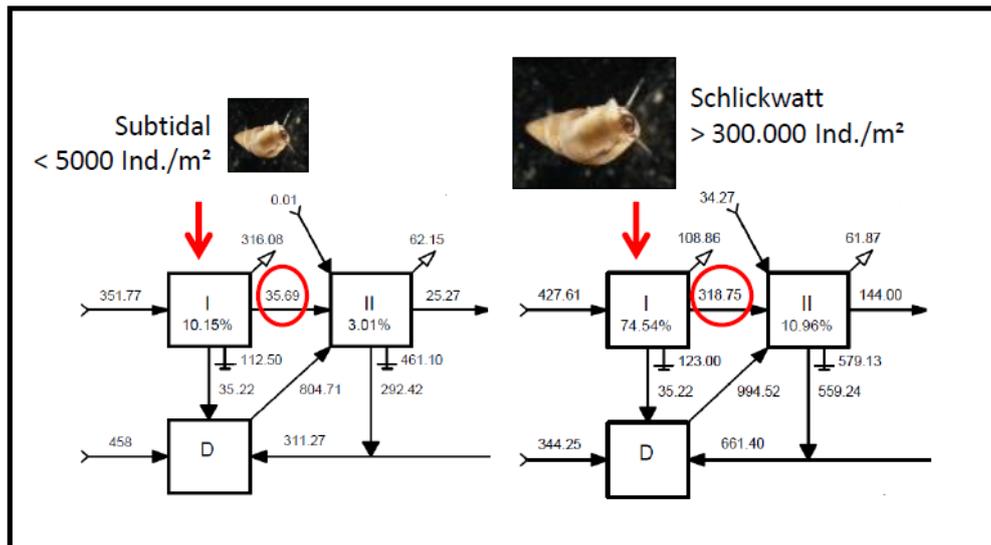Die Wattschnecke konnte als Schlüsselart für das benthische Nahrungsnetz im Jadebusen identifiziert werden.

Fig. 16: Einfluss der Wattschnecke (*Peringia ulvae*) auf die Konsumption der Primärproduktion und der trophischen Effizienz im Sublitoral und dem Schlickwatt.

2.1.4. WP 3: NAHRUNGSNETZMODELL SYLT – RØMØ BUCHT

As a first step to assess the role of invasive species within the food web of the Sylt-Rømø Bight, we constructed different models based on the original model representing the situation in the Sylt-Rømø Bight in 1990 – 1995 (model SRB 1). We constructed two additional models reflecting two different situations, one for the time 2007, when the introduced Pacific oyster *Crassostrea gigas* had the highest biomass (model SRB 2) and an additional model that represents the situation after the hard winter 2009/2010 for the year 2010 (model SRB 3) when the biomass of oysters drastically decreased (Fig. 7).

These three models were all C-based and included about 60 compartments. In addition to the invasive Pacific oyster we included also the Australian barnacle *Austrominius modestus*. Oyster and Australian barnacle increased from virtually zero in 1995 to 15 and 1.3 g C m^{-2}, respectively in 2007 and then decreased to 0.6 and 0.12 g C m^{-2}, respectively, in 2010. Reasons for the increases of oysters and Australian barnacles are related to climate change which favoured strong recruitment of the invasive species during unseasonably warm summers and supported survival of adults during mild winters. The subsequent decline during 2009/10 was due to the cold winter. Results from Ecological network analysis (ENA) showed an increase in most of the system attributes, but a decline in number of cycles, the trophic efficiency, the ascendency ratios, and the relative redundancy from

1995 to 2007 (Table 3). These are ascribed to the impact of the invasive species on system organisation and function. Following the dramatic decline of invasive species from 2007 to 2010 most of the system attributes decreased (Table 3). The variance in biomass and associated flows of other compartments in addition to that of the invasive species has also played a role in the changes in system attributes and function.

Table 3. Global system indices and attributes derived from network analysis of the Sylt- Rømø Bight representing models (SRB1, SRB2, SRB3) over 3 different time periods. Abbreviations see in

System attributes	SRB1 1995	SRB2 2007	Percent change SRB1 to SRB2	SRB3 2010	Percent change SRB2 to SRB3	Percent change SRB1 to SRB3
Number of compartments	59	63		63		
Trophic efficiency (logarithmic mean, %)	5.47	4.82	−11.9	5.91	22.6	8.0
Number of cycles	1197	691	−42.3	737	6.7	−38.4
Finn cycling index (%)	16.61	16.83	1.3	21.59	28.3	30.0
Average path length (APL = TST − Z/Z)	2.69	2.58	−4.1	2.61	1.2	−3.0
Average residence time (ART; days)	19.1	26.5	38.7	24.4	−7.9	27.7
Total system throughput (TST; g C m^{-2} yr^{-1})	6993	8292	18.6	7874.0	−5.0	12.6
Development capacity (DC; g C m^{-2} yr^{-1} bits)	34 608	44 012	27.2	41 341	−6.1	19.5
Ascendency (A; g C m^{-2} yr^{-1} bits)	13 447	15 960	18.7	14 853	−6.9	10.5
Relative ascendency (A/DC; %)	38.9	36.3	−6.7	35.9	−0.9	−7.5
Average mutual information (A/TST, normalized A)	1.92	1.92	0.00	1.89	−2.0	−1.9
Flow diversity (DC/TST, normalized DC)	4.95	5.31	7.3	5.25	−1.1	6.1
Overheads on imports (g C m^{-2} yr^{-1} bits)	3529	5004	41.8	4665	−6.8	32.2
Overheads on exports (g C m^{-2} yr^{-1} bits)	1434	1920	33.9	2216	15.4	54.5
Dissipative overheads (g C m^{-2} yr^{-1} bits)	4672	6519	39.5	6140	−5.8	31.4
Redundancy (R; g C m^{-2} yr^{-1} bits)	11 527	14 610	26.7	13 467	−7.8	16
Relative redundancy (R/DC; %)	33.3	33.2	−0.3	32.6	−1.9	−2.2
Normalized redundancy (R/TST)	1.65	1.76	6.9	1.71	−2.9	3.8
Internal development capacity (DC$_i$; g C m^{-2} yr^{-1} bits)	18 427	22 994	24.8	21 469	−6.6	16.5
Internal ascendency (A_i; g C m^{-2} d^{-1} bits)	6900	8384	21.5	8002	−4.6	16
Relative internal ascendency (A_i/DC$_i$; %)	37.4	36.5	−2.6	37.3	2.2	−0.5
Average internal mutual information (A_i/TST)	0.99	1.01	2.5	1.02	0.5	3.0
Internal redundancy (R_i; g C m^{-2} yr^{-1} bits)	11 527	14 610	26.7	13 467	−7.8	16.8
Normalized internal redundancy (R_i/TST)	1.6	1.8	6.9	1.7	−2.9	3.8
Φ (sum of overheads/TST)	1.38	1.62	17.7	1.65	2.0	20.0
Overall connectance	2.285	2.411	5.5	2.426	0.6	6.2
Intercompartmental connectance	2.843	3.159	11.1	3.030	−4.1	6.6
Food web connectance (living compartments only)	2.283	2.500	9.5	2.398	−4.1	5.0

In the Sylt – Rømø Bight the Pacific oyster *Crassostrea gigas* is one of the most conspicuous invasive species that has been introduced to the system by oyster culture activities already in the early eighties of the last century. In 2001 first specimen were found in the wild on mussel beds outside the culture, and showed an increase in biomass in the following years (Fig. 17). In 2007 it shows a maximum density at the mussel beds and formed also pure oyster reefs. Spawning of Pacific oysters is promoted by a climate regime of warm summers (19 °C spawning temperature) and survival of the recruits and adults is facilitated in mild winters.
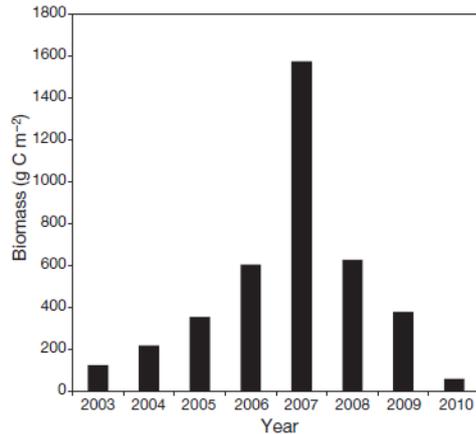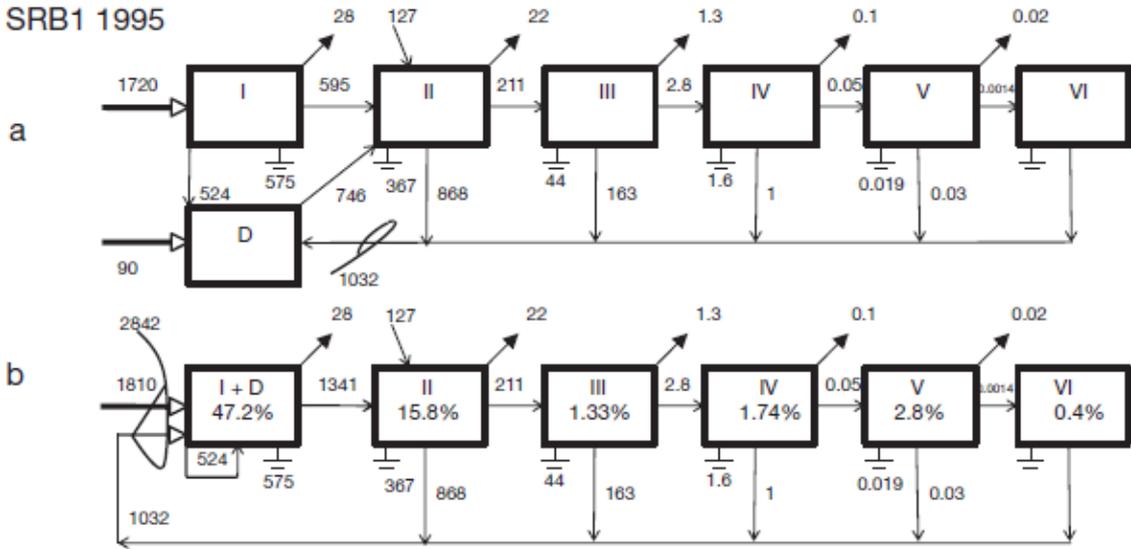
Fig. 17. *Crassostrea gigas*. Trend in the biomass of the Pacific oyster in the intertidal mussel beds of the Sylt- Rømø Bight for the period 2003 to 2010 (data extracted from Büttger et al. 2010)
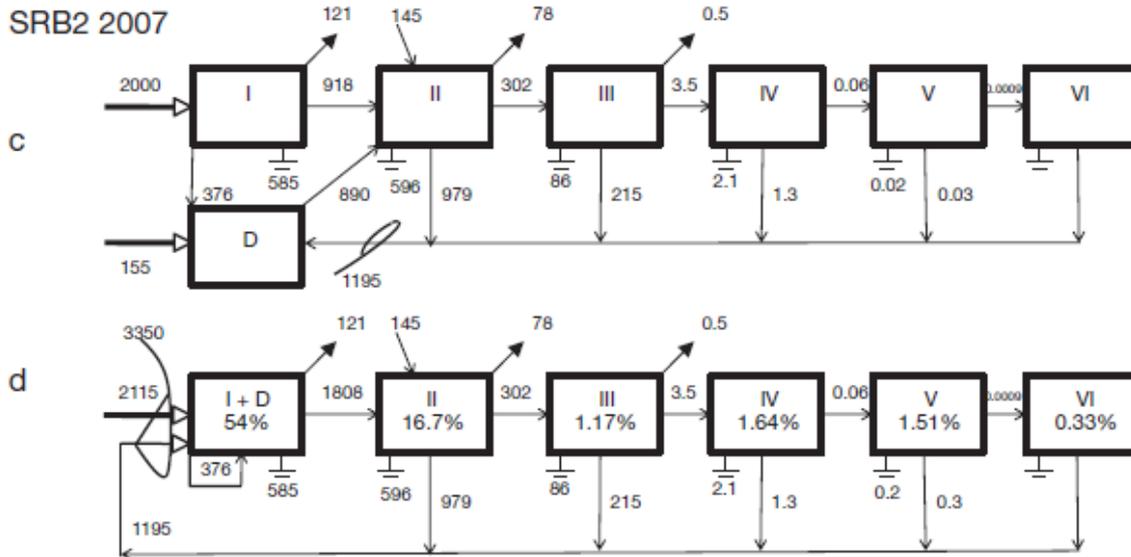
Although the Pacific oyster is abundant and in some years the dominant suspension feeder in the Sylt- Rømø Bight, there was until now no indication on its function within the food web of the Wadden Sea. In contrast to blue mussels, oysters play a minor or not a role as food source for predators such as invertebrates, birds and fish. They therefore accumulate a lot of energy in there biomass whithout transferring it to upper trophic levels.

The carbon flow networks of the 3 models were cast into the simplified Lindeman Spines, illustrated in Fig 18. In the top panel of each model (Fig 18 a, c, e) the detritus pool is separated from the primary producers and shows the relevant amounts of herbivory and detrivory, as well as the returns from each trophic level to the detritus pool and the contribution of plants to the detritus pool. These figures also illustrate that about 56, 50, ad 56 of the total energy passing from the 1st to the 2nd trophic level (TL) consist of recycled material of the SRB1, SRB2, and SRB3 models, respectively and that approximately 92, 89, and 94% of detritus inputs into the respective detritus pools of the 3 models are derived from recycling within the system. Returns from each trophic level and the import into detrital pool, GPP (an energy input into TL I), the canonical exports, and respiration leaving each trophic level are also shown in Fig. 18. When detritus pool and the primary producers are combined in the first trophic level, the inputs and outputs from that level show the total amount of energy passed on to the second level in Fig 18 b,d,f. Roman numerals identify each trophic level, and the carbon received from the previous lower TL to the next higher TL is indicated in the trophic level boxes of each model. Eight trophic levels were identified in each model, although only miniscule amounts (< 0.0005% on average of the initial inputs at level I) were transferred from the fifth to higher TLs so that any effective measure of trophic transfer would hardly be affected by the higher levels. In all 3 models , the efficiency of transfer of the third level is lower than that of TL IV and V which can be ascribed to the relatively high returns of cycled material to the detrital pool from that level (74% on average for the 3 models) The mean trophic efficiencies (ie. the efficiency by which energy is transferred within the system) calculated over the first 3 trophic levels of the SRB1, SRB2, and SRB3 mosdels are, respectively , 5.476, 4.82, and 5.91%; a notable decline was seen in the 2007 model by about 12 % compared to the 1995 model, but was followed by an increase of nearly 23% in 2010 after the decrease in oyster and *Austrominius modestus* abundance.

SRB1 1995

a

1720 28 127 22 1.3 0.1 0.02
I 595 II 211 III 2.8 IV 0.05 V 0.0014 VI
524 575 746 367 868 44 163 1.6 1 0.019 0.03
90 D 1032

b

2842 28 127 22 1.3 0.1 0.02
1810 I + D 47.2% 1341 II 15.8% 211 III 1.33% 2.8 IV 1.74% 0.05 V 2.8% 0.0014 VI 0.4%
524 575 367 868 44 163 1.6 1 0.019 0.03
1032

SRB2 2007

c

2000 121 145 78 0.5
I 918 II 302 III 3.5 IV 0.06 V 0.0009 VI
376 585 890 596 979 86 215 2.1 1.3 0.02 0.03
155 D 1195

d

3350 121 145 78 0.5
2115 I + D 54% 1808 II 16.7% 302 III 1.17% 3.5 IV 1.64% 0.06 V 1.51% 0.0009 VI 0.33%
376 585 596 979 86 215 2.1 1.3 0.2 0.3
1195

SRB3 2010

e

1930 205 86 0.6 0.07 0.003
I 756 II 316 III 3.4 IV 0.09 V 0.002 VI
332 640 961 380 936 80 232 1.8 1.4 0.02 0.05
79 D 1169

f

3178 205 86 0.6 0.07 0.003
2009 I + D 54% 1717 II 18.4% 316 III 1.08% 3.4 IV 2.65% 0.09 V 1.51% 0.002 VI 0.33%
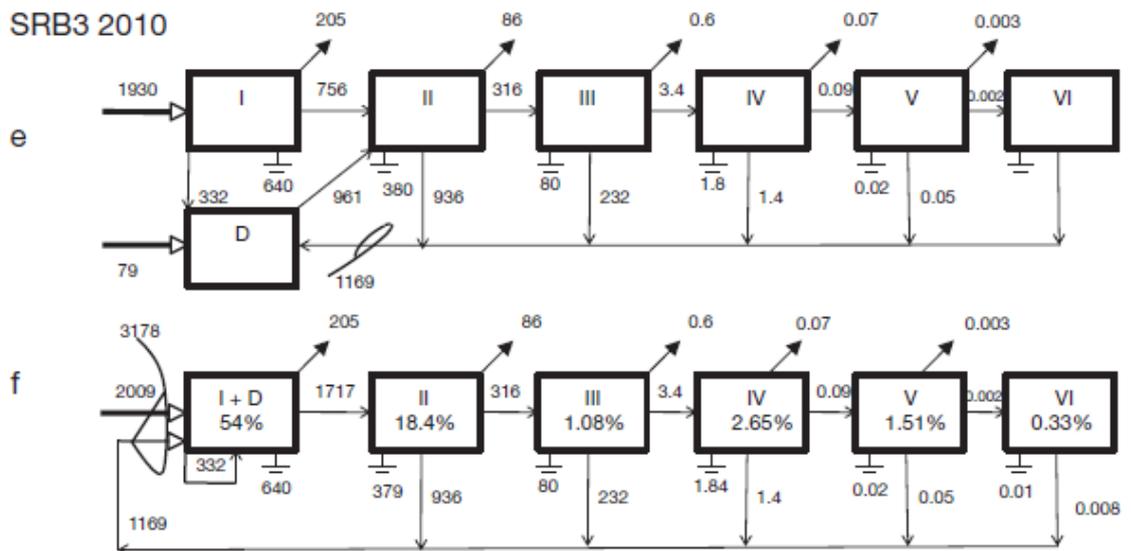332 640 379 936 80 232 1.84 1.4 0.02 0.05 0.01 0.008
1169

Fig.18: The Lindeman Spines for each of the 3 models (a,b) SRB1 (1995), (c,d) SRB 2 (2007) and (e,f) SRB3 (2010). In panels a,c and e the detritus pool (D) is separate from the primary producers at trophic level TL1 (box I) where all the inputs into D are shown as well as the uptake of detritus at TL II. In panels b, d, and f TL 1 and D are merged in the concatenated Lindeman Spines. The percent value in each of the TL boxes gives the amount of input into that level that is passed on to the next higher TL (Trophic transfer in %). Roman numerals in each box indicate the different trophic levels. Open arrows indicate inputs to TL 1 and D, filled arrows indivcate exports from different trophic levels. Arrows between trophic levels (boxes) show amount of carbon passed from the lower to the next higher trophioc level. Respiration at each trophic level is indicated by ⊥. All inputs, exports, respirations, and flows are given in mg C m^{-2} d^{-1}.

IMPACTS analysis performed on the SRB2 model shows that the oyster has negative as well as positive effects on virtually all the system compartments (Fig 19). The oyster has positive impacts particularly on the benthic detritus feeders, benthic omnivores, sediment bacteria and meiobenthos mainly due to a greater detritus production by an oyster reef due to the large amount of egesta that promotes the development of these groups. Indirectly oysters supported zooplankton. Its negative impacts, which are quantitatively greater than the positive effects, are mainly on other suspension feeders that compete for the same energy sources such as phytoplankton and suspended POC, but also on some benthic feeding fish.
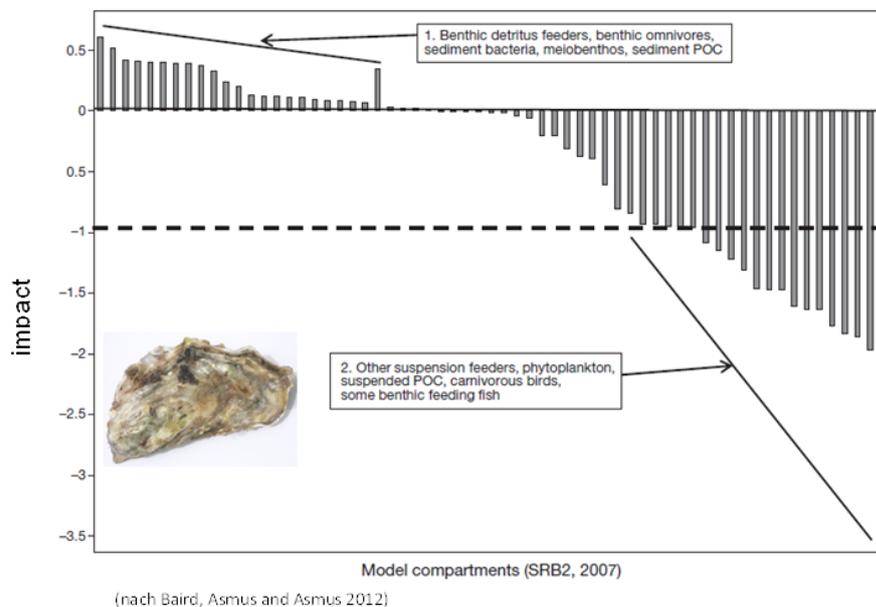

(nach Baird, Asmus and Asmus 2012)

Fig.19: *Crassostrea gigas* . Impact of the Pacific oyster on the on all other compartments of the ecosystem (relative value, estimated from the ENA-routine). Dashed line below the zero line refers to those compartment most affected by the oyster. Box 1 and arrow indicate compartments positively affected by the oyster. Box 2 and arrow indicate the compartments most impacted by the oyster.

Implementation of marine mammals into the Wadden Sea food web model: The harbor seal (*Phoca vitulina*) is the most abundant marine mammal species in the Wadden Sea which plays an important role for marine mammals in terms of resting, nursing and foraging. Due to their large body size and their high abundance in the Wadden Sea, seals exert a strong pressure of predation on their

environment. There are needs to improve the understanding of the trophic behavior of seals in the North Sea and in the Wadden Sea, in order to determine spatio-temporal variations of their foraging activities and to implement better estimations of their diets into food web models.

Trophic markers such as stable isotope and fatty acids have been proven to be a reliable method for the determination of food resources used by marine mammals, and were used to determine the seasonal variation of the diet of the harbor seal from the Sylt-Rømø Bight (See previous report, 2014, 2015). The results of stable isotope and fatty acid analyses revealed two main seasonal trends in the diet of harbor seals from the Wadden Sea/North Sea. Indeed, harbor seals change seasonally their main feeding location, relying more on coastal (i.e. Sylt-Rømø Bight) food resources in the warm seasons than in the cold seasons, when they migrate to the open North Sea to forage. Furthermore, a shift from a diet more strongly influenced by pelagic prey items in spring to a diet of more influenced by benthic prey items in summer was observed in both locations (Sylt-Rømø Bight and North Sea). These seasonal variations in both foraging location and prey items are in accordance with the seasonal variation of the prey species biomass and abundance.

New results and developments (2016):

Abundance and distribution of harbor seals can have a large effect on the structure and the functioning of coastal food webs, and assessing their role in the functioning of ecosystems is a central issue in ecology and management. Ecosystem-based management has been proclaimed as the solution needed to improve the efficiency of ecosystem management measures, contrary to single species based studies. Ecological Network Analysis (ENA) methodologies have been proven to be an efficient tool to study the structure and functioning of a food web. But studies about marine bird and mammal populations are classically based on abundance data, which cannot be directly used to study matter or energy flow within ecosystems. Most of the mass balanced food web models, including ENA are often based on carbon and the flows are therefore expressed in carbon weight per space and time (e.g. mg carbon per m^2 and per day). A graphical realisation of the updated version of the Sylt – Rømø Bight Model is indicated in Fig. 10.
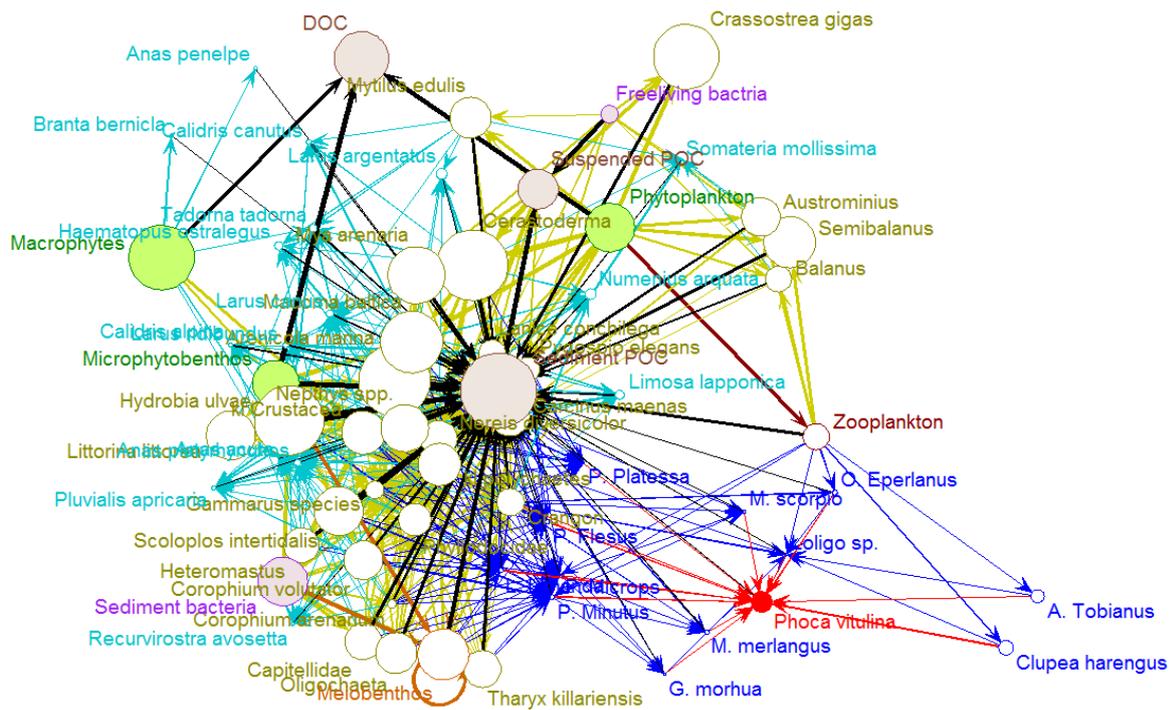
Fig. 20: Updated version of the food web of the Sylt – Rømø Bight including 67 compartments especially harbour seals (red dot) and its prey organisms (fish indicated in blue; birds in blue green; invertebrates in light green; meiobenthos in light brown; non-living compartments. dark brown: primary producers in green).

Essential relationships between fresh weight and other biomass measures such as carbon content were determined 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 for harbor seal. 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.

These conversion factors were then used to include harbor seals and updated biomass of birds in four food web models (one for each season) of the Sylt-Rømø Bight. Ecological Network Analysis (ENA) methodologies were used to assess the seasonal variation of the structure and functioning of the Sylt-Rømø Bight food web, in relation with the presence of top predators (e.g. fish, birds and seals). An "uncertainty analysis" was run on each of the four models to estimate the robustness of the ENA output. The interpretation of the numerous indices and indicators provided by ENA showed that the Sylt-Rømø Bight ecosystem varies seasonally in food web size, stability and resistance in front of external disturbances.

Definition of the indices:

TST = Total system throughput: a high TST reflects a big and active system

FCI = Finn Cycling Index: a high FCI indicates a high proportion of recycled flows in the system

IDF = Ratio of indirect on direct flows: a value greater than 1 can be related to a greater complexity of the web of interaction

APL = Average Path Length: a high value indicates the presence of long cycles

ELD = Effective Link Density: a high ELD indicates a high degree of connectivity in the system and a high number of links flowing into or out of a compartment i

RelOH = Relative Overhead: a high RelOH indicates high system resilience and a high capacity to adapt to novel perturbations. Thus, RelOH is a measure of stability in the meaning of resistance to external disturbances.

Robustness = index combining the organization constraint and the redundancy of the system and therefore measuring and assessing the necessary configuration for sustainability of the system

The results revealed no significant seasonal variation in the whole system indicators. This lack of significant seasonal differences shows that, despite clear seasonal changes in species composition, the general ecosystem functioning is constant all year long. The high hierarchical level of whole system indicators used in this study, provide a broad view of the system but can damp out potentially important signals when describing network attributes, which might suggest a high functional redundancy in the system.

However, some seasonal trends could be observed. In spring and summer, the system is stable, well developed and resistant (Fig. 21a: relatively high values of TST, Fig. 21b: relatively high value of all the indices reflecting the cycling, Fig. 21c: relatively high values of all the indices reflecting the resistance of the system to external perturbations). The winter season is characterized by a small and stable system which is sensitive to external perturbations (Fig. 21a: relatively low value of TST, Fig. 1b: relatively high values of all the indices reflecting the cycling, Fig. 21c: relatively high values of all the indices reflecting the resistance of the system to external perturbations). The system in fall appears to be in an unstable transition state (Fig. 21b: relatively low values of all the indices reflecting the cycling, Fig. 21c: relatively low values of all the indices reflecting the resistance of the system to external perturbations) between these two stable periods (i.e. spring/summer and winter), characterized by a high excess of primary production and a large unevenness of flows.

The higher connectivity and number of parallel pathways observed in spring and summer compared to fall and winter might be explained by the increase of predators in spring and summer. Indeed, the presence of opportunistic predators (i.e. macrofauna and fish species, and seals) relying on

numerous prey species probably increases the number of parallel flows and the pathway length, and therefore the resistance of the system to external disturbances.

The Sylt-Rømø Bight ecosystem is stable and resistant on a yearly basis. Despite the large seasonal variation of species composition and biomass, the whole system indicators are constant across seasons. In spring and summer, the system tends to be more stable, developed and resistant than in the cold seasons, maybe due to the presence of opportunistic predators which seem to have a structural role in the system.

General conclusion: The results from the present study, showed that harbor seals seasonally use the Wadden Sea to forage, and that they probably have a structural role in the system, as the presence of opportunistic carnivorous species seems to increase the stability and resistance of the Wadden Sea ecosystem. The use of ecological network results including top predators, and especially seal species, would improve conservation and management measures in the Wadden Sea.
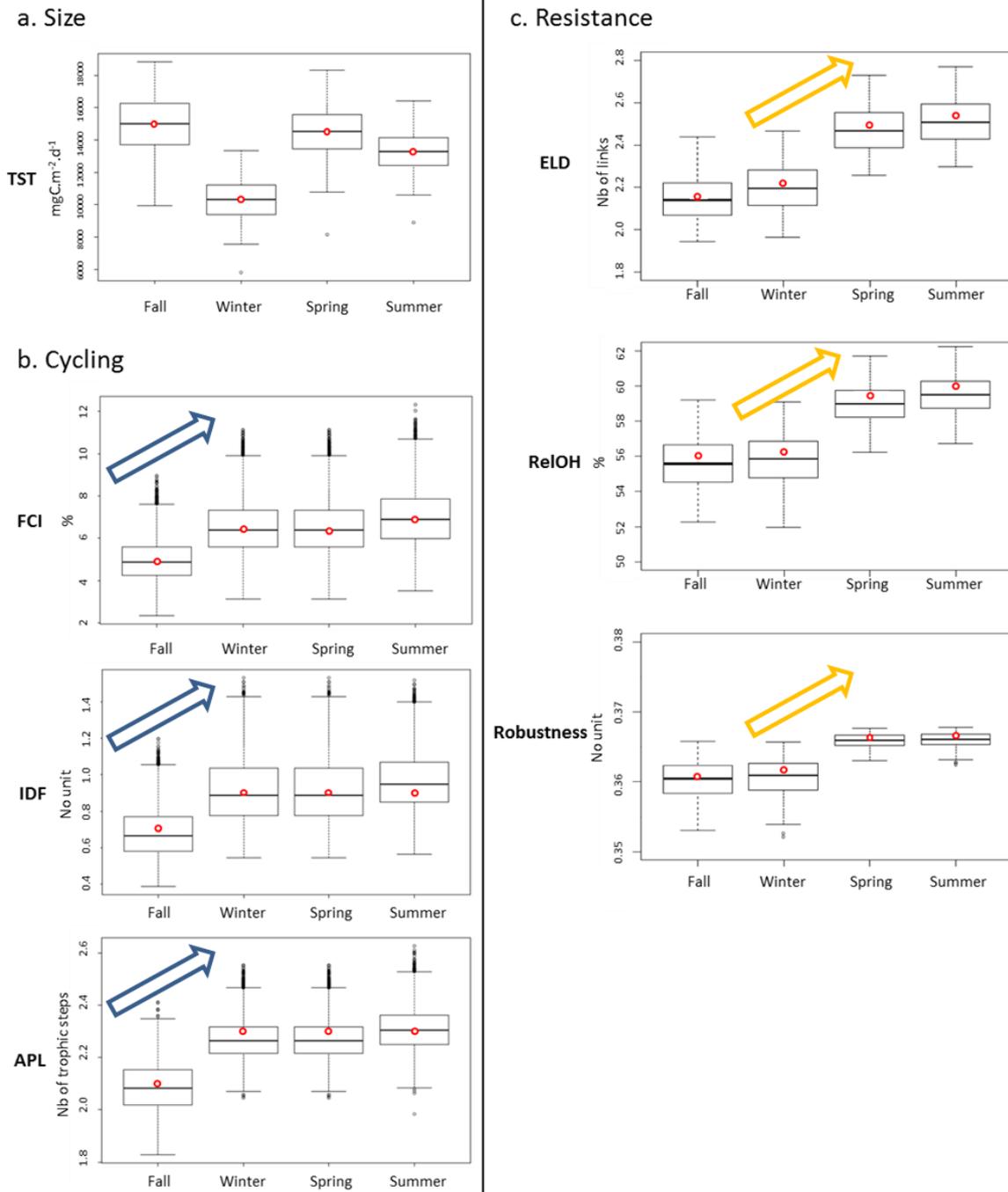
Fig. 21: Whole system indices values per season, based on 10000 plausible network parametrizations. Red circles indicate the values calculated by the initial network parametrization. The median value is shown as a bar in the boxes. The boxes and the whiskers represent the 50%CI and 95%CI respectively.

2.1.5. SONSTIGE ARBEITEN: NAHRUNGSNETZMODELL EMS- ÄSTUAR

In 2014 Prof Dr V.N. de Jonge (Institute of Estuarine and Coastal Studies, Hull, United Kingdom) decided to contribute to INFOWEB by analysing the food web of the Ems estuary. This food web represents an ecosystem that greatly differs from that of the Balgzand, the Jade and the Sylt-Rømø

Bight because it is not a bight or a system with estuarine characteristics but a real estuary with associated gradients in salinity, turbidity, nutrients and temperature. The contribution was carried out in close collaboration with Dr U Schückel (INFOWEB partner Jade, Senckenberg Institut Wilhelmshaven, Germany) and Prof Dr D Baird (University of Stellenbosch, South Africa).

The 80 independent analyses performed made an enormous contribution to the understanding of the functioning of this estuarine food web but also demonstrated benefits and restrictions in using Ecological Network Analysis.

The Ems system was geographically sectioned in three parts (Lower Reaches, Middle Reaches, Dollard) covering channels and intertidal flats. Eighty different analyses were carried out for the three reaches and the entire estuary. The analyses were applied to a full food web covering all species and four fragmented food webs (benthos, full benthos, full fish and full birds). Each flow network consisted of maximally 57 compartments (species and/or functional groups) depicting their respective standing stocks and flows of energy between them. The food web models were analysed in their unbalanced and balanced states. The efficiency of the flow structure (relative ascendency) for the full food web at the species level increased in upstream direction from 0.39 at the Lower Reaches (LR), 0.51 at Middle Reaches (MR) to 0.54 in the Dollard (DO). The mean trophic efficiencies were higher in the LR (2.29%) than the other two reaches (MR: 1.35%, DO: 1.75%). Carbon cycling (Finn Cycling Index) increased in the upstream direction from 0.16 (LR), 0.45 (MR) to 0.52 (DO). The analyses indicate that naturally unbalanced systems should not be balanced with the offered mathematical routine because the results then suggest an increased carbon flow efficiency compared to the unbalanced situation and also an unexplainable change in the positioning of the MR compared to the other reaches. Fragmented food webs can further not be used as indicator for the status of the entire estuarine system because the original range in the relative ascendency for the full food web for the different reaches at the species level of ~0.4 to ~0.55 then increases by a factor of 2.3. The most intriguing figure of this work (submitted to MEPS) can be summarized in Fig. 22.
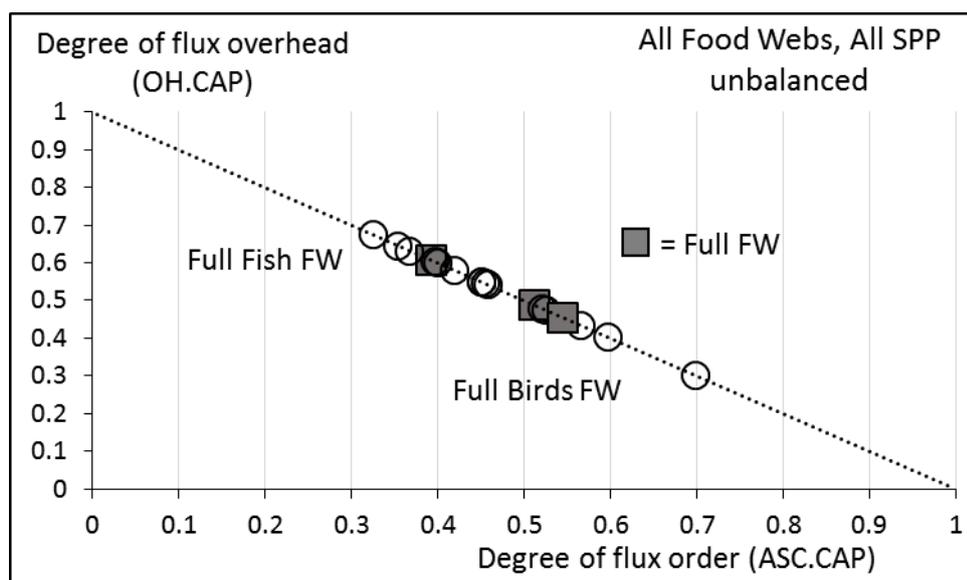

Fig. 22: Plot of the relative overhead (OH.CAP) versus the relative ascendency (ASC.CAP) for the Full Food Web and the 4 fragmented Food Webs represented by All Species (full quadrats) of the Lower

Reaches, Middle Reaches and the Dollard and for an unbalanced carbon flow state.

The above figure clearly shows the variation in the values that occurs only as a result of analysing just parts of the total food web instead of the full food web.

Another result (paper in preparation) is that we have been successful in connecting biodiversity as proxy for the 'system structure' with relative ascendency (or relative overhead) as proxy for the 'system functioning' in a way that opens possibilities for application for assessing the ecosystem status under several European Environmental Directives (Water Framework Directive, Marine Strategy Framework Directive, Maritime Spatial Planning Directive and more).
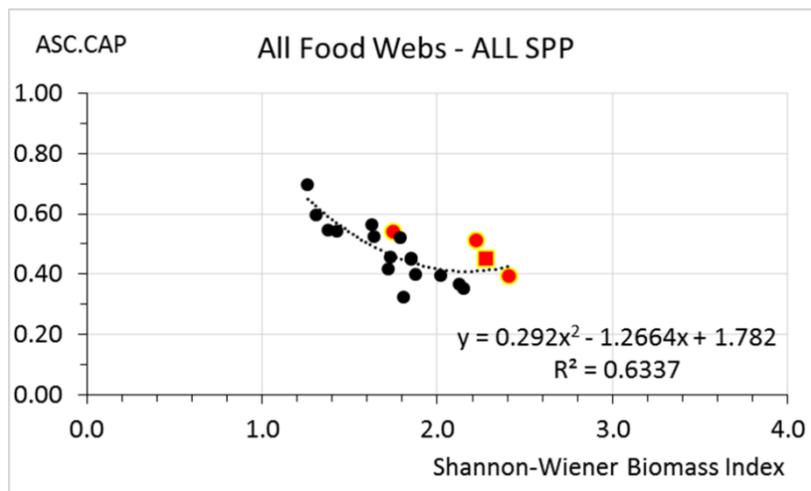

Fig. 23: Plot of the relative ascendency (ASC.CAP) against the Shannon-Wiener Biomass Index for the studied Full Food Web and the 4 fragmented Food Webs as carried out for the most detailed level (All SPP) of Lower Reaches, Middle Reaches and Dollard and for an unbalanced carbon flow state.

2.2 WICHTIGE POSITIONEN DES ZAHLENMÄSSIGEN NACHWEISES

Aufgrund der Konstruktion des INFOWEB Projektes haben die beteiligten Partner den zahlenmäßigen Nachweis mit entsprechenden Positionen gemäß Einzelbewilligung einzeln zu erbringen. An dieser Stelle wird darauf verwiesen.

2.3 NOTWENDIGKEIT UND ANGEMESSENHEIT DER GELEISTETEN ARBEIT

Durch die Beteiligung von nur insgesamt 3 verschiedenen Institutionen (NIOZ, Senckenberg; Alfred-Wegener- Institut) am INFOWEB Vorhaben waren keine Personalmittel zur Koordinierung der Arbeiten beantragt.

Die Ziele des Vorhabens wurden durch das Zusammenspiel der verschiedenen Schwerpunkte der 3 durch Personalmittel finanzierten Doktoranden erreicht in enger Zusammenarbeit mit den assoziierten, integrierten Workpackages, die als Expertenforum fungierten, aber keine Personalmittel erforderten. Reisemittel für Geländearbeiten, Schiffszeiten, Meetings für Diskussionen und Expertenaustausch wurden von dem jeweiligen Institut übernommen.

2.4 VERWERTBARKEIT DER ERGEBNISSE

Es handelt sich in erster Linie um ein Grundlagenforschungsprojekt, das aber Anwendung in Natur- und Umweltschutz findet. Durch die Beurteilung des ökologischen Zustands eines Ökosystems wie dem Wattenmeer mittels Ökologischer Netzwerkanalyse werden Funktion, Struktur und Interaktionen im Ökosystem dargestellt und über spezifische Indikatoren charakterisiert. Diese Indikatoren helfen, den ökologischen Zustand des Systems gemäß EU-Meeresstrategie Rahmenrichtlinie (MSRL) zu bewerten. Die Ökologische Netzwerkanalyse ist als „candidate indicator" vorgeschlagen. Die in diesem Projekt erarbeiteten Ergebnisse tragen essentiell zur Bewertung relevanter Indikatoren des MSRL-Deskriptors Nahrungsnetz (D4) bei.

2.5 STAND VON WISSENSCHAFT UND TECHNIK

Vergleichbare Arbeiten wurden über die Laufzeit des Projektes bis heute nicht verfasst. Andere Veröffentlichungen des Themenkreise auf die die Arbeiten im Projekt Bezug nehmen, wurden im Teil Stand von Wissenschaft und Technik Kapitel 1.3 dieses Berichtes zusammengestellt.

2.6 VERÖFFENTLICHUNGEN

Most project relevant publications by the applying research group

Publications from the INFOWEB project:
(*Publikationen, die aus INFOWEB hervorgegangen sind*)

WP 1: NIOZ - Contribution:

Jung AS, Brinkman AG, Folmer EO, Herman PMJ, **van der Veer HW**, **Philippart CJM** (2017). Long-term trends in nutrient budgets of the western Dutch Wadden Sea (1976 - 2012). J. Sea Res (under review).

Jung AS, Bijkerk R, **van der Veer HW**, **Philippart CJM** (2017). Spatial and temporal trends in order richness of marine phytoplankton as a tracer for the exchange zone between coastal and open waters. J. mar. biol. Ass UK (in press) Published online: 20 October 2016. DOI: https://doi.org/10.1017/S0025315416001326.

Jung AS, Dekker R, Germain M, **Philippart CJM,** Witte JIJ, **van der Veer HW** (2017). Decadal shifts in intertidal predator and prey communities in the Wadden Sea and consequences for food requirements and supply. Mar. Ecol. Prog. Ser. (submitted)

van der Veer HW, Dapper R, Henderson PA, **Jung AS, Philippart CJM**, Witte JIJ, Henderson PA (2015). Long–term changes of the marine fish fauna in the temperate western Dutch Wadden: degradation of trophic structure and nursery function. Est Coastal Shelf Sci 155, 156-166

Van der Veer HW, **Jung AS**, Freitas V, Philippart CJM, Witte JIJ (2016) Possible causes for growth variability and summer growth reduction in juvenile plaice *Pleuronectes platessa* L. in the western Dutch Wadden Sea. J. Sea Res 111, 97-106

van Walraven L, Langenberg VT, Dapper R, Witte JIJ, Zuur AF, **Van der Veer HW** (2015). Long-term patterns in 50 years of scyphomedusae catches in the western Dutch Wadden Sea in relation to climate change and eutrophication. J Plankton Res 37, 151-167.

van Walraven L, Langenberg VT, Daan R, **Van der Veer HW** (2017) Impact of the invasive ctenophore *Mnemiopsis leidyi* on the gelatinous zooplankton community in the western Dutch Wadden Sea. Aquat Invas (accepted)

van Walraven L, van Looijengoed W, Jung AS, Langenberg VT, **van der Veer HW** (2017).Trophic overlap of the invasive ctenophore *Mnemiopsis leidyi* with other zooplanktivores in the western Dutch Wadden Sea

WP 2: Senckenberg- contribution:

Kohlmorgen, L.R. (2013) Temporal changes in the spatial distribution of the macrofauna communities in the sublittoral of the Jade Bay, Germany, Bachelor-Thesis, 62 pp.

Offermanns, C. (2013) Kieselalgenvorkommen im Jadebusen – Quantitative und qualitative Erfassung und Biomasseberechnungen in unterschiedlichen Faziesräumen des Intertidals, Bachelor-Thesis, 59 pp

Schückel, U., Beck, M., **Kröncke, I.** (2013) Spatial variability in structural and functional aspects of macrofauna communities and their environmental parameters in the Jade Bay (Wadden Sea Lower Saxony, southern North Sea). Helgoland Marine Research: 67 Issue: 1: 121-136

Schückel, U., Kröncke, I., (2013) Temporal changes in intertidal macrofauna communities over eight decades: A result of eutrophication and climate change. Estuarine Coastal and Shelf Science: 117 : 210-218.

Schückel, U.; Beck, M.; **Kröncke, I.** (2015) Macrofauna communities of tidal channels in Jade Bay (German Wadden Sea): spatial patterns, relationships with environmental characteristics, and comparative aspects. Marine Biodiversity,45 ,Issue 4 : 841-855

Schückel, U., Kohlmorgen, L.R., **Kröncke, I.** (subm.) Long-term ecological changes in subtidal benthic communities of the Wadden Sea: Overall shift from habitat-structuring to opportunistic species, Journal of Sea Research

Schückel, U., Kröncke, I., Baird, D. (2015) Linking long-term changes in trophic structure and function of an intertidal macrobenthic system to eutrophication and climate change by using ecological network analysis. Marine Ecology Progress Series,536:25-38.

Schückel, U., Beck, M., **Kröncke, I**. (2015) Macrofauna communities of tidal channels in Jade Bay (German Wadden Sea): spatial patterns, relationships with environmental characteristics, and comparative aspects. Marine Biodiversity, doi 10.1007/s12526-014-0308-2

WP 3: AWI- contribution:

Asmus, H. and **Asmus, R.** (2012): Food web of intertidal mussel and oyster beds / J. Wilson and J. Luczkovich (editors) , In: Trophic Relationships of Coastal and Estuarine Ecosystems, Treatise on estuarine and coastal science, Vol.6 E. Wolanski & D. McLusky (eds.), Elsevier, ISBN: 9780123747112 . doi: 10.1016/B978-0-12-374711-2.00627-6

Baird, D. , **Asmus, H.** and **Asmus, R**. (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, Inter-Research, 462 , pp. 143-162 . doi:10.3354/meps09837 , hdl:10013/epic.39878

Niquil, N. , Chaumillon, E. , Johnson, G. , Bertin, X. , Grami, B. , David, V. , Bacher, C. , **Asmus, H.** , Baird, D. and **Asmus, R.** (2012): The effect of physical drivers on ecosystem indices derived from ecological network comparison across estuarine ecosystems , Estuarine, Coastal and Shelf Science, 108 , pp. 132-143 . doi: 10.1016/j.ecss.2011.12.031

Kellnreitner, F. , Pockberger, M. , **Asmus, R.** and **Asmus, H.** (2013): Feeding interactions between the introduced ctenophore *Mnemiopsis leidyi* and juvenile herring *Clupea harengus* in the Wadden Sea , Biological Invasions, 15 , pp. 871-884 . doi: 10.1007/s10530-012-0336-4

Pockberger, M. , Kellnreitner, F. , Ahnelt, H. **, Asmus, R**. and **Asmus, H.** (2013): 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 modelling approach, Journal of Sea Reserach, 86 , pp. 86-96 . doi: 10.1016/j.seares.2013.11.008

Saint-Béat, B. , Vézina, A. F. , **Asmus, R.** , **Asmus, H.** and Niquil, N. (2013) The mean function provides robustness to linear inverse modelling flow estimation in food webs: A comparison of functions derived from statistics and ecological theories , Ecological Modelling, 258 , pp. 53-64 . doi:10.1016/j.ecolmodel.2013.01.023 , hdl:10013/epic.41377

Saint-Béat, B. , Baird, D. **, Asmus, H.** , **Asmus, R.** , Bacher, C. , Pacella, S. R. , Johnson, G. A. , David, V. , Vézina, A. F. and Niquil, N. (2015) Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review , Ecological Indicators, 52 , pp. 458-471 . doi:10.1016/j.ecolind.2014.12.017

De la Vega C., Lebreton B., Siebert U., Guillou G., Lepoint G., Das K., **Asmus R.**, **Asmus H.** (2016). Seasonal variation of harbor seal´s diet from the Wadden Sea in relation to prey availability, PlosOne: 11:e0155727

Horn S., **de la Vega C**. (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

submitted or in preparation:

De la Vega C., Lebreton B., Lehnert K., **Asmus R.,** Siebert U., **Asmus H.** (2016). Stable isotope composition and parasitic infections of harbor seal young-of-the-year used as prey-based diet indicators, Marine Mammal Science (submitted)

De la Vega C., Lebreton B., Asmus R., Siebert U**., Asmus H.** (2016) Shift between spring and summer in the diet of harbor seals of the Sylt-Rømø Bight assessed with fatty acid analysis (submitted)

De la Vega C., Horn S., Baird D., Hines D., Borret S., Fast Jensen L., Schwemmer P., Asmus R., Siebert U., **Asmus H.** (2016) Seasonal dynamics and functioning of the Wadden Sea ecosystem food web (submitted)

Other relevant publications by the applying research group:

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

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

Barrett RT, Camphuysen CJ, Anker-Nilssen T, Chardine JW, Furness RW, **Garthe S**, Hüppop O, Leopold MF, Montevecchi WA, Veit RR (2007). Diet studies of seabirds: a review and recommendations. ICES Journal of Marine Science 64, 1675-1691.

Beusekom JEE van, Buschbaum, C, Loebl M, **Martens P, Reise K** (2010). Long Term Ecological change in the Northern Wadden Sea, In: Müller F, Baessler C, Schubert H, Klotz S (Eds.), Long-Term Ecological Research Between Theory and Application, Springer, 145-153.

Bos OG, Hendriks IE, Strasser M, **Dolmer P** (2006). Estimation of food limitation of bivalve larvae in coastal waters of north-western Europe. Journal of Sea Research 55, 191-206.

Campos J, Bio A, Cardoso JFMF, Dapper R, Witte JIJ, **Van der Veer HW** (2010). Fluctuations of brown shrimp *Crangon crangon* abundance in the western Dutch Wadden Sea, The Netherlands. Marine Ecology Progress Series 405, 203-219.

Dolch T, **Hass, HC** (2008). Long-term changes of intertidal and subtidal sediment compositions in a tidal basin in the northern Wadden Sea (SE North Sea), Helgoland Marine Research 62, 3-11.

Eriksson BK, Van der Heide T, Van der Koppel J, Piersma T, **Van der Veer HW**, Olff H (2010). Human driven regime shifts in soft-sediment systems. Ecosystems 13, 752-764.

Fontaine MC, Tolley KA, **Siebert U**, Gobert S, Lepoint G, Bouquegneau JM, Das K (2007). Ecological variation of harbour porpoises (*Phocoena phocoena*) from Scandinavian waters inferred from trace elements and stable isotopes. BMC Ecology 7, 1, doi: 10.1186/1472-6785-7-1.

Kröncke I, Stoeck T, Wieking G, Palojärvi A (2004). Relationship between structural and trophic aspects of microbial and macrofaunal communities in different areas of the North Sea. Marine Ecology Progress Series 282, 13-31.

Kröncke I (2006). Structure and function of macrofaunal communities influenced by hydrodynamicvally controlled food availability in the wadden sea, the open North Sea and the deep-sea. A synopsis. Senckenbergiana maritime 36(2),123-164

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

Malzahn AM, Hantzsche F, Schoo KL, **Boersma M**, Aberle N (2010). Differential effects of nutrient-limited primary production on primary, secondary or tertiary consumers. Oecologia 162(1), 35-48.

Markert A, **Kröncke I**, Wehrmann A (2010). Recently established *Crassostrea*-reefs vs. native *Mytilus*-beds: Differences in habitat engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). Biological Invasions 12 (1), 15-32.

Musat N, Werner U, Knittel K, Kolb S, Dodenhof T, **van Beusekom JEE**, **de Beer D**, Dubilier N, Amann R (2006). Microbial community structure of sandy intertidal sediments in the North Sea, Sylt-Rømø Basin, Wadden Sea. Systematic and Applied Microbiology 29, 333-348.

Neumann H, **Kröncke I** (2010). Long term effects of sea surface temperature on the ecological functioning of epifauna in the German Bight. Marine Ecology 32 (Suppl. 1),1-9.

Olff H, Alonso DA, Berg MP, **Eriksson BK**, Loreau M, Piersma T, Rooney N (2009). Parallel interaction webs in ecosystems. Philosophical Transactions of the Royal Society B 364, 1755-1779.

Pehlke C, **Bartsch I** (2008). Changes in depth distribution and biomass of sublittoral seaweeds at Helgoland (North Sea) between 1970 and 2005. Climate Research 37, 135-147.

Philippart, C. J., Cadée, G. C., van Raaphorst, W., & Riegman, R. (2000). Long-term phytoplankton-nutrient interactions in a shallow coastal sea: Algal community structure, nutrient budgets, and denitrification potential. Limnology and Oceanography, 45(1), 131-144.

Philippart CJM, Beukema JJ, Cadée GC, Dekker R, Goedhart PW, van Iperen JM, Leopold MF, Herman PMJ (2007). Impact of Nutrient Reduction on Coastal Communities. Ecosystems 10, 187-203.

Philippart CJM, Epping HG (2010). The Wadden Sea: A Coastal Ecosystem under Continuous Change. In: Kennish JM, Paerl H (Eds), Coastal Lagoons: Critical Habitats of Environmental Change. CRC Press - Marine Science Book Series, 399-431.

Philippart CJM, van Aken HM, Beukema JJ, Bos OG, Cadée GC, Dekker R (2003). Climate-related changes in recruitment of the bivalve *Macoma balthica*. Limnology and Oceanography 48, 2171-2185.

Reuter R, Badewien TH, **Bartholomä A**, Braun A, Lübben A, Rullkötter J (2009). A hydrographic time series station in the Wadden Sea (southern North Sea). Ocean Dynamics, 59, 195-212.

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.

Siebert U, Gilles A, Lucke K, Ludwig M, Benke H, Kock KH, Scheidat M (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.

Van Oevelen D, Middelburg JJ, Soetaert K, Moodley L (2006). The fate of bacterial carbon in an intertidal sediment: Modeling an in situ isotope tracer experiment. Limnology and Oceanography 51,1302-1314.

Van Oevelen D, Van den Meersche K, Meysman FJR, Soetaert K, Middelburg JJ, Vézina AF (2010). Quantifying food web flows using linear inverse models. Ecosystems 13, 32–45.

Van Oevelen D, Moodley L, Soetaert K, Middelburg JJ (2006). The trophic significance of bacterial carbon in a marine intertidal sediment: Results of an in situ stable isotope labeling study. Limnology and Oceanography 51(5), 2349-2359.

Van Oevelen D, Soetaert K, Middelburg JJ, Herman PMJ, Moodley L, Hamels I, Moens T, Heip CHR (2006). Carbon flows through a benthic food web: Integrating biomass, isotope and tracer data. Journal of Marine Research 64(3), 1-30.

Van der Veer HW, Freitas V, Koot J, Witte JIJ, Zuur AF (2010). Are epibenthic species at temperate intertidal systems food limited in summer? An analysis for 0-group plaice *Pleuronectes platessa* L. in the Dutch Wadden Sea. Marine Ecology Progress Series 416, 215-227.

Van Walraven L, Langenberg VT, Witte JIJ, **van der Veer HW** (2011). Long term patterns in gelatinous zooplankton in the western Dutch coastal Wadden Sea: trends or regime shifts? Hydrobiologia (in prep.).

Vorträge, die im Rahmen von INFOWEB gehalten wurden:

Presentations at Meetings, Workshops and Symposia

AWI – contributions to Presentations :

Asmus, H. and Asmus R. (2012): Which conditions are stabilising food web functioning? A foresight for the Wadden Sea at WTC Leeuwarden, The Netherlands 13th International Scientific Wadden Sea Symposium (ISWSS) - An integrated approach to emerging challenges in a World Heritage site. 21 – 23.11. 2012:

Asmus H., Asmus R. and de la Vega C. (2014): The impact of biological invasions on the food web of the Wadden Sea (INFOWEB) – an introduction and outlook. 14th International Scientific Wadden Sea Symposium (ISWSS) A foresight for the Wadden Sea at WTC Leeuwarden, The Netherlands

de la Vega, C. and Asmus, H. (2014): Impact of biological invasion on the food web of the Sylt Rømø Bight: a modeling approach with special focus on top predators. PhD days, Helgoland, 5 May 2014 - 8 May 2014 . hdl:10013/epic.45198 <http://hdl.handle.net/10013/epic.45198> Conference -Talk

de la Vega, C. , Lebreton, b. , Asmus, R. , Siebert, u. and Asmus, H.(2014) The impact of top predators on the Sylt-Rømø Bight food web: assessment of harbour seal diet using stable isotope analysis, 5th early career scientists conference for marine and climate research: Natural and

Social Aspect of the Earth System, Bremen, September 2014 - September 2014. hdl:10013/epic.45199 <http://hdl.handle.net/10013/epic.45199> Conference -Poster

de la Vega, C. , Lebreton, B. , Asmus, R. and Siebert, U. (2014): Impact of Top predators on the Wadden Sea food-webs,a modelling approach , Wadden Sea Symposium, Leeuwarden (The Netherlands), December 2014 -.

Horn, S. , de la Vega, C. , Asmus, R. and Asmus, H. (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, Maritimhotel, Bremen, 4 - 7 September 2016 .

Horn, S. , Asmus, R. , Enners, L. , Garthe, S. , Schwemmer, P. and Asmus, H. , (2015): Top-down or bottom-up – The role of birds in the Wadden Sea food web , 50th European Marine Biology Symposium EMBS, Helgoland, 21 - 25 September 2015 .

Horn, S. , Asmus, R. , Enners, L. , Garthe, S. , Schwemmer, P. and Asmus, H. , (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, 6 - 9 September 2015 .

Meetings held at AWI :

Asmus, H., Asmus R., Baird D.,(2012): **-** The impact of biological invasions on the food web of theWadden Sea (INFOWEB)- Introduction into ecological network analysis. Food web analysis workshop 16- 20.4.2012 at the Alfred- Wegener- Institute for Polar and Marine Research, Wadden Sea Station Sylt, Hafenstrasse 43, 25992 List/Sylt

Asmus H. Asmus R. de la Vega C.(2014): The role of biodiversity in food webs. Status Meeting INFOWEB Bilateral Wadden Sea Research 30.9. – 1.10. 2014 at the Alfred–Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Wattenmeerstation Sylt, Hafenstraße 43, 25992 List Sylt.

Asmus H. Asmus R. de la Vega C.(2014): The impact of biological invasions on the food web of the Wadden Sea (INFOWEB). Oral presentation at the workshop on AWI – NIOZ- Cooperation March 2015 at the Alfred–Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Am Alten Hafen 26, 27568 Bremerhaven

de la Vega, C. , Lebreton, b. , Asmus, R. , Siebert, u. and Asmus, H.(2014) The impact of top predators on the Sylt-Rømø Bight food web: assessment of harbour seal diet using stable isotope analysis. Status Meeting INFOWEB Bilateral Wadden Sea Research 30.9. – 1.10. 2014 at the Alfred–Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Wattenmeerstation Sylt, Hafenstraße 43, 25992 List Sylt.

de la Vega, C. and Asmus, H. (2014): Impact of biological invasion on the food web of the Sylt Rømø Bight: a modeling approach with special focus on top predators. , PhD days, Helgoland, 5 - 8 May 2014 .

Horn, S., Asmus, R. and Asmus, H. , (2016): Die ökologische Netzwerkanalyse – Das Wattenmeer als Nahrungsnetz , STopP Statusseminar, 10 - 11 February 2016 .

Meetings held at Senckenberg Institute:

Kickoff Meeting INFOWEB at the 6 -8.3.2012 – Bilateral Wadden Sea Research: The impact of biological invasions on the food web of the Wadden Sea (INFOWEB) at the Institute Senckenberg am Meer, Abteilung Meeresforschung, Südstrand 40, 26382 Wilhelmshaven

Status Meeting INFOWEB 26-27.2.2013: Bilateral Wadden Sea Research: The impact of biological invasions on the food web of the Wadden Sea (INFOWEB) at the Institute Senckenberg am Meer, Abteilung Meeresforschung, Südstrand 40, 26382 Wilhelmshaven

Meetings held at Thünen Institute:
Status meeting INFOWEB 14.4. 2015: Bilateral Wadden Sea Research: The impact of biological invasions on the food web of the Wadden Sea (INFOWEB) at the Thünen Institute for Sea Fishery, Palmaille 9, 22767 Hamburg

Joint AWI/Senckenberg contribution:
Status Meeting PACE 24-25.4.2013: Bilateral Wadden Sea Research: Georisk project meeting: PACE (The future of the Wadden Sea: sediment fluxes: still keeping pace with sea level rise?)

Courses (all held at and organized by AWI Wadden Sea station Sylt.)
Food web analysis workshop 16- 20.4.2012 - The impact of biological invasions on the food web of theWadden Sea (INFOWEB)- Introduction into ecological network analysis at the Alfred-Wegener- Institute for Polar and Marine Research, Wadden Sea Station Sylt, Hafenstrasse 43, 25992 List/Sylt
Ecosystem analysis Wadden Sea; 8-14.6.2012 Introduction into network analysis for students and INFOWEB- participants at the AWI -Wadden Sea Station Sylt.
Food web analysis Wadden Sea; 14-18.1.2013 and Introduction into network analysis for students and INFOWEB- participants at the AWI -Wadden Sea Station Sylt.
Food web analysis Wadden Sea; 10-17.9.2013 and Introduction into network analysis for students and INFOWEB- participants at the AWI -Wadden Sea Station Sylt.
Food web analysis Wadden Sea; 7.-16.7.2015 and Introduction into network analysis for students and INFOWEB- participants at the AWI -Wadden Sea Station Sylt.
Food web analysis Wadden Sea; 19.-28.7.2016 and Introduction into network analysis for students and INFOWEB- participants at the AWI -Wadden Sea Station Sylt.

Studentische Abschlußarbeiten, die im Rahmen von INFOWEB erstellt wurden:

Bachelorarbeiten:

von Palubitzki T. (2013) Gemeinschaftsstruktur und Biomasse von *Sargassum muticum* im Sylter Wattenmeer. Bachelorarbeit Universität Osnabrück. 59 pp

Höfs C. (2013) Long term recruitment patterns of three intrertidal bivalves (Cerastoderma edule, Macoma balthica and mya arenaria) in the Sylt-Rømø Bight –Northern Wadden Sea. Bachelerarbeit, Philipps Universität Marburg. 21 pp

Rische B. (2013) Gemeinschaftsstruktur und Biomasse von Seegraswiesen im Watt der Nordsee Bachelorarbeit Universität Osnabrück.64 pp.

Auch D. (2013) Community structure and biomass of an intertidal oyster bed in Königshafen, Germany. Bachelor Thesis Christian Albrechts Universität Kiel 41pp.

Masterarbeiten

Merkel C.(2015). Ermittlung des Energiebudgets von *Ensis directus* im Eulitoral der Insel Sylt, Diplomarbeit Philipps-Universität Marburg. 51 pp

Busch N.(2012). Untersuchungen zur Nutzung eulitoraler Seegraswiesen durch Wattenmeervögel während des Frühjahrszuges, Diplomarbeit Christian-Albrechts- Universität, Kiel. 119 pp

Promotionen die im Rahmen von INFOWEB erstellt wurden:

De la Vega C. (2016). Influence of top predators on the Wadden Sea food web. Doctoral Thesis in Marine Ecology at the Christian- Albrechts- Universität, Kiel. 221 pp

Jung SA (2016): Impacts of major invasions in the western Wadden Sea food-web structure since the 1970's, Utrecht University (in prep.)

2.7. VERTRAULICHKEIT

Dieser Bericht enthält keine Bestandteile, die zur Wahrung berechtigter Interessen des Zuwendungsempfängers oder Dritter oder aus anderen sachlichen Gründen vertraulich zu behandeln sind.