Long-term changes in the western Dutch Wadden Sea food web and the impact of invasive species

Alexa Sarina Jung

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Long-term changes in the western Dutch Wadden Sea food web and the impact of invasive species

Langetermijn veranderingen in het voedselweb van de westelijke Waddenzee en de invloed van invasieve soorten

(met een samenvatting in het Nederlands)

Proefschrift

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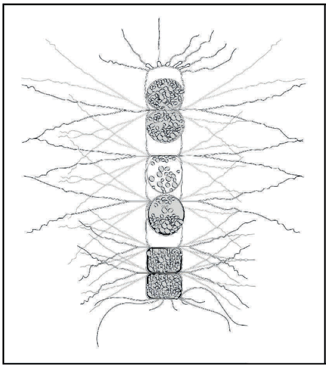
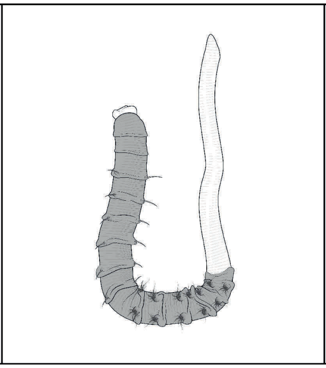
CONTENTS

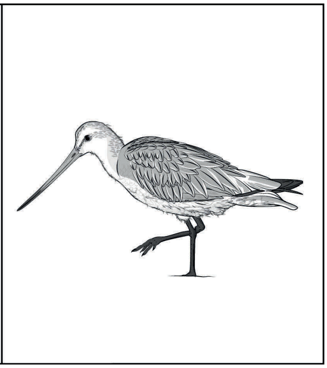
1

GENERAL INTRODUCTION

A. S. Jung







1.1 CONTEXT

1.1.1 *Long-term shifts in the Wadden Sea*

The Wadden Sea is one of the largest intertidal systems in the world; it is located in the south-eastern part of the North Sea following the coastlines of Denmark, Germany and the Netherlands. With its intertidal as well as shallow subtidal flats, drainage gullies and deeper inlets and channels it forms an unique system that, due to its outstanding universal values, became a UNESCO world heritage site in 2009 for the German and Dutch part, and in 2014 for the Danish part (`www.waddensea-worldheritage.org`, Fig. 1.1 left). 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. In addition, the degree of establishment of invasive species and the human impact shows differences due to the geographical region (Reise et al., 2006).

The outstanding values especially include the importance of the Wadden Sea area as nursery areas for a variety of commercial and non-commercial fish species (Zijlstra, 1972) and as a stopover for many migratory bird species that use the area on their migration from northern areas in summer to the wintering grounds in southern Europe and Africa and back (van de Kam et al., 2004; Blew et al., 2005).

Historically the Wadden Sea is relatively young (7500 years old, Flemming, 2002). It is however highly influenced by humans (de Jonge et al., 1993; Lotze, 2005; Lotze et al., 2005). Humans started using the Wadden Sea for food collection (hunting whales, seals and birds, collecting shellfish and fishing) as early as the prehistoric times, but in the last 2000 years this influence has increased. In this time frame humans have been changing the Wadden Sea through habitat destruction, resource depletion and pollution, including excess nutrient supply (Wolff, 1992; Lotze, 2005; Lotze et al., 2005). The introduction of non-native species by humans that became invasive are recorded from the Pleistocene (Strasser, 1998) and around the 13th century (Petersen et al., 1992; Essink et al., 2017) onwards. Since the mid-1980s, the Wadden Sea started to experience the consequences of climate change, including the increase in water temperatures (van Aken, 2008*b*).

These human-induced changes in the coastal environment have left their traces on the habitats and species in the Wadden Sea. The removal of top predators from the food web, such as a reduction in whales, seals and birds (Reijnders and Lankester, 1990) have changed the trophic interactions and top-down control within the system (Lotze, 2005; Lotze et al., 2005). Habitat destruction such as the closure of the Zuiderzee, for example, has changed the hydrodynamics in the western Wadden Sea (Dastgheib and Roelvink, 2012). Increase and decrease in riverine nutrient supply was accompanied by changes in biomass, productivity and species composition of the phytoplankton (van der Veer et al., 1989; Philippart et al., 2000). Introduction of the non-native Pacific oyster in the 2000s resulted in changes in system organization and functioning (Baird et al., 2012). The warming waters resulted in an import of warm-water species and in shifts in phenology, i.e. the timing of seasonal life-history events such as recruitment (Beukema et al., 1998; Philippart et al., 2003; Beukema and Dekker, 2010, 2014; Dekker and Beukema, 2014) and migration (Beukema, 1992; Beukema and Dekker, 2014; Dekker and Beukema, 2014) and fish migration (van Walraven et al., 2017).

Shifts in the relative abundance of species and in the timing of their activities are bound to have repercussions for the trophic interactions within the food web of the Wadden Sea. Removal of top predators may have released small fish and macrozoobenthic species from predation pressure (Strong and Frank, 2010). On the other hand, invasions can have outcompeted native species with the same or a similar trophic niche such as suspension feeding bivalves (Bøhn et al., 2008). The above-mentioned shifts in the timing of recruitment of bivalves and their predator the brown shrimp can lead to match/mismatch situations (Beukema and Dekker, 2014; Dekker and Beukema, 2014).

To improve our understanding of ecosystem functioning of the Wadden Sea, the consequences of these shifts for trophic interactions need to be examined. Such information can be derived from analyses of long-term field observations. For the Wadden Sea such observations exist in many different forms. All countries bordering the Wadden Sea have set up different kinds of monitoring programs and since the early 2000s these efforts are united in the Trilateral Monitoring and Assessment Program (TMAP), which is also used as a basis for the Quality Status Reports (QSR) of the Wadden Sea. Due to the time-consuming efforts of sampling and sample analyses, the temporal resolution of many of those series is restricted to one or two times per year with the timing aligned to expectations with regard to seasonality (e.g. sampling of macrozoobenthos after the winter period to get the surviving biomass of last years recruitment and after summer to include recruits of the new year, Beukema, 1974). This implies that part of a signal in year-to-year variation might be due to shifts in seasonality (e.g. Philippart and Cadée, 2000; Philippart et al., 2010).

1.1.2 *Objectives*

The aim of this study is to identify multi-annual and seasonal changes and variability of several aspects of the Balgzand ecosystem such as nutrients, changes in biodiversity, and changes in trophic interactions. One of the main goals of these investigations is to be able to construct ENA food web models of several decades and examine the changes in the system in terms of trophic structure, cycling and other system properties with a focus on the effect that the invasion of three macrozoobenthic species (*Ensis leei*, *Magallana gigas*, and *Marenzelleria viridis*) had on the system.

Among the most prominent changes within the ecosystem were changes in nutrient supply (de Jonge and Postma, 1974; van Raaphorst and van der Veer, 1990; Philippart et al., 2000), primary production (Cadée and Hegeman, 2002;

Philippart et al., 2010), macrozoobenthic species composition and biomass (Beukema and Cadée, 1997; Beukema and Dekker, 2011), as well as changes in the biomass of different flatfish species (van der Veer et al., 2011). The aims stated above lead to the following research questions:

1. Which changes in the food web, including the invasions, happened on the Balgzand tidal flats over the course of the last decades?
2. Did those changes happened concurrently to each other and, if so, how did they interact?
3. How did these changes influence the trophic interactions between different native and invasive species?

This PhD is part of a larger NWO-BMBF project with multiple PhD and post-doctoral researchers called "INFOWEB" (Impact of invasive species on the Wadden Sea food web). The main aim of the larger project was to investigate the impact of invasions on different parts of the Wadden Sea ecosystem, this can only be understood if the changes in the food web are looked upon in the light of all major changes within these systems.

INFOWEB focuses on the impact of invasive species on the food webs of different intertidal areas of the Wadden Sea: Balgzand, Jade Bay and the Sylt-Rømø Bight (Fig. 1.1). All three areas are well studied and represent typical parts in the different regions of the Wadden Sea and presently exhibit a different degree of establishment of invasive species. Research on the Jade Bay so far showed that the invasive species *M. gigas* and *E. leei* had a higher biomasses in the Sylt-Rømø-Bight that in the Jade Bay, leading to a more specialised system, vulnerable to disturbances in the Sylt-Rømø-Bight (de la Vega et al., 2018).

This PhD thesis focuses on shifts in trophic interactions in the Balgzand area, being the most intensely studied tidal flat system in terms of trophic levels as well as the time frame of data collection in the Dutch part of the Wadden Sea during the last decades. This makes it a perfect study area to be used as a representative of the western Wadden Sea in a comparison of the food webs of different Wadden Sea areas within the framework of the INFOWEB project. Therefore, most of the references and literature of the following sections will be focused on this area and its immediate surroundings.

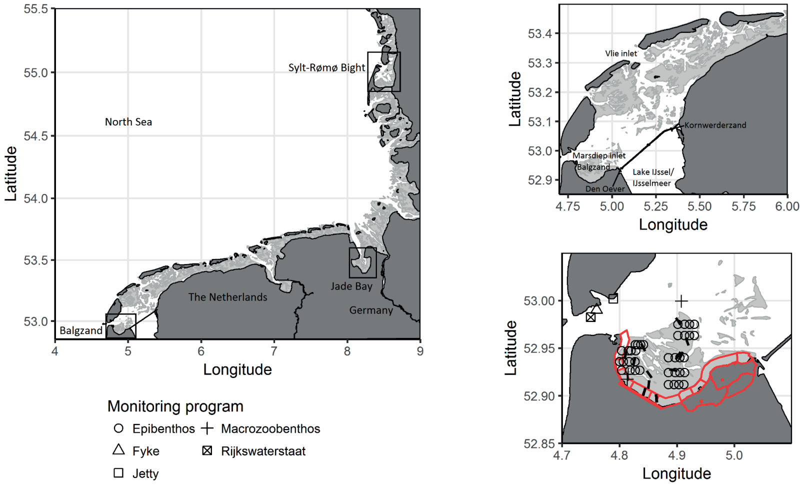


Figure 1.1: Overview map of the Wadden Sea (left) with the different research areas of the INFOWEB indicated in black boxes, the western Wadden Sea (upper right) as well as a map of the sampling stations used for this thesis from several long-term monitoring programs (lower right), for details see Table 1.1.

1.2 STUDY AREA

1.2.1 *Balgzand tidal flat system*

The Balgzand area is an approximately 60 km^2 part in the south west of the Marsdiep tidal basin in the western Dutch Wadden Sea (Fig. 1.1), representing 8 % of the total Marsdiep basin. The tidal flats of the area cover 83 % of the area (50 km^2) and are heavily influenced by the local diurnal tide with a mean tidal range of 1.4 m. Direct freshwater inflow enters the Marsdiep tidal basin mainly from discharges of the Lake IJssel (van Aken, 2008*a*) with annual discharges up to 3000 m^3 s^{-1} and indirect freshwater supply also reaches the area from river runoffs transported via the coastal zone to the Marsdiep inlet (Postma, 1950; Ridderinkhof et al., 1990). As a consequence, salinity in the basin is highly variable and can be down to 0 PSU in front of the sluices from Lake IJssel during discharge. Recent model studies show that most of the freshwater that enters the western Dutch Wadden Sea through the western sluice of the Afsluitdijk (Den Oever, Fig. 1.1 upper right) is circulating the Balgzand area and then leaving the Wadden Sea through the Marsdiep inlet (Duran-Matute et al., 2014).

1.2.2 *Developments during the last decades*

In the past decades the western Wadden Sea has suffered from many threads of the abiotic kind such as an increase in mean sea surface temperature by 1.5 °C in the time between 1980 and 2005 (van Aken, 2008*b*), an increased supply of nutrients (nitrogen and phosphorus) in the 1980s that started to decrease again afterwards (van Raaphorst and van der Veer, 1990; Philippart et al., 2000), pollution that was especially high between 1960s and 1980s due to the use of toxic PCBs and drainage of industrial waste into rivers, which led to high concentrations of heavy metals in the water (Wolff, 1992), an increased fishery in the area (after 1980, Tulp et al., 2008), as well as increased beach nourishments after 1980 (Baptist and Leopold, 2009). Beach nourishment was first done by supplying sand directly on the beach but this method was changed into shore-face nourishment later (Grunnet and Ruessink, 2005; Steijn, 2005) and since 1997 has been applied regularly and since 2001 in higher volumes along the Dutch coastline (Baptist and Leopold, 2009).

Also in the biotic part of the ecosystem changes occurred, sometimes directly depending on the abiotic changes mentioned above. Increases in phytoplankton biomass and production in the 1980s and subsequent declines have been linked to the eutrophication and the efforts to reduce nutrient supply of the European coastal waters in that time (Cadée and Hegeman, 2002). Changes have also been observed in the macrozoobenthic community especially with the almost complete disappearance of mussels and cockles in the early 1990s due to recruitment failure and heavy commercial fishing of these species in the area (Beukema and Cadée, 1996). Within the epibenthic predators a decline of juvenile plaice has been observed (van der Veer et al., 2011) as well as an increase in shrimps (Tulp et al., 2012; Temming and Hufnagl, 2015).

1.2.3 *Historical invasions*

Since its origin, the Wadden Sea system has also undergone the loss and introduction of new species that were not part of the initial ecosystem (Wolff, 2005; Troost, 2010; Beukema and Dekker, 2011). Species can expand or restrict their natural habitat as a consequence of natural processes such as climate change or, alternatively, species can actively be transported to other ecosystems, also over wide geographical ranges (Hulme, 2009). In case these introductions result in surviving and expanding populations these are often referred to as invasive species.

Since several hundreds of years, humans are triggering such transfers. Invasive species that are transferred by humans, unintentionally or intentionally, are called 'introduced'. Introduced invasions usually occur suddenly and show no correlation to environmental conditions. Some invasive species have acclimated themselves with the native ecosystem in such a way that they are now no longer seen as invasive species, they are then called 'naturalized'. A prominent example for such a species is the bivalve *Mya arenaria* at the North Sea coasts, it is believed to have invaded the European coastline twice, first before the Pleistocene (5.0×10^6 to 1.6×10^6 years ago, Strasser, 1998) and then a second time around the 13th or 14th century by the Vikings (Petersen et al., 1992; Essink et al., 2017) and is now seen as part of the native ecosystem. Especially during the last decades, e.g. due to ballast water transport (Reise et al., 1998; Lotze, 2005; Reise et al., 2006), the number of invasive species has increased substantially. Some of the species are intentionally transferred (e.g. *M. gigas* in the Wadden Sea; Troost, 2010), some unintentionally (e.g. *Mnemiopsis leidyi* in the Black Sea, Baltic Sea and the North Sea; Shiganova et al., 2001; Javidpour et al., 2006; Boersma et al., 2007).

Invasions seem to follow a specific pattern (Fig. 1.2 after Reise et al., 2006). They begin with one or more occasions of arrival after which a small group of fully reproducing individuals of the invading species get established in the new ecosystem. This may lead to an exponential growth of the population, after which a phase of adjustment will follow (Essink and Dekker, 2002; Reise et al., 2006). During this phase of adjustment, the population decreases or remains more or less stable in numbers (Reise et al., 2006, 2017). There are different possible causes for this decrease: predators in the recipient community get accustomed to the new prey, an increased abundance of indigenous predators or parasites, low genetic variability leading to poor adaptive strength and decline in genetic vigor (due to small population sizes and an inevitable consanguinity) or loss of specific alleles (Ribera and Boudouresque, 1995; Essink and Dekker, 2002).

Not all invasive species follow this pattern in the same time frame and speed. Some will go through it within several years (e.g. *M. viridis* at the North Sea coast) others will take several decades (e.g. *M. gigas* in the Wadden Sea). Some invaders do have a 'lag' phase during their establishment phase (Reise et al., 2006), that means that they have invaded a specific ecosystem and are reproducing there, but in such small numbers that they have almost no impact on the system. But when favourable conditions occur they will start to expand (e.g. the American slipper limpet *Crepidula fornicata* that arrived with introduced oysters in 1887 and showed only small abundances for long and now is increasing because of milder winters; Thieltges et al., 2004; Reise et al., 2006). Some invaders may never get to the expansion phase and will always occur in small numbers or even get extinct.

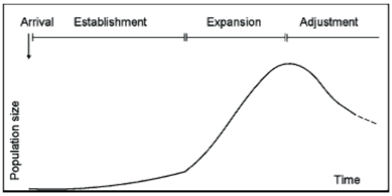


Figure 1.2: Phases in population size of invasive species after Reise et al. (2006).

In the western Dutch Wadden Sea several invasions by alien species were successful and followed the proposed phases in their population sizes. *M. gigas* were first found on the Balgzand in 2001, reached peak biomass (1.9 g AFDM m^{-2}) in 2008, after which the biomass declined again (<1 g AFDM m^{-2}, unpubl. Data, Fig. 1.3). *E. leei* was first detected in 1984 and was then first found in relative low biomass in the area (<1 g AFDM m^{-2}) until a rapid increase occurred in 2005/2006 with biomass values up to 9.7 g AFDM m^{-2}, in the 10 years since then biomass decreased again to levels <5 g AFDM m^{-2} (unpubl. Data Fig. 1.3). The polychaete *M. viridis* was first found in 1989 and occurred in low biomass (<1 g AFDM m^{-2}) in the first 10 years after this it showed a steep increase to a maximum of 7.8 g AFDM m^{-2} in 2003, after which it decreased again to levels around 0.5 g AFDM m^{-2} after 2009 (unpubl. Data Fig. 1.3).

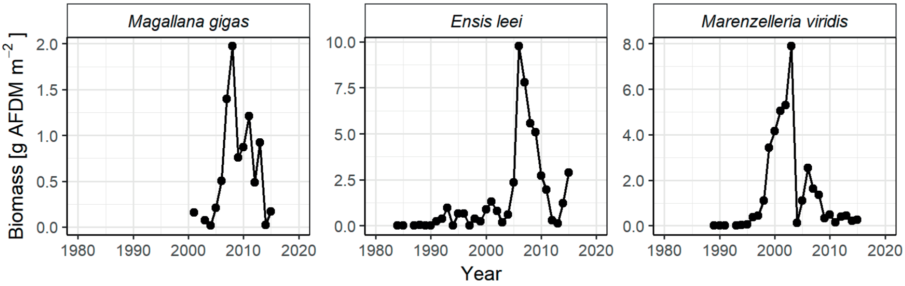


Figure 1.3: Biomass of three common invaders at the Balgzand intertidal in winter, Data courtesy: Jan Beukema & Rob Dekker (NIOZ).

1.2.4 *Seasonal variation*

Not only interannual variations play a role for the functioning of the ecosystem and the food web but also seasonal changes. Within the Wadden Sea this is especially prominent due to its nature as a nursery area for juvenile flat fish and as a stopover area for migratory birds. Seasonal variation however also starts with variation in abiotic parameters. At the Marsdiep tidal inlet mean monthly salinity in the 2000s showed a seasonal pattern with the lowest salinity in February (28.85) and the highest in September (30.72; van Aken, 2008*b*). The mean monthly temperature of the Marsdiep in the 2000s varied between 3 °C in February and 18 °C in August (van Aken, 2008*a*). Nutrients supporting primary production, such as phosphate, nitrogen (in form of nitrate, nitrite and ammonium) and silicate, generally follow a seasonal pattern with high concentrations in winter that are followed by a steep decline in spring and low concentrations in summer after which the concentrations increase again in autumn (Cadée and Hegeman, 2002). Seasonality in pelagic phytoplankton follows the typical pattern of a temperate northern coastal area with a prominent spring bloom that is followed by a weaker autumn bloom (Philippart et al., 2010). However, the height of this autumn bloom seems to be getting smaller over the last few decades (Philippart et al., 2010) thereby shortening the period of ample food supply for consumers. Benthic microalgae (microphytobenthos; MPB) seem to have a peak in their biomass in summer (van der Wal et al., 2010). Many of the macrozoobenthic and epibenthic species show a peak in densities in summer due to recruitment in spring/early summer (Beukema, 1974; Beukema and de Vlas, 1979; Beukema and Dekker, 2010; van der Veer et al., 2011; Beukema et al., 2015) and various fish species visit the area annually during the growing season (van Walraven et al., 2017).

1.3 APPROACH

1.3.1 *Analyses of long-term field observations*

Since the 1970s several long-term monitoring programs (with a length of 10 years or more) have been carried out in the western Dutch Wadden Sea by various research institutes and governmental organizations. They cover nutrients as well as most trophic levels of the food web including phytoplankton, macrozoobenthos, epibenthos, fish and birds. The different programs used in this thesis have been summarized in Table 1.1. Several trophic levels, such as zooplankton and microphytobenthos, are not monitored for the Balgzand area.

These long-term data sets can be used to help with identifying the points of major changes within the Wadden Sea as well as looking at seasonal effects. Afterwards they can be used to build ENA models of the respective phases of change in the ecosystem.

Table 1.1: Overview of long-term field observations used in this thesis in the Marsdiep, the westernmost tidal basin of the Wadden Sea for locations see Fig. 1.1 lower right panel; * data series was not done every year; RWS= Rijkswaterstaat, NIOZ= Royal Netherlands Institute for Sea Research, KNMI = Koninklijk Nederlands Meteorologisch Instituut.

Name	Institution	Variable	Time frame	sampling time	frequency	nr stations
Rijkswaterstaat	RWS	Nutrients	1970-2014	variable	monthly/bimonthly	2
Rijkswaterstaat	RWS	Phytoplankton	2000-2014	variable	monthly/bimonthly	2
Jetty	NIOZ	Phytoplankton	1974-2014	high water	monthly/bimonthly	1
Macrozoobenthos	NIOZ	Macrozoobenthos	1975-2014	variable	February & August	15
Epibenthos	NIOZ	Epibenthos	1975-2014*	high water	monthly/bimonthly	36
Fyke	NIOZ	Fish, Jellyfish	1960-2014	continuous	Spring & Autumn	1
Birds	Sovon	Birds	1980-2014	high tide	monthly	16
De Kooy	KNMI	Air Temperature	1906-2019	continous	continous	1

1.3.2 *Determining trophic interactions*

Within the ecosystem of the western Dutch Wadden Sea and in particular the Balgzand a lot is known about trophic interactions between certain trophic levels (Swennen, 1975; van Beek, 1976; van der Gaag, 1977; van Lissa, 1977; Kühl and Kuipers, 1978; de Vlas, 1979; Afman, 1980; Hummel, 1985; Kamermans, 1994; van der Veer et al., 2011; van Walraven, 2016). Already in the 1980s, first attempts to describe part of the food web or even the whole food web were done (Kuipers and Dapper, 1981; Anonymous, 1988*a*,*b*). However these models were constructed before or during the long-term changes mentioned above. New analysis should be done to assess the effects caused by these changes.

Connections between certain species in form of predator and prey trophic interactions are so far mostly based on stomach content analysis (e.g. Kühl and Kuipers, 1978; Deb, 1997). This type of analysis gives a good overview about potential prey items, however it can only give a snapshot in time with the possibility to miss entire prey items because they do not have any hard body parts that can be found as left overs in the stomach such as bones or otoliths and/or be digested fast (Deb, 1997). In recent years stable carbon and nitrogen isotope analysis have been used as a tool to give additional information on trophic interactions within a food web (among others Fry and Sherr, 1984; Minagawa and Wada, 1984; Fry, 2006).

1.3.3 *Ecological Network Analysis (ENA)*

Assessment of changes in ecosystems on the food web such as the impact of invasive species is not easy and single species approaches are not a reasonable approach to look at these effects on the whole ecosystem. A holistic approach is needed and Ecological Network Analysis (ENA) is such a holistic approach to ecosystem modelling. It looks at flows of one unit (e.g. carbon, nitrogen or phosphorus) through the system via connections over biological compartments. It provides insight into the fundamental functioning of the ecosystem (Ulanowicz, 1980, 1983, 1986; Kay et al., 1989; Mann et al., 1989; Ulanowicz, 1992; Fath, 2015). The methodology of ENA is based on economic input-output theory (Leontief, 1951) and was first applied to ecological systems by Hannon (1973). A set of algorithms was developed for this purpose and the methodological details have been described by Kay et al. (1989); Ulanowicz (2004).

ENA works with compartments that interact with each other in form of flows. Compartments in an ENA model can be everything from species, over genus, to functional groups such as phytoplankton. However, ENA is not a dynamic simulation model but is a static model that analyses a certain point in time depending on the input data. If you want to assess whether an ecosystem has changed over time and how these changes influenced the system the way forward is to construct a number of models covering different time steps with distinctive changes in the ecosystem and compare the results of these models (Miehls et al., 2009*b*,*a*; Schückel et al., 2015). The analyses of such food web models are based on empirical data, which ideally should be obtained by observations or experiments, and depicts a realistic representation of an ecosystem (Ulanowicz, 2004). To establish a quantitative food web model, biomass, respiration, consumption, and egestion of all compartments, and energy flows between the compartments as well as export and import of energy or material from adjacent systems are required to be included in the analysis (Fath et al., 2007, Fig. 1.4).

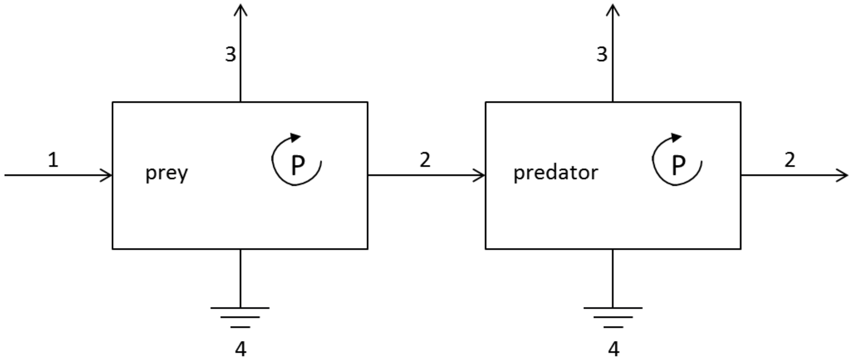


Figure 1.4: Possibilities of energy flows in an ecosystem. 1 = input (e.g. migration or passive transport of individuals into the system); 2 = exchange between compartments (e.g. predation); 3 = export of material (e.g. migration of individuals from the system); 4 = Export of inorganic material (e.g. loss of CO_2 due to respiration); after de la Vega (2016); Horn (2016).

1.4 THESIS OUTLINE

Although both long-term changes and trophic interactions are often interacting, this thesis is structured into two main parts, the first section (Chapter 2 to 4) will deal with long-term changes within the system in an order from nutrients over the bottom of a food web to the top, with a focus on single trophic levels. The second section (Chapter 5 to 8) takes a closer look at the food web interactions of the Balgzand intertidal, some of these chapters still include long-term changes but they focus on trophic interactions between one or more trophic levels within the system.

In **Chapter 2** nutrient budgets of the western part of the Dutch Wadden Sea (1976-2012) is build for phosphorus and nitrogen and a look at the changes in it over the last 45 years is taken in order the see whether a change has occurred in this time frame that could influence the food web.

In **Chapter 3** the exchange zone between the Dutch Wadden Sea and the North Sea is investigated with the help of INLA by analyzing the higher taxonomic richness of phytoplankton (2001-2009) as a proxy for exchange between the two systems. The extent of exchange between the two systems can influence the food web by changing the food supply for higher trophic levels.

In **Chapter 4** a closer look is taken at the changes in the fish community in the tidal inlet of the westernmost part of the Wadden Sea over the last 50 years (1960-2011) and if they are connected to changes in abiotic or biotic variables.

In **Chapter 5** the food requirement of several epibenthic species at the Balgzand tidal flat system (1975-2014) is estimated and compared to the prey availability in order to see if changes in these higher trophic levels occurred and to assess the influence of the different epibenthic species on the food web structure over the years.

In **Chapter 6** a look at the possible cause for an observed growth reduction in summer in juvenile plaice in the western part of the Dutch Wadden Sea is taken. This growth reduction in summer was observed in the area (1975-2009) and is therefor investigated for a potential intra- and interspecific competition.

In **Chapter 7** the seasonal variation within the food web of the Balgzand tidal flat system is investigated (2014) with the means of stable carbon and nitrogen isotopes with special attention paid to the influence of freshwater algae as a food source.

In **Chapter 8** four ENA food web models (1980s, 1990s, 2000s and 2010s) are build to investigate the impact of the invasion of several macrozoobenthic species on the food web of the Balgzand tidal flat system.

The Chapters 2-8 are published as peer-reviewed papers. Over the course of this research some species names were changed for the sake of consistency within this thesis these names have been adjusted also within chapters that have been published already. The refernces to all published papers can be found on page 319. In Chapter 9, the findings of the research presented in this thesis are integrated and discussed with respect to the research questions.

Part I

Long-term changes

2

LONG-TERM TRENDS IN NUTRIENT BUDGETS OF THE WESTERN DUTCH WADDEN SEA (1976 - 2012)

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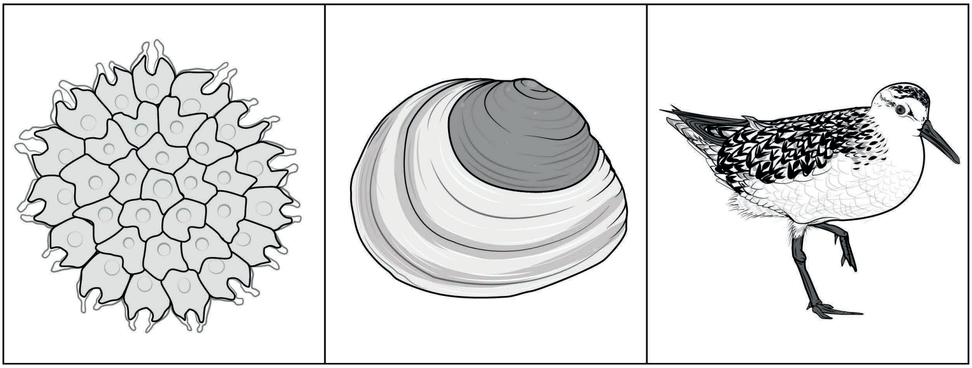

ABSTRACT

Long-term field observations of nitrogen [N] and phosphorus [P] concentrations were used to construct nutrient budgets for the western Dutch Wadden Sea between 1976 and 2012. Nutrients come into the western Dutch Wadden Sea via river runoff, through exchange with the coastal zone of the North Sea, neighbouring tidal basins and through atmospheric deposition (for N). The highest concentrations in phosphorus and nitrogen were observed 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 suggest that the period of the initial net import of phosphorus and nitrogen switched to a net export in 1981 for nitrogen and in 1992 for phosphorus. Such different behaviour in nutrient budgets during the rise and fall of external nutrient concentrations may be the result of different sediment-water exchange dynamics for P and N. It is hypothesized that during the period of increasing eutrophication (1976-1981) P, and to a lesser degree N, were stored in sediments as organic and inorganic nutrients. In the following period (1981-1992) external nutrient concentrations (especially in the North Sea) decreased, but P concentrations in the Wadden Sea remained high due to prolonged sediment release, while denitrification removed substantial amounts of N.

From 1992 onwards, P and N budgets were closed by net loss, most probably because P stores were then depleted and denitrification continued. Under the present conditions (lower rates of sediment import and depleted P stores), nutrient concentrations in this area are expected to be more strongly influenced by wind-driven exchange with the North Sea and precipitation-driven discharge from Lake IJssel. This implies that the consequences of climate change will be more important, than during the 1970s and 1980s.

2.1 INTRODUCTION

Estuaries are highly productive ecosystems, mainly because they receive large inputs of nutrients and organic matter from both river runoff and the open sea (Cloern et al., 2013; Nixon, 1995). Since the 1960s, there has been much environmental concern about the effects of increased riverine nutrient supply on the structure and functioning of estuarine ecosystems in Europe (Rosenberg, 1985) and the United States (Cloern et al., 2013). Particularly, increased inputs of nutrients had major consequences for the coastal ecosystems, such as an increase of biomass of primary producers leading to oxygen depletion, changing species compositions and biodiversity and shifts to bloom-forming algae species, some of which are toxic (e.g. Cloern, 2001). Eutrophication is, amongst others, referred to as the excessive increase in nutrient inputs (Golterman, 1975) and the increase of organic matter due to an increased nutrient supply (Nixon, 1995). Here, we use the first definition. Worldwide measures in the 1980s following conventions, legislative instruments and other laws on eutrophication (Ferreira et al., 2011) were successful in reducing nutrient loads in the North Sea and Baltic Sea, but less effective in other European and US coastal waters, in particular for nitrogen (Grizzetti et al., 2012; Scavia and Bricker, 2006).

The Wadden Sea, located in the south-eastern part of the North Sea bordering Denmark, Germany and The Netherlands is a shallow, intertidal sea consisting of intertidal flats, shallow subtidal flats, drainage gullies and deeper inlets and channels. Due to its outstanding universal values, it became a UNESCO world heritage site in 2009 (`www.waddensea-worldheritage.org`). The western part of the Dutch Wadden Sea is a highly dynamic estuarine environment with nutrient inputs from two main sources, i.e. from Lake IJssel, receiving water from the river Rhine, and from the coastal waters of the North Sea connected to the tidal basins via tidal inlets between the barrier islands (Duran-Matute et al., 2014; Postma, 1950; Ridderinkhof et al., 1990). Field measurements and information from reflectance images retrieved by means of remote sensing suggest the presence of a coastal zone seaward of the barrier islands in which such an exchange of water, nutrients and organic matter between the Wadden Sea and the North Sea takes place (Chapter 3, Postma, 1981, 1984; van Raaphorst et al., 1998; Visser et al., 1991).

Loadings of nitrogen and phosphorus into the coastal waters of the North Sea, including the western Wadden Sea, strongly increased from the early 1950s until the early 1980s and decreased since the mid-1980s (e.g. Philippart et al., 2007; Prins et al., 2012; van Raaphorst and de Jonge, 2004; van Raaphorst et al., 2000; Vermaat et al., 2008). Between 1978 and 1987, the main nutrient source in the western Wadden Sea was Lake IJssel (approximately 50% for phosphorus and 75% for nitrogen Philippart et al., 2000). Consequently, during the early 1980s, the relative contribution of loading from the coastal North Sea was low; the loading of phosphorus was less than 25% and that of nitrogen less than 5% of the total loading (Philippart et al., 2000; van Raaphorst and van der Veer, 1990). Reduction of nutrients that started in the late 1970s was uneven in that P loadings were more effectively reduced than N loadings. This led to a large imbalance in the N : P stoichiometry in the Wadden Sea (Philippart et al., 2007) and the North Sea (Burson et al., 2016) and has affected the phytoplankton communities and productivity (Burson et al., 2016; Philippart et al., 2007). In particular during the spring bloom, phytoplankton in general is now mainly P-limited, whereas a Si–P-co-limitation is likely for the diatom populations, when present (Ly et al., 2014).

Nutrient dynamics are not only influenced by the loadings of dissolved phosphorus and nitrogen, but also by sedimentary processes (storage, burial, remineralization, and denitrification) and sediment-water exchange of their particulate and dissolved forms. A recent study on sediment budgets showed that sedimentation rates in the western Wadden Sea are under the long-term influence of the closure of the southern part of the former Zuiderzee in 1932 (Elias et al., 2012). The closure has formed the present Lake IJssel and has resulted in an increased net inward transport of sediment and its associated organic matter, as tidal channels had to adjust to lower tidal volumes. Apart from these long-term morphological adjustments, sedimentary processes also interact with eutrophication trends. At the onset of eutrophication, local phosphorus concentrations might be buffered by net storage of P in the sediment, followed by gradual release after reduction of nutrient loads (Prastka et al., 1998). In the western Wadden Sea, remineralization plays an important role in the P cycle (Leote et al., 2015). Here, phosphorus might be stored over a longer time in the sediment and therefore serve as a buffer between the freshwater source of Lake IJssel and the North Sea (Kuipers and van Noort, 2008; Tappin, 2002). Local nitrogen concentrations will be influenced by denitrification, i.e. the reduction of nitrate to dinitrogen gas. Because denitrification rates in coastal sediments are related to the amount and quality of sedimentary organic matter and the concentrations of nitrate in waters overlying the sediment, changes in loads of sediments, organic matter and nutrients influence the magnitude of this flux (Deek et al., 2012).

In this study, we present phosphorus and nitrogen budgets of the western Dutch Wadden Sea for the period 1976-2012 to analyse changes in the relative importance of import of nutrients from the North Sea coastal zone compared to that of other sources (Philippart et al., 2000; van Raaphorst and van der Veer, 1990). Previous budgets assumed that closing residuals of the budgets were related to the import of organic matter (N, P) and denitrification (N). For the present budgets, the possible contribution of changes in sedimentation and pelagic-benthic fluxes to the closing residuals of the budgets are also considered.

2.2 MATERIALS AND METHODS

2.2.1 *Study area*

The Wadden Sea is a seaward barrier of sandy islands and shoals, stretching for 600 km from Denmark in the northeast to The Netherlands in the southwest.

In this study, we focus on the Marsdiep and Vlie tidal basin in the westernmost part of the Dutch Wadden Sea. These basins are connected to the North Sea by two tidal inlets, i.e. the Marsdiep and the Vlie (Fig. 2.1A). Marsdiep and Vlie are the tidal basins with the main tidal inlets of the western Dutch Wadden Sea with tidal prisms of about 1050×10^6 and 1150 to $1070 \times 10^6\,\mathrm{m}^3$, respectively (Duran-Matute et al., 2014; Philippart, 1988; Postma, 1982). The smaller Eierlandse Gat, located north of the Marsdiep and south-west of the Vlie tidal basin, has a tidal prism of 160×10^6 to $200 \times 10^6\,\mathrm{m}^3$ and its water exchange with the Marsdiep and Vlie basins is relatively low (Postma, 1982; Duran-Matute et al., 2014). It was, therefore, decided to exclude this basin from the nutrient budget analyses (c.f. Philippart and Cadée, 2000). On average, the temperature of the Marsdiep tidal basin varies between 3 °C in February and 18 °C in August (van Aken, 2008*b*). Freshwater enters the Marsdiep tidal basin directly from discharges of Lake IJssel and indirectly from river runoffs in the south via the coastal zone (Fig. 2.1A). The salinity shows high variability and depends strongly on the amount of fresh water entering the system (van Aken, 2008*a*).

2.2.2 *Nutrient data*

Time series on nutrient concentrations were obtained from the water quality monitoring database (DONAR, `http://waterinfo.rws.nl/`) of the Dutch Ministry of Transport and Public Works. Details about the locations of the used stations and sampling methods can be found in Philippart et al. (2000); van Raaphorst and van der Veer (1990). Total phosphorus (TP) includes dissolved inorganic phosphate (DIP), dissolved organic phosphorus (DOP) and particulate compounds of phosphorus (POP). Total nitrogen (TN) is the sum of ammonium ($\mathrm{NH_4}^+$), nitrate plus nitrite (NO_x), dissolved organic nitrogen (DON) and particulate compounds of nitrogen (PON). For all stations which were used to construct the nutrient budgets (Fig. 2.1A), TP and TN concentrations were estimated from irregular measurements (see below) for every month from January 1976 to December 2012 (n = 444).

For Stations b and c (Fig. 2.1A), nutrient concentrations were measured during the full study period but sampling occurred at irregular intervals. To construct a regular data set with monthly values for all stations, generalized additive models (GAM) were fitted for nitrogen and phosphorus separately. We used GAM because of its ability to fit the non-linear seasonal and long-term trends.

The nutrient concentrations were modelled as a function of "Station" and as a function of the smoother f_1 for "Year" (for the long-term trend) and as a function of the smoother f_2 for "DayInYear" (for the seasonal trend). To smooth the seasonal trend, a penalized cyclic cubic spline was used to ensure that the ends of the fitted seasonal splines match up. The statistical model for nutrient

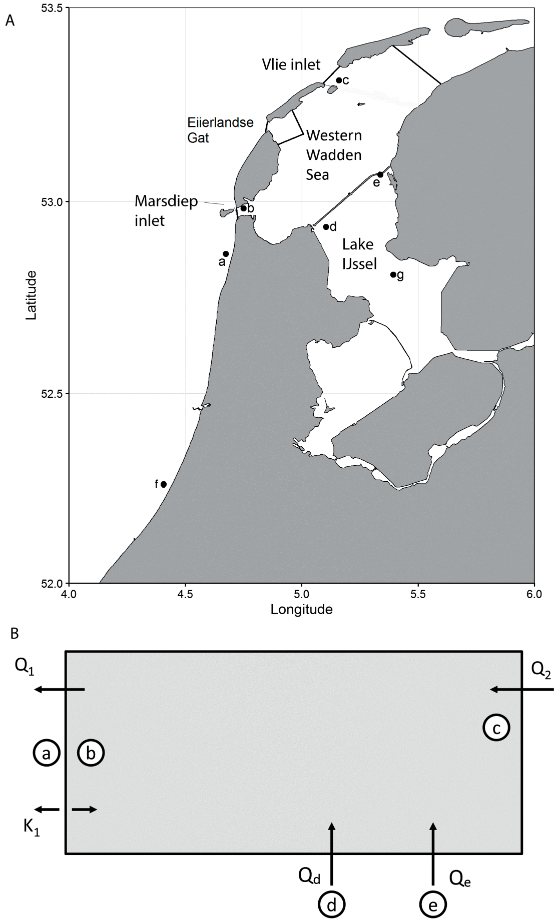

Figure 2.1: The study area with locations of the sampling stations in the North Sea (Station a, Callantsoog) and Noordwijk (Station f), the western Wadden Sea (Station b, Marsdiep; Station c, Vliestroom), and near the sluices in the dam that closes off the man-made freshwater Lake IJssel from the Wadden Sea (Station d, Den Oever; Station e, Kornwerderzand and Station g, Vrouwezand). (A) Geographical map of the study area. (B) One-compartment representation of the western Wadden Sea. Solid arrows represent tidally averaged advective water transport (Q_1, Q_2) and bimonthly averaged major freshwater inputs (Q_d, Q_e); the dashed arrow (K_1) represents the dispersive exchange with the North Sea (Ridderinkhof et al., 1990).

concentrations ([TP] and [TN]; $\text{mol}\,\text{m}^{-3}$) at different stations (S), years (Y) and day in the year (D) reads:

$$[Nutrient]_{SYD} \sim \alpha + \beta \times S + f_1(Y \times S) + f_2(D \times S) + \epsilon \tag{2.1}$$

Measurements at stations a, d and e were, however, terminated in 1988 (a) and 1993 (d and e) (Fig. 2.1A). We estimated the nutrient concentrations at these locations by using measurements at other locations. We used the generated monthly values from the GAM (Eq. 2.1) for Station f in Dutch coastal waters to obtain values for a, and of Station g in Lake IJssel for e and d. In both cases the relationships between the concentrations of the respective stations were obtained by fitting a linear model through the data where both stations were sampled on the same day in the following form:

$$[Nut_{Station2}] \sim \alpha + \beta \times [Nut_{Station1}] + \gamma \times Month + \epsilon \tag{2.2}$$

where $Nut_{Station2}$ is the nutrient concentration ($\text{mol}\,\text{m}^{-3}$) at a station used for the nutrient budget calculations, i.e. Station a, e and d (Fig. 2.1B) and $Nut_{Station1}$ is the measured nutrient concentration ($\text{mol}\,\text{m}^{-3}$) at the reference stations (i.e. f, g). After estimating α and β, the regression model was used to predict missing values at stations a, e and d.

To calculate the budgets the ratio of particulate N and P is needed for the water outside of the Marsdiep tidal inlet and the water inside the Marsdiep tidal inlet. However, the Station a was not sampled for the full period. Therefore concentrations of particulate P and N were derived from concentrations at Station f in a comparable way (GAM, followed by GLM), as done for total nutrients at the other stations but then for this station only.

2.2.3 *Nutrient budgets*

The pelagic nutrient fluxes through the western Wadden Sea were based on a hydrodynamic model containing advective water transport and tidal exchange rates (Ridderinkhof et al., 1990); it implies that we assumed a constant water flow through the system (from an input at the Vlie basin to an output at the Marsdiep basin). The atmospheric nitrogen input was based on values estimated for the southern North Sea by Rendell et al. (1993).

In line with nutrient budget analyses by Philippart et al. (2000); van Raaphorst and van der Veer (1990), mass flows of phosphorus and nitrogen ($\text{mol}\,\text{s}^{-1}$) were calculated by multiplying (i) the net advective water transport rates ($\text{m}^3\,\text{s}^{-1}$; Q_1 and Q_2) with corresponding nutrient concentrations ($\text{mol}\,\text{m}^{-3}$) at Station b ("Marsdiep Noord") and Station c ("Vliestroom") in the western Wadden Sea, and (ii) a tidal exchange rate (K_1 in $\text{m}^3\,\text{s}^{-1}$; Tab. 2.1) with the difference in nutrient concentrations between Station b and Station a ("Callantsoog2"). Dispersive exchange between the North Sea and Vlie tidal basin was assumed to be very low, and therefore not considered separately (c.f. Philippart et al., 2000). Mass flows of phosphorus and nitrogen from Lake IJssel were determined by multiplying the daily averaged freshwater runoff ($\text{m}^3\,\text{s}^{-1}$ at the two discharge sluices Station d ("Den Oever") in the west and Station e ("Kornwerderzand") in the east by their respective nutrient concentrations (mol m^{-3}) (Fig. 2.1B; Tab. 2.1).

For phosphorus, each monthly budget was closed with a residual term labelled TP-flow ($F_{TP,residual}$; mol s^{-1}) which includes the accumulation of particulate matter originating from the open sea, a process described for the Wadden Sea (Postma, 1961) and several other coastal areas (Postma, 1980). For nitrogen, a constant atmospheric import of 0.19 mmol N m^{-2} d^{-1} was assumed (Rendell et al., 1993). Residual flow rates of particulate nitrogen ($F_{TN,residual1}$; mol s^{-1}) coinciding with P ($F_{TP,residual}$; mol s^{-1}) were calculated from the particular phosphorus flows using ambient ratios of particulate nutrients ($N : P_{particular}$; mol mol^{-1}) according to:

$$F_{TN,residual1} = N : P_{particular} \times F_{TP,residual} \tag{2.3}$$

Following (Philippart and Cadée, 2000), the ambient N : P-ratio of the particulate nutrients was computed on the basis of data from Station b. Finally, the nitrogen budget was closed with an additional and N-specific residual flow ($F_{TN,residual2}$; mol s^{-1}). The closing term of P, and the first closing term of N, account for storage and release of nutrients by sediments or microalgae, burial of organic matter in the sediment, unaccounted import from diffuse freshwater sources, and possibly other minor fluxes. The second closing term of N accounts mainly for denitrification, and further for deviations from standard stoichiometry in the fluxes covered by the first residual and for inorganic P burial that is not stoichiometrically related to N burial. Inevitably, estimation errors in the other terms of the budget will also appear in the closing terms.

Table 2.1: Main characteristics and water mass flows of the western Wadden Sea as based on the hydrodynamical model by (Ridderinkhof et al., 1990) and data on freshwater inputs between 1976 and 2012 (456 monthly averages) supplied by the Dutch Ministry of Transport.

Characteristics	Symbol	Value	Unit
Volume		4.66×10^9	m^3
Surface area		1.41×10^9	m^2
Average depth		3.3	m
Tidal exchange		3.60×10^7	m^3 $tide^{-1}$
Tidal frequency		1.92	tide d^{-1}
Residence time		9	days
Freshwater discharges from Lake IJssel	Q_d	295 ± 151	m^3 s^{-1}
	Q_c	210 ± 131	m^3 s^{-1}
Advective transport via Vlie inlet	Q_2	696 ± 65	m^3 s^{-1}
Dispersive transport (tidal exchange)	K_1	3556	m^3 s^{-1}
Advective transport to North Sea	Q_1	1199 ± 210	m^3 s^{-1}

2.2.4 *Sedimentation*

Estimates of the contribution of sedimentation to the residuals of phosphorus ($F_{TP,residual}$; mol s^{-1}) and nitrogen ($F_{TN,residual1}$; mol s^{-1}) were derived from sedimentation and erosion values for 5-year periods of the Marsdiep and Vlie tidal basins ($m^3\,y^{-1}$) as supplied by Elias et al. (2012). After conversion to average sedimentation and erosion rates for the western Dutch Wadden Sea, the sedimentation and erosion rates ($mm\,y^{-1}$) were multiplied with the average phosphorus content of sandy and silty sediments, i.e. 100 and 225 µmol P g^{-1} dry sediment, respectively (Postma, 1954; van Raaphorst and Kloosterhuis, 1994).

2.2.5 *Burial, storage and release of nutrients by the sediment*

No long-term information on storage and release of nutrients by sediments existed. Therefore we constructed a storage and release time series based on the following assumptions. Storage of phosphorus in each year of the study period was estimated by assuming that around 30% of the TP input from the main freshwater source (Lake IJssel) got buried in the sediment after the spring bloom (Nixon et al., 1996). Release of P from the sediment in autumn varies between 10 and 40% of the stored P (Leote et al., 2015), and is inversely related to P concentrations in the water (Hupfer and Lewandowski, 2008). For this study, it was assumed that storage and release were equal during the first year (1976), implying that the maximum release of P is 16.6% of the stored P in the sediment. This rate was derived as follows. A P concentration of 0.066 mol P m^{-2} in the top 1 cm of the sediment as measured in the 1950s by Postma (1954) was taken as a starting point (P_0; mol m^{-2}) for construction of the sediment storage and release time series, as this is the only reliable source for P in the sediment and an estimation of the change that happened in that time was out of the scope of this paper. For example, during the first year (1976) the annual burial was calculated as 30% of the total riverine P loads of 0.042 mol P $m^{-2}\,y^{-1}$ resulting in a burial of 0.013 mol P $m^{-2}\,y^{-1}$. Taking the assumed background value (0.066 mol P m^{-2}) into consideration, this would add up to 0.066 + 0.013 = 0.079 mol P m^{-2} after burial. The release in autumn would then be 16% of the stored P (i.e. 0.013 mol P m^{-2}) leaving 0.066 mol P m^{-2} in the sediment in winter. Within the year 1976, the net change in P in the sediment was by definition kept in balance and would equal to zero.

2.3 RESULTS

2.3.1 *Model results and validation*

Predictions for missing values with GAM models were validated by searching for patterns in the residuals, but no such patterns could be detected (not shown). Predicted values using the GAM models were in line with observations at the different stations (Appendix A). The GAM models were therefore used within this study.

2.3.2 *Nutrient budgets*

Phosphorus

The input of TP from Lake IJssel to the western Wadden Sea (i.e. Marsdiep and Vlie tidal basin) showed strong seasonality ranging between $0.0\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ in summer and $0.6\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ in winter (Fig. 2.2A). The input of TP from the North Sea into the Vlie tidal basin was positive by definition (as it is an advective flux with net inflow) and showed minor seasonality of less than 0.01 $\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ between relatively high inputs in winter and relatively low inputs in summer and autumn (Fig. 2.2B). At Marsdiep, the advective transport of P showed some seasonality with net export of more than $0.5\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ in January in the early years and of less than $0.1\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ in June from 1995 (Fig. 2.2C). The tidally-driven exchange of nutrients between the Marsdiep tidal inlet and the North Sea was generally positive in January (ca. $0.5\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$), February (ca. $0.1\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$) and November (ca. $0.2\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$), implying net import of TP into the Marsdiep during these months, and negative and therefore net exporting P from the Marsdiep during the rest of the year; June is exceptional with high export rates (ca. $0.4\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$; Fig. 2.2D). The residual P load was generally negative in November, January and February, implying a net export up to 0.5 $\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ during these winter months and positive during the rest of the year, in particular in June, with a net import of more than $0.3\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ (Fig. 2.2E).

Figure 2.3A presents the annual averages of the budget terms. The input of phosphorus from Lake IJssel into the Marsdiep tidal inlet peaked in the early 1980s at almost $0.3\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ followed by a decrease until the early 2000s and stabilization hereafter at around $0.1\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ (Fig. 2.3A). Between 1976 and 2012, the average positive loading from the North Sea to the Vlie tidal basin gradually declined from 0.17 to $0.06\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ (Fig. 2.3B). The advective export from the Wadden Sea to the North Sea via Marsdiep declined from almost 0.4 in the 1980s to less than $0.2\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ in the 2000s (Fig. 2.3C).The tidally driven export of phosphorus between the Wadden Sea and the North Sea generally declined during the study period and even became positive in 2011 and 2012, implying higher TP concentrations in the North Sea than in the Wadden Sea during these years (Fig. 2.3D). Between 1976 and 2012, the residual P-load changed from an annually averaged accumulation (>0.2 $\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ in 1976) to a net loss since 1992 of almost $0.1\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ in 2012 (Fig. 2.3E).

Nitrogen

The input of total nitrogen from Lake IJssel to the western Wadden Sea also showed a strong seasonality. It varied between $0\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$ in summer

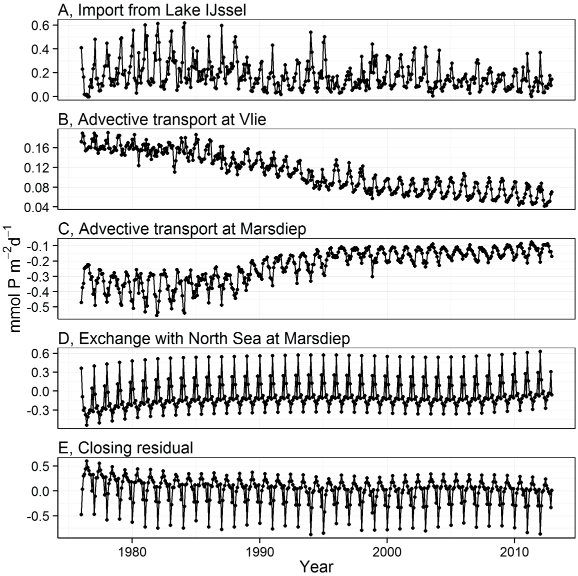

Figure 2.2: Time series of monthly total phosphorus budget terms (mmol P m^{-2} d^{-1}) in the western Wadden Sea with points being drawn at the first of the month as a representative for the whole month, A) Import from Lake IJssel, B) advective transport at Vlie tidal inlet, C) advective transport at the Marsdiep tidal inlet, D) exchange with North Sea at the Marsdiep tidal inlet, E) closing residual. Positive values indicate input into the tidal basins. Note the difference in the scale of the y-axes.

and 30 mmol N m^{-2} d^{-1} in winter (Fig. 2.4A). Nitrogen input into the Vlie basin from the North Sea was always positive, with values ranging between more than 6 mmol N m^{-2} d^{-1} in late winter / early spring and 0.8 mmol N m^{-2} d^{-1} in summer (Fig. 2.4B). The advective transport at the Marsdiep tidal inlet was always negative by definition with only minor seasonal signals whereas a minimum was reached in summer (less negative values, 1.5 mmol N m^{-2} d^{-1}) and the highest export in winter (12 mmol N m^{-2} d^{-1}, Fig. 2.4C). The tidally driven exchange between the western Wadden Sea and the North Sea was mostly negative (net export, around 5 mmol N m^{-2} d^{-1} and in spring even up to 15 mmol N m^{-2} d^{-1}), with net gain only in November (up to almost 4 mmol N m^{-2} d^{-1}) and on occasion in January (Fig. 2.4D). In the nitrogen budget two residual terms were present. The first was estimated based on the phosphorus budget where the amount of exchange of phosphorus was assumed to be connected with a certain N : P ratio to organic matter exchange with the North Sea . This residual of the nitrogen budget therefore followed the same pattern as in the phosphorus budget. Highest values were found in summer, with a net import of up to 10 mmol N m^{-2} d^{-1}. In January as well as in most of February and November, a net export up to 15 mmol N m^{-2} d^{-1} was found (Fig. 2.4E). The second residual in the nitrogen budget represented the

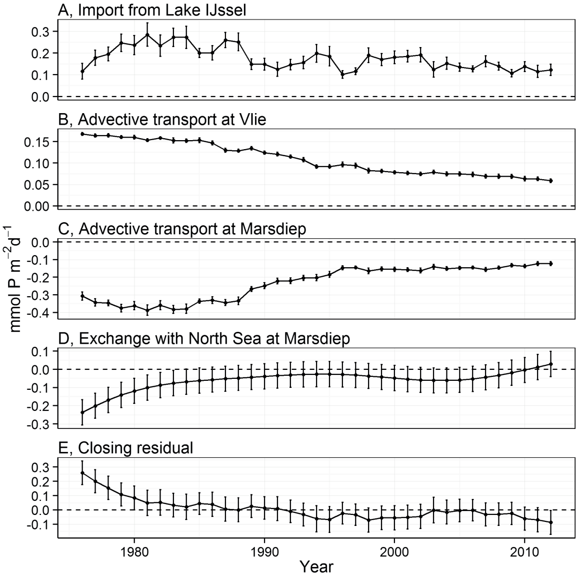

Figure 2.3: Time series of annual total phosphorus (TP) budget terms (mmol P m^{-2} d^{-1}) in the western Wadden Sea (means ± SD) with points being drawn at the first of the year as a representative for the whole year, A) Import from Lake IJssel, B) advective transport at Vlie tidal inlet, C) advective transport at the Marsdiep tidal inlet, D) exchange with North Sea at the Marsdiep tidal inlet, E) closing residual. Positive values indicate input into the tidal basins. Note the difference in the scale of the y-axes.

closing term and showed a less clear seasonality than the other components of the nitrogen budget (Fig. 2.4F).

The annual averages of the nitrogen budget showed that the input into the western Wadden Sea from Lake IJssel peaked in the late 1980's (12.5 mmol N m^{-2} d^{-1}) with some variation in the 1990's (between 12 and 7 mmol N m^{-2} d^{-1}) and a relatively stable period after 1995 with an average 7.6 mmol N m^{-2} d^{-1} (Fig. 2.5A). The exchange between the North Sea and the Vlie basin was always a net gain but it decreased over time from about 5 mmol N m^{-2} d^{-1} to 1.5 mmol N m^{-2} d^{-1} in the mid 1980s and stayed constant since then (Fig. 2.5B). The advective transport at the Marsdiep inlet was always negative by definition, indicating a net export around 1975 with less variability over time but still a slight decrease from 7.8 mmol N m^{-2} d^{-1} to 3.5 mmol N m^{-2} d^{-1} in 2012 (Fig. 2.5C). For the tidally driven exchange with the North Sea a net export decreasing over time from almost 12 mmol N m^{-2} d^{-1} around 1975 to around 2 mmol N m^{-2} d^{-1} in the mid 1980s and constant since then was found (Fig. 2.5D). Between 1976 and 2012, the exchange of nitrogen in the first residual changed from an annually averaged inward transport (5 mmol N m^{-2} d^{-1} in 1976) to values around zero since 1980 (Fig. 2.5E). The second residual showed a change from about 5 mmol N m^{-2} d^{-1} in 1976 to a net export of nitrogen

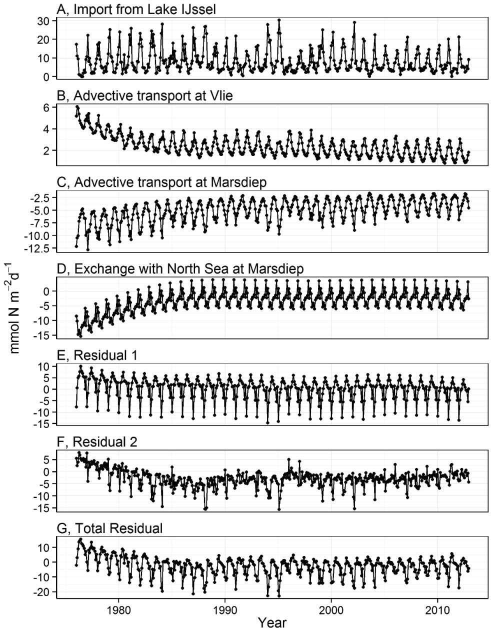

Figure 2.4: Time series of monthly total nitrogen budget terms (mmol N m^{-2} d^{-1}) in the western Wadden Sea with points being drawn at the first of the month as a representative for the whole month, A) Import from Lake IJssel, B) advective transport at Vlie tidal inlet, C) advective transport at the Marsdiep tidal inlet, D) exchange with North Sea at the Marsdiep tidal inlet, E) closing residual. Positive values indicate input into the tidal basins. Note the difference in the scale of the y-axes.

since 1980 with a maximum in 1988 of 7.5 mmol N m^{-2} d^{-1} to a lesser value (>2 mmol N m^{-2} d^{-1}) in recent years (Fig. 2.5F).

Residual vs freshwater import

The influence of freshwater import versus exchange with the North Sea was analysed by a comparison of the import from Lake IJssel with the respective annual residuals of the two nutrients (Fig. 2.6). For phosphorus the residual was highest (0.26 mmol P m^{-2} d^{-1}) in 1976 and at the same time the import from Lake IJssel was small (0.12 mmol P m^{-2} d^{-1}) compared to later years (Fig. 2.6A). From 1976 to 1981, the residuals of P continuously decreased to 0.04 mmol P m^{-2} d^{-1} whilst the import of P from Lake IJssel increased to 0.28 mmol P m^{-2} d^{-1}. From 1982 onwards, the residual of P started to be more variable but in general continued to decrease till the lowest value in this study (-0.08 mmol P m^{-2} d^{-1}) was reached in 2012. The import from Lake IJssel has decreased over time to relatively stable values between 0.1 to 0.2 mmol P m^{-2} d^{-1} in the most recent years (Fig. 2.6A). These trends suggest two main phases, the first one (1976-1981) where the annual P residuals de-

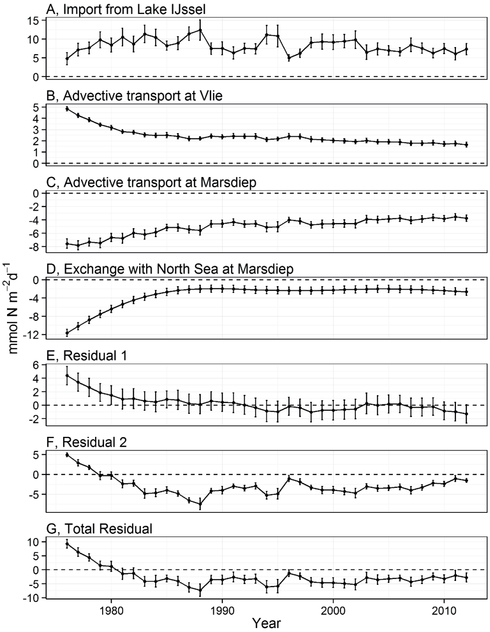

Figure 2.5: Time series of annual total nitrogen (NP) budget terms (mmol N m^{-2} d^{-1}) in the western Wadden Sea (means ± SD) with points being drawn at the first of the year as a representative for the whole year, A) Import from Lake IJssel, B) advective transport at Vlie tidal inlet, C) advective transport at the Marsdiep tidal inlet, D) exchange with North Sea at the Marsdiep tidal inlet, E) closing residual. Positive values indicate input into the tidal basins. Note the difference in the scale of the y-axes.

creased and annual P imports from Lake IJssel increased, and the second one (1982-2012) were the P residuals decreased as did the P imports from Lake IJssel (Fig. 2.6A).

The pattern was similar for the first residual of the nitrogen budget with highest values for the residual at the start of the series in 1976 (4.39 mmol N m^{-2} d^{-1}) and relatively small values for the import from Lake IJssel (4.8 mmol N m^{-2} d^{-1}) followed by a period with decreasing residual and increasing import from Lake IJssel (Fig. 2.6B). In the nitrogen budget, the highest N import from Lake IJssel (12.4 mmol N m^{-2} d^{-1}) occurred in 1988 (Fig. 2.6B). In that year, the N residual was 0.14 mmol N m^{-2} d^{-1}. From 1989 onwards, the annual N residuals continued to decrease but less steeply and with occasional increases in between until a minimum was reached at the end of the study period in 2012 (-1.29 mmol N m^{-2} d^{-1}). At the same time the annual N imports from Lake IJssel decreased to values of less than 10 mmol N m^{-2} d^{-1} with two exceptions in 1994 and 1995 and a minimum in 1996 with 5 mmol N m^{-2} d^{-1}. This suggests that the change in this relative behaviour within the annual N budgets occurred between 1988 and 1989 (Fig. 2.6B), which is seven years later than observed for P (i.e. between 1981 and 1982; Fig. 2.6A).

In the second residual of the nitrogen budget the trend was less pronounced than for the first N residual (Fig. 2.6C), but again this residual started in 1976 with the highest value ($4.92\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$) observed during the study period and reached its lowest value ($-7.40\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$) in 1988. From 1988 onwards, this second N residual varied between $-5.23\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$ (1994) and $-1.05\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$ (1996). The behaviour of the second N residual in relation to the import of annual N from Lake IJssel suggests two phases, a period with a decreasing residual and an increasing import (1976-1988) followed by a period where relatively high residuals coincided with relatively low imports from Lake IJssel (Fig. 2.6C).

Comparing the trends in the closing residual of the P budget (Fig. 2.3E) and the total residual of the N budget (Fig. 2.5G) suggests three periods during the observational period, being (i) 1976-1980: where additional import of both phosphorus and nitrogen is required to close the respective P and N budgets, (ii) 1981-1991: where additional import of phosphorus is still needed to close the P budget, but additional export of N to close the N budget, and (iii) 1992-2012: where additional export of phosphorus and nitrogen is needed to close both nutrient budgets for the western Wadden Sea (Fig. 2.7).

Sedimentation, erosion, storage and release

The particle exchange between the North Sea and the western Wadden Sea (i.e. Marsdiep and Vlie tidal basin) changed from net sedimentation in the period before 2000 to net erosion hereafter (Elias et al., 2012). This means that also the net loading of particulate nutrients most probably switched from net import into the western Wadden Sea to net export to the North Sea. In case of phosphorus this changed from an import into the western Wadden Sea of around $0.03\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ in the period 1975-1980 to an export of $0.01\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$ in the period 2000-2005 (Fig. 2.8).

Assuming that the amount of stored phosphorus in the sediment had not changed between the early 1950s and the early 1970s, a net burial of P in the sediment was found in the beginning of the study period in the early 1970s, followed by a period of net release of P since 1985, after which most years showed a net release with a maximum found in 1991 ($0.03\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$), which is 10 years after the highest import from Lake IJssel in 1981 (Fig. 2.8). After 1997, the net annual storage/release of P levelled out to around zero (Fig. 2.8).

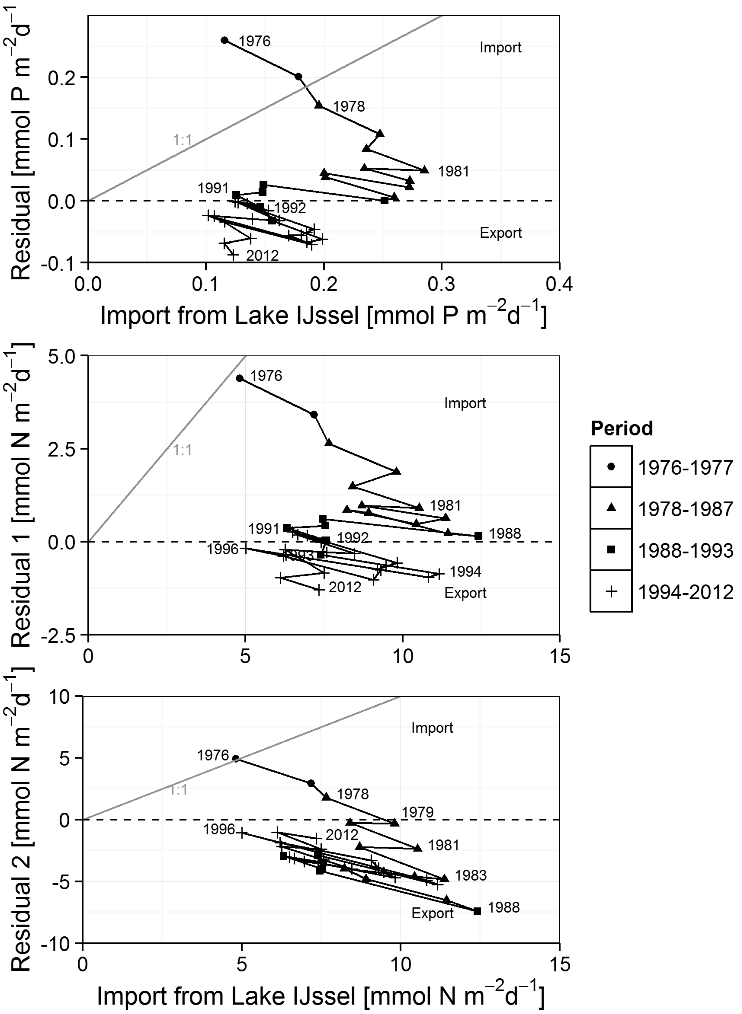

Figure 2.6: Closing residuals versus import from Lake IJssel. Residual of phosphorus budget vs import of P from Lake IJssel (A). Residual 1 of nitrogen budget (B) and Residual 2 of nitrogen budget (C) vs import of N from Lake IJssel in different periods; grey line represents the 1:1 line. Note the difference in the scale of the axes.

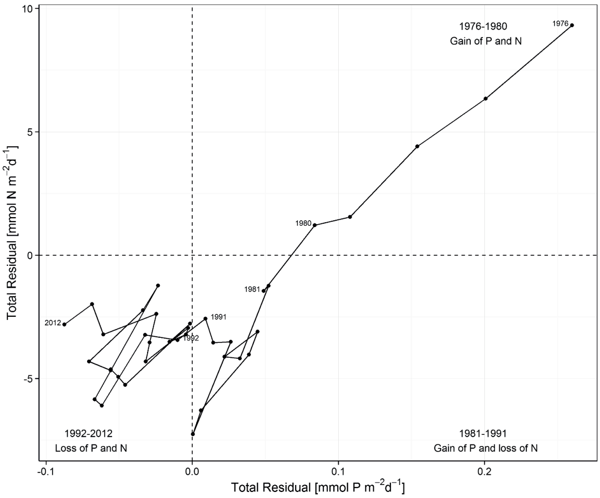

Figure 2.7: Residual of phosphorus budget vs total residuals of nitrogen budget over study period.

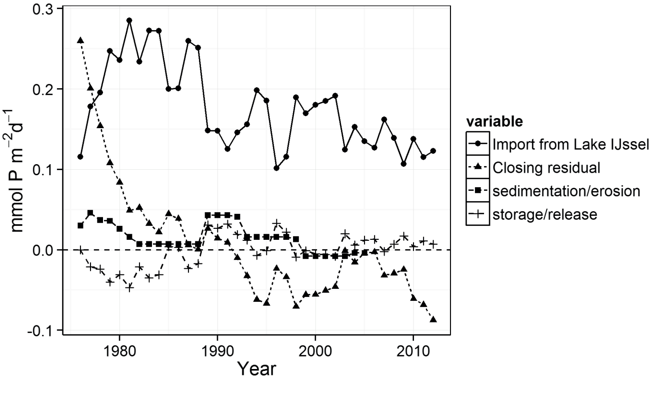

Figure 2.8: Time series of import of phosphorus from Lake IJssel (circles), the residual of the P budget (triangles), the estimated phosphorus transported by sediment (squares) and the estimated amount of phosphorus exchanged with the sediment (cross) in the western Wadden Sea.

2.4 DISCUSSION

2.4.1 *Accuracy of model predictions for nutrient concentrations*

The analyses were computed partly using model estimates of nutrient concentrations based on measurements with a certain uncertainty. Model validations showed a good fit of all the models, giving an indication that at least the general direction of the budget should be trustworthy. However the fact that some of the model estimates are based on a combination of two different time series should be kept in mind. In addition, the relationships between nutrient concentrations of various stations used for estimating local nutrient concentrations when no data were available were assumed to be fixed in time, which might not have been true. So far there is no better alternative to this method.

Import of nutrients in the western Dutch Wadden Sea from the freshwater can be direct (from Lake IJssel and other sources, e.g. van Raaphorst and van der Veer, 1990) and indirect (via the coast line of The Netherlands from the rivers, mainly the Rhine, e.g. de Jonge, 1990) in our study area. From these sources, only the freshwater import from Lake IJssel can be quantified as consistent long-term information since other freshwater nutrient sources are lacking. For 1950-1951, however, Postma (1954) estimated the import of total phosphorus from the canal “Noordhollands Kanaal” via the harbour of Den Helder into the Marsdiep to be 650 kg per tide ($0.03\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$), i.e. in the same order of magnitude as the total P supplied via Lake IJssel (1,050 kg per tide, $0.05\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$). For 1985, van Meerendonk et al. (1988) estimated the import of total P from this canal into the Marsdiep to be 426 ton per year ($0.03\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$), i.e. similar as in the early 1950s (632 kg per tide or $0.02\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$) but now almost an order of magnitude lower than the total P supplied via Lake IJssel (3,721 ton per year, $0.23\,\mathrm{mmol\,P\,m^{-2}\,d^{-1}}$). For the year 1985, the import of total N was estimated to be 1,837 ton per year ($0.25\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$) from the canal and 59,725 ton per year ($8.26\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$) from Lake IJssel (van Meerendonk et al., 1988). Although the freshwater discharge from this canal is relatively low (i.e. 3% of the total freshwater discharges into the western Wadden Sea; van Meerendonk et al., 1988), its importance as an additional nutrient source cannot be excluded, in particular for P during the beginning of the study period before the maximum concentrations were reached in the mid-1980s.

Several compartments in our nutrient budget refer to the exchange of nutrients between North Sea and Wadden Sea as well as internal circulation (e.g. "Wadden Sea Throughput" and "Exchange North Sea") and they were calculated using a fixed coefficient. Recent models of the hydrodynamics of the western Wadden Sea revealed that these coefficients could be variable depending on wind velocity and direction that can be so strong as to even reverse the normal tidal flow (Duran-Matute et al., 2014) and lead to an average variability of the tidal prism of 20 %. So far, however, the outcomes of such hydrodynamic models are not available for the full study period of the nutrient budgets. Moreover, although variations in weather could explain some of the between-year variation, it is unlikely that they will explain the long-term changes discussed in this paper.

2.4.2 *Long-term trends*

Overall, there is a general increase of import of nutrients from Lake IJssel till the beginning of the 1980s and a subsequent reduction afterwards. Furthermore, the initial net gain of phosphorus and nitrogen in the system switched to net loss in the mid-1990s and the first residual of the nitrogen budget switched from positive (indicating an additional N gain) in the late 1970s to negative (indicating net N loss) around 1980. There are several nutrient budgets available for the Wadden Sea, but often they only look at very short time spans (Grunwald et al., 2010) or were conducted before the 1990s (Philippart et al., 2000; van Raaphorst and van der Veer, 1990), when we detected a major change within our nutrient budgets.

Different behaviour in nutrients during nutrient increase and reduction, as were detected in this study, may be the result of changing boundary concentrations, temporary storage of nutrients in the sediment (as has been described for phosphorus) or enhanced denitrification (Cornwell et al., 1999; Kana et al., 1998; Nielsen et al., 1995).

In the 1970s freshwater runoff within Europe was highly loaded with nutrients and reached a peak in the early 1980s (van Raaphorst and de Jonge, 2004; van Raaphorst and van der Veer, 1990). Hereafter eutrophication was reduced and nutrient loads went down, also within the Wadden Sea (Grizzetti et al., 2012; Philippart and Cadée, 2000; Scavia and Bricker, 2006; van Raaphorst and van der Veer, 1990). This pattern is also clear in our study where the import from Lake IJssel into the western Wadden Sea peaked in 1981. However, our study period started in 1976 and is missing the early years in the eutrophication process that started in the 1960s (van Raaphorst and van der Veer, 1990), making it difficult to assess whether the observed changes are showing signs of the system going back to the original state as it has been before the eutrophication in the 1970s or if it reached a new and different state of nutrient dynamics.

High internal loadings from a large historical P-pool in sediments can delay recovery after P reduction for 10–15 years or longer in lakes (Jeppesen et al., 2005; Søndergaard et al., 2013) and has been proposed for estuaries as well (Prastka et al., 1998). Leote et al. (2015) stated that internal recycling might be the most important source for phosphorus in the system by the way of remineralization of stored material in the sediment, at least in recent years. Also van Beusekom and de Jonge (1998) suggested that part of the primary production in the Wadden Sea could only be sustained by this mechanism. We explored this possibility by estimating the stored and released P in the sediment and found a similarity with the order of magnitude and trend of the residual term of the P budget, indicating that this would at least be a possibility.

It is striking that the largest values of the residuals occur at the start of the study period, between 1976 and approximately 1984 for P (Fig. 2.3) and between 1976 and 1980 for N (Fig. 2.6G). The monotonic decrease of the P import at the Vlie tidal inlet during the full study period (Fig. 2.3B) indicates that the rise in P concentrations of the freshwater in Lake IJssel in the 1970s and 1980s is not reflected in the North Sea waters that enter through the Vlie during those years. This is pointing in the direction that the decrease in freshwater P sources for the North Sea coastal area has started earlier than the decrease in Lake IJssel concentrations (i.e. prior to 1976, whereas the decrease started in 1981 for Lake IJssel concentrations), which was also observed by de Jonge (1997). This would make sense, if one assumes that the same sediment burial and release mechanisms work in Lake IJssel as in the Wadden Sea. The advective exchange through the Marsdiep, in contrast (Fig. 2.3C), does reflect the initial rise in P concentrations in the western Wadden Sea, and the decrease from approximately 1983 onwards. However, the rise between 1976 and 1981 has been slower than the rise in input from Lake IJssel, in accordance with the hypothesis of internal storage within the western Wadden Sea and Lake IJssel.

By far the largest contribution to the strongly positive residual of P in the first years stems from the dispersive exchange in Marsdiep, showing that the concentration difference between western Wadden Sea and the North Sea in the surface water was much larger in 1976 than ten years later. If the P residual reflects import of P, then there the concentration difference is directed towards the Wadden Sea, with higher concentrations in the North Sea than in the Wadden Sea in the mid-1970s, and smaller differences later on. This is in line with winter concentrations of phosphate in the river Rhine at the Dutch-German border, which peaked in the early 1970s, i.e. before the period covered by the nutrient budgets of this study (van Bennekom and Wetsteijn, 1990).

This could mean that the effects of reduced nutrient import from the rivers could be observed earlier in the North Sea than in the Wadden Sea. Most likely this is caused by internal (storage) processes in Lake IJssel and in the western Wadden Sea that may have been stronger than in the North Sea, leading to lower concentrations in the 1970s, but eventually breaking down and releasing large amounts of P until the mid-1980s, even after the input of riverine input had been peaking. In particular, the enhanced release of P in anoxic sediment conditions, induced by enhanced organic carbon deposition, may have played a role in this process. It would be stronger in shallow systems such as Wadden Sea and Lake IJssel, than in the North Sea. Note, in this respect, that residual 2 of N, related to denitrification, has its strongest negative values during the mid-1980s. As denitrification is an anoxic process, this would naturally be accompanied by a relatively strong P release.

For the nitrogen budget, the first residual was previously completely attributed to the import of organic matter containing P and N (Philippart et al., 2000). Present findings on the phosphorus budget now point, however, to additional process such as (i) import of dissolved nutrients and/or organic matter from a canal near Den Helder at the beginning of the study period, (ii) long-term variation in net sedimentation rates, and (iii) multi-annual storage and delayed release from the sediment. In contrast to P, N is not expected to have been stored and released over a multi-annual period (Tappin, 2002). However, the influence of import by an additional freshwater source and role of long-term changes in sedimentation rates on the N residual cannot be excluded. Due to insufficient information on, for example, N : P ratios of the freshwater discharge from the Den Helder canal, we cannot estimate how large this fraction is.

The second and closing residual of the nitrogen budget was assumed to represent the atmospheric part of the nitrogen cycle, i.e. denitrification, the reduction of nitrate to nitrogen-gas (Deek et al., 2012; Gao et al., 2012; Philippart et al., 2000). For parts of the eastern Dutch and western German Wadden Sea, Gao et al. (2012) estimated an annual loss of $745\,\mathrm{mmol\,N\,m^{-2}\,y^{-1}}$, corresponding to a daily loss of $2.04\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$ which is in the range of what has been found by Deek et al. (2012) in the northern German Wadden Sea ($2.1\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$ close to Sylt and $3.8\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$ close to Meldorf and the Elbe river) and in this study (average of $3.14\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$ in the period 1994-2012, Table 2.2).

Comparison of the total residuals of P and N suggests that the western Wadden Sea was characterized by three different periods within the study period with regard to the nutrient budgets. During the first years (1976-1980), the budgets were closed by net gain of P and N, most probably as the result of net import from the already nutrient-rich North Sea. From 1981 to 1991, the net gain of P continued but the N budget was closed by a net loss, possibly as a result of net release from the sediment for P and denitrification for N. From 1992, budgets were closed by a net loss of P and N, possible because there was no longer a release of stored P and denitrification of N continued.

2.4.3 *Future budgets*

Several studies showed that wind and rainfall affect the hydrodynamics of the Wadden Sea substantially (Donker, 2015; Duran-Matute et al., 2014; Duran-Matute and Gerkema, 2015). Duran-Matute et al. (2014) found how wind can change the advective transport. Both of these effects will have an impact on the nutrient budgets since the exchange with the North Sea will be affected, as is the exchange between basins, however these changes are mainly short term. There is no study so far that analysed the changes in wind speed and direction over a long term perspective. Note, however, that the main emphasis of this study is on the long multi-year time scale, and that the time scale of wind-driven variability is much shorter than this. Unless it could be shown that wind patterns have systematically changed over the decades, and with that have changed the residual transport rates (which to our knowledge has never been proven), our estimates should be robust on longer time scales, even if there is wind-driven variability (besides variability from a multitude of other sources) in the short-term budget terms. An increased wind speed and bottom shear stress can also lead to an increased remineralization of phosphorus from

Table 2.2: Annual averages of phosphorus and nitrogen loads ($\mathrm{mmol\,m^{-2}\,d^{-1}}$) of the western Wadden Sea. P and N refer to total phosphorus and nitrogen concentrations, respectively, small letters a to f to the respective stations used in the budgets (see Fig. 2.1).

Nutrient	Fluxes	Name	Function	1976-1977	1978-1987	1988-1993	1994-2012
Phosphorus	Input	Outflow Lake IJssel	$Q_d \times P_d + Q_e \times Pe$	0.15	0.24	0.16	0.15
	Input	Advective transport Vlie	$Q_2 \times P_c$	0.17	0.15	0.12	0.08
	Output	Advective transport Marsdiep	$Q_1 \times P_b$	-0.32	-0.36	-0.25	-0.15
	Output	Exchange North Sea	$K_1 \times (P_a - P_b)$	-0.22	-0.09	-0.04	-0.03
	Residual	Residual1	$F_{TP,residual}$	0.23	0.06	0	-0.04
Nitrogen	Input	Outflow Lake IJssel	$Q_d \times N_d + Q_e \times N_e$	6	9.55	8.12	7.94
	Input	Atmosphere	F_{atm}	0.19	0.19	0.19	0.19
	Input	Advective transport Vlie	$Q_2 \times N_c$	4.56	2.82	2.37	1.97
	Output	Advective transport Marsdiep	$Q_1 \times N_b$	-7.68	-6.18	-4.71	-4.18
	Output	Exchange North Sea	$K_1 \times (N_a - N_b)$	-10.91	-4.65	-2.03	-2.25
	Residual	Residual1	$F_{TN,residual1}$	3.91	1.08	0.21	-0.5
	Residual	Residual2	$F_{TN,residual2}$	3.93	-2.81	-4.13	-3.18

the sediment due to increased disturbance (Leote et al., 2013). Rainfall may also affect the hydrodynamics, in direct and indirect ways. The direct way, being local rainfall, will have a minor effect on the nutrient concentration since maximum volume rates involved are at least two orders of a magnitude smaller than the tidal exchanges. However there are studies indicating that rainfall may influence the density gradient especially of flat areas and therefor is influencing the estuarine circulation and the respective exchange coefficient with the North Sea (Burchard et al., 2008). Indirect effects are larger, maximum fresh water discharge from Lake IJssel after periods with heavy rainfall may be up to 2000 $m^3\,s^{-1}$(`http://waterinfo.rws.nl/`), which is almost the same as the regular residual advective transport of $3556\,m^3\,s^{-1}$ through the tidal inlets.

Not all tidal basins in the Wadden Sea have inflow of freshwater. It is not clear how the nutrient budgets of these tidal basins are and how they are affected by changing wind and rain conditions. A study by Grunwald et al. (2010) in the tidal basin behind the German Wadden Sea island Spiekeroog, with only limited fresh water influence indicates that in these tidal basins an export of inorganic material is taking place that is not outbalanced by organic material being imported in the case of phosphorus. In their budget the import of organic material into the basin is higher for nitrogen than the export estimated, however they do not take Ammonium into account when looking at the export of inorganic material. This makes it difficult to directly compare the results from our study with the results of Grunwald et al. (2010). There is an indication that also denitrification might be higher in sediments with a lager freshwater inflow (Deek et al., 2012), which would at least partly explain the differences between the model by Grunwald et al. (2010) and this study.

The budgets of this study require extensive nutrient data. However, extensive data sets are rare and most of the tidal basins have not been investigated extensively over a long period. Recently developed hydrodynamical models such as the GETM model of the Wadden Sea (Duran-Matute et al., 2014) could help in revealing previous hydrodynamics and water budgets of all tidal basins and could help developing nutrient budgets also for other basins by predicting water flow and nutrient concentrations at stations not directly monitored (Tiessen et al., 2012). Such models also bear the potential to allow an estimate how future changes in climate, like increased rainfall and stronger storms as projected by the Dutch Meteorological Institute (van den Hurk et al., 2006), may affect the nutrient budgets and subsequently primary production of the Wadden Sea.

2.5 ACKNOWLEDGMENTS

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3

SPATIAL AND TEMPORAL TRENDS IN ORDER RICHNESS OF MARINE PHYTOPLANKTON AS A TRACER FOR THE EXCHANGE ZONE BETWEEN COASTAL AND OPEN WATERS

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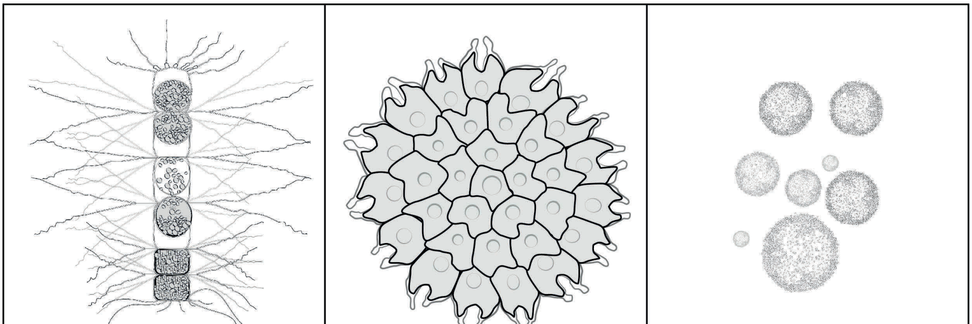

ABSTRACT

Quantifying exchange of particulate matter between coastal and open waters is an important and often unresolved issue. Here, we apply phytoplankton order richness as an innovative marine tracer to identify the geographical position of a coastal exchange zone in the SE North Sea, including its variability in time and space. Previous observations on dynamics of suspended particulate matter accumulation resulted in a hypothesized boundary between coastal waters (including the Wadden Sea) and open North Sea waters, the so-called "line-of-no-return". Our study along two transects (Terschelling, Noordwijk) in the Dutch coastal zone showed seasonality patterns in phytoplankton order richness, both for diatoms and flagellates. 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". Our 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.

3.1 INTRODUCTION

Coastal areas are among the most productive marine ecosystems (among others: Field et al., 1998). Functioning of these coastal systems is determined by the interplay of global drivers with local hydrodynamic and morphological conditions (Cloern and Jassby, 2008). The interactions between land, rivers, coastal zones and open waters are complex with transitions being gradual or more abrupt, and reliable proxies for the detection of such gradients in time and space are not easy to find. Exchange of particulate matter between coastal and open waters has been studied for several decades, especially for the highly productive estuarine areas such as the Wadden Sea (Postma, 1961, 1982, 1984; Visser et al., 1991; van Beusekom and de Jonge, 2002). This coastal zone is separated from the North Sea by a chain of barrier islands and bordering the Dutch, German and Danish coastline. The Wadden Sea is one of the largest estuarine coastal systems worldwide; it fulfils an important nursery function for commercial and non-commercial fish species and provides an important feeding area for migrating coastal birds (for overview see Zijlstra, 1972; Wolff, 1983).

The productivity of the Wadden Sea is mainly the result of pelagic and benthic primary production by microalgae, which is partly fueled by the import of nutrients and accumulating organic matter from the North Sea (Verwey, 1954; Postma, 1984; van Beusekom et al., 1999). The strong impact of increased nutrient loads from rivers into the area in the 1970s-1980s (e.g. de Jonge et al., 1993; van Raaphorst and de Jonge, 2004; Philippart et al., 2007) on primary and secondary production in the western Wadden Sea (Beukema and Cadée, 1986; Beukema et al., 1998) illustrates the importance of variation in local conditions on productivity and ecosystem functioning. However, to what extent the exchange and input of organic matter from the North Sea is spatially and temporally contributing to these local conditions and productivity of this shallow coastal sea remains an open issue.

Nutrient budgets of the western Wadden Sea suggest a relatively limited contribution of imported organic nitrogen and phosphorus from the North Sea compared to the import by rivers (van Raaphorst and van der Veer, 1990; Philippart et al., 2000). Van Beusekom et al. (2012) state that local nutrient dynamics are mainly driven by organic matter import from the North Sea (e.g. van Beusekom and de Jonge, 2002) and, as a consequence, the Wadden Sea should be considered to be predominantly heterotrophic, i.e. consuming more organic matter through respiration than produced through local photosynthesis (e.g. Verwey, 1954; Postma, 1984; van Beusekom et al., 1999). These different views might be related to the time frame of the various studies, e.g. before, during or after the peak in eutrophication in the 1980s (van Raaphorst and de Jonge, 2004). This at least warrants a re-examination of the importance of exchange and import from the North Sea and to what extent spatial and temporal variation does occur.

Identifying the importance of input of the North Sea requires identifying of the mixing and the area of exchange between the Wadden Sea and the North

Sea by an inert tracer with sufficient variation between endmembers and robust in time and space. Suspended particulate matter (SPM) is more or less inert, but exhibits a strong spatial and temporal variability both in amount and size composition in the North Sea (Postma, 1981; van Raaphorst et al., 1998) and especially inside the Wadden Sea (e.g. Postma, 1961). Despite these disadvantages, cross-shore gradients in suspended particulate matter showed indeed on average a minimum outside the Wadden islands, at approximately 50 to 100 km from the shore (Postma, 1981; Visser et al., 1991). A compilation of scarce field measurements and satellite information on SPM concentrations revealed a narrow turbidity minimum zone of a few kilometres width just outside the barrier islands of the Wadden Sea extending from the Netherlands to Denmark (van Raaphorst et al., 1998), which was considered to represent the boundary between coastal Wadden Sea and open North Sea waters. This has led to the confirmation of the so-called "line-of-no-return" in front of the Wadden Sea postulated by Postma (1984). The boundary is enhanced due to the residual transport in north-easterly directions that decreases the exchange between the water masses and increases the accumulation of suspended matter in the coastal zone (de Jonge and de Jong, 2002). However, it is unknown how well defined this boundary is and, if present, if this boundary shows spatiotemporal variation, e.g. as a result of variation in temperature, wind or rainfall (Postma, 1984).

For identification and an analysis of spatial and temporal variability in exchange of SPM, a precise tracer with high temporal resolution is required. Salinity potentially is such an inert tracer, and differences in salinity between open North Sea and the estuarine Wadden Sea are large enough. However, salinity in the area of interest is not only influenced by fresh water input directly into the Wadden Sea via Lake IJssel, the most prominent fresh water input, but also by a narrow band of coastal water with river Rhine input from the south (Zimmerman and Rommets, 1974; Postma, 1982; Philippart, 1988; de Jonge, 1990; de Vries et al., 1998) as well as smaller canals and rivers. Due to these different sources and the fact that the most prominent fresh water sources is separated from the area by a dike and fresh water inflow is controlled via sluices, the salinity in the area is not following the classical estuarine pattern with a gradual salinity gradient. This means that the hydrodynamic situation prevents the use of salinity as a mixing tracer in this area. Also nutrient concentrations are not suited as tracer due to their high turnover rate, and are therefore not inert over longer time scales (Pinckney et al., 2001).

Phytoplankton seems be an alternative candidate. Comparison of chlorophyll a time series has revealed different patterns of phytoplankton biomass variability, and also species composition in oceans and coastal waters (Cloern and Jassby, 2010; Winder and Cloern, 2010). Phytoplankton species composition might be a more sensitive tracer than biomass as each water mass with its own seasonal fluctuations in environmental conditions and biological forcing will contain its own unique plankton community due to specific physiological preferences and tolerances (Hutchinson, 1961; Cloern and Dufford, 2005; Carstensen et al., 2015). Deviations from the "classical seasonal pattern", in the North Sea of a spring bloom dominated by diatoms followed by a summer bloom of dinoflagellates (Alvarez-Fernandez et al., 2012; Carstensen et al., 2015), might then be indicative for potential boundaries between water masses exchanging SPM in the coastal zone.

If indices based on phytoplankton species richness are used as a tracer we face a major problem, as species identification of all algae within a sample is often incomplete (Zingone et al., 2015), A solution is a reduction of the taxonomic resolution to family or genus level to make the dataset more homogeneous and more robust to variations in species' identification (Heino and Soininen, 2007; Ptacnik et al., 2008; Carneiro et al., 2013; Olli et al., 2013). This implies, however, that algae that were not indentified up to this level are subsequently excluded from further analyses. In order to keep the samples as complete as possible, we decided to use phytoplankton order richness that was calculated as the number of orders of which phytoplankton species or species groups were found in a sample. We assumed that this index still contains the information on seasonality on phytoplankton community structure, whilst the possible bias as a result of reducing the actual sample size is relatively low.

Applying the phytoplankton order richness as a tracer to identify the area of exchange between Wadden Sea and North Sea, including its spatial and temporal variability, requires long-term data sets that are consistently collected and analysed without any methodological changes in time. Within the framework of the Dutch national marine monitoring program (`http://waterinfo.rws.nl/`), phytoplankton species composition was determined along two transects from the Dutch coast (including the Wadden Sea) to the central North Sea and consistently analysed since 2000. For each sample, the order richness of diatoms and flagellates was calculated as the number of orders of which phytoplankton species of these functional groups were present. Diatoms and flagellates were selected because they are two of the species richest groups of the phytoplankton (Guiry, 2012) and therefore expected to be most sensitive to variations in environmental conditions. We used the order richness data set to examine (I) if there is a seasonality in the order richness of phytoplankton, and, if so, (II) if there are differences in seasonality from the coast (Wadden Sea) to the central North Sea, (III) if there are specific spatial patterns in this seasonality which covary with spatial variation in environmental conditions such as the "line of no return", and (IV) if seasonal patterns in order richness can be attributed to specific phytoplankton groups related to environmental conditions.

3.2 MATERIALS AND METHODS

3.2.1 *Study area*

The stations used in this study were part of the Dutch national marine monitoring program (`http://waterinfo.rws.nl/`) and located at two transects perpendicular to the Dutch coast with one ("Terschelling") off the Wadden Sea island Terschelling and the other ("Noordwijk") just north of the outflows of the rivers Rhine and Meuse (Fig. 3.1). In addition, information on phytoplankton species composition from two stations within the Wadden Sea ("Danziggat" (TDG), "Marsdiep Noord" (TMD)) was added. The numbering of the stations at these transects reflects their distance (km) to the coastline, e.g. sampling station "T100" is located 100 km from the shoreline of the island of Terschelling.

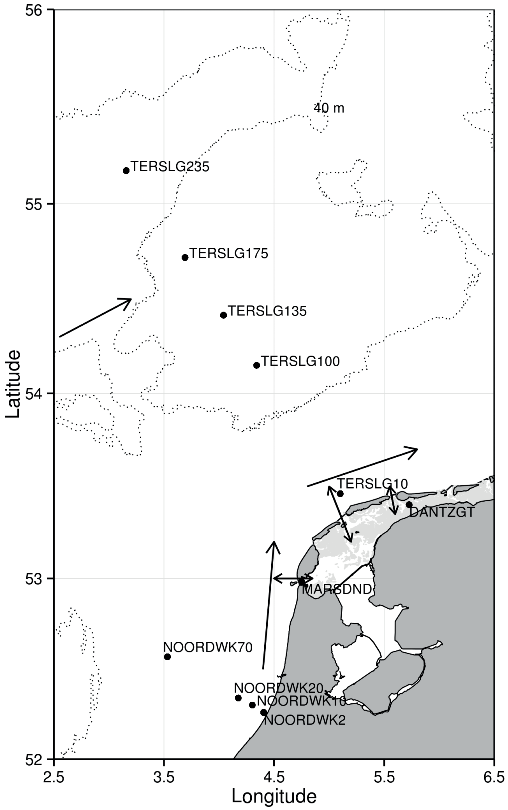

Figure 3.1: Map of study area with phytoplankton sampling stations (red points) and residual currents (black arrows; van Raaphorst et al., 1998), see Table 3.1 for description of stations.

The Terschelling transect covers a range of environmental conditions (Fig. 3.1 & Tab. 3.1) from shallow permanently mixed waters in the coastal zone ("T10") via the relatively shallow Oyster Grounds and a deeper channel (around 50 m) with mostly muddy ground and summer stratification ("T100", "T135") to the Dogger Bank that is a really shallow (18 m) sand bank in the middle of the central North Sea ("T235"). Except for the "T10", which is closest to the coast, thermal stratification occurs on all stations during summer (Baretta-Bekker et al., 2009).

The Noordwijk transect ranges from the coastal zone to 70 km offshore ("N70"). Except for the shallowest station ("N2") all stations are in permanently mixed waters (Fig. 3.1). At this transect, thermal and haline stratification occur intermittently for short periods (Baretta-Bekker et al., 2009).

Table 3.1: Names, codes (1: this paper; 2: original data base RWS) and geographical position (latitude in °N; longitude in °E) of sampling stations of phytoplankton with their distance to shore (in km), depth (in m), average salinity (in PSU) and indication if summer stratification occurs or not as obtained from Otto et al. (1990).

Transect	Station Code 1	Station Code 2	Latitude	Longitude	Distance	Depth	Salinity	Stratification
Terschelling	TDG	DANTZGT	53.401140	5.726982	0	5	28.89	No
	TMD	MARSDND	52.982540	4.749931	0	16	28.43	No
	T10	TERSLG10	53.461111	5.100833	10	24	32.68	No
	T100	TERSLG100	54.149444	4.341944	100	49	34.57	Yes
	T135	TERSLG135	54.415556	4.041111	135	35	34.64	Yes
	T175	TERSLG175	54.719167	3.691667	175	35	34.74	Yes
	T235	TERSLG235	55.172222	3.157500	235	18	34.8	Yes
Noordwijk	N2	NOORDWK2	52.261389	4.406111	2	13	29.14	No
	N10	NOORDWK10	52.302222	4.302500	10	18	30.65	Transition
	N20	NOORDWK20	52.341667	4.175000	20	20	32	Transition
	N70	NOORDWK70	52.569444	3.531389	70	28	34.92	Transition

3.2.2 *Sampling*

The data used in this study are part of the Dutch monitoring program that is executed by the Dutch Ministry of Transport and Public Works. Methods of sampling and counting of the samples were described in detail by Prins et al. (2012). The data was accessed through the national database (DONAR, `http://waterinfo.rws.nl/`) and cell counts were separated into taxonomical groups (in this case Order). Taxonomical classification for each (group of) species was obtained from Koeman et al. (2005) and the database WoRMS (World Register of Marine Species; `www.marinespecies.org`).

3.2.3 *Statistical analysis*

Data exploration was applied following the protocol described in Zuur et al. (2010). Time series were plotted for each location and inspected for outliers and zero inflation.

Spatial and temporal trends and variability in phytoplankton order richness was analyzed by testing a set of different models. Since the order richness is a count, a Poisson distribution with a log-link was used. This means that the basic model is of the form:

$$
\begin{gathered}
Order\ richness_{it} \sim Poisson(\mu_{it}) \\
E(Order\ richness_{it}) = \mu_{it}
\end{gathered}
$$

$$\mu_{it} = exp(\eta_{it})$$

$Order\ richness_{it}$ is defined here as the number of taxonomical orders for which phytoplankton of a taxonomical group (i.e. diatoms or flagellates) was found at location i at time t. The predictor function µit is a function of the covariate terms representing a long-term trend, seasonality and location. Due to the non-linearity of seasonal patterns, generalized additive models (GAM) were applied (Wood, 2006; Zuur et al., 2013, 2014).

The basic model was of the following form:

$$\eta_{it} = \alpha + f(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$$

The notation $f(DayInSeason_t)$ is a smoothing function of the seasonal pattern. In model M1 we use one long-term smoother for the all the locations (i.e. the $Year_i$ term) and also one seasonal smoother for all locations. The categorical covariate $Location_i$ allows for a different mean value per location. This basic model was subsequently adjusted to test the different hypotheses (see "Model selection" and Tab. 3.2).

The time series were highly irregular spaced in time, and sampling days differed per location, so the auto-correlation function could not be used. Therefore, a variogram was used via the gstat package (Pebesma, 2004) in R to assess temporal and spatial residual correlation. Variograms of Pearson residuals from each location did not show temporal correlation. However, when all residuals were combined, temporal correlation up to 6 days (indicating spatial correlation) were found and therefore a spatially correlated residual term was added and fitted to all models using integrated nested Laplace approximation via R (INLA Rue et al., 2009, 2015).

As in other Bayesian approaches, INLA estimates the posterior distribution of all random effects and parameters that are included into the model. It can handle different distributions as well as complex temporal and spatial correlations. The tools available for smoothing techniques in the current version of INLA are limited, especially for interaction terms between smoothers and categorical variables. However, the INLA package allows specification of a smoother in terms of its basis functions. Most smoothers can be written as $\mathbf{X} \times \mathbf{b} + \mathbf{Z} \times \mathbf{u}$, where the $\mathbf{u}$'s as normally distributed random intercepts, see Zuur et al. (2014) for a detailed explanation. This notation is accepted by INLA. Here we used 35 knots (Ruppert et al., 2003) and O'Sullivan splines as the most widely used smoother functions and being implemented into the mgcv package (Wand and Ormerod, 2008). For models with interactions between the smoother and the categorical variable location or group, the matrices $\mathbf{X}$ and $\mathbf{Z}$ are defined as block diagonal matrices.

3.2.4 *Model selection*

Outcomes of fits of different models were compared to examine if seasonal patterns in the phytoplankton order richness of diatoms and flagellates at stations

Table 3.2: Hypotheses and statistical models for patterns in seasonality in phytoplankton order richness (η_{it}) along a transect.

#	Hypothesis	Statistical model	Description	Model
H0	There is no trend, just noise (local variation dominates geographic variation in phytoplankton order richness)	$\eta_{it} = \alpha + Location_i + \epsilon_{it}$		
H1	All the time series have one (similar) underlying seasonal trend	$\eta_{it} = \alpha + f(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$	The notation $f(DayInSeason_t)$ is as smoothing function of the seasonal pattern. In this model we use one seasonal smoother for all locations and year ($factor(Year_t)$) as a categorical variable. The categorical covariate $Location_i$ allows for a different mean value per location	Model# 1
H2	Seasonality changes over the transect which is related to salinity	$\eta_{it} = \alpha + f_j(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$	$j = 1, 2$; where j refers to the Salinity zone with avg. Salinity below 30 PSU refers to brackish, above to marine	Model# 2
H3	All the time series havethree underlying seasonal trends which are related to stratification	$\eta_{it} = \alpha + f_k(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$	$k = 1, \ldots, 3$; where k refers to stratification zones (mixed, transit and stratified)	Model# 3
H4	All the time series have two underlying seasonal trends which are related to the line of no return two underlying seasonal trends which are related to the line of no return	$\eta_{it} = \alpha + f_l(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$	$l = 1, 2$; where l refers to zone inside or outside line of no return nb: no predefined clustering, so 5 submodels possible	Model# 2, Model# 3, Model# 4c-e
4c	Terschelling: separation between "T100" and "T135" Noordwijk: separation between "N10" and "N20"			
4d	Terschelling: separation between "T135" and "T175" Noordwijk: separation between "N20" and "N70"			
4e	Terschelling: separation between "T175" and "T235" Noordwijk: Not possible			
H5	All the time series have two underlying seasonal trends which are related to the depth of the station	$\eta_{it} = \alpha + f_m(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$	$m = 1, \ldots, 3$; where m refers to the depth of the station (only Terschelling transect)	Model# 5
H6	All the time series have two underlying seasonal trends which are related to a combination of depth of the station and it's distance to the shore	$\eta_{it} = \alpha + f_n(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$	$n = 1, \ldots, 4$; where n refers to a combination of depth and distance to the shore (only Terschelling transect)	Model# 6
H7	All the time series alongthe transect have a different seasonal trend	$\eta_{it} = \alpha + f_o(DayInSeason_t) + factor(Year_t) + Location_i + \epsilon_{it}$	$o = 1, \ldots,$ max station number; where o refers to the station code	Model# 7

along the two transects perpendicular to the coastline could be best explained:

(I) by local variation dominating the geographical variation in phytoplankton order richness (null hypothesis), or

(II) by one common seasonality pattern for all stations within a transect (Hypothesis 1), or

(III) by a gradual shift in seasonality from the central North Sea to the coast (Hypotheses 2), or

(IV) by groups of seasonal patterns related to specific spatial processes such as summer stratification or the "line of no return" (Hypotheses 3-4), or

(V) by groups of seasonal patterns related to specific physical properties such as water depth and distance to the shore (Hypotheses 5-6, only possible for the Terschelling transect), or

(VI) by local seasonal variation dominating variation at large spatial scales (Hypothesis 7; Tab. 3.2).

Models fitted with the INLA package were compared by the DIC (Deviance Information Criterion). DIC is the Bayesian equivalent to the Akaike's information criterion (AIC), a tool to measure the goodness-of-fit of an estimated statistical model and model complexity. If competing models are ranked according to their DIC, the one having the lowest DIC is the best. Differences ($\Delta DIC = DIC_i - DIC_{min}$) between the DIC of a particular model (DIC_i) and the that of the best model (DIC_{min}) of more than 10 might definitely rule out the particular model i with the higher DIC, and differences between 2 and 10 imply substantially less good fit of the particular model compared to the best model. If the difference in DIC is less than 2, then the fit of the particular model is considered to be comparably good as that of the best model (Burnham and Anderson, 2002). In case one of these two models is simpler than the other, this one should be considered being the best. However, if models with DIC differences of less than 2 are comparably complex, then there is no best model. The likelihood of a particular model i to be the best one was calculated following Burnham and Anderson (2002) by applying the following formula: $Likelihood = exp\left(\frac{(DIC_{min} - DIC_i)}{2}\right)$
where DIC_{min} is the lowest found DIC of the different models tested and DIC_i is the DIC of the model i for which the likelihood is calculated.

3.3 RESULTS

3.3.1 *Phytoplankton order richness*

A total of 26 different orders of diatoms were found within the study area and study period, of which six were only found occasionally (Achnanthales, Aulacoseriales, Corethales, Licmophorales, Striatellales and Thalassiophysales, App. Fig. B.1). Several orders (among others Anaulales, Centrales and Thalassiosirales) were more abundant close to the shore than further offshore. For diatoms, the highest number of orders (20) was found at the "Marsdiep Noord" station orders on 17th October 2005, and the lowest (0) at the stations "T100" and "T235" on 2nd May 2007. For diatoms, the order richness showed a seasonal pattern that differed spatially (Fig. 3.2). The Wadden Sea stations ("TMD" and "TDG") had the highest order richness in summer/autumn. At the Terschelling transect, the station 10 km off the coast showed the highest order richness of diatoms in winter and the stations at 100, 135 and 175 km off the coast showed a less clear seasonal pattern (Fig. 3.2, right). The diatoms at the station at 235 km off the coast ("T235") had relatively low order richness in summer, but not as low as at the "T10" station (Fig. 3.2, right). The Noordwijk transect showed low order richness in diatoms at all stations during summer (Fig. 3.2).

For flagellates, a total number of 31 different orders were found of which 13 occurred only occasionally (Chlorodendrales, Coccidiniales, Coccosphaerales, Euglenida, Floenciellales, Isochrysidales, Mischococcales, Nephroselmidales, Pyrocystales, Synurales, Synacosphaerales, Thannatomonadida and Volvocales, App. Fig. B.2). Several orders of flagellates had a higher presence closer to the shore (Noctilucales and Sphaeropleales), whilst others showed a clear offshore preference (Dinophysiales, Gonyaulacales and Prorocentrales). Flagellates order richness showed less variation than that of diatoms with a maximum value of 16 orders at "T235" (21st February 2006, 22nd June 2004 and 2nd May 2007). The minimum order richness in flagellates (0) was found at stations "N10" and "N2" on various dates. For flagellates, the seasonal pattern appeared to be less variable than for diatoms and more or less similar between the stations with a relatively high order richness found in summer compared to winter (Fig. 3.2).

Table 3.3: DIC and likelihood of the different models at the Terschelling transect for diatoms and flagellates ΔDIC refers to the difference of the DIC from this model to the one with the lowest DIC.

	Diatom			**Flagellates**		
Model	**DIC**	**ΔDIC**	**likelihood**	**DIC**	**ΔDIC**	**likelihood**
1	5462.04	274.75	0	4622.72	0	1
2	5227.82	40.53	0	4637.92	15.2	0
3	5301.13	113.84	0	4786.88	164.16	0
4c	5392.32	205.03	0	4734.75	112.03	0
4d	5420.46	233.17	0	4771.45	148.73	0
4e	5485.49	298.2	0	4783.38	160.66	0
5	5267.23	79.94	0	4655.45	32.73	0
6	5187.29	0	1	5187.29	564.57	0
7	5372.51	185.22	0	5372.51	749.79	0

Table 3.4: DIC and likelihood of the different models at the Noordwijk transect for diatoms and flagellates ΔDIC refers to the difference of the DIC from this model to the one with the lowest DIC.

	Diatom			Flagellates		
Model	**DIC**	**ΔDIC**	**likelihood**	**DIC**	**ΔDIC**	**likelihood**
1	3609.79	35.54	0	3089.59	21.46	0
2/3	3590.21	15.97	0	3068.12	0	1
4c	3578.66	4.42	0.11	3069.67	1.54	0.46
4d	3574.24	0	1	3072.14	4.01	0.13
7	3584.15	9.91	0.01	3584.15	516.03	0

3.3.2 *Spatial and temporal trends*

Terschelling transect

For diatoms, spatial and temporal trends in order richness was best explained by Model # 6 with a grouping of stations into four areas according to the combination of water depth and the distance to the shore (Tab. 3.3). The difference in DIC compared to the next best model (# 2) was more than 40, indicating that other explanations (Models) were not competing with Model # 6. The results of this model indicated a seasonal pattern with generally high order richness in summer in the Wadden Sea (Area 1) compared to the three areas in the North Sea (Fig. 3.3). In the North Sea, lowest summer values were found at "T10" (Area 2). The other stations at this transect showed a pattern with a peak in the middle of the summer and two phases with lower order richness and the furthest offshore station, which was more pronounced in Area 3 ("T100", "T135" and "T175") than in Area 4 ("T235") (Fig. 3.3). For this model, the diatom order richness in Area 1 (Wadden Sea) was significantly higher compared to the other areas in the North Sea and appeared to decrease within the North Sea from inshore to offshore areas (Tab. 3.5). The annual estimates for seasonality showed no significant difference between the year 2001 and the other years, implying the seasonal variation in order richness of diatoms was more or less similarly strong for all years (Tab. 3.5, Fig. 3.7A).

For flagellates, Model # 1 with only one seasonal trend with a peak in summer and lower values in winter for all stations had the lowest DIC (Tab. 3.3; Fig. 3.4). The DIC of the next best model was considerably higher (>10), so Model # 1 was selected as the best model. The posterior estimates of model parameters of this model indicted, however, that the flagellate order richness at Area 1 ("TDG") was significantly lower than that at all other stations (Tab. 3.6). Annual signals showed no significant differences between years, implying that all years experienced more or less the same strength in seasonality in order richness of flagellates (Tab. 3.6, Fig. 3.7B).

Table 3.5: Posterior estimates (mean and 95% credibility interval) of model parameters of Model #6 for diatoms, Area 1 refers to the Wadden Sea stations ("TMD", "TDG"), Area 2 refers to "T10", Area 3 to "T100", "T135" and "T175" and Area 4 to "T235". The parameters values of the year 2001 and Area 1 ("Wadden Sea") are zero by definition.

Parameter	**mean**	$Q_{0.025}$	$Q_{0.975}$
Intercept	2.5557	-2.2538	7.1897
2002	-0.0794	-0.2615	0.1231
2003	-0.0773	-0.3818	0.2826
2004	-0.0504	-0.4711	0.4856
2005	-0.067	-0.6041	0.6432
2006	-0.1053	-0.7526	0.7854
2007	-0.1462	-0.9554	0.8639
2008	-0.1334	-1.1553	0.9411
2009	-0.2434	-1.4424	0.9171
Area 2	-0.2846	-0.3509	-0.219
Area 3	-0.298	-0.3446	-0.2515
Area 4	-0.3517	-0.4195	-0.2845
Smoother Area 1	0.0133	-0.0319	0.0586
Smoother Area 2	0.0079	-0.0549	0.0706
Smoother Area 3	0.0189	-0.028	0.0652
Smoother Area 4	-0.0402	-0.1046	0.0235

Table 3.6: Table 6. Posterior estimates (mean and 95% credibility interval) of model parameters of Model #1 for flagellates, Area 1 refers to "TMD", Area 2 to "TDG", Area 3 to "T10", Area 4 to "T100", Area 5 to "T135", Area 6 to "T175" and Area 7 to "T235". The parameters values of the year 2001 and Area 1 (station "TMD") are zero by definition.

Parameter	**mean**	$Q_{0.025}$	$Q_{0.975}$
Intercept	1.7436	0.2919	1.1564
2002	-0.1248	0.1511	-0.4379
2003	-0.1283	0.2045	-0.5704
2004	-0.1993	0.2498	-0.774
2005	-0.3584	0.2933	-1.0664
2006	-0.1973	0.3134	-0.9535
2007	-0.2503	0.3416	-1.0708
2008	-0.2779	0.3794	-1.2217
2009	-0.1264	0.4136	-1.1442
Area 2	0.2381	0.0433	0.1533
Area 3	0.3456	0.0449	0.2575
Area 4	0.4708	0.0438	0.3848
Area 5	0.4479	0.044	0.3615
Area 6	0.4198	0.0446	0.3324
Area 7	0.4226	0.0444	0.3355
Smoother	0.0724	0.0205	0.0313

Noordwijk transect

For diatoms, the model with the lowest DIC was Model # 4d (Tab. 3.4), i.e. one of the models where the grouping of the stations was tested according to a possible presence of a "line-of-no-return". The difference in DIC between this model and other second best model (Model # 4c) was larger than 2, so Model # 4d was considered to be the best model. This model implied that the pattern in seasonality shifted between station "N20" and "N70", with the relatively low diatom order richness in summer at the outermost station of the Noordwijk transect (Area 2; "N70") being more pronounced than those in Area 1, comprising the other three stations closer to the shore (Fig. 3.5) and having an overall lower order richness (Tab. 3.7). Compared to the year 2001, the overall order richness in diatoms was significantly lower in the years 2005 and 2009 (Tab. 3.7, Fig. 3.7C).

Table 3.7: Posterior estimates (mean and 95% credibility interval) of model parameters of Model #4d for diatoms, Area 1 refers to "N2", "N10" and "N20", Area 2 to "N70". The parameters values of the year 2001 and Area 1 ("N2", "N10","N20") are zero by definition.

Parameter	**mean**	$Q_{0.025}$	$Q_{0.975}$
Intercept	2.4292	2.288	2.5727
2002	-0.1205	-0.2875	0.0565
2003	-0.0844	-0.2851	0.0921
2004	-0.1293	-0.324	0.0678
2005	-0.2548	-0.4516	-0.0525
2006	-0.1544	-0.3553	0.0415
2007	-0.1803	-0.3679	0.0352
2008	-0.162	-0.3561	0.0485
2009	-0.2433	-0.4526	-0.046
Area 2	-0.058	-0.1163	-0.0003
Smoother Area 1	0.01	-0.0215	0.0415
Smoother Area 2	-0.037	-0.0845	0.0103

With regard to flagellates, the combined Model # 2/ Model # 3 had the lowest DIC, however the difference in DIC to the next best model was less than 2 (Model # 4c). As both model have the same complexity they should be treated as equally good in their prediction of the seasonal pattern (Tab. 3.4). Model # 2/3 implied that the pattern in seasonality shifts between station "N2" (Area 1, where there is no stratification) and Area 2 ("N10", N20" and "N70") that is considered as a transition zone between waters that are continuously mixed and that experience summer stratification (Tab. 3.8) with a peak in late summer order richness being higher in the outermost stations (Fig. 3.6A). The most inshore station "N2" had overall higher order richness in flagellates (Tab. 3.8). Model # 4c implied that the pattern in seasonality shifts between Area 1 ("N2" and "N10") and Area 2 ("N20" and "N70"; Tab. 3.8) with a peak in late summer order richness being higher in the outermost stations (Fig. 3.6B). The most inshore station "N2" had overall higher order richness in flagellates (Tab. 3.8). In both models seasonal signals did not significantly differ between years and showed the same overall pattern (Tab. 3.8, Fig. 3.7D; only graph from best model shown).

Table 3.8: Posterior estimates (mean and 95% credibility interval) of model parameters of Model #2 /3 and Model #4c for flagellates, Area 1 refers to "N2" in Model #2 /3 and "N2" & "N10" in Model #4c and Area 2 to "N10", "N20" and "N70" in Model #2 /3 and "N20" and "N70" in Model #4c. The parameters values of the year 2001 and Area 1 ("N2" or "N2"and "N10") are zero by definition.

	Model #2 /3			**Model #4c**		
Parameter	**mean**	**Q0.025**	**Q0.975**	**mean**	**Q0.025**	**Q0.975**
Intercept	1.8072	0.6227	0.3746	1.9805	1.3662	2.7155
2002	-0.0816	0.134	-0.3704	-0.1082	-0.4253	0.185
2003	0.0359	0.1955	-0.4123	-0.0984	-0.5471	0.2991
2004	-0.1279	0.26	-0.7776	-0.1827	-0.7728	0.2782
2005	-0.0929	0.3232	-0.9231	-0.3483	-1.0812	0.1531
2006	0.0461	0.3664	-0.872	-0.186	-0.9726	0.4055
2007	-0.0187	0.4195	-1.0202	-0.2267	-1.0769	0.4587
2008	-0.063	0.4726	-1.224	-0.2583	-1.2352	0.4804
2009	-0.0112	0.5261	-1.3292	-0.0974	-1.1536	0.7611
Area 2	-0.1502	0.041	-0.2313	0.2016	0.152	0.2511
Smoother Area 1	0.06	0.0435	-0.0258	0.0612	0.0135	0.1082
Smoother Area 2	0.0858	0.0256	0.0343	0.0782	0.0261	0.1298

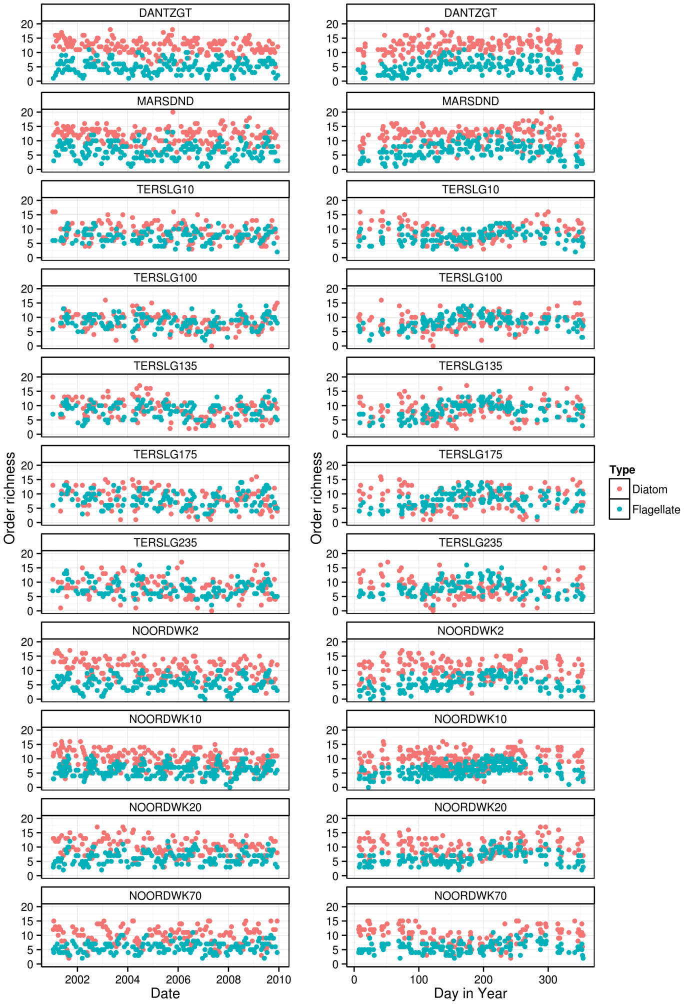

Figure 3.2: Order richness (η_{it}) based on the number of taxonomical orders of diatoms and flagellates in a sample for stations in the Wadden Sea and North Sea for the period 2001-2009 (left panels) and during the season (right panels).

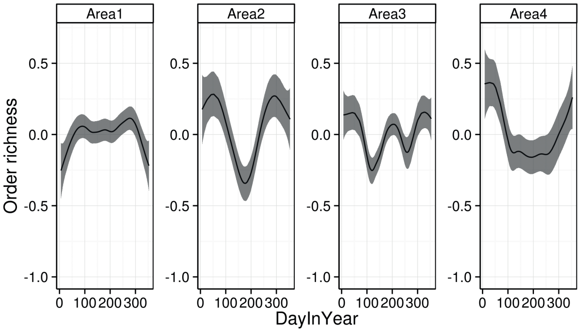

Figure 3.3: Seasonal smoother for order richness in diatoms at the Terschelling transect for four different areas as described by Model #6, i.e. Area 1 ("TMD", "TDG"), Area 2 ("T10"), Area 3 ("T100", "T135", "T175") and Area 4 ("T235").

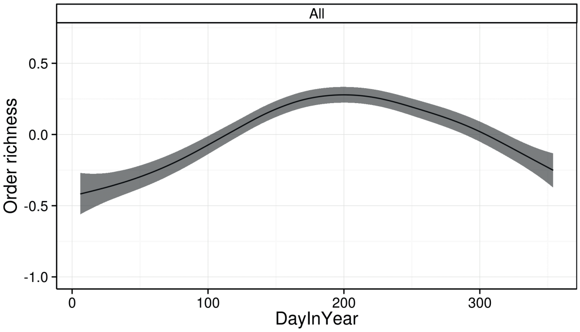

Figure 3.4: Seasonal smoother for order richness in flagellates at the Terschelling transect as described by Model # 1, i.e. one common smoother for seasonality at all stations in the Wadden Sea and North Sea.

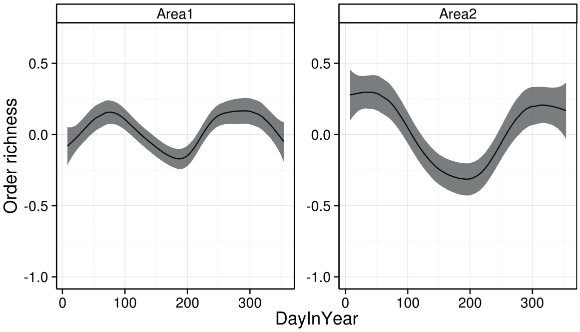

Figure 3.5: Seasonal smoother for order richness in diatoms at the Noordwijk transect for two different areas as described by Model 4d, i.e. Area 1 ("N2", "N10", "N20") that is assumed to be inside the " line-of-no-return" and Area 2 ("N70") that is assumed to be outside the exchange area.

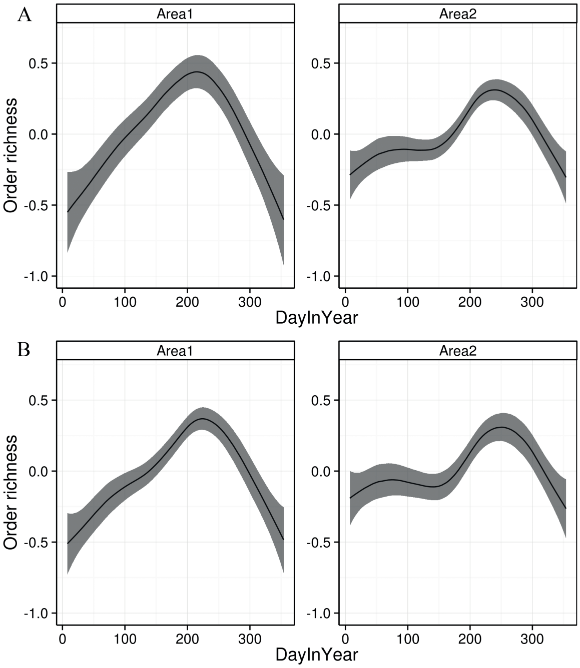

Figure 3.6: Seasonal smoother for order richness in flagellates at the Noordwijk transect for two different areas as described by A) Model 2/3, i.e. Area 1 ("N2") that is permanently mixed and Area 2 ("N10", "N20", "N70") that occasionally experiences thermal and haline stratification and B) Model 4c, i.e. Area 1 ("N2" and "N10") and Area 2 ("N20", and "N70").

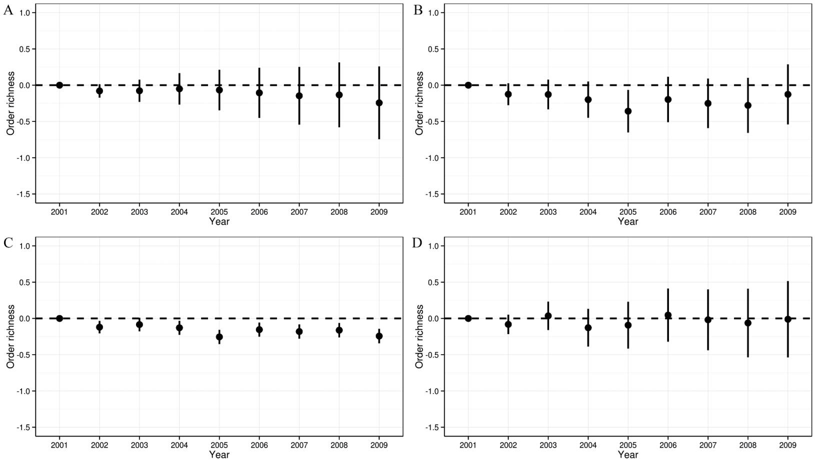

Figure 3.7: The year effect of the various models, i.e. Model #6 for diatom order richness along the Terschelling transect (A), Model #1 for flagellate order richness along the Terschelling transect (B), Model #4d for diatom order richness along the Noordwijk transect (C) and Model #2 / Model #3 for flagellate order richness along Noordwijk transect (D).

3.4 DISCUSSION

The seasonality patterns in phytoplankton order richness along transects perpendicular to the shore, both for diatoms and flagellates suggests that it might be a promising tracer for identifying mixing of particulate organic matter between coastal and open waters. Several other studies indicate that the number of species is related to the general functioning of an ecosystem (Naeem et al., 1994) such as nutrient cycling, production and resource use efficiency (Loreau et al., 2001; Naeem et al., 2009; Finkel et al., 2010). However, not only richness on a species level can be used to assess such ecological relationships (Gaston et al., 1993). The higher taxon approach was first used for terrestrial ecosystem (Balmford et al., 1996, and literature therein) and is now also transferred to aquatic ecosystems (Passy and Legendre, 2006; Heino and Soininen, 2007; Gallego et al., 2012; Carneiro et al., 2013; Mueller et al., 2013; Machado et al., 2015). Several studies dealing with the higher taxon approach in freshwater algae (e.g. Heino and Soininen, 2007; Carneiro et al., 2013) and marine phytoplankton (e.g. Ptacnik et al., 2008; Olli et al., 2013, 2014) showed that higher taxa can be used to assess eutrophication state and resource use. Also our findings with regard to exchange of particulate matter based upon seasonality patterns in order richness underlines the strength of the higher taxon approach.

For the two transects (Terschelling, Noordwijk) and the two phytoplankton groups (diatoms, flagellates), there was no common model that could explain the observed seasonality in phytoplankton order richness. For the group of Terschelling stations (in total six stations, including two stations in the Wadden Sea), seasonality in order richness varied according to depth and distance to shore for diatoms and was uniform along this transect for flagellates. At the four Noordwijk transect stations, there appeared to be two groups in seasonality with the outermost station ("N70") being separated from the rest for the diatoms, and the seasonality at innermost non-stratified station ("N2") being different from the rest for the order richness in flagellates. This implies that the seasonality pattern in diatom order richness at Noordwijk was not explained by ambient environmental conditions with respect to depth, distance to shore, salinity and stratification, and may therefore be the result of a "line-of-no-return" between 20 and 70km from the shore. For the Terschelling transect, there are no stations at comparable distances from the shore and there appears to be a change in seasonality of diatoms somewhere between 10km and 100 km. This implies that a "line-of-no-return" might also exists in this part (10 – 100 km) of the Terschelling transect. Our findings on a possible "line-of-no-return" between 20 and 70 km from the shore at Noordwijk and between 10 and 100 km at Terschelling is in line with previous observations of a minimum in suspended particulate matter (SPM) concentrations at 50 to 100 km from the shore (Postma, 1981; Visser et al., 1991). The sampling grid of this data set was, however, not fine enough to narrow down the exact position of the "line-of-no-return".

Within coastal waters, the phytoplankton spring bloom is generally dominated by large, fast-growing diatoms, followed by a number of summer and autumn blooms comprised of diatoms and flagellates (Tett et al., 1986; Mallin et al., 1991; Carstensen et al., 2015). Diatoms often dominate phytoplankton blooms in the coastal zone because they are so highly adaptable to different environmental conditions such as varying light and other physical stress (Armbrust, 2009; Carstensen et al., 2015). As phytoplankton blooms are mostly dominated by a single species (e.g. the flagellate *Phaeocystis globosa*), highest observed order richness is expected outside blooms but still within the growing season. Different patterns in seasonality in the order richness (as, for example, found for diatoms along the Terschelling transect) might, therefore, reflect different timing in (low diversity) blooms. Different strength in seasonality (as, for example, found for diatoms along the Noordwijk transect) might reflect different strength of coinciding blooms at these stations. In addition, however, higher overall densities increase the probability of finding more species in a sample of a given volume (Gotelli and Colwell, 2001).

In Dutch coastal waters, dinoflagellates tend to have a higher biomass in summer-stratified (lower turbulence) offshore stations, thus attaining highest biomass on stations further from the coast where thermal and/or haline stratification occurs (Baretta-Bekker et al., 2009). However, biodiversity is expected to be low during blooms (Baretta-Bekker et al., 2009), with the lowest order richness of flagellates in summer months. Our results contradict these expectations, as we find the highest order richness in flagellates at both transects in summer. We also found an increase in seasonality along the Noordwijk transect, being subject to short periods of intermittent thermal and haline stratification. This signal of stratification was not observed for flagellate order richness along the Terschelling transect where thermal stratification occurs on almost all (with exception of "T10") stations during summer. During periods of haline stratification, phytoplankton samples taken from the water surface at "N2" might have contained (more) freshwater flagellates closer to shore. This is in agreement with the gradual decline of the presence of the freshwater order "Sphaeropleales" between "N2" and "N20" at the Noordwijk transect (see Appendix Fig. B.2). From these observations, it appears that seasonality in order richness in flagellates is more driven by an overall seasonality in phytoplankton communities, driven by nutrient cycling and inflow of freshwater algae, then by thermal stratification during summer.

Our findings suggest that patterns in seasonality in order richness of diatoms and flagellates reflect different water masses and drivers of phytoplankton dynamics along the coastline of the Netherlands. The Wadden Sea was found to be clearly different from the North Sea, implying that seasonality in Wadden Sea phytoplankton is at least partly driven by local environmental conditions and /or that the exchange between the Wadden Sea and the North Sea is limited, in particular during summer. The stations "N2", "N10", "N20" and "T10" appear to be at the inside of the "line-of-no-return". Similarity in seasonality in diatom order richness at "T100", "T135" and "T175" compared to the more shallow stations in the close surroundings suggests that depth is a strong driver for phytoplankton dynamics and that this signal is not diffused as the result of mixing along the transect. Our findings with regard to clear grouping of stations based on seasonality and long-term variation in order richness of diatoms and flagellates underline the potential of using information at higher taxonomic levels to detect spatial and temporal patterns in mixing. In order to take full advantage of this technique, a grid on order richness with a higher resolution in time and space is required.

3.5 ACKNOWLEDGMENTS

We are most grateful to Rijkswaterstaat for the start and continuation of the long-term monitoring programme on phytoplankton species abundance in the North Sea and the Wadden Sea, and to all who were involved in sampling and analyses. We thank Alain F. Zuur for the support with the statistical analysis. We furthermore acknowledge the scientific interactions with our colleagues of the INFOWEB project, i.e. the NIOZ Netherlands Institute of Sea Research (Texel & Yerseke, NL), the Alfred Wegener Institute for Polar and Marine Research (Sylt, D), Senckenberg Institute (Wilhelsmhaven, D) and the University of Groningen (Groningen, NL). We also like to thank the two anonymous reviewers for their helpful comments on earlier versions of this manuscript. The supplementary material for this article can be found at `https://doi.org/10.1017/S0025315416001326`.

4

CHANGES OVER 50 YEARS IN FISH FAUNA OF A TEMPERATE COASTAL SEA: DEGRADATION OF TROPHIC STRUCTURE AND NURSERY FUNCTION

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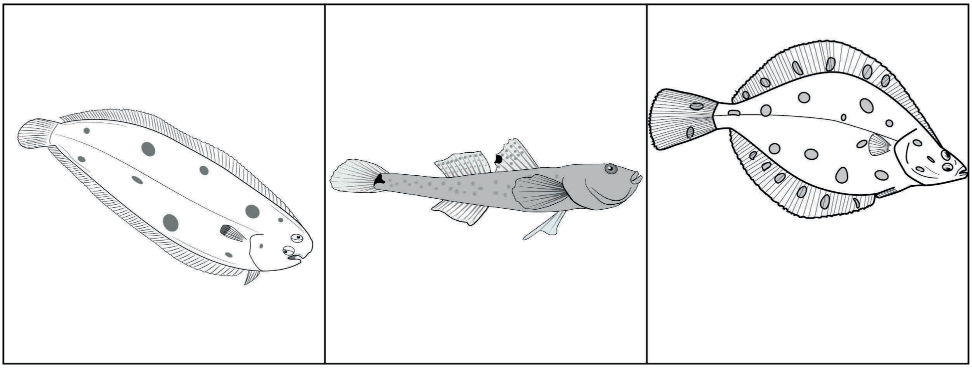

ABSTRACT

The 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. 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.

4.1 INTRODUCTION

Coastal ecosystems have been under pervasive human disturbance for centuries (Jackson et al., 2001) with historical evidence worldwide for major structural and functional change due to overfishing. The current challenges relate not only to overfishing, but the combined effects of it with climate change (e.g., warming, acidification, deoxygenation), habitat destruction and pollution (Bijma et al., 2013; European Marine Board, 2013).

Present findings on long-term changes in fish communities are primarily based upon information from commercial catches, landings and stock assessments. Most ecological research addressing full communities is of shorter duration and cannot give a long historical perspective. Furthermore, most observations are from the open sea while cumulative impacts of human behaviour are considered most severe in shallow coastal waters. To examine long-term changes in coastal fish communities and identify their possible causes, we analyse a 50 year consistent time series of fish fauna in the Dutch part of the international Wadden Sea, the largest coastal ecosystem bordering the North Sea.

The Wadden Sea is a typical example of a coastal ecosystem under long-term anthropogenic pressure. Key changes in the Dutch part include the decline of the harbour seal (Reijnders and Lankester, 1990); disappearance of the bottlenose dolphin (Reijnders and Wolff, 1983); loss of the commercial spring herring fishery; pollution events (Essink and Wolff, 1983); embankments; eutrophication (de Jonge et al., 1996; Philippart et al., 2007) and species introductions (Wolff, 1992; van Walraven et al., 2013).

Daily monitoring of the fish fauna using fyke nets in the western part of the Dutch Wadden Sea started in 1960 and has continued without change in methodology ever since (van der Meer et al., 1995). The main advantage of this passive sampling device is that it samples both pelagic and benthic components of mobile fauna. It has been demonstrated that fyke catches are representative of a much larger area and that they represent an, on-average, constant sampling fraction of the fauna for all the abundant and most of the rare species (van der Meer et al., 1995). Non-commercial fyke catches such as these supply the best available data of changes in the marine ecosystem as sampling methods have not been influenced by economics, management, fishing technology and targeting patterns as normally occurs citepBranch2010.

Previous papers on these fyke catches dealt with fish recruitment (Philippart et al., 1996), long-term variability in the abundance of the brown shrimp *Crangon crangon* (Campos et al., 2010), bass *Dicentrarchus labrax* (Cardoso et al., 2015) and gelatinous zooplankton (van Walraven et al., 2015). In this paper, long-term trends in the coastal fish community are analysed by addressing the following questions: [1] what are the long-term patterns in the fish community; [2] are these long-term trends associated with environmental factors, and [3] is there an impact of climate change visible?

4.2 MATERIAL AND METHODS

4.2.1 *Sampling*

A passive fish trap near the entrance of the Dutch Wadden Sea (Fig. 4.1) was used. This 'kom-fyke' (Nédélec and Prado, 1982) has a leader of 200 m running from above the high water mark into the subtidal where two chambers collect the fish and other specimens. The stretched mesh-size of the leader and the chambers was 20 mm. In the area, the semidiurnal lunar tide is dominating and tidal range varies between 1 and 2 m depending on weather conditions and lunar phase. Tidal currents normally do not exceed $1\,\mathrm{m\,s^{-1}}$, except for periods with strong wind stress. Fishing started in 1960 and has continued ever since where the kom-fyke was emptied every morning irrespective of tidal phase, except when prevented by bad weather. In most years, the kom-fyke was removed just before winter because of potential damage by ice floes and in summer because of fouling of the net and potential clogging by macroalgae and jellyfish. Catches were sorted immediately, and all individuals were identified up to species level. For each species, numbers were counted and sometimes, when numbers were large, only wet mass was determined. Prior to data analysis, wet masses were transformed into counts, using a fixed ratio per month, i.e. a fixed mean individual mass based on the actual measurements from 1970 onwards. All information was stored in a database.

A suite of environmental parameters was collected which were considered to potentially influence fish communities (Table 4.1). Large-scale hydrodynamic circulation was indexed by the North Atlantic Oscillation (NAO) during winter (Dec-March). Fish performance during winter (Dec-Feb) and summer (July-Aug) was indexed by water temperature, salinity and visibility (Secchi disk readings), obtained from long-term monitoring programmes at the NIOZ sampling jetty, located < 1 km east of the kom-fyke. Primary productivity was indexed by mean summer values (May-Sept) of concentrations of chlorophyll-a ($\mu\mathrm{g\,L^{-1}}$), total-N and total-P ($\mathrm{mg\,L^{-1}}$; sum of dissolved inorganic, dissolved organic, and particulate compounds) in the Marsdiep basin. As nutrient concentrations only covered part of the sampling period, loadings of total-N and total-P discharged from Lake IJssel (the main freshwater source of the Marsdiep) were also included. Habitat destruction was captured by the amount of sand dredging, the amount of beach nourishment and the intensity of shrimp fisheries in the coastal zone of the North Sea and cockle fisheries in the intertidal of the Wadden Sea. To index predation pressure by top predators, abundance estimates of cormorants in the western Wadden Sea, and numbers of harbour and grey seals in the Dutch Wadden Sea and coastal zone were multiplied by their respective daily food requirements [cormorants: $575\,\mathrm{g\,wet\,mass\,d^{-1}}$ (Leopold et al., 1998); harbour seal: $2.5\,\mathrm{kg\,wet\,mass\,d^{-1}}$, grey seal: $3\,\mathrm{kg\,wet\,mass\,d^{-1}}$ (IMARES, Brasseur pers. comm.)] and summed.

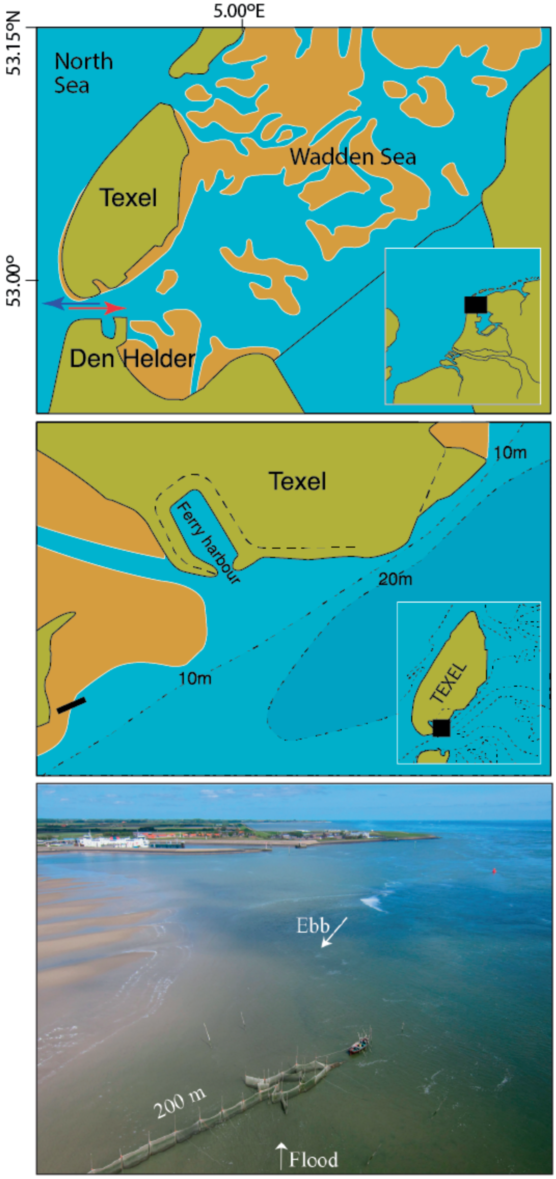

Figure 4.1: The sampling location near the island of Texel. Upper panel: western Dutch Wadden Sea; red arrow indicates inwards migration in spring and blue arrow outward migration in autumn. Middle panel: fyke net position (black bar); Orange: intertidal areas. Lower panel: Arial photograph taken from a southwestern angle (courtesy of Lodewijk van Walraven)

Table 4.1: Environmental variables used with references.

	Environmental parameter	Area	Time series	Unit	References
Hydrodynamic circulation	NAO Dec- March	Coastal zone Wadden Sea	1960-2011	-	Jones et al. (1997) `http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm`
Fish performance	Water temperature	western Wadden Sea	1960–2011	°C	van Aken (2003, 2010) (`www.nioz.nl`)
	Salinity	western Wadden Sea	1960–2011	o/oo	van Aken (2003) (`www.nioz.nl`)
	Secchi disc	western Wadden Sea	1974-2010	m	Philippart et al. (2013)
Productivity	Chlorophyll	western Wadden Sea	1976–2007	$\mu g\,L^{-1}$	(`http://waterinfo.rws.nl/`)
	Total-N and total-P	western Wadden Sea	1972-2010	$mg\,L^{-1}$	(`http://waterinfo.rws.nl/`)
	Total-N and total-P loadings	western Wadden Sea	1960-2004	$mol\,s^{-1}$	van Raaphorst and de Jonge (2004)
			1977–2009	$kg\,s^{-1}$	van Beusekom et al. (2009)
Habitat destruction	Sand mining	Coastal zone	1960-2011	$10^6\,m^3\,y^{-1}$	Anonymous (2013*b*)
	Beach nourishment	Coastal zone	1960–2011	$10^6\,m^3\,y^{-1}$	Rijkswaterstaat Zee en Delta Stolk, pers. comm.
	Shrimp fisheries	Coastal zone	1970-2011	$10^3\,km^2$	Landings: Anonymous (2013*a*)
		Wadden Sea			Densities: IMARES DFS survey; Tulp pers. comm.
	Intertidal cockle fisheries	Wadden Sea	1971-2011	$10^6\,kg\,y^{-1}$	Landings: IMARES; Troost pers. comm.
Top predators	Cormorants	western Wadden Sea	1980-2011	Ind.	Sovon Vogelonderzoek Nederland/Netwerk Ecologische Monitoring.
	Harbor and grey seals	Dutch Wadden Sea	1960-2011	Ind.	CBS et al. (2016)

4.2.2 *Data analysis*

For each species, the length-weight relationship was determined, based on individuals collected between 1990 and 2002 (Leopold et al., 2001). For some rare species, length-weight relationships were taken from Fishbase (`www.fishbase.org`). For all catches, total wet biomass was estimated. First, for each species, the size-frequency distribution of the catch was converted to wet mass using the length-weight relationship. Then the total biomass of the catch was estimated by summing the individual masses (direct estimate). For the period from 1960 to 1980, no size frequency distributions were available and, therefore, total biomass of the catch could only be calculated indirectly by taking the average monthly individual mass for each species from the period 1980-2010. For comparison, this indirect estimate was also applied for the period 1980-2010. Finally, the average daily biomass of the catch was calculated for both spring (April, May, June) and autumn (September, October). Species were characterized based on number of years found as core ($\leq$20 y) or transient species (<20 y), by mode of life (pelagic, demersal, benthopelagic) and to trophic level (the position of a species in the food chain) using Fishbase (`www.fishbase.org`). In addition, the biogeographic guild (northern and southern species) was determined based on Daan (2006). For each sampling date, the tropic level of the fish fauna was estimated by taking the trophic level of the various species caught and calculating the massweighted average trophic level. All information is presented in Appendix D.

4.2.3 *Statistical analysis*

Statistical treatments used R (R Core Team, 2011). Preliminary data explorationwas carried out following the protocol described in Zuur et al. (2010). Multi-panel scatterplots using the xyplot function from the lattice package (Sarkar, 2008) were applied to identify the type of relationship between environmental variables and the presence of collinearity. Common trends in the biomass time series of the various species were extracted by min/max autocorrelation factor analysis (MAFA) (Solow, 1994), all species present for >10 years were included. This analysis is a type of principal component analysis where the axes represent a measure of autocorrelation and indicate the association between the values of the principal component at Z_t and Z_{t+k}, where k is a time lag of 1, 2 etc. The first MAFA axis has the highest autocorrelation with a time lag of 1 year and therefore represents the main trend in the data and the loadings determine the relationship of individual species time series to particular MAFA axes.

Subsequently, the second MAFA axis has the second highest autocorrelation with a time lag of 1 year. Cross-correlations between MAFA axes and environmental variables, also known as canonical correlations, allow identification of significant correlations between trends in species biomass and explanatory variables. The software package Brodgar (`http://www.brodgar.com`) was used to carry out MAFA (see also Erzini et al., 2005).

4.3 RESULTS

4.3.1 *Environmental variables*

The environmental variables showed different temporal patterns (Fig. 4.2). The NAO index showed large variability with maximum values at the beginning of the 1990s. Both local winter and summer temperature increased over the years in contrast to salinity. Secchi disc measurements were missing until mid-1970s, and showed an irregular pattern without trend. Summer chlorophyll-a concentration was available from the 1970s and peaked in the late 1980s, followed by a steady decrease. Total-N and total-P loadings increased until the beginning of the 1980s followed by a decrease. Nutrient concentrations only covered part of the period, but were in line with the loadings. In the coastal zone, sand mining and beach nourishment increased steadily from the 1980s and also shrimp fisheries increased over time, but with large inter-annual variability. In the Dutch Wadden Sea cockle fisheries increased until around 2000 and then decreased partly because mechanical dredging was banned in 2004. Since 1990, predation pressure by top predators increased strongly as the result of the increased abundance of cormorants, harbour seals and grey seals.

Environmental variables displayed collinearity (Table 4.2). Summer temperature was correlated with a number of variables that also increased over time. Strong collinearity was also found between sand mining, beach nourishment, shrimp fisheries and top predators. Furthermore, summer chlorophyll was correlated with total-N and total-P loadings.

4.3.2 *Fish fauna*

In total 82 fish species were identified (Appendix D). Both in spring and autumn, the total number of core species showed no consistent trend; the number increased at an average rate of approximately 1 species every 3 years between 1960 and ca. 1987, and subsequently declined (Fig. 4.3). Over time, the total number of transient species increased. Between 1965 and the mid-1980s, cold water-adapted species were most abundant; their subsequent decline was not fully compensated by warm water species, resulting in a recent small decline in species number. Spring catches were, on average, dominated by demersal species (40). In addition 16 pelagic and 9 benthopelagic species were found. Most of the rare species were demersal species. Most of the pelagic species were caught frequently; only 4 pelagic species were rarely caught.

Between 1980 and 2011, the estimated and the reconstructed mean daily total biomass were significantly correlated for both spring (Pearson correlation $r = 0.98$; $n = 33$; $p < 0.01$) and autumn ($r = 0.90$; $n = 33$; $p < 0.01$) values.

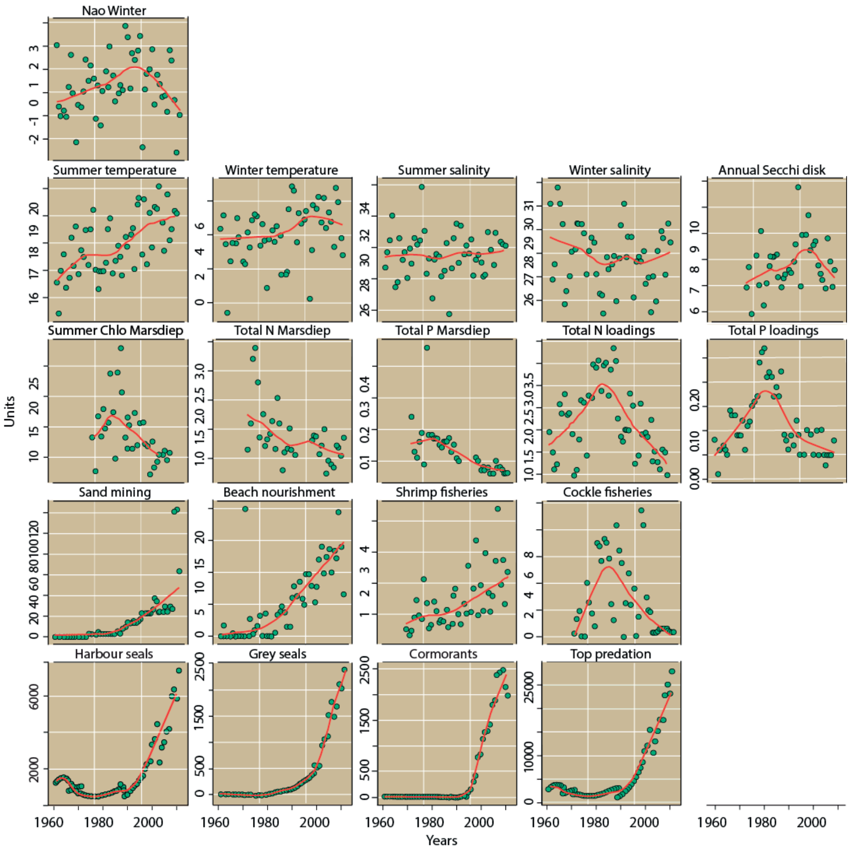

Figure 4.2: Time series of environmental variables in the western Dutch Wadden Sea for the period 1960-2011. For units and references see Table 4.1. A LOESS smoother with a span of 0.5 was fitted to aid visual interpretation.

Table 4.2: Pearson correlation coefficients between the various environmental factors. Significant relationships are indicated in bold ($p < 0.01$). For more information see Table 4.1.

		Winter temp	Winter salinity	Summer temp	Summer salinity	Secchi disc	Summer chl-a	Loading total-N	Loading total-P	Sand mining	Beach nourishment	Shrimp fisheries	Cockle fisheries	Top predators
Hydrodynamic circulation	NAO index	0.26	-0.11	0.17	0.06	0.31	0.07	0.16	0	-0.23	-0.11	0.19	0.19	-0.18
Fish performance	Winter temperature		-0.07	0.26	0.27	-0.14	**-0.46**	-0.28	-0.32	0.22	0.26	0.15	-0.15	0.22
	Winter salinity			-0.21	0.06	-0.13	-0.16	-0.3	-0.37	0.06	-0.01	0	-0.39	-0.03
	Summer temperature				0.35	0.18	-0.34	-0.28	-0.21	**0.45**	**0.47**	0.26	-0.27	**0.46**
	Summer salinity					-0.4	-0.35	-0.41	-0.2	0.07	0.05	0.06	-0.13	0.03
	Secchi disc						-0.16	0.05	-0.2	0	0.11	0.3	0.19	0.06
Productivity	Summer chlorophyll a							**0.63**	**0.53**	**-0.55**	**-0.49**	-0.4	0.16	**-0.50**
	Total N loadings								**0.81**	**-0.38**	**-0.50**	-0.26	**0.51**	**-0.48**
	Total P loadings									-0.32	**-0.43**	**-0.40**	**0.49**	**-0.45**
Habitat destruction	Sand mining										**0.67**	**0.41**	-0.31	**0.83**
	Beach nourishment											**0.42**	**-0.48**	**0.69**
	Shrimp fisheries												-0.1	**0.58**
	Cockle fisheries													-0.4
Predation	Top predators													

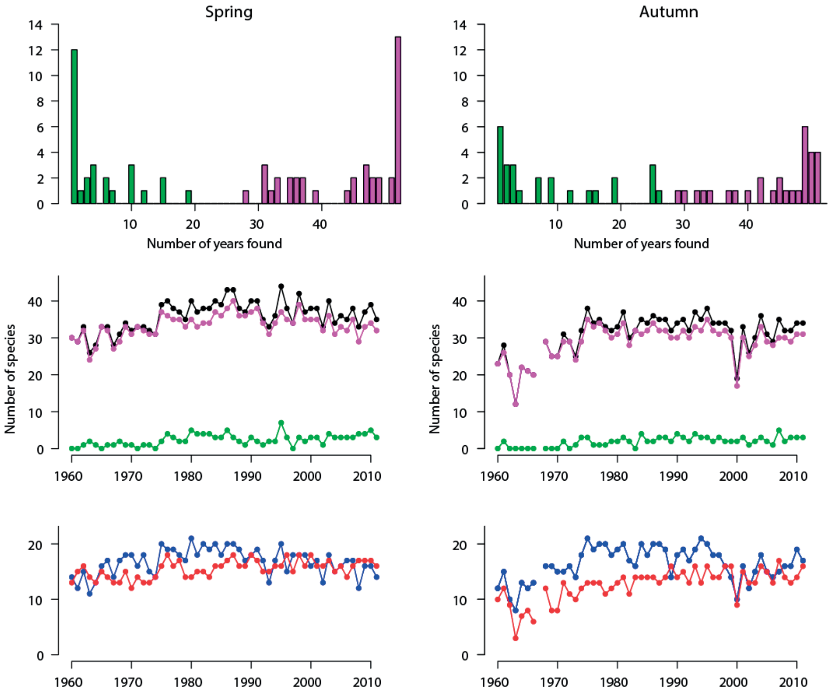

Figure 4.3: Characterization fish species in spring (left column) and autumn (right column). Top panel: Number of species per number of years found, colors depict core (pink) and transient (green) species; Middle panel: Trends in total (black), core (pink) and transient (green) species over time; Lower panel: Trends fish fauna in warm-water adapted (red) and cold-water adapted (blue) species over time.

Large interannual variability in total biomass occurred between 1960 and 1970, followed by a period of steady increase with peak values of about 90 $kg\,d^{-1}$ in spring and $40\,kg\,d^{-1}$ in autumn, and finally a steady decrease to catches of around 5 to $10\,kg\,d^{-1}$ at present (Fig. 4.4). Pelagic and demersal species biomass fluctuated (Fig. 4.4), the largest decrease was in the demersal group in spring. Demersal species remained the dominant spring group, in autumn pelagic species became the dominant from the 1980s onwards.

In general, mean daily numbers caught were much lower in spring than in autumn (Fig. 4.5). In contrast, mean individual wet mass was larger in spring than in autumn (Fig. 4.5). Mean individual wet mass showed a decrease over time, especially in spring from around 100-150 g in the 1980s-1990s to less than 50 g in more recent years. The decrease in autumn was less clear and mean individual mass even increased in recent years.

The average trophic level showed a significant decrease in spring of about 0.5 units from 1980 to 2011 (Pearson correlation r =-0.48; n = 33; $p < 0.01$). This decrease was mainly caused by the pelagic species (Fig. 4.6), which showed a significant decrease over time in spring (Pearson r =-0.71) and autumn (r =-

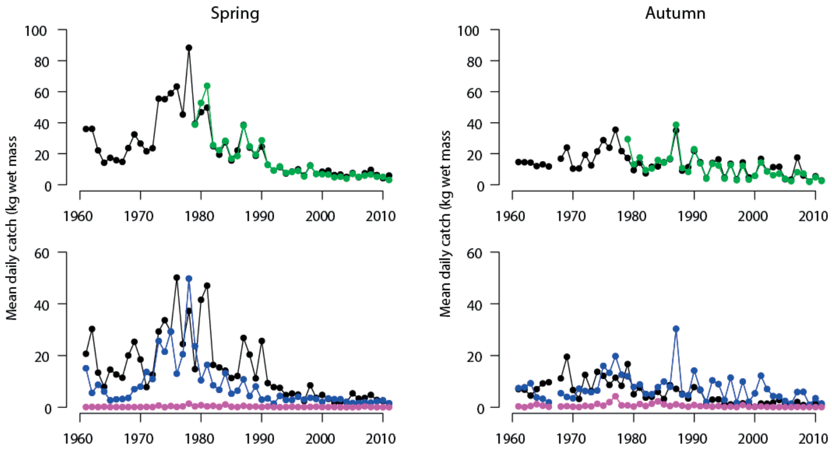

Figure 4.4: Trends in total daily catch (kg d^{-1}) in wet mass in spring (left column) and autumn (right column). Top panel: Total daily catch based on direct measurements of fish size (green line) and based on reconstructed size, i.e. fixed ratio (black line); Bottom panel: Daily catch of demersal (black line), pelagic (blue line) and benthopelagic (pink line) fish species.

0.47). Neither the demersal nor the benthopelagic species showed a trend in trophic level.

4.3.3 *Trend analysis*

Catches of individual fish species displayed different types of pattern (Appendix B) ranging from a continuous decrease (*Zoarces viviparous*) via maximum catches around the 1970s-1980s (*Belone belone*, *Gadus morhua*, *Atherina presbyter*, *Cyclopterus lumpus*, *Scophthalmus maximus*, *Pleuronectes platessa*, *Platichthys flesus*) to a steady increase (*Dicentrarchus labrax*). For many species, trends in catches differed for spring and autumn. Some species showed consistently higher catches in spring (*Alosa fallax*, *Salmo trutta*, *B. belone*, *Chelon labrosus*) or in autumn (*Clupea harengus*, *Osmerus eperlanus*, *Anguilla anguilla*, *Melangius merlangus*, *Pollachius pollachius*, *Scomber scombrus*), or showed different patterns between spring and autumn catches (*G. morhua*, *Liza ramada*).

The MAFA was performed on species that were present for at least 10 years. To reduce the influence of the most abundant species on the outcome, data were also square root transformed, but results were the same (Fig. 4.7). The scores of the first MAFA axis showed a continuous change over time. In spring, the decreasing trend seemed to stabilize in the mid-1990s, in contrast to autumn where the trend continued. The second axis showed for both spring and autumn an increasing trend from 1960 to a maximum around 1980 followed by a steady decrease.

The canonical correlations illustrate the relationships between species and the first two axes. Spring and autumn showed a slightly different pattern for axis 1 and a more similar pattern for spring axis 2 (Fig. 4.8). For the first axis significant relationships were present for 18 species in spring and for 21 in autumn, whilst for the second axis this accounted for 17 (spring) and 10 (autumn) species. For the first axis, *Anguilla anguilla*, *Belone belone*, *Trachurus trachurus*, *Zoarces viviparus*, *Myoxocephalus scorpius*, *Scophthalmus rhombus* and *Limanda limanda* had a strong declining trend and showed a significant correlation (r > 0.50) in either spring or autumn. *Dicentrarchus labrax* was the only species with a strong increasing trend. For the second axis, four species showed a significant correlation (r > 0.50) and only during spring: *B. belone*, *Callionymus lyra*, *Chelon labrosus* and *Pleuronectes platessa*. For some groups, the spring and autumn patterns were similar. Clupeids, Gadoids, Muglids showed a strong positive correlation with the second axis, while for flatfishes the first axis was more important.

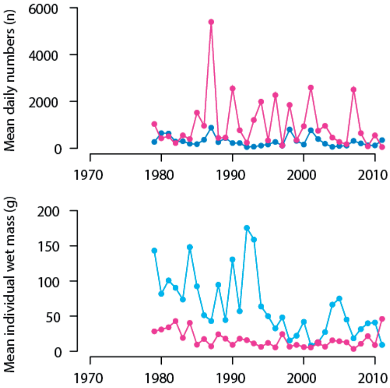

Figure 4.5: Trends in mean daily numbers (n) (top) and individual fish biomass (g wet mass) (bottom) in spring (blue) and autumn (red).

The correlations between the two MAFA axes and the explanatory variables are presented in Table 4.3. Highly significant correlations with the first MAFA axis existed with summer temperature, sand mining, beach nourishment, top predators and to a lesser extend with shrimp fisheries. The second MAFA axis showed highly significant correlations with the NAO winter index in spring and autumn and with parameters linked to the productivity of the area.

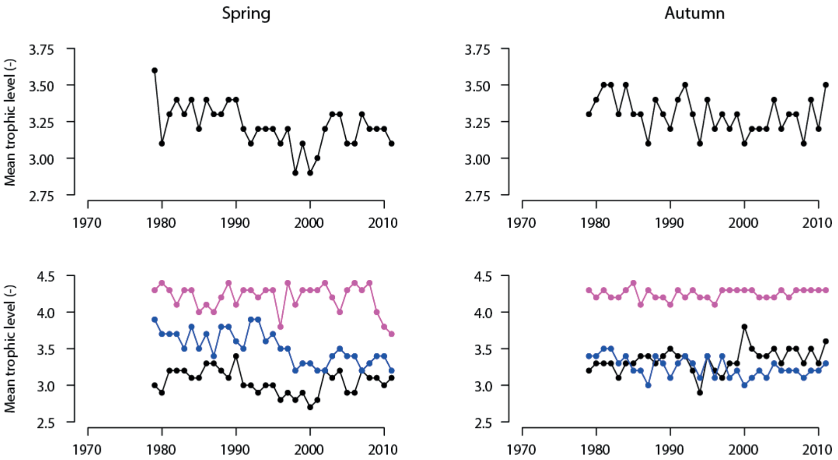

Figure 4.6: Trends in trophic level (-) in spring (left panel) and autumn (right panel). Top panel: all species; Lower panel: demersal (black), pelagic (blue) and benthopelagic species (pink)

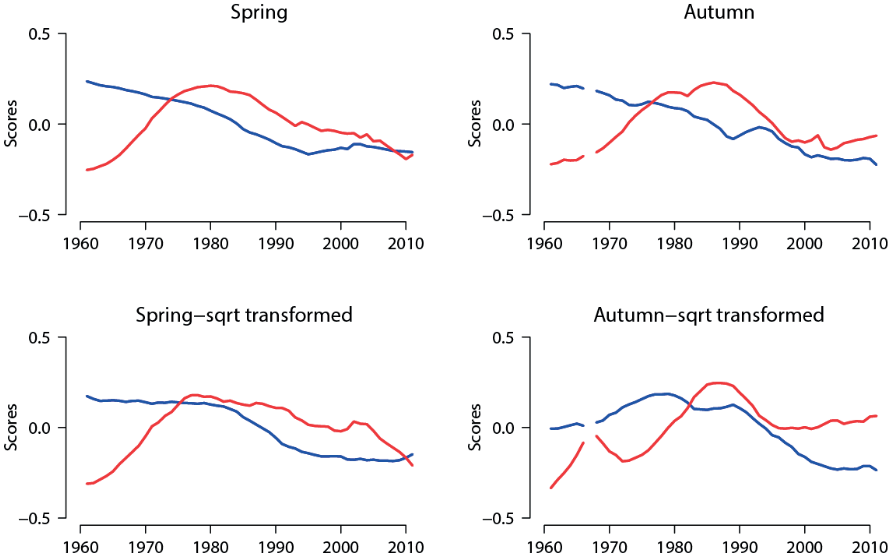

Figure 4.7: First (red) and second (blue) axis of min/max auto-correlation factor analysis (MAFA) of total biomass of 34 common fish species (caught in at least 10 years during the study period; see Appendix E) for spring (left panels) and autumn (right panels). Top panel: non-transformed data; lower panel: square root transformed data.

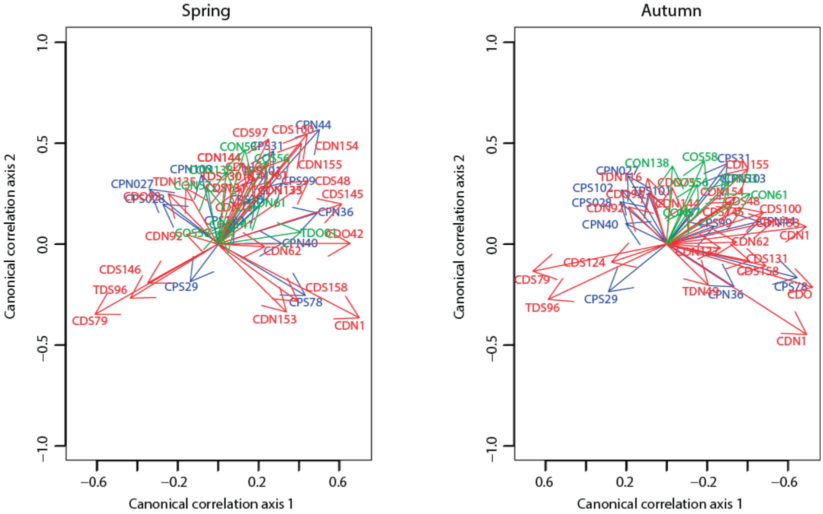

Figure 4.8: Canonical correlations between first and second MAFA axis and trends of the total biomass of 34 common (caught in at least 10 yrs during the study period; see Appendix E) fish species in spring (left panel) and autumn (right panel). Demersal species (red), pelagic species (blue) and benthopelagic species (green). For coding see Appendix D (Significance level $p < 0.01$ and $n = 51$: $r > 0.28$).

Table 4.3: Pearson correlation coefficients between the various environmental factors and the first and second axis of the min/max auto-correlation factor analysis (MAFA) for spring and autumn. Significant relationships are indicated in bold ($p < 0.01$).

		Spring		Autumn	
		First axis	Second axis	First axis	Second axis
Hydrodynamic circulation	NAO winter index	0.34	**0.72**	0.45	**0.75**
Fish performance	Winter temperature	-0.31	-0.06	-0.33	-0.05
	Winter salinity	0.18	-0.20	0.24	-0.19
	Summer temperature	-0.58*	-0.03	**-0.62**	-0.04
	Summer salinity	0.01	-0.04	0.02	-0.04
	Secchi disc	-0.37	-0.22	-0.21	-0.24
Productivity	Summer chlorophyll a	0.26	**0.49**	0.41	**0.61**
	Total N loadings	0.10	**0.61**	0.21	**0.68**
	Total P loadings	0.18	**0.76**	0.25	**0.74**
Habitat destruction	Sand mining	**-0.58**	-0.38	**-0.67**	-0.22
	Beach nourishment	**-0.67**	-0.29	**-0.74**	-0.25
	Shrimp fisheries	**-0.49**	**-0.52**	**-0.59**	**-0.44**
	Cockle fisheries	0.04	0.40	0.19	0.45
Predation	Top predators	**-0.57**	**-0.53**	**-0.75**	-0.41

4.4 DISCUSSION

Capture by fixed gears requires the active movement of the organism. The kom-fyke is located near a large tidal inlet of the Wadden Sea and it is expected that spring catches will contain fish that were migrating from the North Sea into the Wadden Sea whilst autumn catches will comprise fish on their way to migrate to the North Sea including the locally produced young-of-the-year (Fonds, 1983). Therefore, spring catches are considered to reflect the fauna of the coastal zone of the North Sea and autumn catches the productivity of the Wadden Sea nursery. The geographical origin of the fish species caught in the kom-fyke suggests that the observed long-term trends in fish communities may reflect a more general pattern occurring not only locally within the Wadden Sea.

4.4.1 *Trends in environmental conditions*

Climatic variability over western Europe determines the fluctuations in temperature and fresh water input (reflected in salinity) in the Wadden Sea: seasonal variation in sea surface temperature only lags a few days behind the coastal surface air temperature (van Aken, 2008*b*) and the precipitation over western Europe, and the connected changes in the Rhine discharge, are mainly responsible for the inter-annual variations in the salinity (van Aken, 2008*a*). This climate variability can be captured with the NAO index that shows a significant correlation with winter, spring and mean annual temperature (van Aken, 2008*b*): a positive NAO index means mild and wet winters and a negative one cold, dry weather (Jones et al., 1997).

Temperature and salinity are the main forcing functions affecting fish performance. Salinity is reflecting river runoff which is found to be correlated with riverine nutrient loads, affecting chlorophyll-a and primary production (Philippart et al., 2007), and possibly riverine sediment loads and hence visibility. The length of the time series determines the perceived pattern. In the last 25 years, a clear warming of about 1.5 °C has occurred in the western Wadden Sea (van Aken, 2008*b*). However, over a centennial period, a cooling of about 1.5 °C is observed in first 30 years and a warming in the last 25 years. An explicit greenhouse effect is not required as a forcing factor to explain recent warming because coincident variations in wind statistics and cloudiness can explain the increase (van Aken, 2010).

Measurements of the nutrients and chlorophyll started only just before the peak in nutrient loads and concentrations in this area (Cadée and Hegeman, 2002; Philippart et al., 2007) and hence overall decreasing trends are observed. These truncated time series limit our ability to identify candidate explanatory variables for the trends in the fish fauna using correlation analyses. Anthropogenic habitat destruction, sand mining and beach nourishment in the coastal zone, have affected the area especially since the 1980s, while fisheries were impacting over even longer time scales. Top predators have increased recently and hence these factors showed collinearity. The correlation of these variables with productivity might be causally misleading because of the short length of the time series.

In this study we are forced to accept different baselines; 19th century for temperature, salinity and NAO winter index; 1980s for nutrients, chlorophyll, Secchi disc; 1960s for habitat destruction and top predators.

4.4.2 *Long-term trends in the fish community*

In the 1980s and 1990s the fish fauna of the Dutch Wadden Sea comprised 97 species, varying from very abundant to extremely rare (Witte and Zijlstra, 1983). In the present study, 82 species were caught over the period 1960 to 2011, indicating that these catches are a good representation of the species composition described by Witte and Zijlstra (1983). The absence of a trend in the number of species caught suggests that with respect to species richness the function of the area is unchanged.

Species composition is slowly shifting from core to transient species indicating that rare species occur more often. From the mid-1980s especially coldwater-adapted forms have declined and warm water species have increased, however losses have not been fully compensated. Shifts in species or abundance due to changes in sea water temperature have also been observed in the Bristol Channel (Henderson et al., 2011) and in the eastern North Atlantic (ter Hofstede et al., 2010). The change in the eastern North Atlantic has been linked to the decline of cod and plaice and the increase of sprat, anchovy and horse mackerel (Rijnsdorp et al., 2009). In this study, bass *Dicentrarchus labrax* in particular has increased explosively in biomass contemporaneously with the decline in eelpout *Zoarces viviparous*.

The decrease in catch biomass from the mid-1970s was much stronger in spring than in autumn. There are indications that these trends are large-scale ones and reflect those of fish communities in the entire the Dutch Wadden Sea: beam trawl surveys showed an increase in the Wadden Sea from the 1970s to 1985 followed by a steep decrease until the mid-1990s and a temporary period of increase until 2002 (Tulp et al., 2008), a trend corresponding roughly with that of demersal fish in the kom-fyke. In these trawl surveys, the most important change has been the disappearance of I- and II-group flatfish, especially plaice *Pleuronectes platessa*, (van der Veer et al., 2011), which were abundant in earlier times (Kuipers, 1977; de Vlas, 1979). Time series of North Sea plaice do not show decreasing trends of recruitment over the last decades (Anonymous, 2006) implying a change in the distribution of the older juvenile stages.

Seasonal variation in numbers and mean individual biomass illustrates the nursery function of the Wadden Sea (Zijlstra, 1983): in spring low numbers of juvenile and adult fish enter the area and in autumn much higher numbers of mainly small juveniles leave. The large fluctuations in numbers of juveniles illustrate the interannual variability in year-class strength of the young-of-the-year of the various nursery species (especially Clupeidae and flatfish species).

A slight, but clear, negative trend in both numbers and individual biomass in autumn, implies that the overall nursery function of the area has been reduced. The main changes seem to have occurred in the coastal zone as this is reflected in the spring catches. This negative pattern in both pelagic and demersal catches was not clearly observed in the long-term beam trawl survey (Tulp et al., 2008). The trends in trophic level illustrate that the composition of the pelagic fauna has been particularly affected: both in the coastal zone (spring) and the Wadden Sea (autumn): the trophic level of the pelagic fish fauna (typical species herring *Clupea harengus* and garfish *Belone belone*) has decreased strongly in spring, reflecting the situation amongst the coastal zone fauna. This study shows similar common trends in both spring and autumn suggesting a strong link between the coastal zone and the Wadden Sea. This implies that in both areas underlying mechanisms might be similar, which is supported by the fact that Gadoids, Clupeids and flatfish species showed similar patterns in spring and autumn. However, in terms of biomass the absolute impact seems less in the Wadden Sea than in the coastal zone of the North Sea.

4.4.3 *Correlations between environmental factors and the fish community*

In the perspective of the radical changes in coastal ecosystems including the Wadden Sea over the last 2000 years (Lotze, 2005), the present study only reflects a short moment in a history of constantly shifting baselines (Jackson et al., 2001; Pinnegar and Engelhard, 2008; Lotze and Worm, 2009). Furthermore, correlations between environmental factors and the fish community may not point to underlying relationships and potentially miss causal factors: there is collinearity among the environmental factors; the time series are relatively short; certain events such as eutrophication have only occurred once and the fish community consists of a variety of species with different life cycles and preferences. The most important trend in the fish community as depicted by the fyke catches is the decreasing biomass from 1960 to 2000 and the stabilization hereafter. We consider the correlation with summer temperature spurious as warming by 1.5 °C only started 25 years ago (van Aken, 2010). The correlation with nutrient concentration in summer (total-N and total-P) may hint at eutrophication as an explanation in support of Boddeke (1991). However, for the fish fauna this correlation does not imply causality as this time series is relatively short (31 years) and only started when eutrophication was almost at its maximum. The reconstructed pattern of eutrophication since the 1930s (van Raaphorst and de Jonge, 2004) agrees with the relatively low total fish biomass during spring in the 1960s and relatively high values in the 1980s (Fig. 4.4). The impact of eutrophication on productivity should act either via increased recruitment (numbers) or growth (individual biomass) or a combination of both. Neither seems to be the case: there has not been an increase in numbers nor in individual fish mass in the kom-fyke catches. Also growth patterns of 0-group plaice in the intertidal of the Wadden Sea did not show any pattern from 1975 to 2007 (van der Veer et al., 2010).

The strong correlations of fish biomass with habitat destruction and top predators are more likely to reflect causality. Bottom trawling fishing activities destroy the surface layer of the sediment whereas sand extraction and beach nourishment physically removes and covers the habitat consisting of sediment and the associated benthic communities. Attempts to identify the impact of beach nourishment on marine life have so far focused on benthos and birds (Baptist and Leopold, 2009; Leewis et al., 2012). Sand extraction in the coastal zone at a depth from about 20 m has increased from a few million m^3 per annum at the beginning of the 1980s to 35 million m^3 at present whilst a further increase is expected (Anonymous, 2013*b*), and this links in with sand nourishment. Along most of the Dutch coastline sand nourishment takes place regularly at intervals of a few years. Recovery of the benthic community takes a number of years (van der Veer and Oorthuysen, 1985; Newell et al., 1998; van Dalfsen and Essink, 2001) and often the community structure differs from the original due to a shift in sediment type (Desprez, 2000; Wilber and Clarke, 2001). Finally, a link with the abundance and hence consumption of top predators seems likely: cormorants and seals have increased considerably since the 1990s (e.g., Brasseur et al., 2015) and this also holds true for the harbour porpoise (Camphuysen, 2004).

The second most important trend in the fish community is an increasing trend in species abundance from 1960 to a maximum around 1980 followed by a steady decrease. This second MAFA axis showed a significant correlation with the NAO winter index and also with chlorophyll-a in summer. Following Alheit and Bakun (2010), the NAO winter index predicts synchronicity in a region comprising the North Sea, the Baltic Sea, the northwestern Mediterranean and north and central European lakes. Even shifts in species composition in Narragansett Bay (east coast of the US) could be correlated with the winter NAO index (Collie et al., 2008). Therefore, this correlation might reflect the large-scale influence of weather conditions in northern Europe acting via the food chain on the fish fauna; the strong significant correlation between NAO winter index and subsequent summer chlorophyll-a in the Wadden Sea supports this view.

The fact that approximately similar types of patterns were found in related species, i.e. the Clupeids, Gadoids, Mulids and flatfishes,suggests general underlying mechanisms. However, the present study is not suited to unravel them. An exception might be the strongly decreasing trend in eelpout *Zoarces viviparous* and increasing trend of bass *Dicentrarchus labrax*. It is very likely that they reflect a northwards shift in distribution as a response of climate change (increased water temperature) (eelpout: Pörtner and Knust 2007; bass: Henderson and Corps 1997).

Given that the Dutch Wadden Sea is open to migration and many fish species range over large areas, the change in trophic structure of the fish assemblage of the western Wadden Sea may reflect a more general pattern occurring in other coastal areas. On the other hand, coastal waters and open North Sea regions might differ in their response as shown by McQuatters-Gollop et al. (2011). The present results are based on correlations only. The next step in the identification of underlying relationships should not only focus on climate change, habitat destruction, top predators and impact of large-scale hydrodynamic circulation but also on regime shifts (Beaugrand, 2004; Weijerman et al., 2005; Möllmann and Diekmann, 2012) and factors indicated as responsible for these shifts such as temperature increase, gradual warming, temperature-induced modified predatoreprey relationships and high fishing pressure (Beaugrand, 2004; Freitas et al., 2007; Kenny et al., 2009; Kirby et al., 2009).

This study confirms the alarming observations for offshore fisheries of Jackson et al. (2001); ecological changes occurred in the past and continue at a rapid rate in coastal ecosystems, they are damaging the ecological health of these coastal areas.

4.5 ACKNOWLEDGMENTS

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Part II

Trophic interactions

5

LONG-TERM SHIFTS IN INTERTIDAL PREDATOR AND PREY COMMUNITIES IN THE WADDEN SEA AND CONSEQUENCES FOR FOOD REQUIREMENTS AND SUPPLY

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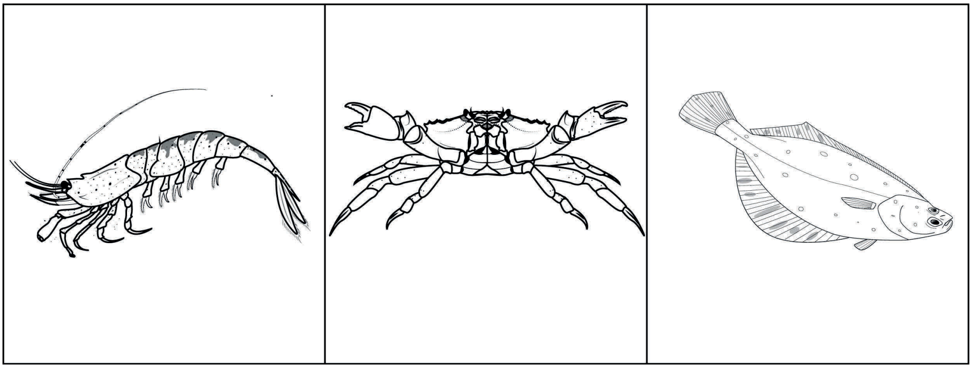

ABSTRACT

Fluctuations in species composition can have major effects on the functionality of an ecosystem; however, studying such impacts is often complicated because fluctuations coincide with changes in other parts of the ecosystem. In this study, we explored long-term (1975 to 2014) changes in predator–prey interactions following concurrent changes in predatory epibenthic fish and crustaceans and macrozoobenthic bivalves and polychaetes in the western Wadden Sea. Historical and recent invasions have resulted in an increase in relatively large and long-lived bivalves (*Mya arenaria*, *Ensis leei*, *Magallana gigas*) which have found a size refuge from epibenthic predators in the Wadden Sea. While bivalves dominated the macrozoobenthic biomass, polychaetes were the main food source of epibenthic predators, with the invasive polychaete *Marenzelleria viridis* probably becoming an important food source during the early 2000s. Food requirements of epibenthic crustaceans, mainly *Crangon crangon*, almost doubled from 5 to 10 g ash-free dry mass (AFDM) $m^{-2}\,y^{-1}$, and requirements of epibenthic fish decreased by more than 80%, mainly due to the local disappearance of *Pleuronectes platessa*. While the overall food requirements of the epibenthic predators stayed more or less constant, the edible fraction of the macrozoobenthic biomass increased from 5 to $20\,\mathrm{g\,AFDM\,m^{-2}}$ until the 2000s and decreased to $10\,\mathrm{g\,AFDM\,m^{-2}}$ thereafter. This was the result of changes in native (*Nereis diversicolor* and *Heteromastus filiformis*) and invasive (*M. viridis*) polychaetes. These findings illustrate that coinciding species-specific changes and interactions of both predators and prey should be taken into account to determine the impact of invasions on the food web structure and functioning of coastal systems.

5.1 INTRODUCTION

Within coastal ecosystems, fluctuations in species composition and abundance within the macrozoobenthic community can considerably change the functionality of such an ecosystem (Vitousek et al., 1987; Baird et al., 2012) by altering the energy transfer within the food web (Mack et al., 2000; Baxter et al., 2004; Baird et al., 2012). This is especially illustrated by the impact of successful invasive species. The western Dutch Wadden Sea, for example, has experienced several invasions in the past, such as the bivalves *Mya arenaria* (400-700 years ago, Strasser, 1998), *Ensis leei* (formerly known as *Ensis directus*, around 1982 Beukema and Dekker, 2011), and *Magallana gigas* (around 2001 Beukema and Dekker, 2011) and the polychaete *Marenzelleria viridis* (formerly also known as *M. cf. wireni*, Essink and Dekker, 2002; around 1989, Beukema and Dekker, 2011), that increased to high biomass within the system (Beukema and Dekker, 1995; Essink and Dekker, 2002; Troost, 2010; Beukema and Dekker, 2011). These invaders not only competed for food such as phytoplankton or microphytobenthos with native macrozoobenthic species (Essink and Dekker, 2002; Troost, 2010), but also changed the amount of attractive food sources for predators (Essink and Dekker, 2002; Troost, 2010).

The intertidal macrozoobenthic community of the Wadden Sea experiences a continuous predation over the whole tidal cycle. While wading birds feed on emerged tidal flats during low tide (Swennen, 1975), high tide gives access to epibenthic fishes and crustaceans (Kuipers, 1977; Kuipers et al., 1981).

Different predators have different prey, and many of them only consume a part of the total macrozoobenthos (Kuipers, 1977; del Norte-Campos and Temming, 1994; van der Veer et al., 2011). For example, shrimp feed on small bivalves and crustaceans (Pihl and Rosenberg, 1984), whereas plaice *Pleuronectes platessa* may also feed on regenerating body sections such as tails of lugworms and siphons of bivalves (Kuipers, 1977; del Norte-Campos and Temming, 1994). In addition, other factors such as the burrowing depth of macrozoobenthos can be of influence if an individual has a risk of being preyed on (Zwarts and Wanink, 1989, and literature therein), which is often correlated to the size of the animal (Zwarts and Wanink, 1989). Other factors influencing prey selection include thick shells (e.g. cockles, Bijleveld et al., 2015 and mussels, Leonard et al., 1999; Smith and Jennings, 2000) and clumping behaviour (e.g. mussels, Côté and Jelnikar, 1999).

This means that for a new invasive species, success is influenced by whether it fits the native predators prey spectra with regard to size and palatability and how well it can avoid predation by means of burrowing, aggregation or other behaviour (López et al., 2010; Stokesbury and Himmelman, 1996). In the western Wadden Sea, for instance, the invasive bivalve species *M. arenaria* and *M. gigas* can grow large enough to outgrow their suitable size as a prey even for birds (Scheiffarth et al., 2007; Markert et al., 2013). In addition, predation of adult *M. arenaria* is reduced as the result of deep burrowing (Zwarts and Wanink, 1993) and that of *M. gigas* by formation of extensive and dense reef structures (Troost, 2010). This means that only early life stages (*M. arenaria*) or the occasionally loose individual (*M. gigas*) of these invaders can be considered prey items for fish, crustaceans and birds. The relatively small invasive polychaete *M. viridis* which lives in the top layer of the sediment can, however, be considered a potential food item for the epibenthic community during its whole life cycle.

Studying the consequences of invasions on food web dynamics within coastal ecosystems is often complicated by the occurrence of coinciding changes in other structuring factors of trophic relationships (e.g. Halpern et al., 2007). During the same period in which several of the invasions in the macrozoobenthic community in the Wadden Sea occurred, for example, changes in epibenthic predators were also observed. Juvenile flatfish, mainly plaice, declined in the western Wadden Sea between the 1970s and late 1980s (van der Veer et al., 2011; Freitas et al., 2016), possibly as the result of climate-induced temperature changes (Rijnsdorp et al., 2009; Teal et al., 2012). Large brown shrimp *Crangon crangon* appear to have increased since the 1990s (Temming and Hufnagl, 2015; Tulp et al., 2012). This is most likely due to a decline in numbers and a shift in the distributional range of the shrimp's key predators (Temming and Hufnagl, 2015) as well as an increase in small brown shrimp in the area, at least in spring (Beukema and Dekker, 2014). Because predatory flatfish and shrimp feed on different food items at different rates, these changes in the epibenthic community must have had consequences for the trophic interactions with and within the macrozoobenthic community.

In this study, we explore the potential consequences of these observed changes in the epibenthic and macrozoobenthic community for their trophic interactions. We compare the food requirements of fish and crustaceans with the availability of macrozoobenthos as a food source. This analysis is based on data from long-term sampling programs on macrozoobenthos (since 1970) and epibenthos (since 1975) performed at the Balgzand tidal flats. From epibenthic abundances and information on the diets of these predators, we calculate the food requirements of all fish and crustacean species and the part of this intake that is probably represented by macrozoobenthic prey items. Food availability is derived from macrozoobenthic abundances and information on the fraction of this community that is available as prey for epibenthic predators. This information on long-term changes in food requirements versus food availability is subsequently used to explore if the food web structure and functioning of the coastal Wadden Sea system have changed over time.

5.2 MATERIALS AND METHODS

5.2.1 *Sampling*

Study area

All sampling took place at Balgzand, a tidal flat system of 50 km^2 bordering the Marsdiep tidal inlet in the western part of the Wadden Sea (Fig. 5.1). The area is isolated from the mainland by dikes in the south and west and from other tidal flats by tidal channels ranging in depth from 5 to 20 m. The area consists of barren flats with only a few mussel and oyster beds. Median grain size and silt content are about 150 µm and 5 % respectively and there is a gradient from coarse sand in the northern, more exposed flats to fine sands and mud in the sheltered southern areas (Dapper and van der Veer, 1981; Christianen et al., 2015). On average, the majority of the flats are drained for 2 to 4 h and submerged for 8 to 10 h of the tidal cycle. At high tide most of the area is, on average, covered by 1.0 to 1.5 m of water, with ambient depth depending on weather (wind) conditions and lunar phase.

Epibenthic surveys

The epibenthic community was sampled in 24 years over the period 1975 to 2014 (1975-1983, 1986, 1991, 1993-2002, 2007, 2009 and 2014, App. Tab. F.1). Over the years, sampling methods remained the same, but the number of samples varied. Fishing was done on a grid of 36 stations distributed over the area (Fig. 5.1); however, often not all stations could be visited due to prevailing weather conditions (water depth). In most years, sampling from started in February and continued at frequent intervals (usually every 2 to 4 weeks) until autumn at a period of 3 h around high tide, because the flatfish population is randomly distributed over the area during this time (Kuipers, 1977). Hauls of about 100 m were made during daytime using a 1.9 m beam trawl with one tickler chain, towed at a speed of about $35\,\mathrm{m\,min^{-1}}$ following Riley and Corlett (1966). Location of the hauls was established at the start of the series by wooden poles and later by GPS. The length of the trawls was assessed with a meter-wheel fitted outside the trawl. Water temperature and, in later years, salinity were measured during each cruise. All samples were stored in plastic bags, transported to the laboratory and preserved the same day in a 4 % formaline-seawater solution until 1990 and by deep-freezing after 1990.

Samples were sorted to species level and the length of the individuals were measured to the nearest 1 mm total length (0-group flatfish) or nearest 5 mm (all others) within a few weeks after sampling. If the number of individuals per for a certain species were high (approximatly more than 100 Ind.) the sample was subsampled and densities were corrected by this supsampling factor. For the most abundant species, except for the shore crab *Carcinus maenas*, information about catch efficiency (plaice - *Pleuronectes platessa*, Kuipers, 1975; flounder - *Platichthys flesus*, van der Veer et al., 1991, sole – *Solea solea*, van der Veer et al., 2001; shrimps – *Crangon crangon*, van Lissa, 1977; gobies (*Pomatoschistus microps* and *P. minutus*), van Beek, 1976, App. Fig. G.1). For these species, the number of individuals caught was corrected and catch efficiency and converted into age-specific densities. For all other species, which were present in low numbers only, catches were converted into densities without correcting for net efficiency. Subsequently, total densities were split into densities per age-class based upon species-specific length classes. In case of doubt with regard to age-length relationships in fish, individual age was verified by means of otolith reading. Following previous methodology (Zijlstra et al., 1982; van der

Veer, 1986; van der Veer et al., 1998, 2011), total mean densities at Balgzand per species i per age-class j were calculated as the arithmetic means of the age-specific species' densities (n_{ij}; m^{-2}) at all stations sampled during a survey (maximum 36).

In 1983, 1986 and 1991, fewer than 50 stations were sampled during various cruises over the whole year. In 1998, 1999 and 2002, 150 stations were sampled and in the other years, between 260 and 400 stations were sampled.

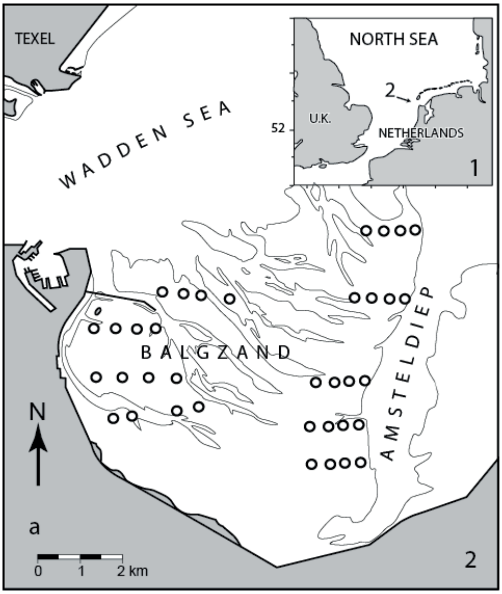

Figure 5.1: Balgzand intertidal in the western Dutch Wadden Sea. Sampling of epibenthic species was based on 9 transects, each consisting of 4 hauls (open circles). Thin lines indicate the low-tide mark; thick lines the high-tide mark.

Macrozoobenthic surveys

The macrozoobenthic community has been monitored since the 1970, with all groups being monitored consistently and quantitatively from around 1988 onwards. Sampling was done at 15 stations scattered over Balgzand, twice a year; once in late winter (February-March) and once in late summer (August-September)For the present analysis, only data for late summer were used. However, from 1975 up to and including 1987, polychaetes were not, or inadequately sampled and quantified in summer. For this reason, polychaete data for this period were calculated from the winter data of the following year ($\sim$ 0.5 y after the summer sampling) which was always sampled and quantified completely. A correction factor of 1.87 times the winter biomass values was applied, a factor derived from the period 1988-2009 (R. Dekker, unplubl.). This fixed factor predicted summer values with a standard deviation of $\sim$ 20%. The 15 stations consisted of 12 fixed transects and 3 permanent quadrats. At each of the 12 transect, cores were taken to a depth of approximately 35 cm at equal intervals (20 m), covering $0.45\,\mathrm{m}^2$ in summer. At the 3 permanent quadrats, a total of $0.95\,\mathrm{m}^2$ of sediment was taken also to a depth of approximately 35 cm, which consisted of 18 randomly divided positioned cores (9 of $\sim 0.1\,\mathrm{m}^2$ and 9 of $0.009\,\mathrm{m}^2$). For more information about sampling strategy, see Beukema (1976). Transect and quadrat cores were sieved in the field over 1-mm square mesh screens. All macrozoobenthic organisms retained were collected and sorted alive in the laboratory down to species and, if possible, year-class level (bivalves, assesed by means of the number of year marks on the shell) within 1 or 2 days after sampling. For each species (and year-class), the number per sample was counted. Each group of a particular species of a particular age class was put into one container, which was dried for 3 days in a ventilated stove at 60 °C, weighted, incinerated for 3 h at 560 °C and weighed again. Weight loss after incineration, defined as ash-free dry mass (AFDM), was considered a measure for biomass. After conversion to total biomass (all age classes combined) per surface area per station for each species i, the species-specific total mean biomass (B_i; $\mathrm{g\,AFDM\,m^{-2}}$) at Balgzand was calculated as the arithmetic mean of the total biomass at all 15 stations sampled during a survey.

5.2.2 *Trophic interactions*

Total food requirements of epibenthic predatory species

For each species i (and age class j), the total food requirement of epibenthic predators was assumed to be equal to the total daily food requirement ($\mathrm{g\,AFDM\,m^{-2}\,d^{-1}}$). To allow for comparison with previous estimates, the methodology of de Vlas (1979) was followed with some minor modifications as previously used by van der Veer et al. (2011). The species-specific daily food requirement was considered to be the sum of daily maintenance requirements (DMR; $\mathrm{g\,AFDM\,m^{-2}\,d^{-1}}$) and daily growth requirements (DGR; $\mathrm{g\,AFDM\,m^{-2}\,d^{-1}}$), whereby, energy requirements for locomotion and other expenditures were assumed to be included in the DMR.

The estimation of daily maintenance requirements was based on species-specific metabolic mass (M_{ij}; $\mathrm{g\,WM\,m^{-2}}$, where WM= wet mass) and temperature. First, for each species i at each age-class j and each size-class k, the wet mass (W_{ijk}; g WM) was determined from an average length per size class of 0.5 cm (L_{ijk}; cm) using species-specific length-mass relationships:

$$W_{ijk} = (a \times L_{ijk})^b \tag{5.1}$$

where a (shape coefficient; $\mathrm{g\,WM^{1/3}\,cm^{-1}}$) and b (-) are species-specific parameters (App. Tab. G.1). Second, the species-, age- and size-specific wet mass W_{ijk} (gWM) was converted into species-, age- and size-specific metabolic mass (M_{ijk}; $\mathrm{g\,WM^{0.8}}$) as $M_{ijk} = W_{ijk}^{0.8}$. For each species from each age-class, the corresponding metabolic mass was multiplied by the density of that size-class (n_{ijk};

m^{-2}). Subsequently, the sum for all size classes was calculated to obtain the total metabolic wet mass of the age class of each species per square meter, so:

$$M_{ij} = \sum k(n_{ijk} \times M_{ijk}) \tag{5.2}$$

The species-specific daily food requirement needed to meet DMR_{ij} as part of the total food requirement equals:

$$DMR_{ij} = c_i Q_{10i}^{0.1T} m_i M_{ij} \tag{5.3}$$

where c_i ($\mathrm{g\,AFDM\,g^{-1}\,WM}$) is the species-specific conversion factor from wet mass to AFDM (Tab. 5.1), T is temperature (°C), Q_{10i} is the species-specific increase in physiological rates with a temperature increase of 10 °C (Tab. 5.1), m_i ($\mathrm{g\,WM^{0.8}\,d^{-1}}$) is the maintenance coefficient (Tab. 5.1), and M_{ij} ($\mathrm{g\,WM\,m^{-2}}$) is the species' metabolic mass per age class. DMR_{ij} was calculated for each species for each age class for each sampling event.

Table 5.1: Adjusted coefficients for different species for calculating the food requirement. Q_{10i} values were taken from Freitas, Cardoso, Lika, Peck, Campos, Kooijman and van der Veer (2010); wet weight ash-free dry mass conversion factor (c_i; Brey et al. 2010); and maintenance coefficient (m_i) values were taken from de Vlas 1979 for *Pleuronectes platessa*, van Beek 1976 for *Pomatoschistus microps* and *P. minutus*, van der Veer et al. 2001 for *Solea solea* and van Lissa 1977 for *Crangon crangon*.

Species	Q_{10i}	c_i	m_i
Solea solea	2.79	0.2	0.02
Pleuronectes platessa	2.33	0.17	0.02
Pomatoschistus microps	1.53	0.19	0.01
Pomatoschistus minutus	1.53	0.19	0.01
Platichthys flesus	2.33	0.17	0.02
Carcinus maenas	2.16	0.14	0.01
Crangon crangon	2.9	0.19	0.02

DGR_{ij} was based on the observed increase in length (L_{ijt}) within cohorts of size classes of species between sampling events. First, the arithmetic mean length (L_{ijt}; cm) was determined for each species i and each age-class j during each sampling event t. Subsequently, L_{ijt} were converted to mean wet mass (W_{ijt}; g WM) using species-specific length-mass relationships (see Eq. 5.1). Hereafter, instantaneous growth rate (g_{ijt}; $\mathrm{d^{-1}}$) between two sampling events (from t to $t+1$) was determined from the change in W_{ijt} in the period t to $t+1$ between the two surveys (Δt; days) according to:

$$g_{ijt*} = (lnW_{ijt+1} - lnW_{ijt})/\Delta t \tag{5.4}$$

Here, g_{ijt*} ($\mathrm{d^{-1}}$) was considered to represent the instantaneous growth rate at the midpoint in time ($t*$; day number) between the two successive sampling events. To get estimates for g_{ijt}, an exponential curve was fitted through g_{ijt*} for each year. From this relationship of g at $t*$, estimates of g for the exact sampling date could be determined. This estimate of g on a sampling date was taken to represent growth of all size classes of an age group, and applied to determine daily growth in mass for each size class. For those species for which this approach was not possible (e.g. crustaceans which show a continuous immigration of small individuals and emigration of large individuals), g_{ijt} were derived from observations where clear shifts in size frequency distribution over time were found and peaks in settlement could be followed during successive sampling events.

DGR_{ij} or each sampling event (t) (DGR_{ijt}; g AFDM m^{-2} d^{-1}) was calculated as the sum of the products of g_{ijt} and W_{ijkt}:

$$DGR_{ijt} = \sum k(g_{ijt}W_{ijkt}) \tag{5.5}$$

For the conversion from daily growth requirements (DGR_{ijt}) to daily food requirements for growth ($DFRG_{ijt}$; g AFDM m^{-2} d^{-1}), it was assumed that the $DFRG$ needed to be twice as high as the DGR for fish species (de Vlas, 1979) and three times as high for crustaceans as they are considered to be "sloppy" feeders (van Lissa, 1977, M. Fonds pers. comm.), i.e. a net food efficiency factor E_i of 0.5 and 0.33 g WM growth per g WM food requirement, respectively. For each species i of each age class j at each sampling date t, $DFRG_{ijt}$ was calculated as:

$$DFRG_{ijt} = c_i DGR_{ijt}/E_i \tag{5.6}$$

For each sampling event t, the total daily food requirement (DFI_{ijt}; g AFDM m^{-2} d^{-1}) of each species i and each age class j was then calculated as:

$$DFI_{ijt} = DMR_{ijt} + DFGR_{ijt} \tag{5.7}$$

To estimate the total food requirement per year (DFI_{ij}, g AFDM m^{-2} y^{-1}), a polynomial was fitted through DFI_{ijt} for each year separately. A maximum fourth-order polynomial was fitted through the individual data points and the surface area during the growing season (1 March - 31 October) was calculated by integration of the polynomial function from days 60 to 300. In some cases, a third-order or second-order polynomial was sufficient. The growing season was not sampled completely in all years, pleading to a potential underestimation of the annual food requirement. Monthly total food requirement (DFI_{ijm}, g AFDM m^{-2} mon^{-1}) was estimated by integration of the polynomial function for the time of each month.

The approach followed in this study does not take into account any loss due to ingestion (e.g. spilling, rejection of prey) that can be off the order of 20% (Brett and Groves, 1979). This means most likely that the food requirement estimated in terms of energy required for maintenance and growth will be an underestimation for all species.

Food requirement by epibenthic predators on macrozoobenthos

For each predator that was encountered during the epibenthic surveys, potential food items were defined in line with van der Veer et al. (2011); Freitas et al. (2016), taking into account (1) juvenile bivalve spat (newly settled), (2) siphons of adult bivalves (except *Mytilus edulis*) (about 3% of total biomass),

(3) tail tips of the polychaete *Arenicola marina* (corresponding to 15% of total biomass), and (4) total biomass off all other polychaetes. The species- and age-specific contribution of potential prey items (as weight fraction of total stomach contents) to total food requirement was based on published information from various sources, i.e. Baeta et al. (2006) for shore crabs (*C. maenas*), del Norte-Campos and Temming (1994) for brown shrimp (*Crangon crangon*) and Kühl and Kuipers (1978) for various fish species. For predation on macrozoobenthos, this fraction (f; -) ranged from 0.15 for gobies (*Pomatoschistus microps* and *P. minutus*) to 1.00 for sole (*Solea solea*) (Tab. 5.2). The annual food requirement of macrozoobenthos by a particular epibenthic predator species i of a particular age class j ($DFIm_{ij}$, g AFDM m^{-2} y^{-1}) was subsequently calculated as this weight fraction multiplied with the total food requirement per year (DFI_{ij}, g AFDM m^{-2} y^{-1}).

Available macrozoobenthic prey for epibenthos

For each of the individuals of each species that was encountered during the macrozoobenthic surveys, its potential as food item for epibenthos was defined in line with the previous subsection (Tab. H.1). So for each survey, the average biomass (g AFDM m^{-2}) was calculated for (1) juvenile bivalve spat, (2) siphons of adult bivalves (except *M. edulis*), (3) tail tips of the polychaete *A. marina*, and (4) total biomass off all other polychaetes.

All data were stored in a Microsoft Access 2010 database, which was directly accessed with the open source program R (R Core Team, 2016) that was used for all calculations and estimations.

Table 5.2: Food selection of the different species at different age groups according to various studies. Food selection is according to weight proportions of stomach content. Data for all species taken from Kühl and Kuipers (1978), except for *Carcinus maenas* (Baeta et al., 2006) and *Crangon crangon* (del Norte-Campos and Temming, 1994).

Age	Prey	*Pleuronectes platessa*	*Platichthys flesus*	*Solea solea*	*Pomatoschistus minutus*	*Pomatoschistus microps*	*Carcinus maenas*	*Crangon crangon*
0-group all-groups for crustaceans	Macrozoobenthos	0.95	0.95	1	0.15	0.15	0.4	0.3
	Crangon crangon				0.6	0.2		
	small crustaceans				0.26	0.64		0.35
	Other	0.05	0.05				0.5	0.3
	Cannibalism						0.1	0.05
I group	Macrozoobenthos	0.95	0.95	1	0.35	0.28		
	Crangon crangon				0.57	0.32		
	small crustaceans				0.06	0.16		
	Other	0.05	0.05		0.02	0.06		
II group	Macrozoobenthos	0.95	0.95					
	Other	0.05	0.05					

5.3 RESULTS

5.3.1 *Sampling*

In principle, abundance estimates were based on surveys consisting of 36 hauls spread out over the Balgzand intertidal. However, the intensity of the surveys varied among years; also, due to weather conditions, not all hauls were sampled during a survey. Especially during periods of easterly winds, water depth became too low in part of the area to allow fishing. This means that the number of stations, their location and the month changed per year and therefore the accuracy of the estimation of density, biomass and annual food requirements by the epibenthic community may be negatively affected. Also subsampling could have an influence on the abundance estimations and was relatively high in some cases (e.g. up to a factor of 512 in brown shrimps (*Crangon crangon*), meaning that only 1/512 was counted and measured, and the rest of the sample was estimated from this). Furthermore, some species or size classes are not distributed randomly over the area: flounder only occurred in the siltier areas and just settled shrimps mainly occurred in the most sheltered part (closer to the shore) of the Balgzand tidal flats. The accuracy of the results largely depended on the abundance estimates of species in the system, e.g. for plaice Zijlstra et al. (1982) estimated a sampling error of up to 35%.

5.3.2 *Food requirements*

During the study period (1975-2014), the total biomass ($\mathrm{g\,WM\,m^{-2}}$) of epibenthic predators at the Balgzand tidal flats was, on average, dominated by brown shrimp (*C. crangon*) and juvenile plaice (*Pleuronectes platessa*). While the biomass of shrimp was higher at the end of the study period (Fig. 5.2), the biomass of juvenile plaice (of all age groups) was high in the 1970s and early 1980s but much lower thereafter (Fig. 5.3). Other relatively dominant fish with regard to biomass were the European flounder (*Platichthys flesus*, in particular the II-group) and the two goby species (*Pomatoschistus minutus* and *P. microps*, in particular the 0-group) (Fig. 5.3). Their biomass was, on average, comparable with that of the shore crab (*Carcinus maenas*) (Fig. 5.2). Other rarer fish species caught were lesser sandeel (*Ammodytes tobianus*), Atlantic herring (*Clupea harengus*), three-spined stickleback (*Gasterosteus aculeatus*), shorthorn sculpin (*Myoxocephalus scorpius*), European smelt (*Osmerus eperlanus*) and eelpout (*Zoarces viviparous*) (Fig. 5.2). Because of their generally low numbers, it was not possible to estimate their growth in time and annual food requirement could, therefore, not be calculated for these fish species.

The calculation of food requirements as total annual food requirement was restricted to (1) epibenthic species with the highest biomass, including plaice, flounder, sole and both goby species as well as brown shrimp and shore crab, (2) those years during which at least five cruises were conducted (3) those years during which all these species were sorted, and (4) availability of information for all age classes of the selected fish species. This resulted in analyses of the annual food requirement for five fish species (divided into two or three year classes) and two crustaceans during 12 years between 1975 and 2014 (Tab. H.1).

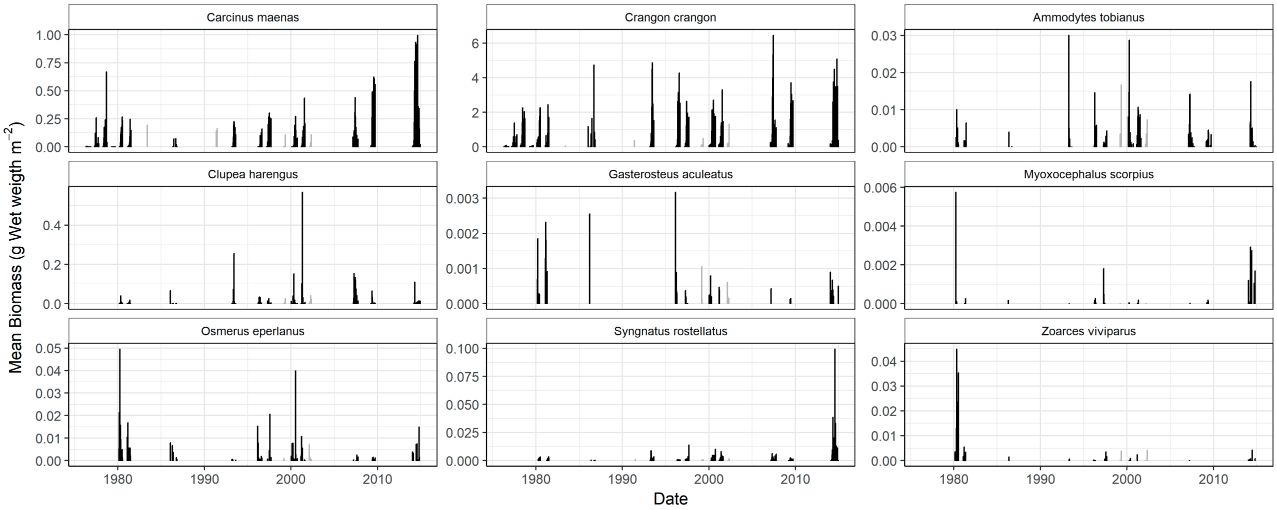

Figure 5.2: Biomass of crustaceans and fish species without age distinction caught during the epibenthic surveys at the Balgzand intertidal flats between 1975 and 2014. Grey bars indicate years with fewer than 4 sample events.

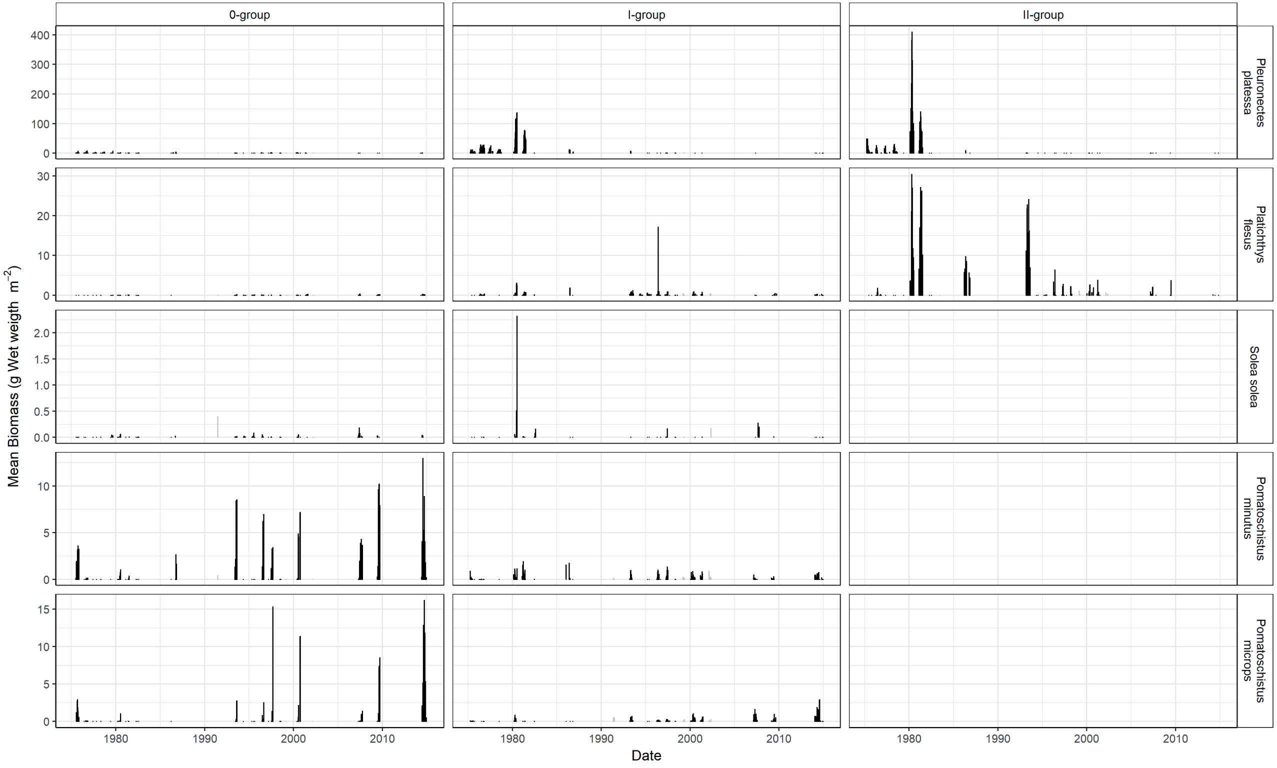

Figure 5.3: Biomass of age classes of various flatfish and goby species caught during the epibenthic surveys at the Balgzand intertidal flats between 1975 and 2014. Grey bars indicate years with fewer than 4 sample events.

Within this period, the sum of the total annual food requirement by these seven epibenthic species ranged from less than 13 g AFDM m^{-2} y^{-1} in 2001 to more than 40 g AFDM m^{-2} y^{-1} in 1980 and 2007 (Tab. H.1). On average, shrimp (*C. crangon*) contributed most with their total food requirement ranging from less than 5 g AFDM m^{-2} y^{-1} in 1999 to almost 40 g AFDM m^{-2} y^{-1} in 2007 (Tab. H.1, Fig. 5.4). The maximum contribution of shore crabs (*C. maenas*) to the sum of total annual food requirement was less than 3 g AFDM m^{-2} y^{-1} in 2009 and 2014 (Tab. H.1, Fig. 5.4). With regard to the fish species, the dominance in annual total food requirement shifted from juvenile plaice (*P. platessa*, in particular the I-group) between 1974 and 1986 to gobies (*P. microps* and *P. minutus*, in particular the 0-groups) during the rest of the study period (Tab. 5.2, Fig. 5.4).

Overall, the summed total annual food requirement of crustaceans appeared to have increased, whereas that of fish decreased (Tab. 5.2, Fig. 5.4). On average, this resulted in a decrease of the contribution of epibenthic fish species to total annual food requirement by fish and crustaceans from approximately 25 to 5% during the study period (Tab. H.1, Fig. 5.4).

Total food requirement by crustaceans (dominated by shrimp, *C. crangon*) was relatively high (>2 g AFDM m^{-2} mon^{-1}) from May to August compared to early spring (March) and late autumn (October) (Fig. 5.5). During the first years of the study period, specifically prior 1990, the dominance in total food requirement shifted from II-group plaice (*P. platessa*) in March to April to I-group plaice in May to July (Fig. 5.5). After 1990, the seasonal pattern in total food requirement showed an increase (June to September) followed by a decrease in October of 0-group gobies (*P. microps* and *P. minutus*, Fig. 5.5).

5.3.3 *Food availability*

On average, the macrozoobenthic biomass at Balgzand in late summer fluctuated strongly but increased, on average, from about 35 g AFDM m^{-2} in the late 1970s to 70 g AFDM m^{-2} in the early 2000s, and showed some decrease hereafter (Fig. 5.6). This trend was apparent in the biomass of both bivalves and polychaetes (Fig. 5.6), as well as *Peringia ulvae* and other groups. On average, the biomass consisted for more than 70% of bivalves, whereas the potential macrozoobenthic prey items consisted of more than 80% of polychaetes (Fig. 5.6), but in the most recent years, *Peringia ulvae* showed biomass values that were comparable with those found for polychaetes.

With respect to the bivalves, only a minor part (approximately 10%) of the total biomass was spat that could be considered as prey for epibenthic fish and crustaceans (Fig. 5.6). Within the study period, the biomass of spat varied from year to year, from 0.1 g AFDM m^{-2} (in 1977), to >8 g AFDM m^{-2} in 1991, 1992, 2006 and 2011. The biomass of the regenerating bivalve siphons was low (<5 g AFDM m^{-2}) and more or less constant in time (Fig. 5.6).

With respect to polychaetes, much of the total biomass (50% to 90%) could be considered as epibenthic prey. The biomass of polychaetes that could be

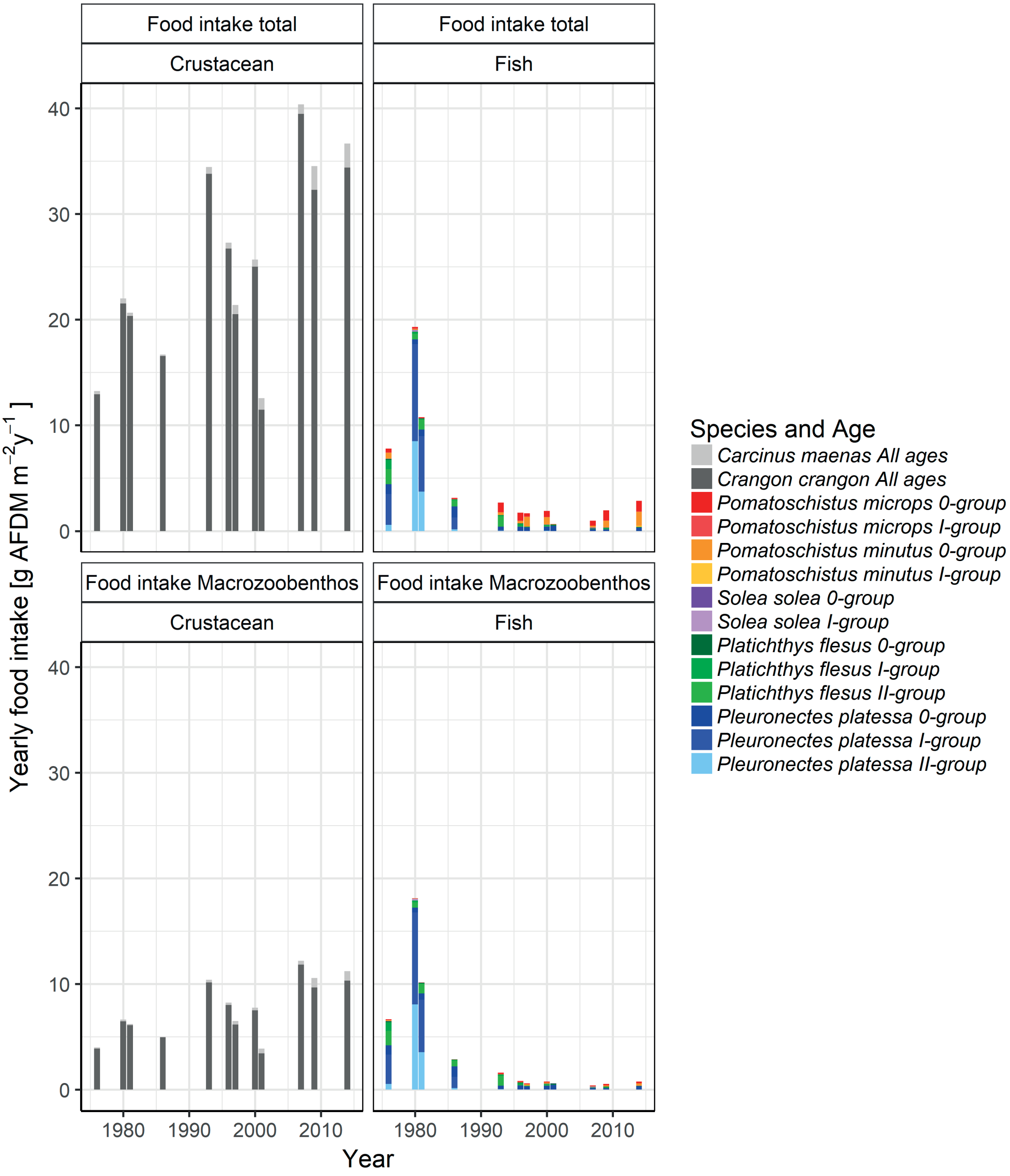

Figure 5.4: Annual food requirement of all prey (top panels) and macrozoobenthic prey only (bottom panels) by crustaceans and fish at the Balgzand intertidal flats during the growing season (March-October) between 1975 and 2014 for those years when sufficient data were available.

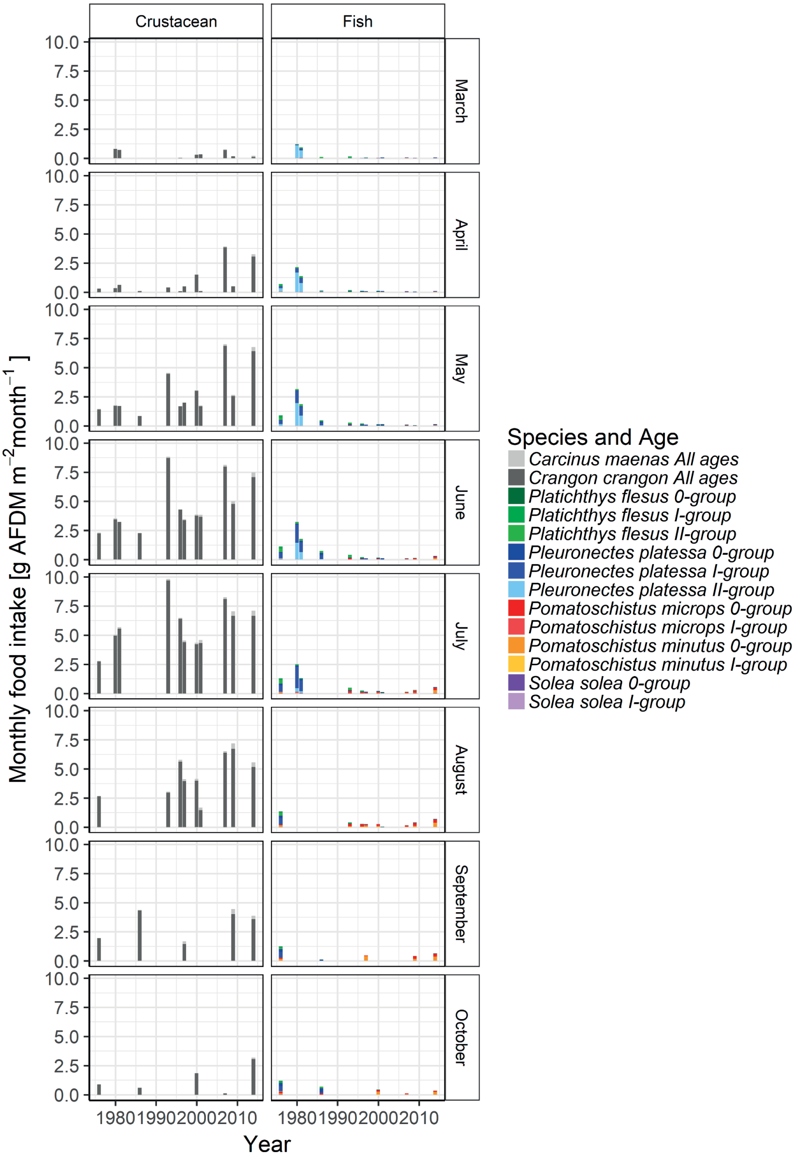

Figure 5.5: Monthly food intake of all prey by crustaceans (left panels) and fish (right panels) at the Balgzand intertidal flats during each month of the growing season (March-October) between 1975 and 2014 for those years when sufficient data were available.

considered as prey (Fig. 5.6 *Arenicola marina* tails and other polychaetes) generally increased from $<5\,\mathrm{g\,AFDM\,m^{-2}}$ in the 1970s to $>20\,\mathrm{g\,AFDM\,m^{-2}}$ in the early 2000s and $<10\,\mathrm{g\,AFDM\,m^{-2}}$ at the end of the study period. The biomass of the regenerating tails of the lugworms was relatively low ($<5\,\mathrm{g\,AFDM\,m^{-2}}$), but higher in the 1980s and 1990s than before and after this period (Fig. 5.6).

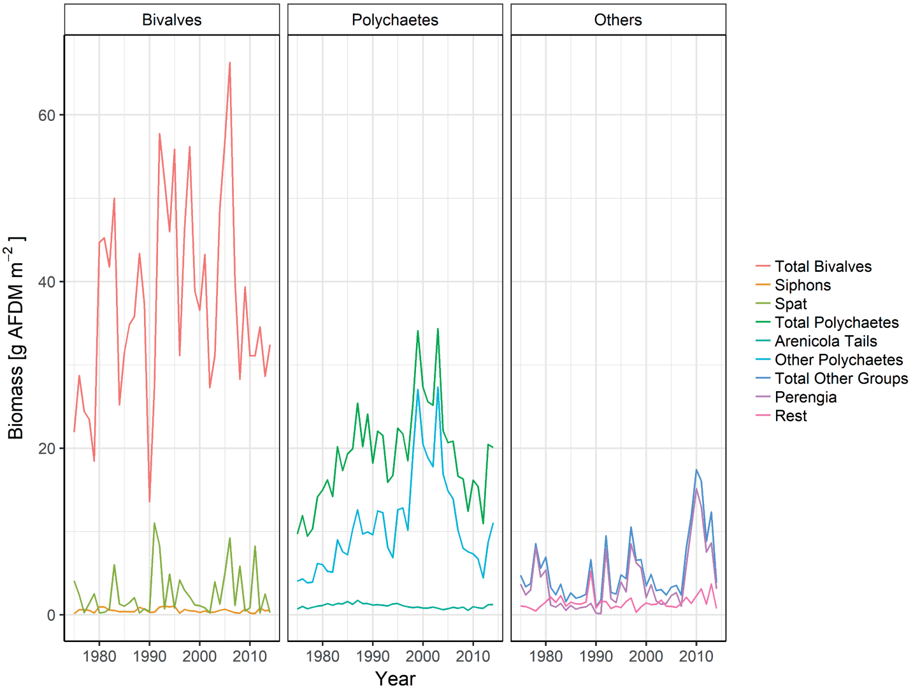

Figure 5.6: Biomass of macrozoobenthos divided into bivalves, polychaetes, and other groups at the Balgzand between 1975 and 2014. Red, turquois and blue represent total biomassin bivalves, polychaetes, and others, respectively; other colours represent biomass of potential food items as part of total biomass.

5.4 DISCUSSION

5.4.1 *Long-term changes in epibenthic predators*

Despite the continuous and/or enhanced impacts of eutrophication, fisheries and climate change during the study period (Philippart and Cadée, 2000; Lotze, 2005; Wolff, 2013, Chapter 2), the food web structure in terms of the species composition of the epibenthos at Balgzand has remained relatively stable from the 1970s to 2014. Observed shifts in abundance over these last decades mainly refer to changes in seasonality in abundance: a decline in juvenile plaice and even absence from July onwards as well as an increase in the abundance of brown shrimp. The ob served decline in juvenile plaice abundance at the Balgzand tidal flats is in line with a 10- fold decrease in total biomass of fyke catches of both pelagic and demersal fish species from 1980 to the present at a location nearby (Chapter 4). The disappearance of juvenile flatfish as a top predator may also release other epibenthic predators such as juvenile shrimp from predation pressure. Average landings of large shrimp (>50 mm) originating from the NE North Sea (including the Wadden Sea) are indeed $\sim$ 40% higher since 2000 than in the 1980s and 1990s, which is attributed to a reduced predation by juvenile whiting and cod (Temming and Hufnagl, 2015). The decline of fish as a competitor may allow other species to take over. From our data, we cannot determine if the increase in food requirement by shrimp is due to a release of predation from juvenile flatfish or reduced competition with other epibenthic species; changes in environmental conditions, food availability or fisheries; or a combination of these factors (Philippart et al., 2003; Campos et al., 2010; Tulp et al., 2012).

5.4.2 *Long-term changes in macrozoobenthic prey*

During the study period, the total biomass of macrozoobenthos at the Balgzand tidal flats was mostly dominated by bivalves except in the autumn of 1990, when a combination of failing recruitment in preceding years and extensive shellfish fisheries resulted in a historical low of mussel and cockle beds (Dankers and Zuidema, 1995; Beukema and Cadée, 1996; Dankers et al., 2003). Biomass of the macrozoobenthos fraction available as prey items for epibenthic predators was, however, mostly dominated by polychaetes with the exception of the first year (1974) of the study period. Thereafter, the biomass of polychaetes as potential prey increased until the early 2000s and started to decrease again after that to levels similar to those found in the 1980s.

The increase in polychaete biomass from the 1970s to the 1980s was mainly due to an increase in the abundance of *Hediste diversicolor* and *Heteromastus filiformis* during a period of eutrophication (Beukema, 1991). In addition, the macrozoobenthic community was invaded by the North American polychaete *Marenzelleria viridis* (Essink and Dekker, 2002). Within the Dutch Wadden Sea, this species was first recorded in the Ems estuary (eastern part) in 1983 and found in the western part from 1989 onwards (Essink and Dekker, 2002). Its relatively high productiovity:biomass (P:B) ratio (ca. $6\,\mathrm{g\,g^{-1}\,y^{-1}}$) compared to native polychaete species (Sarda et al., 1995) in combination with its high standing stock (ca. $10\,\mathrm{g\,AFDM\,m^{-2}}$; Essink and Dekker, 2002, Dekker unpubl.), its edibility (small size) and its accessibility (shallow burrower) most likely made this invasive species an important food source for epibenthic predators in the 2000s.

5.4.3 *Long-term changes in predator-prey relationships*

For the epibenthic fish species, the potential predation on macrozoobenthos more or less covers their total food requirements, in particular for juvenile plaice. During the study period, however, the overall abundance and average size of this flatfish strongly declined. implies that siphon nipping by flatfish was reduced over time. Such a release may affect anti-predatory behaviour of former prey items, e.g. burrowing depth of bivalves, possibly resulting in enhancement of their growth (Persson and Svensson, 2006; Fässler and Kaiser, 2008; Flynn and Smee, 2010).

For epibenthic crustaceans (in particular shrimp), however, the potential predation on macrozoobenthos covers approximately half of their total food requirements. This implies that they require other resources to gather enough energy to survive and grow. The diet of *Crangon crangon* is highly variable in time and space and includes meiofauna, shrimp and 0-group fish (e.g. Pihl and Rosenberg, 1984; van der Veer and Bergman, 1987; del Norte-Campos and Temming, 1994; Oh et al., 2001). Prey selection appears to be related to the abundance of the prey items and the size of the shrimp (e.g. small shrimp feeding 100% on meiofauna; del Norte-Campos and Temming, 1994. Changes in the abundance and size structure of shrimp may, therefore, not only change the food requirement of macrozoobenthos but also of other potential prey items within the ecosystem.

Analysis of the food web structure of the Balgzand intertidal flats in the western Dutch Wadden Sea in the 1970s by Kuipers et al. (1981) indicated a total food requirement by epibenthic carnivores of 15.6 g AFDM m^{-2} y^{-1} (Tab. 5.3). The two groups of these predators took more or less an equal share: the summed predation by the various fish species was 7.4 g AFDM m^{-2} y^{-1} whereas that by the crustacean species accounted for 8.2 g AFDM m^{-2} y^{-1} (Tab. 5.3). A comparison between the study from the 1970s (Kuipers and Dapper, 1981) and the results from this study (based on more accurate estimates for food requirements for maintenance and growth) shows that the present value for the 1970s (23.1 g AFDM m^{-2} y^{-1}) is approximately 45% higher than the previous estimate for this period (Tab. 5.3). In both estimates, however, total food requirement of epibenthic predators is dominated by that of shrimp, which accounts for 43 and 68% of the total food requirement, respectively. These estimates are comparable with those found for total annual food consumption of mobile epibenthic fauna in Gullmarsvik on the Swedish west coast in 1978: 26 g AFDM m^{-2} y^{-1} (Pihl, 1985). As for the Balgzand tidal flats, brown shrimp accounted for most (46%) of the total food requirement in that area in that year (Pihl and Rosenberg, 1984).

Despite shifts in the relative dominance of species and in the size structure of the epibenthic predators, their summed food requirement of macrozoobenthic prey remained more or less constant, around 10 g AFDM m^{-2} y^{-1}, during the study period. Total biomass of the potential food items for epibenthos was <5 g AFDM m^{-2} in the 1970s, >20 g AFDM m^{-2} in the 2000s and again <10 g AFDM m^{-2} thereafter. This implies that the P:B ratio must have been

Table 5.3: Total predation pressure ($\mathrm{g\,AFDM\,m^{-2}\,y^{-1}}$) in around the 1970s as derived from previous findings (Kuipers and Dapper, 1981; original references in Kuipers et al., 1981) and in this paper of main epibenthic predators on the Balgzand tidal flats.

Species	Previous studies			This study	
	Food req. ($\mathrm{g\,AFDM\,m^{-2}\,y^{-1}}$)	Years	Source	Food req. ($\mathrm{g\,AFDM\,m^{-2}\,y^{-1}}$)	Years
Plaice	5.5	1973, 1975, 1976	Kuipers (1977); de Vlas (1979)	4.7	1975, 1976
Flounder	0.9	1975, 1976	de Vlas (1979)	2.4	1976
Gobies	1	1975, 1976	van der Gaag (1977)	0.4	1975, 1976
Shore crab	1.5	1972?	Klein Breteler (1976)	0.3	1976, 1977
Shrimp	6.7	1976-1979	Kuipers and Dapper (1981)	15.3	1976-1979
Sum	15.6			23.1	

between at least $0.5\,\mathrm{g\,g^{-1}\,y^{-1}}$ in the 2000s and $2\,\mathrm{g\,g^{-1}\,y^{-1}}$ in the 1970s to sustain these food requirements, which is within the order of magnitude found for intertidal bivalves and polychaetes (e.g. Beukema, 1976; Kuipers and Dapper, 1981; Sarda et al., 1995). During the 2000s, the macrozoobenthos and hence the potential food supply was dominated by a highly productive invasive polychaete (*M. viridis*). This suggests that food availability was relatively high compared to the required food requirement by the epibenthic predators at that time.

Our findings illustrate that analyses of the impacts of shifts in species composition (invasions or disappearance) on trophic transfer within coastal intertidal systems should take into account species-specific changes and interactions of both prey and predators. Adult bivalves have generally outgrown their epibenthic predators. At the Balgzand tidal flats, bivalve spat was only an important food source for epibenthic predators during years of low polychaete biomass (as in the 1970s) or high bivalve recruitment success (as in 1991). If the adult bivalves such as *Mya arenaria* and *Magallana gigas* get too large to be predated by birds (Zwarts and Wanink, 1989; Scheiffarth et al., 2007; Markert et al., 2013), then this will lead to shorter cycles of energy transfer ("dead-end species") in the food web and disrupt the transport of energy into higher trophic levels (Baird et al., 2012). In contrast to their relatively low total biomass, polychaetes represented the main food source for epibenthic predators in particular after the successful invasion by *M. viridis*.

5.4.4 *Bottom-up or top-down control?*

During the study period, the Balgzand tidal flats changed from a system where the food requirement by juvenile flatfish of macrozoobenthos was still considerable (ca. $5\,\mathrm{g\,AFDM\,m^{-2}\,y^{-1}}$, representing approximately 50% of the total epibenthic food requirement) to a system where these fish almost disappeared and shrimp became more abundant with an increase of their food requirement from 5 to $10\,\mathrm{g\,AFDM\,m^{-2}\,y^{-1}}$. The increase in brown shrimp appears not to be restricted to the Balgzand tidal flats. A fourfold increase in summer densities from the 1970s to the 2000s of relatively small shrimp (20 to 53 mm) in the subtidal of the Marsdiep tidal basin has been observed (Tulp et al., 2012). This increase appeared to be limited to the western part of the Wadden Sea, possibly related to spatial variation in food conditions (Tulp et al., 2012). Our findings strengthen the idea that predation by brown shrimp is key to the regulation of stocks of benthic invertebrates of the Wadden Sea (Pihl and Rosenberg, 1984; van der Veer et al., 1998; Wolff, 2013), in particular during recent years.

Furthermore, the shift from flatfishes to shrimps at Balgzand also implies a shift from predation pressure on siphons of bivalves and tail tips of the lugworm *Arenicola marina* (Kuipers, 1977; de Vlas, 1979) to other prey items, i.e. bivalve spat and small polychaetes (van der Veer et al., 1998; Pihl and Rosenberg, 1984). This might have released adult bivalves and lugworms from flatfish predation. The observation, that the bivalve *Limecola balthica* (formerly known as *Macoma balthica*) now lives deeper and has a higher body condition (Compton et al., 2016) might be an indication that the predation pressure on the siphons from flatfish have been reduced. On the other hand, increased shrimp predation on bivalve spat might have increased their role in regulating bivalve recruitment success (van der Veer et al., 1998). This suggests at least the possibility that some top-down effects on the species and size structure of the macrozoobenthic community are likely in the intertidal Balgzand food web.

Whether bottom-up regulation also occurs cannot be determined in this study; however growth conditions of the epibenthic predators can be used as an indirect indication. For both juvenile flatfishes (Zijlstra et al., 1982; van der Veer, 1986; van der Veer and Witte, 1993; van der Veer et al., 2010; Freitas et al., 2012) and gobies (Freitas et al., 2011), growth conditions at Balgzand appear to be optimal at least until late summer, suggesting the absence of a bottom-up effect. For juvenile flatfish summer growth reduction was observed in the intertidal, but also in the subtidal and tidal gullies (Freitas et al., 2012, Chapter 6). The observed growth reduction coincided with a decrease in stomach content, suggesting the availability of fewer prey items. It was hypothesised that behavioural components acted to produce a less active macrozoobenthos after the spring/summer phytoplankton bloom, reducing prey availability and hence causing a reduction in food requirement.

5.4.5 *Long-term changes: the shifting baseline syndrome*

The ecological time series used in this study all started around the 1970s. However, it is clear that the Wadden Sea had already changed considerably centuries before the 1960s (Wolff, 1983; Lotze et al., 2005; Wolff, 2013), and after the 1960s the Wadden Sea suffered from the cumulative effects of habitat loss, overexploitation, pollution, eutrophication and species invasions (see Lotze et al., 2005).

For the western Wadden Sea and the Balgzand intertidal, severe pollution and eutrophication have occurred (Duinker et al., 1979; van Beusekom et al., 2005) in combination with serious habitat loss. Until the closure of the former

Zuiderzee, extensive subtidal and intertidal seagrass beds were present (Philippart and Dijkema, 1995) and a variety of top predator fish species such as rays were common in the area (Philippart, 1998; Wolff, 2005). Quantification of the impact of these events and losses on the Wadden Sea food web structure and ecosystem functioning is not possible, but Lotze et al. (2005) speculated that via filter and storage capacity and degradation in water quality, these events may have led to a simplification and homogenisation of the system.

With long-term impact studies, the reference or starting point is of importance and is generally represented by the situation that occurred at the beginning of the time series. This points to the so-called shifting baseline syndrome (Pauly, 1995) stating that each generation readjust the baseline and accepts the situation that occurred at the beginning of their careers as reference. For this study, the start of our time series and subsequently our baseline situation was in the early 1970s. Because our study area used to be covered by seagrass beds and was roamed by top predators before that time, the Balgzand food web structure was most likely already partly degraded and simplified by then.

5.5 ACKNOWLEDGMENTS

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6

POSSIBLE CAUSES FOR GROWTH VARIABILITY AND SUMMER GROWTH REDUCTION IN JUVENILE PLAICE *PLEURONECTES PLATESSA* L. IN THE WESTERN DUTCH WADDEN SEA

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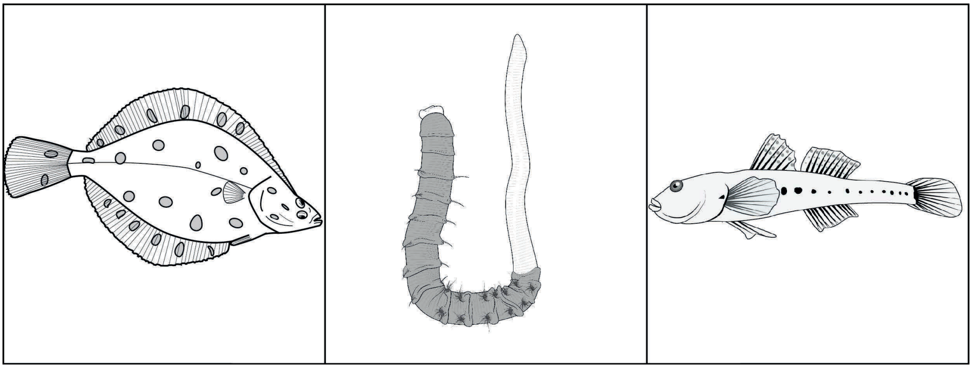

ABSTRACT

Growth variability within individuals and among groups and locations and the phenomenon of summer growth reduction has been described for juvenile flatfish in a variety of European coastal areas whereby the underlying causes still remain elusive. Potential mechanisms were tested for juvenile plaice *Pleuronectes platessa* L. in the western Dutch Wadden Sea, by analysing published and unpublished information from long-term investigations (1986-present). Growth variability did occur and could be explained by differences induced by environmental variability (water temperature), and by non-genetic irreversible adaptation and sex. Dynamic Energy Budget analysis indicated that especially sexually-dimorphic growth in combination with variability in sex ratio could explain most of the variability in growth and the increase in the range of the size of individuals within the population over time. Summer growth reduction was not only observed among 0-group plaice in the intertidal, but also in the subtidal and tidal gullies as well as among I-and II-group plaice. Intraspecific competition for food was not detected but some support for interspecific competition with other predators was found. Also resource competition with the other abundant epibenthic species (0-, I- and II-group flounder *Platichthys flesus*; the brown shrimp *Crangon crangon*; the shore crab *Carcinus maenas*; the goby species *Pomatoschistus minutus* and *P. microps*) could not explain the summer growth reduction. The observed growth reduction coincided with a decrease in stomach content, especially of regenerating body parts of benthic prey items. It is hypothesised that macrozoobenthos becomes less active after the spring phytoplankton bloom, reducing prey availability for juvenile plaice in summer, causing a reduction in food intake and hence in growth.

6.1 INTRODUCTION

Temperate shallow coastal areas such as the international Wadden Sea are important nurseries for various commercial and non-commercial fish species (Zijlstra, 1972), providing a combination of relatively low mortality and fast growth (Bergman et al., 1988). Hence, both of these aspects, as well as the carrying capacity of these areas, have been a research focus over many decades.

Over time, insight into the growth dynamics of shallow coastal areas has changed from the traditional view that field growth of juvenile fish was maximal and only determined by prevailing water temperatures (van der Veer, 1986; Zijlstra et al., 1982), the so-called 'maximum growth-optimal food condition hypothesis' (van der Veer et al., 1994; van der Veer and Witte, 1993), to the view that growth is variable among nursery areas (Berghahn et al., 1995; Karakiri et al., 1991, 1989) and only maximum just after settlement, slowing down during summer. This growth reduction has been found using various methods, annually, at a latitudinal scale, and in multiple juvenile flatfish species (Ciotti et al., 2013*b*,*a*; Fox et al., 2014; Freitas et al., 2012; van der Veer et al., 2010). In combination with experimental work, Fox et al. (2014) points to post-settlement habitat quality in general as the key factor modifying potential growth rates, without indicating in detail the underlying responsible processes.

All of the existing information about growth variability among juvenile flatfish in various nurseries and the evidence of summer growth reduction has been summarized recently by Ciotti et al. (2014). Their main conclusion was that, despite clear evidence for growth heterogeneity at numerous spatiotemporal scales, underlying causes remain elusive, and therefore might even be multifactorial. Nevertheless, there are also arguments in support of the presence of general patterns, such as the observation that summer growth reduction in European waters occurs each year in adjacent populations and among different species (see van der Veer et al., 2010; Freitas et al., 2012; Ciotti et al., 2013*b*,*a*; Fox et al., 2014).

In course of time, various factors have been suggested that might induce variability in juvenile growth, ranging from ontogenetic background (Kinne, 1962; van der Veer et al., 2000), sex (Lozán, 1992; van der Veer et al., 2009) and environmental conditions such as spatial and temporal variability in water temperature (Fonds et al., 1992), salinity (Augley et al., 2008) and food conditions (van der Veer and Witte, 1993); however, so far the quantitative impact of these factors on field growth have not been assessed. Growth reduction appears to be a general phenomenon among various 0-group flatfish species, at least in shallow intertidal and coastal areas (Ciotti et al., 2014; Freitas et al., 2012; van der Veer et al., 2010). It is unclear whether growth reduction also operates in deeper waters and among elder flatfish age groups. This would require information about growth in I- and II-group flatfish and information from deeper waters.

From an energetic perspective, growth reduction boils down to reduced energy availability for growth. According to general Dynamic Energy Budget considerations (Kooijman, 2010), this must translate to a reduced mobilization of stored energy due to less food assimilated. Because juvenile flatfish in European waters are mainly benthic polychaete and mollusc feeders (de Groot, 1971; de Vlas, 1979; Edwards and Steele, 1968; Kuipers, 1977), sudden decreases in benthic food availability seem unlikely. Moreover, long-term intertidal macrozoobenthic data at the Balgzand intertidal in the Dutch Wadden Sea suggest even an increase in food abundance over the last decades (Dekker, unpubl., in van der Veer et al., 2011, Chapter 5). This implies that intra- and/or interspecific food competition might be more likely candidates. If growth reduction of 0-group plaice is caused by intraspecific food competition, a negative relationship between realized growth of the 0-group and the total food uptake of the flatfish species (0, I and II group) would be expected. Growth reduction caused by interspecific food competition would imply a negative relationship between realized growth and food intake by other predatory epibenthic species (e.g., other fish species and crustaceans). An alternative explanation could be resource competition, which would imply a negative relationship between realized growth in 0-group plaice and the population density of all predatory epibenthic species.

In this paper, we first focus on possible (multifactorial) causes for the observed heterogeneity in size as a consequence of variability in growth among juvenile fish and, secondly, we investigate whether similar factors might be operating in space and time by testing various hypotheses (intraspecific, interspecific and resource competition) dealing with the observed growth reduction in summer. The focus is on juvenile plaice, *Pleuronectes platessa* L., because this species has been the subject of numerous studies in the western Dutch Wadden Sea and a wealth of published and unpublished information on various aspects of its ecology is available (for overview see Creutzberg et al., 1978; Kuipers, 1977; de Vlas, 1979; Zijlstra et al., 1982; van der Veer, 1986; van der Veer and Witte, 1993; van der Veer et al., 2000).

6.2 MATERIALS AND METHODS

6.2.1 *Data sources*

Published and unpublished data of two sampling programmes on fish in the western Dutch Wadden Sea were used: the Balgzand and the EMOWAD-ZKO programme.

The Balgzand high water programme covers the period 1975 to 2009 (1975-1976, 1979-1983, 1986, 1991, 1993-2002, 2007, 2009). Fishing was conducted on a grid of 36 stations distributed over the Balgzand, an isolated tidal flat system of 50 km^2 in the western part of the Wadden Sea (Fig. 6.1), using a standard 2-m beam trawl with one tickler chain from February onwards at frequent intervals (in principle every 2 to 4 weeks) over a period of 3 h centred around high water, because during this period the flatfish population is randomly distributed over the area (Kuipers, 1977). Over the years, methodology has remained the same: hauls of about 100 m have been made during daytime at a speed of about

$35\,\mathrm{m\,min^{-1}}$, following the protocols of Riley and Corlett (1966). Location of the hauls was established by wooden poles put in the sediment at tow start, and later by GPS. The length of the trawls was assessed with a meter-wheel fitted outside the trawl. During each cruise bottom water temperature, and in later years also salinity, was measured. All samples were stored in plastic bags, transported to the laboratory at the same day, and for samples collected through 1990 were preserved in a 4 % formaline-seawater; after 1990, samples were deep-frozen after collection. All samples were sorted to species level and each individual was measured to either the nearest mm total length if 0-group flatfish, or to the nearest 5 mm for other specimens, within a few weeks of collection. Juvenile flatfish were separated into age groups based on their length–frequency distribution. In case of doubt, sagitta otoliths were removed and were checked by eye for annual rings. Subsequently, data were stored in a database.

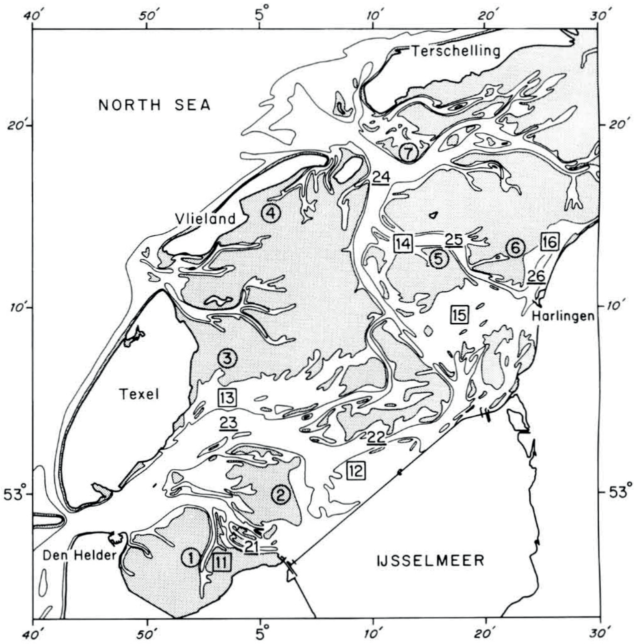

Figure 6.1: Location of the Balgzand and the EMOWAD-ZKO cruises in the western Dutch Wadden Sea. Note EMOWAD-ZKO Station 1: Balgzand area (where the 36 gridded stations of the Balgzand cruises are located). Stations 1 to 6: intertidal stations; Stations 11 to 16: subtidal stations; Stations 21 to 26: tidal channels. Station numbers refer to code used in van der Veer and Witte (1993). Shaded area refer to the intertidal. After van der Veer and Witte (1993).

The EMOWAD-ZKO programme was carried out in 1986 (12 stations) and 2009 (18 stations) in the Marsdiep and Vlie tidal basins of the western Dutch Wadden Sea (Fig. 6.1). In 1986, stations in each basin were visited alternately

(Marsdiep basin in odd months, Vlie stations in even months), in 2009 both basins were sampled every month. Stations were selected at the intertidal (areas with drained tidal flats at lower low water spring tides, LLWS); subtidal (area between LLWS and LLWS - 5 m); and tidal channels (areas deeper than 5 m below LLWS). Sampling was carried out every month from March to October, for about 3 hours around high tide during daytime. Intertidal stations were sampled with a 2-m beam trawl (5-mm mesh in codend, 1 tickler chain) towed from a rubber dinghy powered by an outboard motor at a constant speed of $35\,\mathrm{m\,min}^{-1}$, following the protocols of Riley and Corlett (1966). At each station 2-3 hauls of about 100 m each were conducted. In subtidal and channel stations, fishing was carried out with the RV Navicula -a 20m, low-draft vessel equipped with a stern-mounted trawl gantry- with a 3-m beam trawl (10-mm mesh in codend, 1 tickler chain). Depending on the size of the area, 2-3 hauls were done in subtidal stations and 1 or 2 in the tidal channels. In all cases the total distance covered at each station, from all tows combined, was on average 500 m. The geographic position of the trawls was recorded using a GPS and bottom temperature data were obtained at each trawl location with a CTD. Catches were sorted on board immediately and measured to the nearest mm (0-group) or in 0.5 cm total length classes. For all catches, juvenile flatfish were separated into age groups based on their length–frequency distribution. In case of doubt, sagitta otoliths were removed and were checked by eye on board for annual rings. Subsequently, data were stored in a database.

The number of fish caught was corrected for size-selective mesh and catch efficiency according to Kuipers (1975); Dapper (1978) for the 2-m beam trawl, and after Bergman et al. (1989) for the 3-m beam trawl, and converted into densities. For each station, the arithmetic mean of the plaice density and the mean length were estimated and used as indices of population density and size over time.

6.2.2 *Growth variability*

The effect of environmental variability (bottom water temperature and salinity) on growth was analysed for juvenile plaice at the Balgzand area. Unpublished data for 2000, representing the average situation, were selected. For all cruises, temperature and salinity were measured during each haul (see above) with an accuracy of about 0.50C and 0.5 PSU.

The impact of ontogenetic background on growth was studied by analysing morphometric characteristics for juvenile plaice at the Balgzand area. Published information for 1995 was taken from van der Veer et al. (2000). In short, from each cruise, at least 100 individuals of 0-group were selected and they were after rinsing with 1 % NaCl, and bleached individually in a 1 % NaCl, 0.45 % H_2O_2 and 0.85 % KOH solution for 20 to 60 min depending on their size (Potthoff, 1983). Subsequently, the fish were then kept overnight in 1 % KOH for maceration. Next day the fish skeletons were stained with analizarin red solution for about 3 d. Finally, after rinsing with a 1 % NaCl, 0.5 % KOH solution, the fish were stored and cleared in a solution consisting of 50 % glycerine and 50 % of 0.5 % KOH, 1 % NaCl. All of the dilutions were made with demineralized water. For each individual, the number of vertebrae, dorsal, and anal fin rays were counted, reflecting the temperature conditions experienced during the egg (vertebrae) and larval (fin rays) stages. For more details, see van der Veer et al. (2000).

The potential impact of sex on growth was analysed for juvenile plaice by means of the Dynamic Energy Budget (DEB) theory. The DEB theory (Kooijman, 2010) describes the energy flows through an animal in relation to varying food densities and temperatures conditions. Food uptake in plaice is assumed to follow a (Holling type-II) functional response relationship with food density in line with observations on juvenile flounder (Kiørboe, 1978; Mattila and Bonsdorff, 1998) and whereby food conditions are scaled between 0 to 1 (ad libitum food). With a set of species-specific parameters (for plaice see: van der Veer et al., 2001, 2010), the DEB model can be applied for all combinations of fish size, food conditions and temperature. Due to differences in food intake and in energy participation, males and females have different parameter sets, and hence, growth characteristics (Freitas, Campos, Skreslet and van der Veer, 2010), for a thorough description of the model and relevant equations see van der Veer et al. (2009).

6.2.3 *Growth reduction*

Summer growth conditions among I- and II-group plaice were studied for the Balgzand programme. Until the beginning of the 1980s, both I- and II-group occurred in substantial densities (see Bergman et al., 1988; van der Veer et al., 2011) to allow a growth analyses. For the period 1975 – 1978, observed growth in between two successive sampling periods was compared with predicted maximum possible growth according to the DEB model (sensu the same method as described in Freitas et al., 2012). Under constant food conditions (or at abundant food due to the hyperbolic shape of the functional response), DEB differential equations can be analytically solved and the dynamics of growth then simplifies to Von Bertalanffy growth curve (Kooijman, 2010). This allows predictions of maximum possible growth predictions in between two successive sampling periods and a comparison with observed growth. This approach has already been applied for juvenile plaice previously and for a thorough description of the method and relevant equations, see van der Veer et al. (2010); Freitas et al. (2012).

Summer growth conditions in the subtidal and channel stations were analysed for 0-group plaice for the EMOWAD-ZKO programme in 1986 and 2009. For all field observations, the observed growth rate dL ($\mathrm{cm\,d^{-1}}$) between time $t = i$ and $t = i + 1$ was compared with growth as predicted by the standard Dynamic Energy Budget (DEB) model (sensu Freitas et al., 2012, see above) for the intertidal, subtidal and channel stations. Results are taken from Freitas et al. (2016).

6.2.4 *Growth relationships*

The presence of intraspecific, interspecific and resource competition was analysed for the Balgzand data. First of all, for all data, the ratio of observed and DEB predicted maximum growth rates was estimated and analysed over time. To help visualize patterns, a smoothing curve was added using the LOESS function in R (R Core Team, 2014). Next, daily food intake for juvenile flatfish and the other epibenthic species was estimated in mg ash free dry weight per m^2 per d ($\mathrm{mg\,AFDM\,m^{-2}\,d^{-1}}$) separately for each Balgzand survey, based on specific energy requirements following de Vlas (1979) with some slight modifications van der Veer et al. (2010) and Chapter 5, whereby energy requirements were based on two components: contribution for metabolism (daily maintenance requirements), and contribution for observed growth (daily growth requirements). Energy required for locomotion and other expenditures was not considered and was assumed to be included in the estimate of metabolism. The various coefficients were adjusted for each species separately (Tab. 6.1). Finally, for each Balgzand survey over the years, the ratio between observed and maximum possible growth for 0-group plaice according to the DEB model was compared with the estimated daily food intake of all juvenile plaice (0-, I- and II-group) (possible intraspecific competition); with the estimated daily food intake of all epibenthic predators present (possible interspecific competition) and with the density of all epibentic species (possible resource competition).

Table 6.1: Adjusted coefficients for different Species for calculating the food intake. Q_{10} values were taken from Freitas, Cardoso, Lika, Peck, Campos, Kooijman and van der Veer (2010), the wet weight- ash-free dry mass conversion factors (c_i) and maintenance coefficients (M_i) from de Vlas (1979); van Beek (1976); Brey et al. (2010); van der Veer et al. (2001); van Lissa (1977).

Species	Q_{10}	c_i	M_i
Solea solea	2.79	0.2	0.02
Pleuronectes platessa	2.33	0.17	0.02
Pomatoschistus microps	1.53	0.19	0.01
Pomatoschistus minutus	1.53	0.19	0.01
Platichthys flesus	2.33	0.17	0.02
Carcinus maenas	2.16	0.14	0.01
Crangon crangon	2.9	0.19	0.02

6.2.5 *Statistical analyses*

All calculations were carried out in R version 3.1.1. Linear mixed effects models were fitted using the nlme package (Pinheiro et al., 2009). Generalized additive models using a Normal distribution with log-link were applied using the GAM functions in the mgcv package (Wood, 2006).

6.3 RESULTS

6.3.1 *Growth variability*

Environmental conditions

Environmental variability in water temperature and salinity was low in spring, but increased with increasing temperature and was on the order of 1 to 3 °C during the year (Fig. 6.2). Salinity showed large fluctuations during the year and also among stations on the order of 2 – 18 PSU difference. Variability was not random among stations but showed clear spatial patterns; e.g., relatively cold and saline waters at the lower parts of the tidal flats in spring (Fig. 6.3). According to the maximum growth model of Glazenburg (1983), each degree in water temperature potentially accounted for 1.3 mm mon^{-1} growth difference.

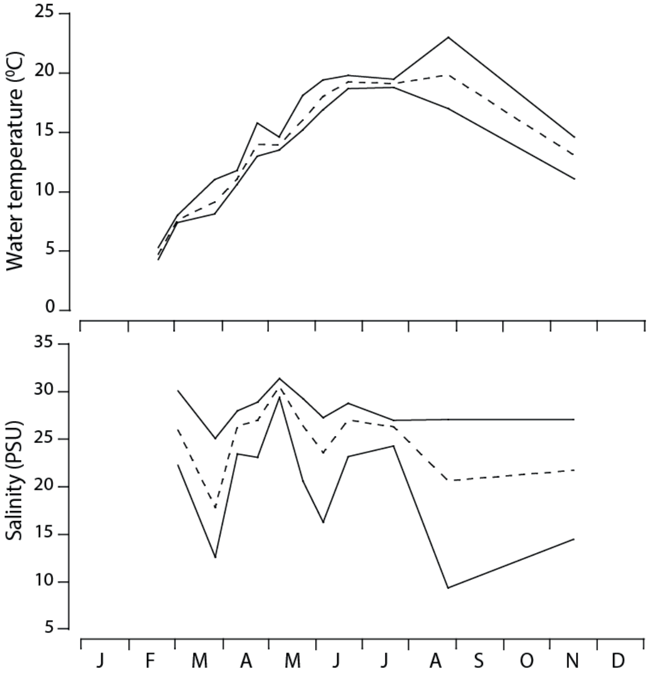

Figure 6.2: Mean (dashed line), minimum (lower line) and maximum (upper line) bottom water temperature (top panel; °C) and salinity (bottom panel; PSU) at Balgzand at 36 fishing stations during high water in 2000.

Ontogenetic background

From the onset of larval immigration in March 1995, individual variability in the number of vertebrae (40 – 45), anal (49-60) and dorsal (66-82) fin rays was found and remained present in substantial enough numbers during the

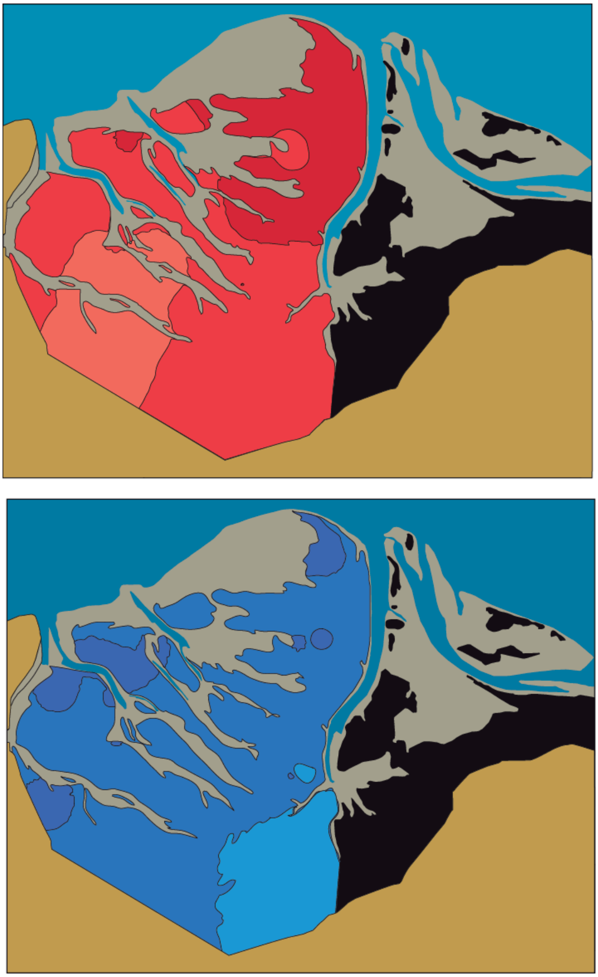

Figure 6.3: Bottom water temperature (top panel; °C) and salinity (bottom panel; PSU) on 18-19 April 2000 at Balgzand at 36 fishing stations. Temperature ranges from 8 °C (dark red) to 11 °C (light red), salinity from 23 (light blue) to 28 (dark blue). Yellow area refers to mainland, light brown is subtidal area (between low water and low water – 5m and black area is no data avaialable.

season to identify subgroups (Fig. 7 in van der Veer et al., 2000). Trends in mean length over time indicated that differences between subgroups were significantly correlated with the number of vertebrae, but not with the number of anal fin or dorsal fin rays (Fig. 6.4). As a consequence, there was a significant relationship between mean growth and number of vertebrae ($rs = 1.00$, $P < 0.05$) and by the end of June mean length of the various subgroups varied from around 45 to 60 mm (Fig. 6.4).

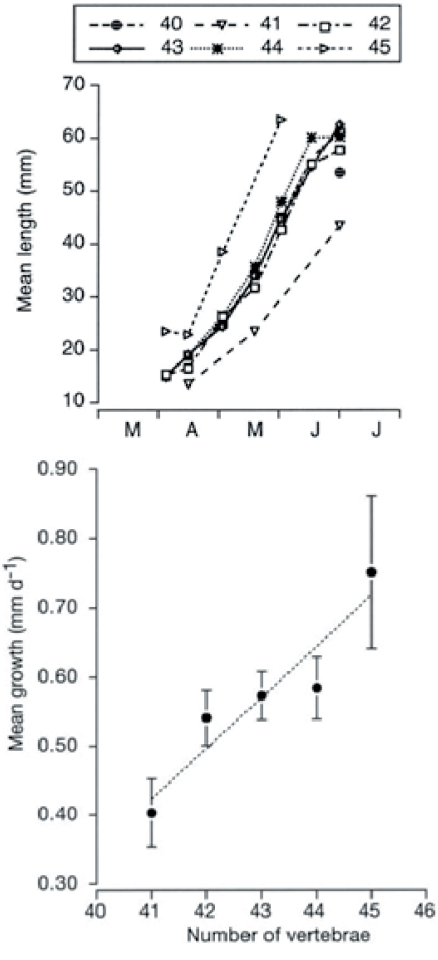

Figure 6.4: Seasonal pattern of mean length (mm) (top panel) and mean growth (bottom panel) of the various meristic subpopulations of 0-group plaice at the Balgzand in 1995 in relation to number of vertebrae.

Sex

The potential impact of sex on growth was illustrated by the predicted difference in growth of male and female 0-group plaice at Balgzand in 1975. Growth curves for both males and females constructed by means of the DEB model at prevailing water temperatures showed clear differences. Starting at a similar size (15 mm) at settlement, predicted mean length differed by more than 4 cm by the end of the season (Fig. 6.5). Plaice growth as predicted by the experimentally established maximum growth model (for an unknown mixture of male and female plaice) by Fonds et al. (1992) was in between male and female growth. Applying the DEB growth model of males and females for 0-group plaice data from 1975 (de Vlas, 1979), showed that much of the observed variation in size at the end of the growing season could be explained by differences in settlement time and in sex (Fig. 6.6).

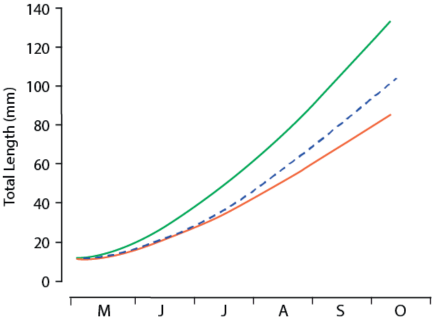

Figure 6.5: Predicted growth of male (red) and female (green) 0-group plaice at the Balgzand in 1995 from May 1th onwards according to the DEB model and according to the experimentally established growth model of Fonds et al. (1992) (blue).

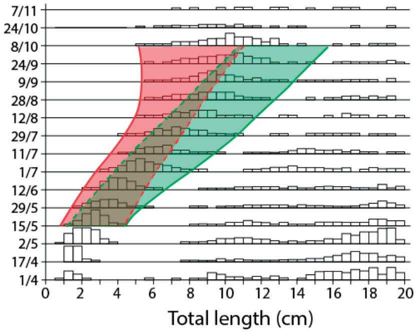

Figure 6.6: Length frequency distribution of juvenile plaice at Balgzand in 1975. Data after de Vlas (1979), together with simulated maximum growth for 0-group plaice according the DEB model for first settlers and last settlers at prevailing temperatures. Green: female; red: males. For more information see text.

6.3.2 *Growth reduction*

Growth reduction was not restricted to 0-group and could also be observed in I- and II-group plaice at Balgzand: the ratio observed growth/maximum possible growth for I- and II-group plaice at Balgzand showed a decrease over time from values around 1.0 in the beginning of the season to values around 0.5 at the end of the summer season (Fig. 6.7). Growth reduction was also not restricted to the intertidal and also occurred.The ratio observed growth/maximum possible growth for 0-group plaice in the subtidal and channel decreased over time in both years for all stations from values around or above 1.0 to about 0.3 at the end of the summer season (Fig. 6.8).

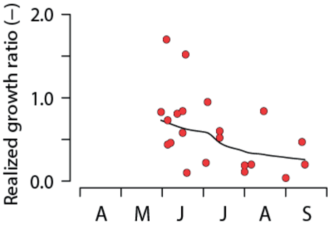

Figure 6.7: Realized growth (ratio of observed growth versus maximum possible growth according to the DEB model) for I- and II-group plaice at Balgzand in the period 1975 – 1978. For methodology see Freitas et al. (2012).

6.3.3 *Growth relationships*

Intraspecific food competition for 0-group plaice did not seem present at Balgzand: there was no relationship between the ratio of observed and maximum possible growth according to the DEB model and the estimated daily food intake of all juvenile plaice (0-, I- and II-group) (Fig. 6.9). Applying a GAM showed that no significant relationship existed: the smoother could be described by a straight line and 0 (no relationship) was within the 95% confidence limits (Fig. 6.9).

To analyse interspecific food competition at Balgand, the ratio between observed and maximum possible growth for 0-group plaice according to the DEB model was compared with the estimated daily food intake of all epibenthic predators present (Fig. 6.10). Applying a GAM showed that a weak significant relationship existed ($P < 0.05$): 0 (no relationship) was not completely within the 95% confidence limits (Fig. 6.10) of the smoother.

Possible resource competition at Balgzand did not seem present: there was no relationship between density of all epibenthic species (mainly flatfishes, gobies and crustaceans) and observed growth reduction in 0-group plaice(Fig. 6.11).

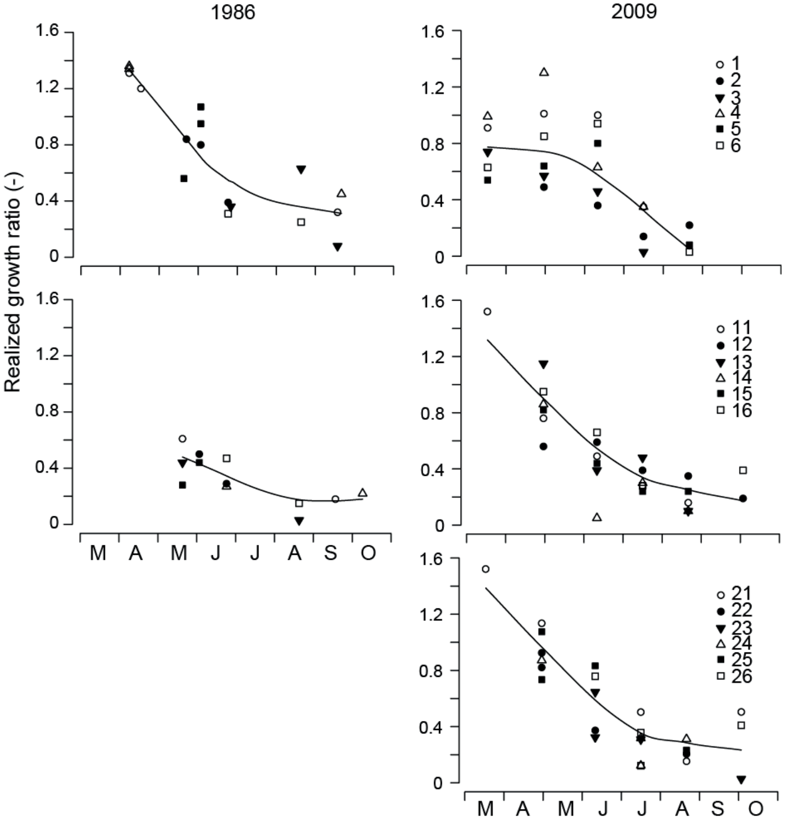

Figure 6.8: Realized growth (fraction of the observed growth versus maximum possible growth according to the DEB model) in 1986 and 2009 at stations located in the intertidal (top panels), subtidal (middle panels) and channels (bottom panel). Solid lines are the LOESS smooth functions fitted to the realized growth ratio data to capture trends over time. For locations of EMOWAD-ZKO stations see Fig. 6.1. Data for 2009 were originally published in Freitas et al. (2016).

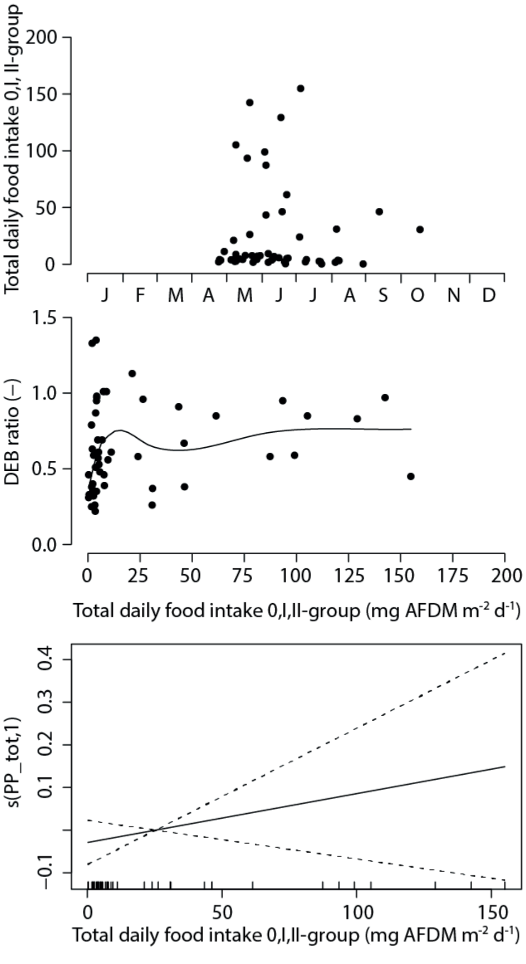

Figure 6.9: Modelled intraspecific competition for food at Balgzand, where daily food intake was estimated on the basis of specific energy requirements, using data that were combined for 1975 – 2009. Top panel: Estimated total daily food intake (mg AFDM m^{-2} d^{-1}) of 0-, I-, and II-group plaice in relation to day number. Middle panel: Realized growth of 0-group plaice (-) in relation to estimated total daily food intake (mg AFDM m^{-2} d^{-1}) of 0-, I-, and II-group plaice. Bottom panel: GAM smoother (n.s.) of relationship between realized growth (-) of 0-group plaice and estimated total daily food intake of 0-, I-, and II-group plaice (mg AFDM m^{-2} d^{-1}).

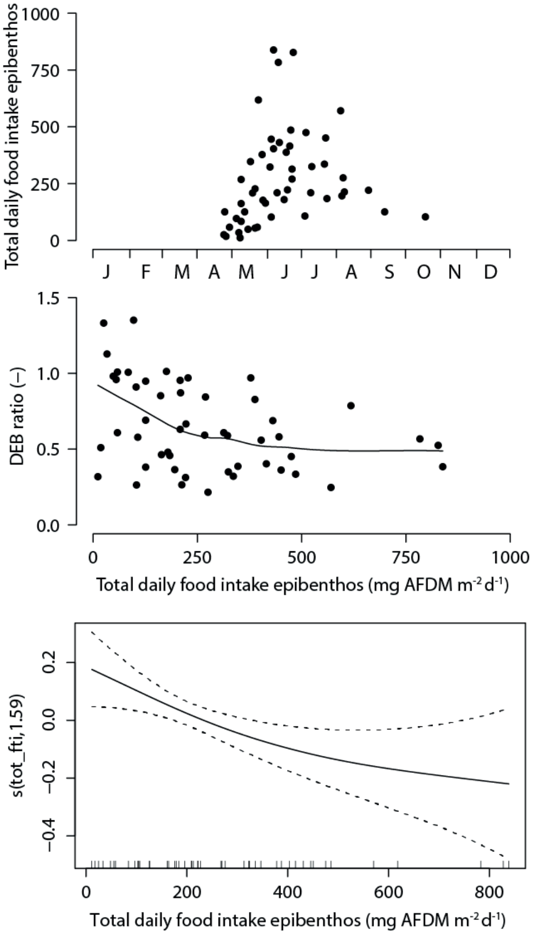

Figure 6.10: Modelled interspecific competition for food at Balgzand, where daily food intake was estimated on the basis of specific energy requirements, using data that were combined for 1975 – 2009. Top panel: Estimated total daily food intake (mg AFDM $\mathrm{m}^{-2}\,\mathrm{d}^{-1}$) of all epibenthic predators (flatfish, gobies and crustaceans) in relation to day number. Middle panel: Realized growth (-) of 0-group plaice in relation to estimated total daily food intake (mg AFDM $\mathrm{m}^{-2}\,\mathrm{d}^{-1}$) of all epibenthic predators. Bottom panel: GAM smootherof relationship between realized growth of 0-group plaice and estimated total daily food intake (mg AFDM $\mathrm{m}^{-2}\,\mathrm{d}^{-1}$) of all epibenthic predators.

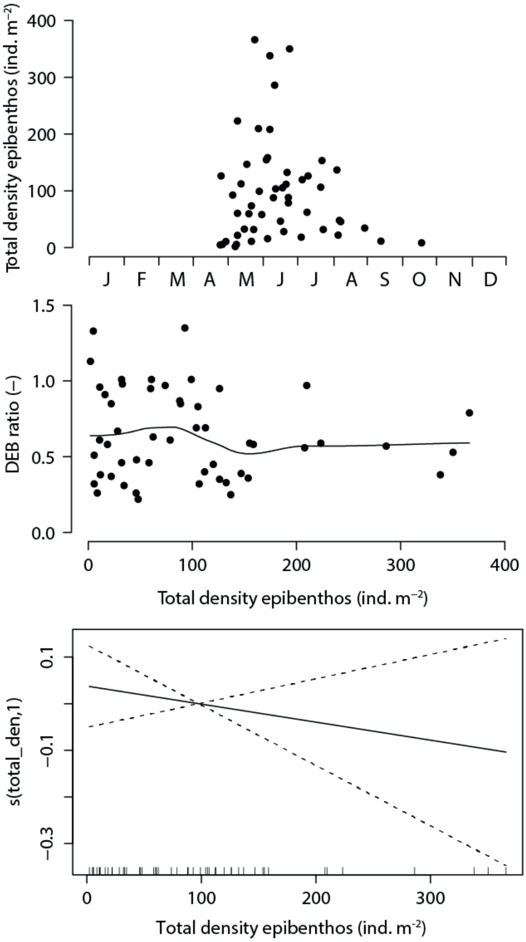

Figure 6.11: Potential for resource competition, for food, at Balgzand, using data that were combined for 1975 – 2009. Top panel: Total density (ind. m^{-2}) of all epibenthic predators (flatfish, gobies and crustaceans) in relation to day number. Middle panel: Realized growth (-) of 0-group plaice in relation to total density (ind. m^{-2}) of all epibenthic predators. Bottom panel: GAM smoother (n.s.) of relationship between realized growth (-) of 0-group plaice and total density (ind. m^{-2}) of all epibenthic predators.

6.4 DISCUSSION

6.4.1 *Growth variability*

Growth, and as a consequence size, is a key life history parameter due to the strong link between growth and mortality, especially in early life (Anderson, 1988; Houde, 1997; Pepin, 1991; van der Veer et al., 1997; Ware, 1975). Hence, variability in growth during early life may directly affect survival, and ultimately recruitment, via size-selective mortality and/or size-dependent onset of maturation (van der Veer et al., 1994).

Variability in growth is the integrated effect of multiple factors acting ultimately on energy consumption and participation between maintenance, growth and reproduction (Kooijman, 2010; van der Veer et al., 2009). They consists of drivers at various levels, as summarized by Ciotti et al. (2014). In this study the focus is on especially some intrinsic (ontogenetic background, sex) and extrinsic (temperature, salinity, food conditions) drivers. Quantification of the various drivers is complicated since they are acting simultaneously and are also partly opposing. Ontogenetic background results in a variability in mean growth during the season of between 0.40 to $0.75\,\mathrm{mm\,d^{-1}}$; however, most of the population falls within 0.50 to $0.75\,\mathrm{mm\,d^{-1}}$ (van der Veer et al., 2000), a range of 50%. Lozán (1992) was among the first who pointed at sexual differences in food intake and growth performance. According to the DEB theory, sex can be responsible in plaice for a size range at the end of the first year of life at Balgzand of between 8.0 cm (for a male) and 13.5 cm (for a female), a 70% difference. Temperature is a controlling factor (Fry, 1947; Neill et al., 1994) directly affecting growth. Temperature conditions at Balgzand varied about 1 to 3 °C between stations, which means a range in size of about 10 – 30% at 10 °C, and of 5 – 15% at 20 °C. Salinity on the other hand is a masking factor, loading metabolism (Fry, 1947; Neill et al., 1994) and therefore potentially negatively affecting growth. The Balgzand surveys have illustrated that salinity conditions at Balgzand can be very variable, sometimes on the order of a few hundred percent; however, the quantitative impact on growth is unknown. Reduced growth rates have been reported for 0-group plaice at low salinities (Karakiri et al., 1989), but experimental work showed faster growth at the lowest salinity levels tested (Augley et al., 2008) in a situation of unlimited food. The interaction of food availability with other variables to generate variability in growth response is widely known (Jobling, 1994). Food resources are a limiting factor that can restrict maximum metabolism (Neill et al., 1994). In the Wadden Sea, clear indications of a relationship between food abundance and growth were found (van der Veer and Witte, 1993), whereby a range in growth of 50% was observed. However, recently Freitas et al. (2016) could not confirm this relationship.

A comparison of temporal with spatial variability in size within and among local populations might give an insight into the relative importance of the various factors generating growth variability (van der Veer et al., 1994). However, size-selective processes such as size-selective mortality and migration (Kuipers, 1977; van der Veer et al., 1997) might interfere and bias such a comparison. By far the most important appears to be intrinsic factors such as sex, being able to generate differences in growth rates within populations on the order of 70%, and ontogenetic background generating a range of 50% in size. However, van der Veer et al. (2000) argued that the impact of ontogenetic background will vary among years and will normally be relatively low since most of the population will have a relatively similar background.

6.4.2 *Summer growth reduction*

The evidence of summer growth reduction in early juvenile flatfish is strong and has been reported for different years, different areas and different species based on different methods (Ciotti et al., 2013*b*,*a*; Fonseca et al., 2006; Freitas et al., 2012; Hurst and Abookire, 2006; van der Veer et al., 2010). Summer growth reduction might be a general phenomenon: in this study, it was also was observed in other age groups (I- and II-group plaice) and in other areas (subtidal, deeper channels). Recently, otolith microstructure analysis of individual flatfish confirmed earlier observations of summer growth reduction at Balgzand; however, relatively smaller than observed from shifts in population size (Cardoso et al., 2016). This difference is most likely caused by size-selective processes, such as size-selective predation (van der Veer et al., 1997) and migration (Kuipers, 1977) biasing estimates from size-frequency distributions. Furthermore, Cardoso et al. (2016) suggested that the observed reduction in growth was most likely caused by an external factor: the growth reduction did not start at a certain fish size (which would suggest being caused by an ontogenetic change such as a shift in prey preference, sensu de Vlas, 1979), but the decline occurred at about the same time in different years irrespective of fish size.

In this study no support was found that the observed summer growth reduction was caused by direct competitive intraspecific interactions between juvenile plaice themselves and only a weak support for interspecific competition with other species. Also resource competition did not seem likely. However, these conclusions were based on hauls with a length of about 100 m at high water, while growth heterogeneity already seems to occur even at a smaller spatial scale of about 100 m (Ciotti et al., 2013*b*,*a*). Therefore, it cannot be excluded that the sampling is inadequate for any analysis of direct and indirect competition: at the scale of the length of a haul heterogeneity in growth already occurs. Furthermore, the present analysis based on mean densities does not take into account the spatial heterogeneity in macrozoobenthos in the intertidal (Compton et al., 2013) and the spatial and temporal variation in the distribution of 0-group plaice (Gibson, 1973; Kuipers, 1973; van der Veer, 1986). It cannot be excluded that the sampling design has been inadequate for analysing competition and interactions among epibenthic predators and that sampling should be conducted at a smaller scale, as was done for shore crabs *Carcinus maenas* in the same area (Smallegange et al., 2009).

Growth reduction induced by changes in food availability does not seem likely at first glance. For benthic predators such as juvenile plaice, predation pressure by juvenile flatfish is rather low compared to the food availability, at least for the Balgzand area (Kuipers, 1977; de Vlas, 1979; van der Veer et al., 2011). Also, part of the diet of juvenile flatfishes at Balgzand and in other areas consists of regenerating body parts of benthic prey (among others Macer, 1967; Edwards and Steele, 1968; Kuipers, 1977; de Vlas, 1979; Poxton et al., 1983; van der Veer and Witte, 1993) and maximum predation at Balgzand appears to coincide with maximum productivity of the benthic invertebrates (Kuipers, 1977). However, these considerations are based on potential food availability, while for a predator only harvestable prey counts: the combination of not only density and size (potential food availability), but also of accessibility (Piersma, 1994; Zwarts and Wanink, 1993).

The potential benthic prey items for juvenile plaice, all live at least partly burrowed in the sediment where they are relatively well hidden and only available for predators when they are actively exposing body parts at the sediment surface for instance during feeding, defecation and spawning. At Balgzand, the growth reduction in plaice corresponds with a (temporal) disappearance of regenerating body parts in the stomachs of juvenile flatfish (Fig. 6 in de Vlas, 1979). At the same period of time, mean stomach content of I- and II-group plaice at Balgzand also showed a dip (Fig 6.12; after Kuipers, 1977).

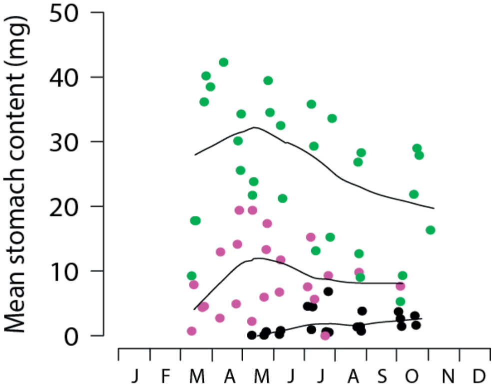

Figure 6.12: Mean stomach content of juvenile plaice at Balgzand in 1973. Data after Fig.6 in Kuipers (1977). Black: 0-group plaice; pink: I-group plaice; green: II-group plaice. Solid lines represent LOESS smooth functions fitted to the data to capture trends over time.

Macrozoobenthic biomass shows a seasonal pattern (Beukema, 1974) in synchrony with primary production in the system (Cadée and Hegeman, 1974*a*; Cadée and Hegeman, 1974*b*) and the (temporal) disappearance of regenerating body parts in the stomachs of juvenile flatfish in summer corresponds with the decrease in primary production after the spring bloom, in between and before the second lower autumn bloom (Beukema and Dekker, 2014; Philippart et al., 2010). This suggests that growth reduction in summer in plaice at Balgzand and possibly in other European waters might be caused by a reduced activity of the benthos after the spring phytoplankton bloom. Temperate coastal benthic ecosystems indeed seem to show a clear seasonality (Coma et al., 2000).

However, to test whether prey searching and handling are indeed key factors determining food intake of juvenile flatfish and are the possible cause of the summer growth reduction would require underwater observations of seasonal pattern in the activity of the benthic community. If true, also spatial differences in prey species composition and abundance would affect food intake of juvenile flatfish and hence growth (sensu van der Veer and Witte, 1993).

6.5 ACKNOWLEDGMENTS

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7

SEASONAL VARIATION IN THE DIET OF ESTUARINE BIVALVES

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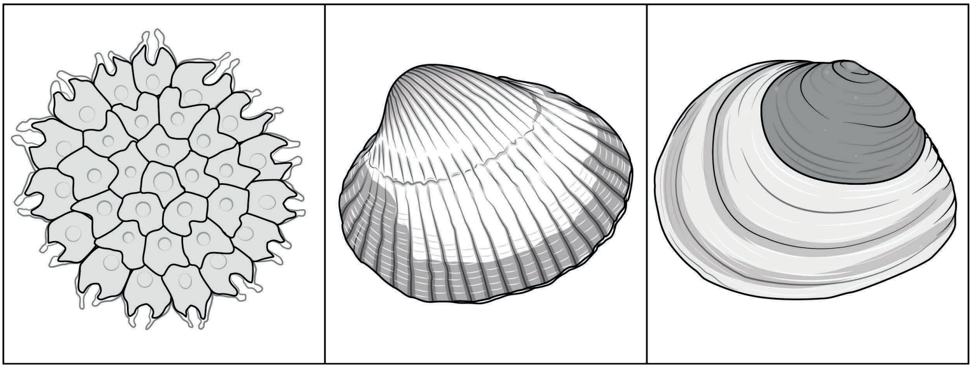

ABSTRACT

Estuarine food webs are generally considered to be supported by marine pelagic and benthic primary producers and by the import of dead organic matter from the open sea. Although estuaries receive considerable amounts of freshwater phytoplankton and organic compounds from adjacent rivers, the potential contribution of these living and dead matter to estuarine food webs is often assumed to be negligible and, therefore, not examined. Based on stable isotope analyses, we report the importance of freshwater suspended particulate organic matter (FW-SPOM) for fuelling estuarine food webs in comparison to estuarine SPOM and microphytobenthos. This previously neglected food source contributed 50-60 % (annual average) of food intake of suspensionfeeding bivalves such as cockles (*Cerastoderma edule*), mussels (*Mytilus edulis*) and Pacific oysters (*Magallana gigas*) at the Balgzand tidal flats, an estuarine site in the western Wadden Sea (12-32 psu). For these species, this proportion was particularly high in autumn during strong run-off of SPOM-rich freshwater, whilst estuarine SPOM (20 %-25 %) and microphytobenthos (15 %-30 %) were relatively important in summer when the freshwater run-off was very low. These findings have implications for our understanding of the trophic interactions within coastal food webs and for freshwater management of estuarine ecosystems.

7.1 INTRODUCTION

Coastal ecosystems and their food webs are under the influence of a variety of tidal and seasonally fluctuating factors in environmental conditions (e.g. temperature, salinity and/or hydrodynamics, (Menge and Olson, 1990)). In addition, long-term (interannual) variation in coastal community structures due to loss or gain of biodiversity (e.g. extinction/disappearance of species, invasions) and anthropogenic changes (e.g. input of nutrients, extraction of biomass by fisheries) occur (Reise et al., 1989; Wolff, 2000; Jackson et al., 2001; Griffiths et al., 2005; Lotze, 2005; Lotze et al., 2005, 2006; Halpern et al., 2008). These variations at different time scales will have consequences for the trophic transfer, isotopic niches and predator-prey interactions within the food web. However, to identify long-term changes from higher-order dynamics is a challenge. This is particularly true for marine organisms such as macrozoobenthos for which long-term trend analyses are based upon data that are gathered once a year during a particular season.

Considering coastal marine bivalves, for example, the sampling is often restricted to one (e.g. Frid et al., 1999; Compton et al., 2013) or two periods (e.g. Beukema and Dekker, 2005; Currie and Small, 2005) in a year. If the seasonal timing of spatfall varies between years, then recruitment success (spat m^{-2}) might be over- or underestimated if sampling is performed at a fixed date (Philippart et al., 2003). If the diet of a marine coastal bivalve depends on body size (e.g. as found for *Limecola balthica* by Rossi et al. 2004 then, as a consequence, the estimate for the total annual trophic transfer by the local stock will be related to the timing of sampling. If the bivalves are opportunistic in their diet and/or the availability of various food sources varies throughout the season, then determination of main diet based upon observations during one season (Christianen et al., 2017) might be biased. In order to extrapolate seasonal values to annual estimates of trophic transfer, insights into the seasonality of the diet of coastal marine bivalves are required.

Based upon the length of their siphons compared to their burrowing depth, coastal marine bivalves are often divided into suspension feeders (filtering suspended particulate organic matter out of the water column with their relatively short siphons) and facultative deposit-feeders (able to graze from sediment surface using their relatively long siphons). Although bivalves prefer living microalgae (e.g. Kamermans, 1994; Hsieh et al., 2000; Riera and Richard, 1997; Kharlamenko et al., 2001; Sauriau and Kang, 2000), detritus might still be part of their diet, even if originating from vascular plants (Navarro et al., 2016). For many bivalve species, main food sources in their direct benthic environment can vary through the year due to sedimentation of pelagic microalgae and organic matter during slack tides and/or calm weather (Cadée, 1996; Cloern, 1996), to wind and tide-driven resuspension of benthic matter (Fischer et al., 1979; de Jonge and de Jong, 2002; Kamermans, 1994; Cloern, 1996), and to seasonal variation in burrowing behaviour of the facultative deposit-feeders (Reading and McGrorty, 1978; Zwarts and Wanink, 1989). Competition of coexisting intertidal bivalves for food might, therefore, differ throughout the year as the result of external (availability of food sources) and internal (e.g. siphon length, shell size and burrowing depth) variation.

Until a few decades ago, stomach content analysis was the main tool to determine the diet of coastal marine bivalves (Ivell, 1981; Hummel, 1985; Kamermans, 1994). However, the approach is very time-consuming and provides diet information of a snapshot in time and requires taxonomic knowledge of prey items (Zacharia et al., 2004). Since the 1970s, the composition of stable nitrogen (^{15}N) and carbon (^{13}C) isotopes of various potential food items in relation to bivalve body mass is used to estimate the trophic position of an organism as well as the source of its diet, integrated over a longer time period (Fry and Sherr, 1984). Because freshwater algae (-36 to -30 ‰) have lower $\delta^{13}C$ values than marine algae (-24 to -20 ‰) and marine microphytobenthos (-20 to -16 ‰) (France, 1996; Riera and Richard, 1996), food source of coastal marine bivalves can often be determined by analysing their stable isotope signature (Riera and Richard, 1996; Kang et al., 1999; Herman et al., 2000; Sauriau and Kang, 2000; Page and Lastra, 2003).

In this study, we expand on the diet studies from the past (Kamermans, 1994) and explore the seasonality in the diet of coastal marine bivalves living on the Balgzand tidal flats in the western Wadden Sea by using stable isotope analyses (Fig. 7.1). Because this area is under the influence of freshwater outputs of Lake IJssel (Postma, 1950; Ridderinkhof et al., 1990; Duran-Matute et al., 2014), we have included freshwater SPOM samples to explore the proportion of this potential food source to estuarine SPOM and benthic organic matter (Canuel et al., 1995; Peterson, 1999; Antonio et al., 2010; Bishop et al., 2017). Seasonal variation in relationships between diet and body size are investigated for all sampled bivalve species, as are trophic niches within and between bivalve species throughout the year. We discuss our results on seasonality in diet with respect to potential food availability, to previous statements on main diet and trophic transfer in this area and to the consequences of using seasonal samples to describe long-term variations in trophic interactions in general.

7.2 MATERIALS AND METHODS

7.2.1 *Study area*

All sampling took place at the Balgzand, a large (50 km^2) isolated tidal flat system bordering the Marsdiep tidal inlet in the western part of the Wadden Sea (Fig. 7.1). The area is surrounded by dikes to the south and west and by tidal channels ranging in depth from 5 to 20 m (relative to mean sea level). Median grain size and silt content of the sediment are about 150 µm and 5%, respectively, with a gradient from coarse sand at more exposed flats in the north to fine sands and mud at the more sheltered areas in the south (Compton et al., 2013). On average, the tidal flats are drained for 2 to 4 hours of the 13-hour tidal cycle. At high tide, most of the area is covered by 0.7 to 1 m of water, the actual depth depending on the lunar phase and weather conditions.

The Balgzand tidal flat area has been studied by the Royal Netherlands Institute for Sea Research (NIOZ) since the early 1970s for macrozoobenthos (Beukema, 1976; Beukema and Dekker, 2006; Dekker and Beukema, 2007), crustaceans (Klein Breteler, 1976; van Lissa, 1977, Chapter 5) and fish (de Vlas, 1979; van der Veer et al., 2011, Chapter 5). These long-term studies revealed strong year-to-year variation and multi-annual trends, including the impacts of long-term variation in nutrient supply (Beukema and Cadée, 1986; van der Veer et al., 1989; Philippart and Cadée, 2000, Chapter 2), the invasion and establishment of Pacific oysters (Troost, 2010), and the shift from juvenile flatfish to shrimps as main predators of small macrozoobenthic prey (Chapter 5). Since 2008, the Balgzand tidal flats are also covered by the SIBES (Synoptic Intertidal BEnthic Surveys of the Wadden Sea) surveys, during which intertidal macroozoobenthos is sampled in summer (July/Aug) in a grid of 500 mx500 m (Bijleveld et al., 2012). In addition to the long-term field observations, this area was subject to a suite of field experiments and other in-depth studies, including studies on the diet of bivalves based upon stomach analyses (Hummel, 1985; Kamermans, 1994).

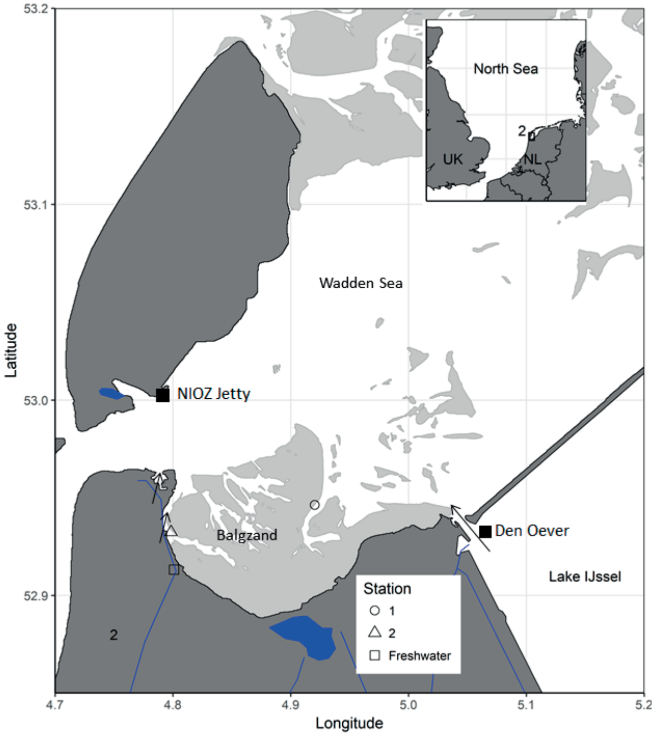

Figure 7.1: Map of the study area, the two sampling stations on the Balgzand tidal flats are indicated, as well as the freshwater station and the NIOZ jetty (star). The arrows depict the locations (sluice in Den Oever, the Balgzand channel and the harbour of Den Helder) where freshwater is discharged into the western Wadden Sea.

7.2.2 *Sampling*

Field work was conducted under the general permit (permit number 01028628) for the Coastal Systems department of the NIOZ for 2012-2015. The permission was granted by the department "Stéd en Plattelân" of the "provinsje fryslân" at 7 December 2012 (for 3 years). At the Balgzand tidal flats, samples were collected around high water (temperature, salinity, suspended particulate organic matter, SPOM; Table 7.1) and low water (macrozoobenthos, microphytobenthos; Table 7.2) at two stations (Fig. 7.1) during four different periods in time (March, June, September and December of 2014), either by foot or from board of the R.V. Stern and rubber dinghies (Table 7.1). In addition, freshwater SPOM samples were collected (one sample per period) one day after the estuarine SPOM samples in a small channel that is supplying freshwater to the Balgzand tidal flats (52.913° N, 4.801° E; Fig. 7.1). Estuarine and freshwater SPOM samples were collected from surface water samples with a bucket. For the estuarine samples, water temperature and salinity were measured with handheld automated devices (Delta Ohm HD2105.1 and Delta Ohm HD2105.2). This information was not gathered for the freshwater SPOM samples. Samples were sieved through a 200 µm mesh to exclude larger zooplankton from the sample and stored in an ice chest. In the lab samples were filtered onto pre-combusted 25 mm GF/F filters using a 25 mm filter cartridge mounted on a 60 ml syringe. Between 80 and 250 ml of water was filtered, samples were stored at −20 °C until further processing.

Table 7.1: Sampling dates, local sampling times, mean temperature (°C), mean salinity (PSU) and the number of estuarine SPOM samples collected at high tide at two estuarine stations (Fig. 7.1) at Balgzand tidal flats in 2014. Freshwater SPOM samples were taken one day after the estuarine SPOM samples.

Station	Date	Time span	Mean Temperature	SD	Mean Salinity	SD
1	13.03.2014	09:00-09:40	7.65	0.15	16.55	0.15
2	12.03.2014	10:20-10:50	8.55	0.05	19.95	2.26
1	27.06.2014	11:00-12:15	18.4	0.24	23.72	0.97
2	23.06.2014	13:00-14:10	19.53	0.12	11.77	2.18
1	23.09.2014	09:10-09:40	14.64	0.1	21.67	0.1
2	18.09.2014	12:20-13:20	19.73	0.09	22.85	1.92
1	15.12.2014	12:50-13:20	6.33	0.12	31.14	0.14
2	16.12.2014	12:40-13:30	7.27	0.17	31.55	0.13

Samples for microphytobenthos (MPB) were sampled by collecting the top layer of sediment from visible diatom mats into plastic bottles that were brought back to the research facility cooled. Microphytobenthic diatoms were extracted in the laboratory using the method of Riera and Richard (1996), slightly modified by Herlory et al. (2007). The sediment was spread on a tray, covered by three layers of nylon mesh (2 × 100 µm, 1 × 50 µm) that was kept moist by repeatedly spraying filtered seawater on top. The samples were then left in a temperature regulated room reflecting outside temperature (depending on season 6 to 20 °C) overnight and the following day the algae were washed into a beaker with filtered seawater and concentrated by centrifugation (10 min at 1000x g) and stored at $-20\,^{\circ}\mathrm{C}$ (Lebreton et al., 2012).

Sampling of bivalves was conducted around low water by foot on the dry tidal flats. An area of approximately $20\,\mathrm{m}^2$ area was searched for living animals by collecting organisms on the surface (e.g. the epibenthic *Magallana gigas*, formerly known as *Crassostrea gigas*), by looking for siphon holes or other structures (e.g. the infaunal *Mya arenaria*, of which large specimens burrow up to a depth of 25 cm,Zaklan and Ydenberg 1997), or by randomly sieving the upper 5 cm of sediment over a $1\,\mathrm{mm}^2$ sieve. The collected organisms were transported in separate plastic containers and taken to the lab, where they were washed and stored in filtered seawater for 24–48 h to get rid of stomach and gut contents. They were then measured (nearest mm), shells were removed from bivalves larger than 0.5 cm and organisms were stored separately in glass vials at $-20\,^{\circ}\mathrm{C}$ until stable isotope analyses.

Table 7.2: Sampling dates, number of bivalve species and total number of bivalves sampled at low tide at two estuarine stations (Fig. 7.1) at Balgzand tidal flats in 2014.

Station	Date	No of bivalve species	No of bivalves sampled
1	13.03.2014	5	74
2	12.03.2014	6	46
1	27.06.2014	6	25
2	23.06.2014	7	38
1	23.09.2014	6	21
2	18.09.2014	7	47
1	15.12.2014	3	7
2	16.12.2014	5	17

7.2.3 *Seasonality in primary sources of microalgae*

Seasonality in biomass of potential sources of living pelagic and benthic microalgae (marine pelagic microalgae, freshwater microalgae, microphytobenthos) was based upon relative seasonal variations (compared to the maximum value observed) in chlorophyll-a concentrations of phytoplankton in the Marsdiep tidal inlet and in Lake IJssel, respectively, and NDVI (Normalized Density Vegetation Index) values for the intertidal area of the Dutch Wadden Sea (Table 7.1).

Seasonal variation in estuarine phytoplankton biomass in 2014 ($\mathrm{mg\,m^{-3}}$) was derived from the long-term field observations at the NIOZ jetty (Fig. 7.1; see Philippart et al. (2010) for materials and methods). Since sampling was performed at the tidal inlet at high water, these values are expected to have a relatively high component of materials of marine origin. Seasonal variation in supply of freshwater algal biomass was calculated as the discharge of freshwater ($\mathrm{m^3\,mon^{-1}}$; `http://waterinfo.rws.nl/`) from Den Oever, a sluice complex approximately 25 km east of the Balgzand tidal flats (Fig. 7.1), multiplied by average monthly concentrations of chlorophyll-a ($mg\,m^{-3}$; `http://waterinfo.rws.nl/`) at the sampling station Vrouwezand (52.810 350° N, 5.393 138° E) in the southern part of Lake IJssel (Fig. 7.1, station not shown) in 2014.

Because microphytobenthos biomass ($mg\,Chl - a\,m^{-2}$) was not available for 2014, we based the seasonality of benthic microalgae on NDVI values as derived for the period 2002-2004 from satellite images by van der Wal et al. (2010). The possible fate of freshwater SPOM in seawater (deterioration) was explored by plotting the variations in $\delta^{15}N$ and $\delta^{13}C$ values of estuarine suspended particulate organic matter (SPOM) as a function of local salinity, including the values of the freshwater SPOM as reference levels.

7.2.4 *Stable isotope analysis (SIA)*

Prior to the Stable Isotope Analysis (SIA), all samples were freeze dried for 48 hours at −60 °C to remove water, homogenized and decalcified if necessary. Samples were weighted and folded into tin cups for analysis except for samples that needed to be decalcified. Those samples were decalcified in silver cups with 1 M HCl to remove inorganic carbonate and dried for another 24 h at 60 °C, folded and analysed. Nitrogen and carbon isotope ratios for all samples were determined with a Thermo Scientific Delta V Advantage Isotope Ratio Mass Spectrometer linked with a Flash 2000 Organic Element Analyzer at the NIOZ. Isotope ratios (R) are presented in the δ notation in ‰ relative to an internationally defined reference.

$$X = (R_{sample}/R_{standard} - 1) \times 1000 \tag{7.1}$$

with R being the ratio between the heavy and light isotopes ($^{15}N :^{14} N$ or $^{13}C :^{12} C$). The reference for ^{15}N is atmospheric nitrogen and for ^{13}C is Vienna Peedee-Belemnite (VPDB). For each analytical run monitoring gas, both N_2 and CO_2, with a predetermined isotopic composition was used to determine the δ values for all standards and samples. Three standards with known isotopic composition were included at the beginning, after every twelve samples and at the end of each analytical sequence to monitor performance of the machine and to correct for the offset between the measured and actual isotope ratio. One standard, Acetanilide, was used to correct the measured values and the other two standards, Urea and Casein, to check the correction. Analytical reproducibility was 0.3 ‰ for $\delta^{15}N$ and 0.1 ‰ for $\delta^{13}C$ throughout every sequence. Before the standards each sequence starts with multiple blanks, empty tin cups, to remove air if present and to determine a potential blank contribution to the analysis. Blanks are typically too low to be of any importance.

7.2.5 *Data Analysis*

To establish that the isotope values of the three sources were different they were tested using an ANOVA, when significant this was followed by a pairwise Tukey Honest Significant Differences test corrected for multiple comparisons.

To directly compare the stable isotope signal of the bivalves with their potential food sources, we assumed a trophic fractionation factor of 3.78 ‰ for $\delta^{15}N$ and 2 ‰ for $\delta^{13}C$ per trophic level (Dubois et al., 2007).

To determine the relative contribution of the various food sources to the diet of the bivalves, an isotopic mixing model was applied for each season to the bivalve data available by using the R package simmr (Version 0.3, Parnell et al. 2010). This package is designed to solve mixing equations for stable isotopic data within a Bayesian framework, and includes the possibility of a-posteriori testing of correlations between probabilities of different sources (Parnell and Inger, 2016).

The relationship between the shell length of a bivalve and the $\delta^{13}C$ and $\delta^{15}N$ values was tested for all samples of one species by fitting a linear model through the data according to:

$$\delta^{13}C = \beta_1 \times Shell\ length(mm) + factor(Season) \tag{7.2}$$

$$\delta^{15}N = \beta_2 \times Shell\ length(mm) + factor(Season) \tag{7.3}$$

where β_1 represents the slope of change in $\delta^{13}C$ per mm, and β_2 the slope of change of $\delta^{15}N$ per mm.

The size of the isotopic niche of each bivalve species was analysed for each season separately with the SIBER package (Version 2.1.3, Jackson et al. 2011 in R (R Core Team, 2017). Only bivalve species with more than 4 samples were included in the analysis.

Trophic niche of all bivalve species was investigated by calculating the Standard Ellipse Area corrected for small sample sizes (SEA_c) from $\delta^{13}C$ and $\delta^{15}N$ measurements of individuals. This is a bi-variate measure of variation similar to the standard deviation (Jackson et al., 2011).

Variation in seasonal diet overlap within species and between species was investigated by calculating the percentage of overlap of the area of the SEA_c ellipses of one species in the course of the year and all species for each season separately, respectively.

7.3 RESULTS

7.3.1 *Seasonality in primary sources of microalgae*

In 2014, the chlorophyll-a concentrations within the Marsdiep tidal inlet peaked in March (14.1 $\mu g\,L^{-1}$, Fig. 7.2) after which a steady decline occurred until July (40 % of maximum, Fig. 7.2). A small autumn bloom could be detected with a peak in September (9.1 $\mu g\,L^{-1}$, 64 % of maximum, Fig. 7.2), the minimum concentration was found in January and December (Fig. 7.2).

In 2014, peak chlorophyll a discharge from Lake IJssel via the sluice at Den Oever was found in autumn (August 19.6 $\mu g\,s^{-1}$ and October 21.4 $\mu g\,s^{-1}$) and lowest values were observed in April (0.9 $\mu g\,s^{-1}$, 4 % of maximum, Fig. 7.2).

In the period 2002-2004, NDVI values of microphytobenthos at the Balgzand flats were highest during the summer/autumn period (June- October) with values up to 0.14 NDIV (Fig. 7.2). Comparable to the marine phytoplankton biomass, the lowest NCVI values were found in January (46 %) and December (36 %).

The three primary sources for local concentrations of living microalgae at Balgzand show distinctively different seasonal patterns with respective peaks in spring (marine phytoplankton), summer/autumn (microphytobenthos) and autumn (freshwater phytoplankton).

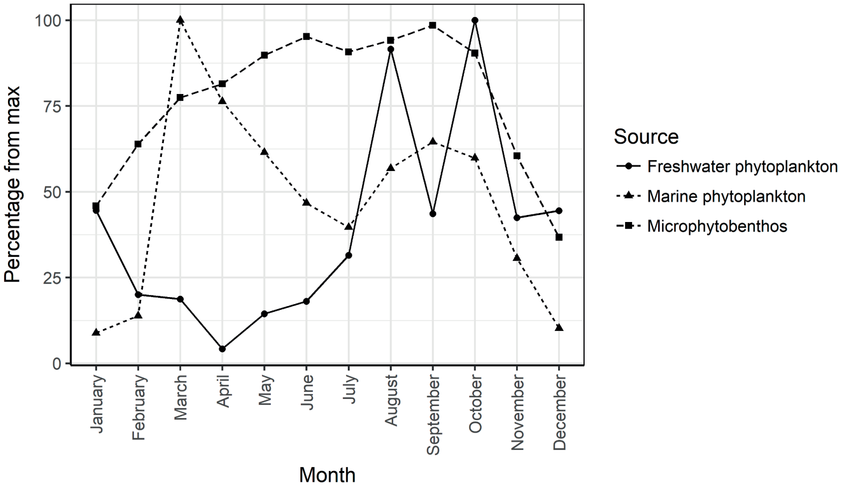

Figure 7.2: Monthly variations in living microalgae as food for the Balgzand bivalve community. Values are relative to their respective maximum (set as 100%) of chlorophyll-a concentrations ($mg\,Chl - a\,m^{-3}$) in the Marsdiep tidal inlet in 2014 (marine phytoplankton), NDVI of the tidal flats of the Dutch Wadden Sea between 2002 and 2004 (microphytobenthos) and input of chlorophyll-a (mg Chl a month-1) from Lake IJssel via the discharge sluices at Den Oever (freshwater phytoplankton). See text for data sources

There were no significant linear relationships between stable isotope signals of the estuarine SPOM and salinity (Fig. 7.3). On average, however, the values of the $\delta^{13}C$ values of the freshwater SPOM were lower than the $\delta^{13}C$ values of the estuarine SPOM (Fig. 7.3).The means of $\delta^{13}C$ of all three sources had significantly ($p < 0.05$) different values, whereas the means of $\delta^{15}N$ were not significantly different between the sources.

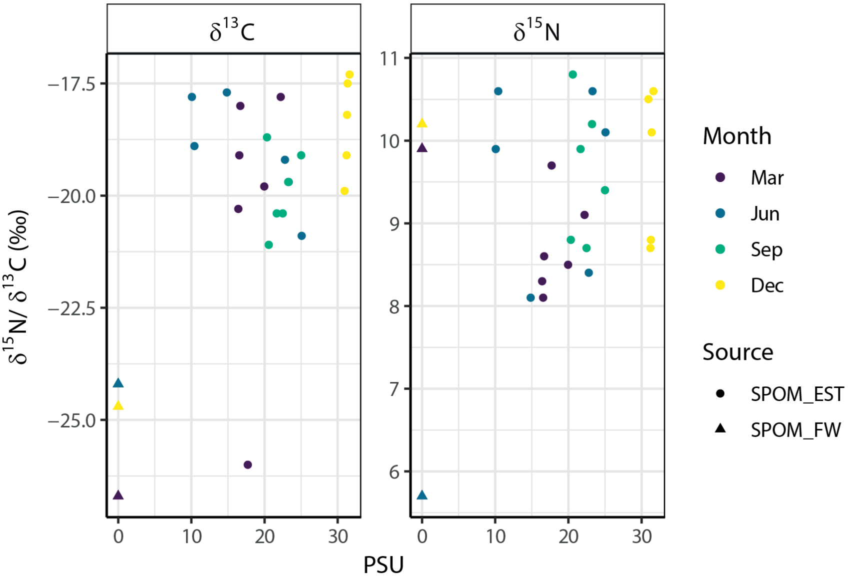

Figure 7.3: Variations in $\delta^{13}C$ (left panel) and $\delta^{15}N$ (right panel) and values of estuarine suspended particulate organic matter (SPOM_EST) as a function of local salinity. The triangles denote the stable isotope values of the freshwater SPOM (SPOM_FW) samples .

7.3.2 *Seasonality in stable isotope signatures of SPOM and microphytobenthos*

Seasonal variation in the average stable isotope signals of the SPOM (estuarine, freshwater) and microphytobenthos samples was most pronounced in the nitrogen isotopic signatures of the freshwater SPOM. The $\delta^{15}N$ value in June (5.7 ‰) was almost 5 ‰ lower than those in March (9.9 ‰) and December (10.2 ‰) (Fig. 7.4) Unfortunately no information is available for September. The average of March, June and December FW_SPOM was used for further analysis, if needed. Average $\delta^{15}N$ values of the estuarine SPOM samples varied between a relatively low 8.7 ‰ in March to more than 9.6 ‰ for all other seasons, whilst those of microphytobenthos ranged between 7.6 ‰ in December to more than 10 ‰ in June (Fig. 7.4, but then without the corrections for trophic enrichment). Variation in the average $\delta^{13}C$ values was around 2 ‰ in all three types of samples (Fig. 7.4).

7.3.3 *Seasonality in stable isotope signatures of estuarine bivalves*

Stable isotope signatures of the estuarine bivalves were more or less centred around the signatures (corrected for trophic enrichment) of the estuarine SPOM samples, in particular in March and June (Fig. 7.4). The stable isotope mixing model results suggest that for *Limecola balthica*, estuarine SPOM is the most probable food source in March (> 0.45; Fig. 7.5) however, the diet of this de-

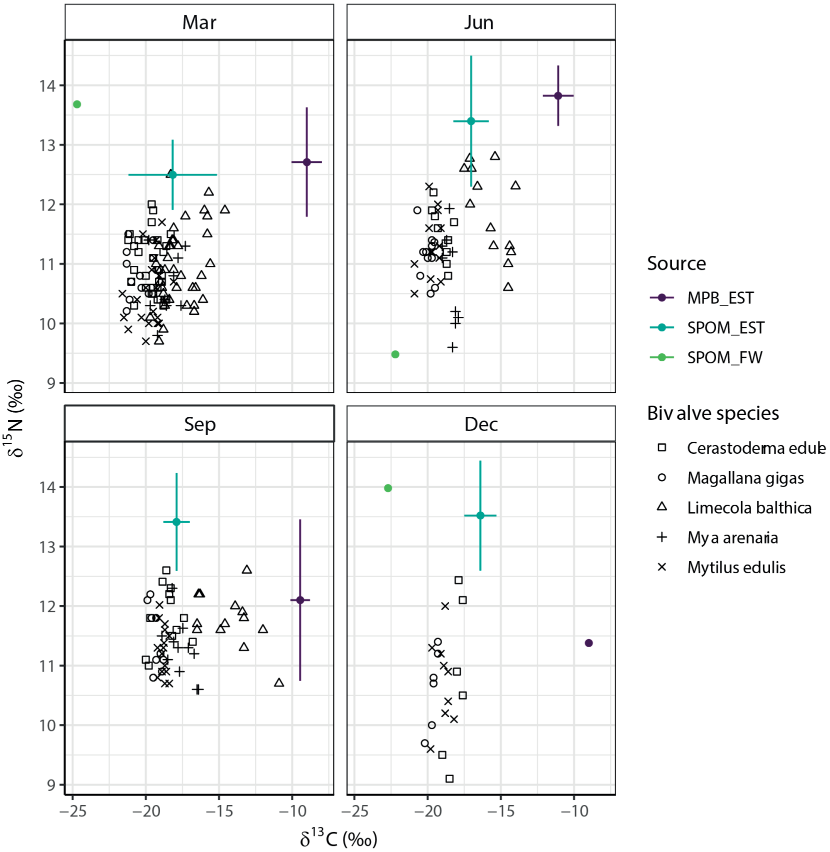

Figure 7.4: Tracer plots of the estuarine bivalve species as sampled in March, June, September and December 2014 at the Balgzand tidal flats in relationship to local pelagic (SPOM_EST) and benthic (microphytobenthos) samples and to pelagic samples taken in an adjacent freshwater channel (SPOM_FW). Note that the isotope signals of the SPOM (estuarine and freshwater) and microphytobenthos samples are already corrected for trophic enrichment by one trophic level (+3.78 $\delta^{15}N$ and +2 δ^{13}C; (Dubois et al., 2007).

posit feeder switched to benthic microalgae in June and Sepetmber (> 0.50; Fig. 7.5). For all other bivalve species sampled during all periods of the year (*Cerastoderma edule*, *Magallana gigas*, *Mya arenaria*, *Mytilus edulis*), the results indicated a high probability of feeding mainly on freshwater SPOM (approximately 0.5) up to more than 0.7 for *M. gigas* in December (Fig. 7.5).

Season-specific matrix plots of food sources showed, however, mostly high ($r > 0.65$) negative (between microphytobenthos and estuarine SPOM, between estuarine and freshwater SPOM) and positive (between microphytobenthos and freshwater SPOM) correlations (Appendix Fig. I.1 and I.2). For several occasions the positive correlation between microphytobenthos and freshwater SPOM was relatively low (< 0.3), for *L. balthica* in June and September (Appendix Fig. I.1).

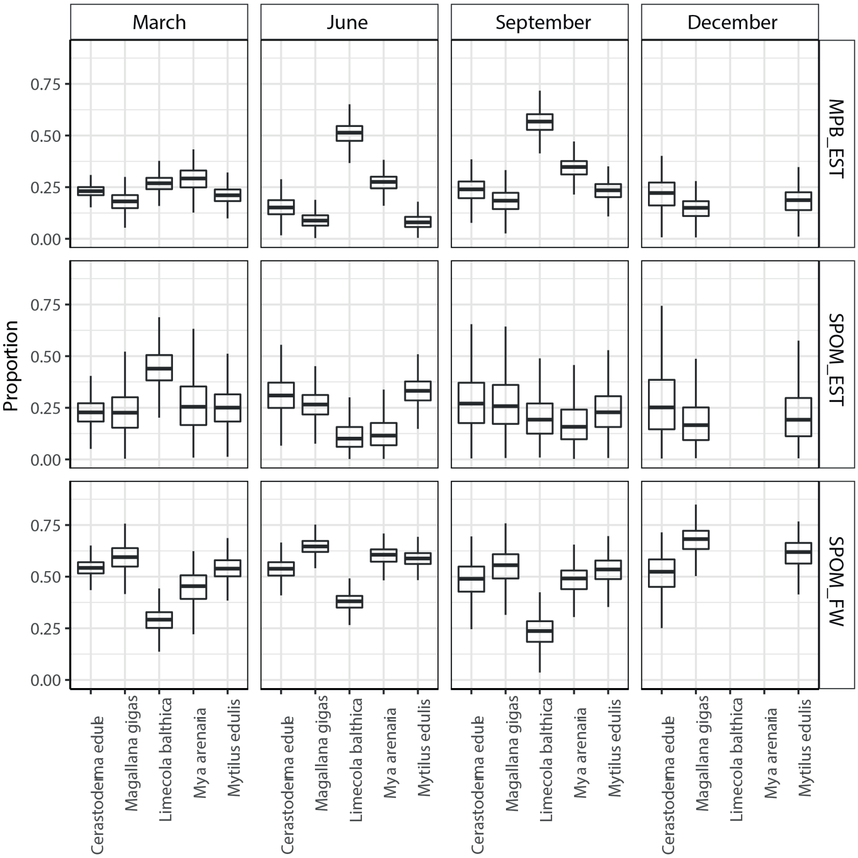

Figure 7.5: Relative contribution of different food sources to the diet of estuarine bivalves at the Balgzand tidal flats in March, June, September and December 2014.

7.3.4 *Correlation of $\delta^{13}C$ and $\delta^{15}N$ with shell length of estuarine bivalves*

For *L. balthica* and *Mya arenaria*, the $\delta^{13}C$ signal significantly decreased with shell length with respective slopes of -0.08 $\delta^{13}C$ mm^{-1} and -0.02 $\delta^{13}C$ mm^{-1} (Fig. 7.6, Table J.1). For the Baltic tellin *L.balthica*, the intercept of this relationship was higher in June and September than in March (Fig. 7.6, Table J.1). For the soft-shell clam *M. arenaria*, the intercept of this relationship was higher in September than in March and June (Fig. 7.6, Table J.1). For *M. edulis*, the $\delta^{13}C$ signal significantly increased with shell length (+0.02 $\delta^{13}C$ mm^{-1}) with the intercept of this relationship being higher in September and December as in March (Fig. 7.6, Table J.1). The slopes of these relationships were not significant for the other three estuarine bivalve species examined (Fig. 7.6, Table J.1).

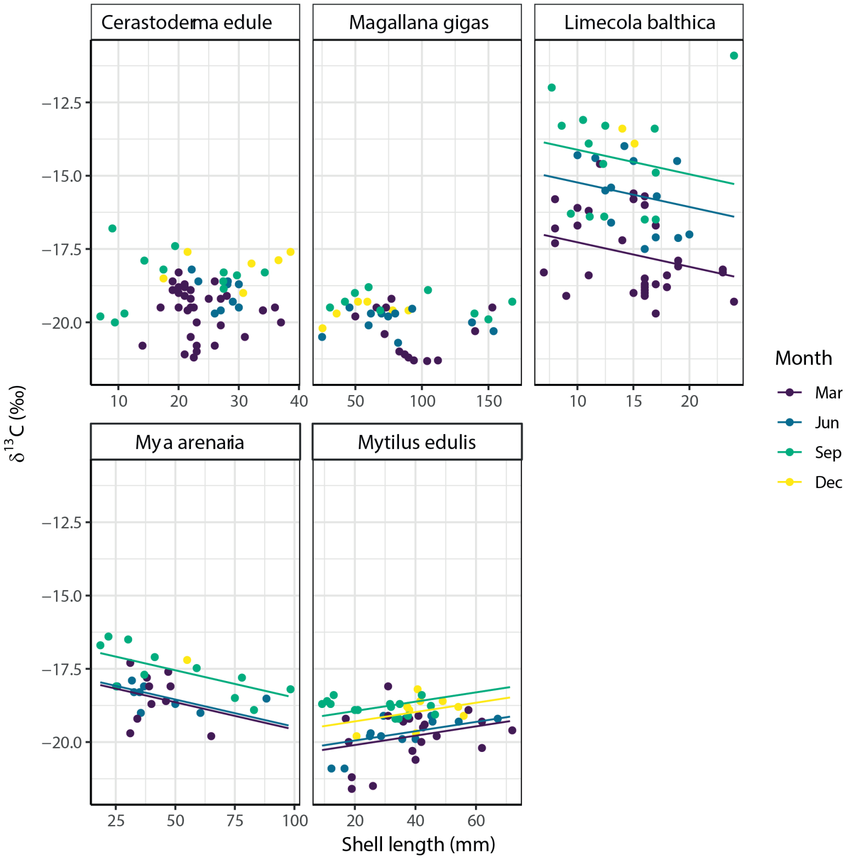

Figure 7.6: Relationships between the $\delta^{13}C$ signals and shell length estuarine bivalves at the Balgzand tidal flats in March, June, September and December 2014. Linear relationships with significant ($p < 0.05$) slopes are plotted as solid lines (see Appendix J.1 for significance of these relationships).

For four bivalve species (*C. edule*, *M. gigas*, *M. arenaria* and *M. edulis*), the $\delta^{15}N$ signal significantly increased with shell length with respective slopes of +0.06, +0.01, +0.02 and +0.03 $\delta^{15}N$ mm^{-1} (Fig. 7.7, Table J.2). For the edible cockle *C. edule*, the intercept of this relationship was higher in June and September and lower in December compared to March (Fig. 7.7, Table J.2). For the Pacific oyster *M. gigas*, and the blue mussel *M. edulis*, the intercept of this relationship was higher in June and September and similar in December as in March (Fig. 7.7, Table J.2). For the soft-shell clam *M. arenaria*, the intercept was higher in September compared to March and June (Fig. 7.7, Table J.2). The slope of these relationship was not significant for *L. balthica* (Fig. 7.7, Table J.2).

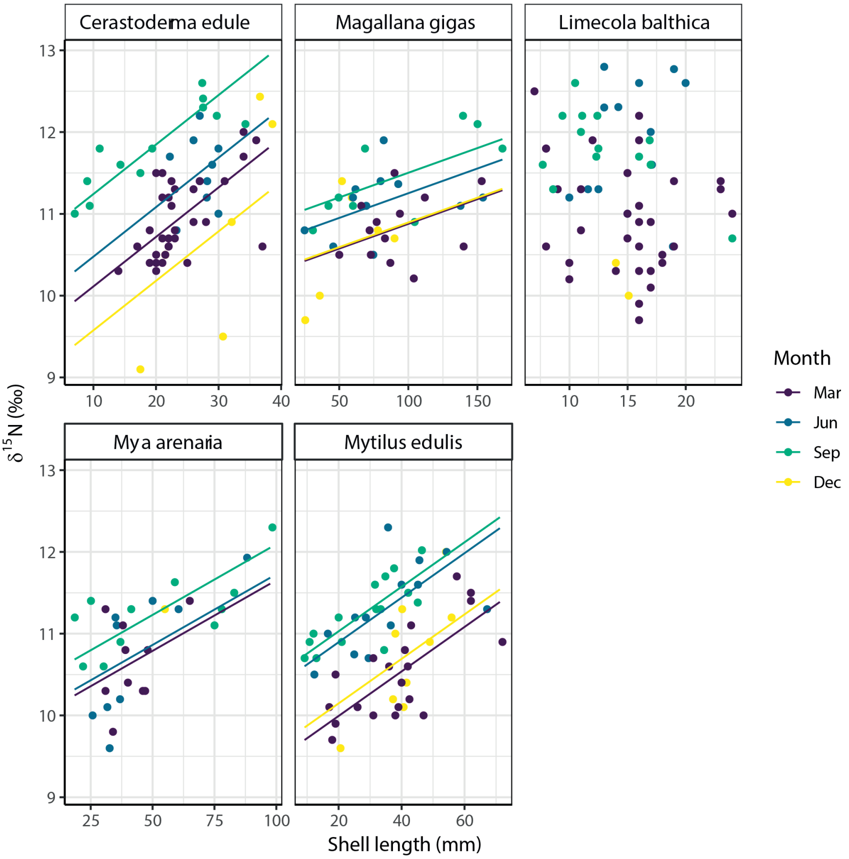

Figure 7.7: Relationships between the $\delta^{15}N$ signals and shell length of estuarine bivalves at the Balgzand tidal flats in March, June, September and December 2014. Significant linear relationships ($p < 0.05$) are plotted as solid lines (see Appendix for significance of these relationships).

7.3.5 *Seasonality in trophic niche overlap within estuarine bivalve species*

On average, the SEA_c (Standard Ellipse Area corrected for small sample sizes) was highest for the Baltic tellin (*L. balthica*) and relatively low for the Pacific oyster (*M. gigas*), implying that the isotopic niche of the Baltic tellin was much wider (more than three times) throughout the year than that of the Pacific oyster (Fig. 7.8, Table 7.3). For *Cerastoderma edule*, the maximum isotopic niche (SEA_c) in December hardly overlapped (< 40%) the niches in March, June and September, whilst the smallest isotopic niche in June fell mostly ($\geq$ 75%) within those of March and September (Fig. 7.8, Table 7.3). For *L. balthica*, the relatively large isotopic niches (SEA_c) in the different months only partly overlapped each other, i.e. an overlap between March and June of less than 40% and an overlap between March and September of less than 35%, with June having the largest overlap (>60%) with September (Fig. 7.8, Table 7.3). For *M. gigas*, the relatively large isotopic niche (SEA_c) in March comprised most of the niches in June (90%), September (58%) and December (60%), but overlap between the isotopic niches of these latter three months was relatively small, i.e. between 17% and 45% (Fig. 7.8, Table 7.3). For *M. arenaria*, the largest isotopic niches in March partly overlapped the ones in June (< 70%) and September (< 65%), the overlap between June and September was less than 50% (Fig. 7.8, Table 7.3). Also for *M. edulis*, the largest isotopic niche in March partly overlapped that of the other months (> 70%), whilst the smallest isotopic niche in September fell largely (> 80%) within those of March, June and December (Fig. 7.8, Table 7.3).

7.3.6 *Seasonality in trophic niche overlap*

In March, the relatively large isotopic niche of *L. balthica* comprised only part of the niches of the others ranging from 59% for *M. arenaria* to 24% for *M. gigas* (Fig. 7.9, Table 7.4).

In June, the sizes and overlaps in isotopic niches appeared to be smaller than in March, with the smallest overlap being between that of *L. balthica* with all other estuarine bivalves, e.g. 0% for *C. edule*, *M. gigas* and *M. arenaria*, 1% for *M. edulis* and 8% for *S. plana* (Fig. 7.9, Table 7.4).

In September, the overlap of the relatively large isotopic niche of *L. balthica* with all other estuarine bivalves was still relatively small, e.g. 0% for *M. gigas*, 1% for *M. edulis*, 15% for *M. arenaria* and 25% for *C. edule* (Fig. 7.9, Table 7.4).

In December, there was no overlap between the isotopic niches of *C. edule* and *M. gigas*, whilst the isotopic niche of *M. edulis* partly overlaps with these two species (Fig. 7.9, Table 7.4).

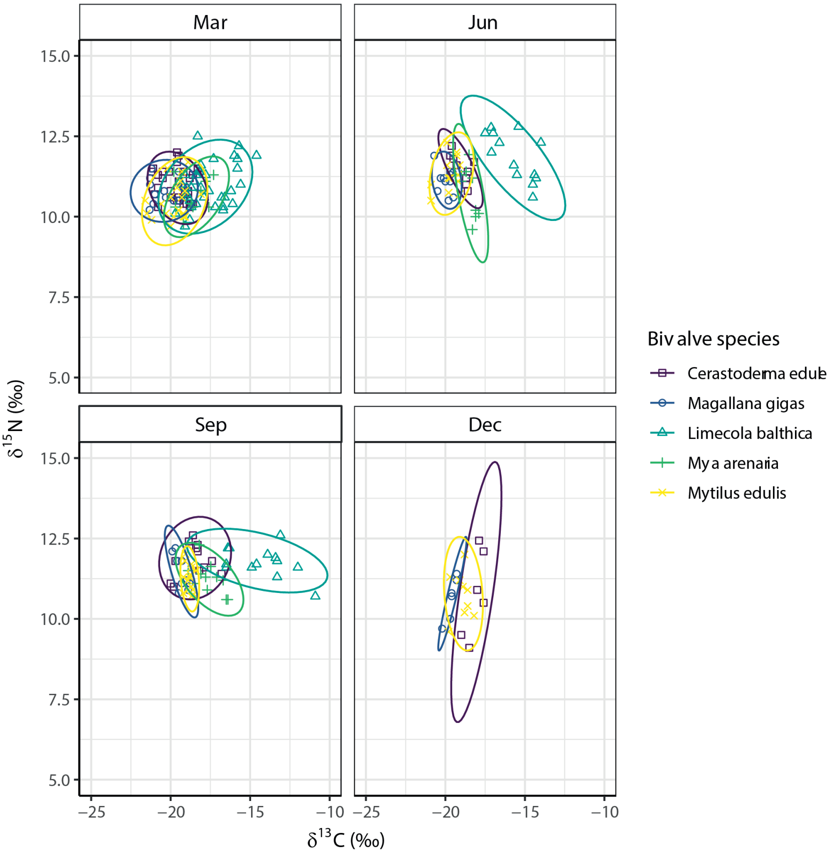

Figure 7.8: Seasonal variation in isotopic niche overlap between estuarine bivalve species at the Balgzand tidal flats in March, June, September and December 2014.

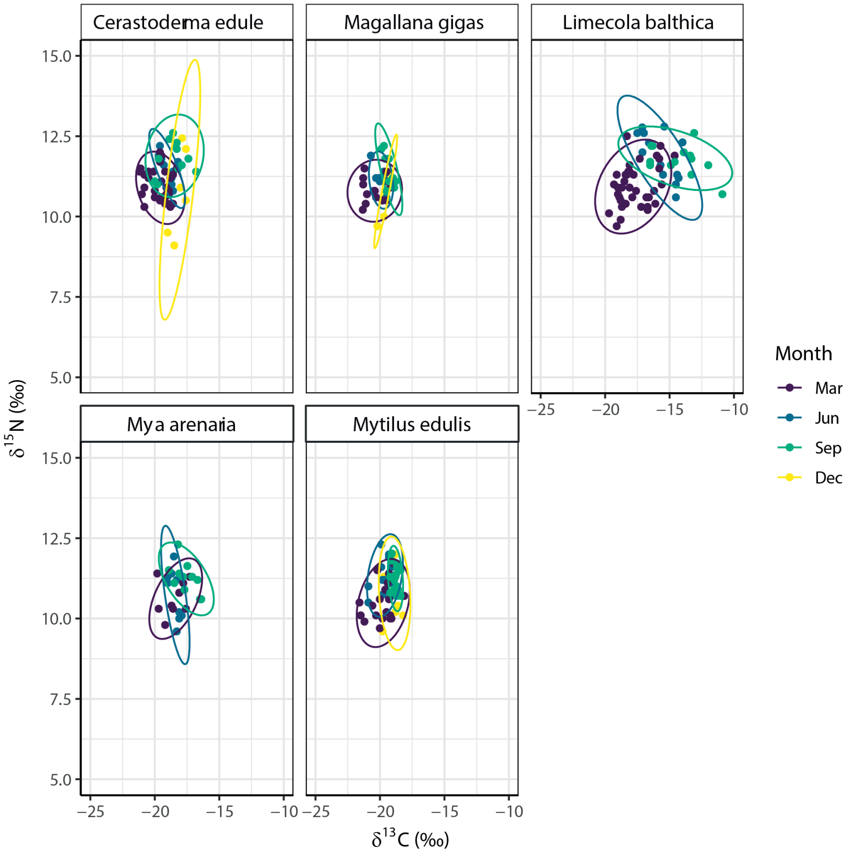

Figure 7.9: Seasonal variation in isotopic niche overlap within estuarine bivalve species at the Balgzand tidal flats in March, June, September and December 2014.

Table 7.3: Standard Ellipse Area corrected for small sample sizes (SEA_c, as δunits^2) and percent overlap of the SEA_c within estuarine bivalve species (%) as sampled in March, June, September and December 2014 at the Balgzand tidal flats.

Speciesname	Month	SEA_c	March	June	September	December
Cerastoderma edule	March	7.55		39	56	33
Cerastoderma edule	June	3.94	75		94	46
Cerastoderma edule	September	10.04	42	37		47
Cerastoderma edule	December	11.92	21	15	39	
Limecola balthica	March	15.32		37	34	
Limecola balthica	June	14.61	39		66	
Limecola balthica	September	15.24	34	63		
Magallana gigas	March	6.69		41	26	17
Magallana gigas	June	3.06	90		39	28
Magallana gigas	September	3.05	58	40		25
Magallana gigas	December	1.92	60	45	39	
Mya arenaria	March	9.11		39	47	
Mya arenaria	June	5.13	69		49	
Mya arenaria	September	6.79	63	37		
Mytilus edulis	March	9.76		47	19	60
Mytilus edulis	June	6.37	73		26	66
Mytilus edulis	September	2.08	88	81		100
Mytilus edulis	December	8.21	71	51	25	

Table 7.4: Standard Ellipse Area corrected for small sample sizes (SEA_c, as δunits^2) and percent overlap of the SEAc between estuarine bivalve species (%) as sampled in March, June, September and December 2014 at the Balgzand tidal flats.

March	SEA_c	*Cerastoderma edule*	*Limecola balthica*	*Magallana gigas*	*Mya arenaria*	*Mytilus edulis*
Cerastoderma edule	7.55		73	67	66	87
Limecola balthica	15.32	36		24	59	42
Magallana gigas	6.69	76	54		48	81
Mya arenaria	9.11	54	99	35		65
Mytilus edulis	9.76	67	66	56	61	

June	SEA_c	*Cerastoderma edule*	*Limecola balthica*	*Magallana gigas*	*Mya arenaria*	*Mytilus edulis*
Cerastoderma edule	3.94		0	24	67	74
Limecola balthica	14.61	0		0	0	1
Magallana gigas	3.06	31	0		11	99
Mya arenaria	5.13	51	1	7		43
Mytilus edulis	6.37	46	2	48	35	

September	SEA_c	*Cerastoderma edule*	*Limecola balthica*	*Magallana gigas*	*Mya arenaria*	*Mytilus edulis*
Cerastoderma edule	10.04		38	26	44	19
Limecola balthica	15.24	25		0	15	1
Magallana gigas	3.05	87	0		37	47
Mya arenaria	6.79	66	33	17		22
Mytilus edulis	2.08	91	9	68	73	

December	SEA_c	*Cerastoderma edule*	*Magallana gigas*	*Mytilus edulis*
Cerastoderma edule	11.92		0	39
Magallana gigas	1.92	0		82
Mytilus edulis	8.21	56	19	

7.4 DISCUSSION

7.4.1 *Food availability*

At the Balgzand tidal flats, the highest availabilities of the three primary food sources occured at different times of the year. Marine phytoplankton had the highest availability in the spring, microphytobenthos peaked in summer, while freshwater phytoplankton had peak values in the autumn. In general, highest values of freshwater that enter this system are found in winter (up to 3000 $m^3\,s^{-1}$) and lowest in summer with no water supply at all on some days (Gräwe et al., 2016). In 2014, the general supply of freshwater algae to the Wadden Sea was highest in autumn as a result of a combination of high freshwater discharge and the highest chlorophyll a concentration in Lake IJssel and lowest in April, mostly due to low levels of water discharge in that month.

Since several unicellular freshwater algal species can be cultured in media consisting up to 60% seawater for 96 hours (Wetherell, 1961), at least part of the freshwater phytoplankton should be able to survive in brackish waters for at least several days. Also the dead organic matter (detritus) can be a valuable food source for estuarine bivalves (Canuel et al., 1995; Peterson, 1999; Antonio et al., 2010; Bishop et al., 2017). Because the local availability of these resources might also vary in time (e.g. tides, seasons) and space (e.g. as the result of sinking and resuspension), diet studies of estuarine bivalves by means of stable isotope analyses should include all potential resources (including freshwater SPOM) during the growing period. Sampling should then preferably be done close to the sediment within the full tidal window when bivalves have direct access to their food.

Ideally the isotopic signal of pure phytoplankton samples would be the best solution to exclude the effect of other particulate matter on the signal. However, this type of sampling is time consuming and might not be a realistic approach. An alternative would be the analysis of compound specific isotopic composition e.g. amino acids (McClelland and Montoya, 2002) or the inclusion of sulfur as an additional isotope to distinguish the influence of freshwater material (MacAvoy et al., 1998; Fry, 2006).

However, several of the averages of food sources in this study (all freshwater SPOM and microphytobenthos in December) were based upon single observations, leading to some uncertainties regarding the stable isotope values of the sources. Also within the mixing model correlations of up to 0.97 between two food sources were found. Such large correlations indicated that the model cannot discern between the two sources, which means that if one source is being consumed at the top of its probability range, then the other is likely to be at the bottom of its probability range, and vice versa (Phillips et al., 2014).

7.4.2 *Seasonal variation in diet*

During this study, two species (*Abra tenuis*, *Scrobicularia plana*) and one period (December) were undersampled and are, therefore, not further considered. In March, June and September 2014, the obligate suspension-feeding bivalves (*Cerastoderma edule*, *Magallana gigas*, *Mya arenaria* and *Mytilus edulis*) appeared to have predominantly utilized freshwater SPOM as their main food source. Only *Limecola balthica*, a bivalve species that can switch between deposit- and suspension-feeding (Bradfield and Newell, 1961; Hummel, 1985), appeared to have fed mainly on estuarine SPOM during spring. In June and September 2014, this Baltic tellin appears to have preferred microphytobenthos, most probably gathered by means of deposit-feeding.

It should be noted, however, that most correlations between food sources were high, indicating that the models could not discern very well between these resources (Phillips et al., 2014). These outcomes are, nevertheless, in concordance with previous findings that freshwater SPOM can be an important food source for estuarine obligate suspension-feeding bivalves (Canuel et al., 1995; Peterson, 1999; Antonio et al., 2010; Bishop et al., 2017) and that main food sources of estuarine facultative deposit-feeding bivalves can vary within the year (Zwarts and Wanink, 1989).

The results of the mixing model are also highly depending on the trophic discrimination factor. Within this study we used values that were measured by Dubois et al. (2007) because these values were based upon a feeding experiment on two estuarine bivalve species also included in our research (*M. gigas* and *M. edulis*). These values differ from the average values reported in literature (Fry, 2006); for $\delta^{13}C$ we used 2 ‰ instead of 1 ‰ and for $\delta^{15}N$ we used 3.78 ‰ instead of 2.2 to 3.4 ‰. Additional analyses (not shown here) with these lower trophic discrimination factors resulted in changes in the probabilities of the three food sources (up to 25-30 %)in the diet of the bivalves. Using other values for trophic discrimination factors did, however, not change our main conclusion that all species feed on a mixture of different sources and that the freshwater SPOM is a relevant part of their diet.

7.4.3 *Ontogenic variation in diet*

The significant correlation of the $\delta^{13}C$ (*C. edule*, *L. balthica*, *M. arenaria* and *M. edulis*) and the increase of the $\delta^{15}N$ signal (*C. edule*, *M. gigas*, *M. arenaria* and *M. edulis*) signals with shell length suggests that the diet of these estuarine bivalves varies through life-cycle stages. This might be due to gradual shifts in their feeding behaviour in life, to different access to various food sources with size and/or to different timing in growing seasons with age. As was observed for edible cockles (*C. edule*) in the Gironde estuary (Sauriau and Kang, 2000), for example, seasonal variation in the availability of food resources combined with non-synchronous growing seasons of juvenile and adult bivalves (spring versus summer) might lead to shifts in main diets with size. In general, relationships between isotopic signals and size might also be explained by differences in growth rates, with juveniles generally growing faster than adults (Gorokhova, 2018). Additional to ontogenetic shifts in bivalves also shifts in the $\delta^{15}N$ baseline are a possible explanation of the observed changes here. The small shift in $\delta^{15}N$ between the March and December values and the slightly higher values during summer months, June and September could be due to a change in food web complexity and an increase in trophic level for most sampled organisms. However, it could also be an indication that the baseline $\delta^{15}N$ values shifted a little from the winter to the summer situation. Based on the data presented here, this is all very speculative, but this question definitely deserves some further attention.

The negative relationship between the $\delta^{13}C$ signal and shell length in combination with the ranges observed for these species indicates that, on average, the diet of *L. balthica* shifted from microphytobenthos to estuarine SPOM when growing from 5 to 25 mm shell length and that of *M. arenaria* from estuarine SPOM to freshwater SPOM when growing from 25 to 100 mm shell length. For Baltic tellins (*L. balthica*), this ontogenic change is in line with observations for the Scheldt estuary where small juveniles were feeding mostly on microphytobenthos, while larger sized bivalves tended to feed more and more on estuarine phytoplankton (Rossi et al., 2004). The shift in the soft-shelled clam *M. arenaria* might be due to thresholds for feeding behaviour as determined by low food concentrations (Riisgård et al., 2003). If the threshold where this species stops feeding increases with its size, then this bivalve might prefer to feed more and more during food-rich waters caused by discharge outflows during its life time.

The positive relationship between the $\delta^{13}C$ signal and shell length in combination with the ranges observed for the blue mussel *M. edulis* indicates that, on average, this species shifted from a relatively higher proportion of estuarine SPOM compared to freshwater SPOM in its diet when growing from 10 to 70 mm shell length. Mussels frequently change position and orientation during their life time (e.g. Butman et al., 1994). If small mussels settle, on average, at the top of a mussel bed and then gradually move down to lower locations as new mussels and oysters settle on top of them, they would get less and less access to the relatively light freshwater (containing freshwater SPOM) and more and more to the denser saline waters (containing marine SPOM).

Estuarine bivalves such as *C. edule* and *M. edulis* were found to ingest a wide range of zooplankton species, including bivalve larvae, selectively consuming smaller categories of zooplankton present (Lehane and Davenport, 2002). If the threshold of edible zooplankton increases with shell size, then it is expected that the proportion of primary consumers increases during the life time of bivalves. Such an increase would then be reflected by a significant increase of the $\delta^{15}N$ signal with shell length as was observed for *C. edule*, *M. gigas*, *M. arenaria* and *M. edulis*.

7.4.4 *Interspecific competition for food*

Within the estuarine bivalve community, the interspecific niche overlap was highest in March. This seasonal variation in niche overlap was partly due to the variation in species-specific niche breadths. Such seasonal variation might indicate that the bivalves were relying on a wider array of resources in March than in June, but also that the bivalves were more food-limited in spring than in summer (Gorokhova, 2018).

Although food limitation is not very likely because the relatively high niche breadth is mainly found within the obligate suspension-feeders during the phytoplankton spring bloom, this possible cause cannot be excluded. More probable, the bivalves took advantage of the high availability of the same food source at that time. Interspecific competition for food was more likely to occur during summer, when marine phytoplankton densities were low as the result of low nutrient concentrations and the supply of freshwater phytoplankton was low due to low inflows from Lake IJssel. During that time, microphytobenthos is probably the main potential food source for estuarine bivalves, which is in line with the findings by Christianen et al. (2017). For obligate suspension-feeding bivalves, their food source might only come available during high wind speeds when benthic algae are resuspended into the water column (de Jonge and van Beusekom, 1992).

7.4.5 *Conclusions*

Our results indicate that freshwater algae may contribute to the food supply of estuarine bivalves in the study area, and that diets of bivalves vary with season and shell length. Although not all parts of the Wadden Sea receive as much freshwater import as the western Wadden Sea, the estuaries of large rivers such as Ems, Elbe and Weser show comparable freshwater inflows (Gräwe et al., 2016). Diet studies should evaluate all food sources utilized by temperate estuarine bivalves and sampling should include all possible resources and be in close proximity to the feeding space of these bivalves.

7.5 ACKNOWLEDGMENTS

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8

IMPACTS OF THE INVASIONS OF THE MACROZOOBENTHOS ON FOOD WEB DYNAMICS OF THE WESTERN DUTCH WADDEN SEA

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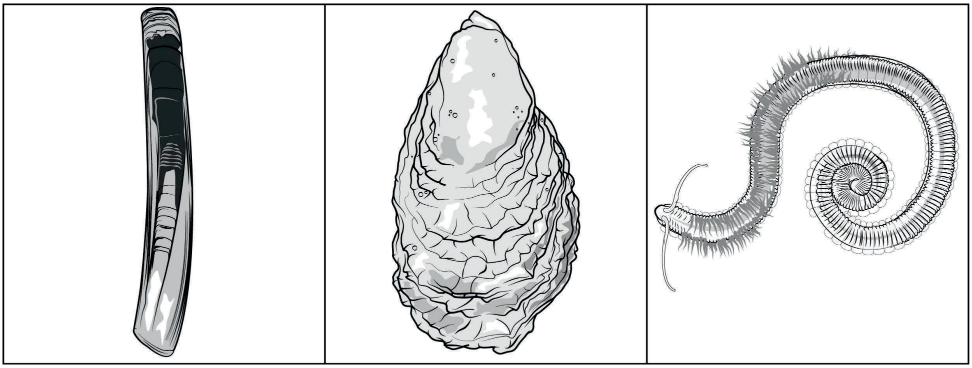


ABSTRACT

Invasions of marine species are changing coastal food webs worldwide, impacting on trophic interactions between native species (e.g. predator-prey relationships). Here, the impact of three macrozoobenthic invasive species on food web structure and functioning at Balgzand (western Wadden Sea) is quantified by using Ecological Network Analysis (ENA). The bivalves *Ensis leei* and *Magallana gigas* were observed for the first time in 1984 and 2001, respectively, and the polychaete *Marenzelleria viridis* appeared in 1989. Although *E. leei* and *M. viridis* reached similar peak biomasses in the 2000s (ca. 1700 and 2000 $\mathrm{mg\,C\,m^{-2}}$, respectively), the bivalve consumption was higher (>45% of total consumption) than that of the polychaete (<10%). Biomass and impact of *M. gigas* remained relatively low. *E. leei* occupied an ecological niche that was partially empty, which led to competitive advantage with respect to other suspension feeders. Increasing biomass of *E. leei* coincided with a 70% increase of trophic carbon transfer from primary to secondary producers and an 80% increase from secondary producers to detritus. Carbon flows from secondary producers to higher trophic levels were reduced by more than 60%. These shifts in trophic transfer were stronger than those observed during the invasion of *M. gigas* in the NE Wadden Sea. At Balgzand, biomass of *M. gigas* and *M. viridis*, rapidly declined to low values in the 2010s, implying a temporally limited impact. In the 2010s, *E. leei* was still responsible for 30% of the total consumption in the 2010s, indicating a longer-term impact.

8.1 INTRODUCTION

Marine species invasions in coastal food webs are common all over the world and are changing coastal systems (Mack et al., 2000; Bax et al., 2003). These invasions often follow a specific pattern: after the introduction of one or more individuals a small population of fully reproductive individuals follows, after which the invading species gets established in its new environment. This may subsequently result in an exponential increase of the new local population, followed by a phase of adjustment with a reduction in abundance and biomass (e.g. Mack et al., 2000; Essink and Dekker, 2002; Reise et al., 2006, 2017). During the adjustment phase, the population may stabilize, strongly fluctuate or drop to negligible numbers (Reise et al., 2017). A decrease might be caused by sevreal factors: combination of predators of the invaded system getting accustomed to the new prey (the invasive species), an increased abundance of also invasive predators from the same system as the invaders, infections by bacteria, viruses and parasites, and changes in environmental conditions (temperature, salinity, etc.) (Ribera and Boudouresque, 1995; Essink and Dekker, 2002).

During this process of increase and establishment, the invasive species can change local species distribution, amongst others due to competition for space and food, facilitation, predation and parasitism (Mack et al., 2000; Rodriguez, 2006), and disruption of ecosystem processes such as trophic interactions (Molnar et al., 2008). Three major factors have been identified to be most important with respect to these impacts. The first factor is how well adapted an invader is to the environmental and biological conditions in the new system. A better adapted species would have a higher impact (Ruesink, 2018). The second factor is the number of individuals that have invaded the system as well as their origin, as a broader genetic base can increase the success of an invader (Ruesink, 2018). This means that a higher number of individuals or individuals of many different origins bring a broader genetic pool increasing their ability to adjust to many different environmental conditions. The third factor that influences the impact of invasive species is whether the invader plays a so far unknown role in the system or inhabits an ecological or trophic niche that is already occupied by a native species (Ricciardi et al., 2013). Assessing the effect of an invasive species on the ecosystem requires a reference situation that provides the relevant knowledge about the situation before the invasion (Blossey, 1999).

The Wadden Sea, a large tidal flat system bordering the coastlines of the Netherlands, Germany and Denmark, which is listed as a World Heritage Site, has been invaded by at least 90 nonnative (alien) species over the last century (Wolff, 2005; Buschbaum et al., 2012; Gittenberger et al., 2017). Approximately 12 % of the invasive marine-brackish macrozoobenthic species were deliberately introduced, all others spread secondarily from adjacent coasts with more active harbours or shellfish cultures (Wolff, 2005; Buschbaum et al., 2012). Recent successful invasive and presently established species include the epibenthic crabs *Hemigrapsus takanoi* and *H. sanguineus*, the parasitic copepod *Mytilicola orientalis* and the pelagic comb jelly *Mnemiopsis leidyi* (Boersma et al., 2007; Buschbaum et al., 2012). Strong invasions by the bivalve *Ensis leei*, the polychaete *Marenzelleria viridis*, and the bivalve *Magallana gigas* have been witnessed within the tidal flats systems of the western Dutch Wadden Sea. These species are expected to have a strong impact on local food web dynamics because substantial populations have developed within the western Dutch Wadden Sea ecosystem (e.g. Essink and Dekker, 2002; Reise et al., 2017).

The American razor clam (*E. leei*; formerly known as *E. directus*; Beukema and Dekker, 2011) was first detected on the Balgzand intertidal in the western Dutch Wadden Sea in 1984 and remained in relative low biomass in the area until a rapid increase started in 2005 followed by a peak in 2008 after which the biomass decreased again. It was considered to be a strong invader due to its long lifespan (von Cosel, 2009) and biannual recruitment (Cardoso et al., 2009). Most importantly, because of its high motility it was able to fill in the so far unoccupied lower edges of the tidal flats where currents were too strong for native species to settle (Dekker and Beukema, 2012).

In the same tidal flat system (Balgzand) the polychaete *M. viridis* (formerly also known as *M. cf. wireni*; Essink and Dekker, 2002) was first found in 1989, showing a consistent increase from 1993 (although really low in the first few years) to a maximum in 2003, after which it decreased again. It may be able to outcompete other benthic fauna that feed on surface deposits of material from primary production (Neideman et al., 2003) because of its high fecundity and its relatively long life span (Zettler, 1997) plus its high tolerance for low oxygen conditions, which allows it to live in deeper sediments then other species on the tidal flats (Bochert et al., 1997; Daunys et al., 2000).

A third invader, the Pacific oyster (*M. gigas*; formerly known as *Crassostrea gigas*; Beukema and Dekker, 2011), was first found on the Balgzand in 2001. Its biomass started to increase exponentially in 2005, peaked in 2008 and then declined again. Pacific oysters are suspension-feeding bivalves which construct reefs on the mudflats and which feed predominantly on phytoplankton. Due to their strong filtering capacity (Smaal et al., 2005; Wheat and Ruesink, 2013) combined with a long lifespan (Cardoso, 2007), fast maturation (Kobayashi et al., 1997) and high fecundity (Helm, 2004), it was feared that they might outcompete the native reef-forming blue mussels for food and space (Fey et al., 2010).

In this paper, we analyse the impact of the bivalves *E. leei* and *M. gigas* and the polychaete *M. viridis* on the food web dynamics of the Balgzand system, located in the western part of the Dutch Wadden Sea. Based on the availability of time series and the observed invasive development of these three species, we compared the carbon flows and several Ecological Network Analysis (ENA)-based indices of the Balgzand food web for four decades, i.e. the 1980s, 1990s, 2000s and 2010s. These periods roughly coincided with different phases of the invasion being, Phase I with no to low biomass, Phase II with low to increasing biomass, Phase III with exponential increase of biomass, and Phase IV with biomass decrease after the peak. We explore if, (and if so, to what extent) the high biomass of the invaders affected the absolute and relative carbon flows in the system compared to the situation when the biomass of these three species was still relatively low.

Carbon flows of the system are analysed by means of Ecological Network Analysis (ENA; Ulanowicz, 1986, 2004; Fath et al., 2007). ENA allows for an investigation of the carbon flows within a local food web (trophic interactions, including grazing and predation) and the exchange of carbon with the environment (import, respiration, and export) in a systematic way. The various flows can subsequently be used to calculate so-called network metrics and other descriptors of the food web for comparison of the carbon budgets in the 1980s, 1990s, 2000s and 2010s and for comparison with other ENA studies on invasions.

Ecological Network Analysis was previously applied to study the impacts of the invasion of the zebra mussel *Dreissena polymorpha* in Oneida Lake (USA) and in the Bay of Quinte (Canada) (Miehls et al., 2009*a*,*b*) and of the Pacific oyster *M. gigas* in the Sylt-Rømø Bight in the northeastern Wadden Sea (Baird et al., 2012). During their peak, their biomass contributions ranged from 25% (Pacific oyster) to 89% (zebra mussel) of the total living biomass (Miehls et al., 2009*a*; Baird et al., 2012). As a result of their high consumption rates and low predation, the invasions by these suspension-feeding bivalves resulted in enhanced carbon flows from primary to secondary producers, and in reduced carbon flows to higher trophic levels (Miehls et al., 2009*a*,*b*; Baird et al., 2012). In this study, we test whether such shifts in trophic transfer also occurred during the invasions in the Balgzand food web.

8.2 MATERIAL AND METHODS

8.2.1 *Study area*

The Balgzand area, covering approx. 50 km^2 of intertidal area and 10 km^2 of subtidal area, represents ~8 % of the Marsdiep tidal basin in the western Dutch Wadden Sea (Fig. 8.1; Table 8.1). This study only considers the intertidal area including the channel edges, because the available long-term studies are mainly located in the intertidal areas. The southwestern part of the Balgzand has a higher elevation (+ 20 cm with respect to mean sea level or MSL) and is more silty (> 10 % silt) than the northwestern part, which is situated well below MSL with a silt content of ~2 % (Beukema, 1988). The central and eastern part of the Balgzand is a mixture of these two extremes (Beukema and Cadée, 1997). Mean tidal range is about 1.40 m (roughly -80 to 60 cm to MSL, Beukema and Cadée, 1997). During each tidal cycle, the tidal flats are exposed for 2-4 hours and are submerged for 8-10 hours (de Vlas, 1979) and at high water, mean water depth varies between a few dm up to 1.4 m (Postma, 1982).

Table 8.1: Geomorphology of the Balgzand tidal flat area and the Marsdiep tidal basin.

Characteristic	Balgzand	Marsdiep	Unit
Volume	30	2900	10^6 m^3
Surface area	50	630	10^6 m^2
Average depth	0.67	4.6	m

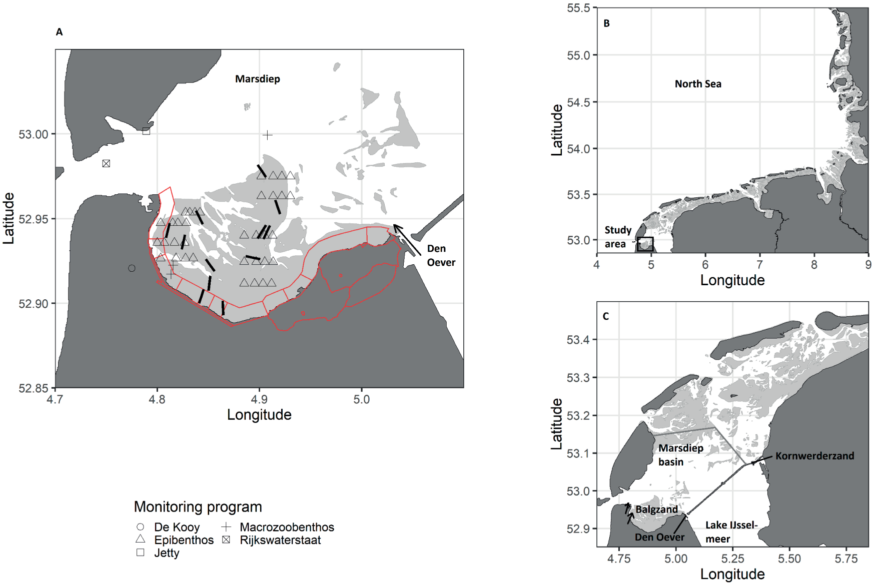


Figure 8.1: (A) Map of the Balgzand, with the red lines indicating the borders of the areas for the bird counting by Sovon (`www.sovon.nl`), the open circle the closest weather station (De Kooy), the black lines and crosses the sampling transects and stations for the macrozoobenthic sampling program by NIOZ (`www.nioz.nl`), the triangles the stations for epibenthic sampling by NIOZ, the square with a cross the station for water quality ("Marsdiep Noord") by RWS (`rijkswaterstaat.nl`) and the square the station for water quality ("Jetty") by NIOZ; (B) The trilateral Wadden Sea; (C) The western Dutch Wadden Sea, with the arrows indicating the locations of the two freshwater discharge sluices close to the Balgzand with "Helsdeur" up north and "Het Kuitje" (also known as "Oostoever" down south.

The macrozoobenthos shows different compositions within these subareas. The southwest is generally characterized by a low diversity and absence of dominating species in terms of biomass. In the central, eastern and north-western part of the Balgzand, suspension-feeding bivalves (viz. *Cerastoderma edule*, *Mytilus edulis* and *Mya arenaria*) as well as the lugworm *Arenicola marina* (Beukema, 1988; Beukema and Cadée, 1997) are dominating with respect to biomass. At present, there are only a few local aggregations of mussels in the intertidal area of the Balgzand (Folmer et al., 2014) and seagrass beds do not occur.

The Balgzand area is under the influence of freshwater discharges from small discharge points at the borders of the Balgzand tidal flat system, e.g. via the "Helsdeur" and "Het Kuitje" (also known as "Oostoever") and from the eastern (Kornwerderzand) and western (Den Oever) sluices of Lake IJssel (Fig. 8.1). The average freshwater discharge via the "Helsdeur" and "Het Kuitje" is relatively low, in total on average $18\,\mathrm{m^3\,s^{-1}}$ (Postma, 1982), compared to approximately $400\,\mathrm{m^3\,s^{-1}}$ (with maximum values up to $3000\,\mathrm{m^3\,s^{-1}}$ in winter) via the sluices of Lake IJssel (van Aken, 2008*a*). Recent hydrodynamic model studies suggested that most of the freshwater entering the westernmost part of the Dutch Wadden Sea via Den Oever is transported over the Balgzand area before leaving the Wadden Sea through the Marsdiep tidal inlet (Duran-Matute et al., 2014). Furthermore, freshwater runoffs from the rivers Scheldt, Meuse and Rhine enter the Marsdiep tidal inlet via the North Sea coastal zone (Postma, 1950; Ridderinkhof et al., 1990; Gräwe et al., 2016). Salinity within the Marsdiep basin is highly variable and ranges between 0 PSU in front of the discharge sluices of Lake IJssel to 32 PSU in the Marsdiep tidal inlet during periods of low freshwater input (van Aken, 2008*a*). Mixing between the water of the Balgzand area and the rest of the tidal basin is strong, with a local flushing time of the Balgzand water mass in the order of approximately three tidal periods (Zimmerman, 1978).

8.2.2 *Ecological network analysis (ENA)*

Model construction

Ecological network analysis (ENA) started with a carbon-based reconstruction of flows within the ecosystem of the Balgzand area for all study periods separately, based upon species composition and biomass and diet matrices for all species. If period-specific and/or site-specific data were not available, then estimates from other periods, other areas or from more generic relationships derived from literature were used. Assuming a steady state within each period, the constructed carbon flow matrices were closed by balancing the inputs and outputs. Four carbon flow networks were constructed, one for each decade (1980s, 1990s, 2000s and 2010s). These four networks consisted of living compartments, with some compartments representing a specific species whilst others comprise functional groups (e.g. phytoplankton and zooplankton) and three non-living compartments susPOC (suspended particulate organic carbon), sedPOC (sediment particulate organic carbon) and DOC (dissolved organic carbon). The first two networks (BZ1980s, BZ1990s) comprised a total of 54 living compartments, including the invasive macrozoobenthic species *Ensis leei* and *Marenzelleria viridis*. The other two networks (BZ2000s, BZ2010s) consisted of 55 living compartments, since they also include the invasive Pacific oyster *Magallana gigas* (Table 8.2).

The analysis was done using R version 3.5.1 (R Core Team, 2018). A full description of the applied enaR package (v. 3.2.3) along with complementary scripts (Schückel unpubl.) can be found in Borrett and Lau (2014); Lau et al. (2017).

Parameter inputs

Carbon budgets of each of the living compartments were constructed using decadal mean biomass data and mean conversion factors to calculate uptake and dissipation (or respiration), growth, and egestion (in the case of heterotrophs) rates. All biomasses or standing stocks of all compartments were measured as (or converted to) $\mathrm{mg\,C\,m^{-2}}$ and all flows were expressed in terms of $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$. Missing data and information were collected from other sources (Table 8.3, see

Table 8.2: Mean biomass (mg C m^{-2}) per compartment per decade as used in the four respective networks (BZ1980s, BZ1990s, BZ2000s and BZ2010s). Sources and conversions are described in Appendix K, POC = Particulate Organic Carbon, DOC = Dissolved Organic Carbon.

Compartment nr			BIOMASS (mg C m^{-2})			
1980/ 1990	2000/ 2010	Compartment name	BZ1980s	BZ1990s	BZ2000s	BZ2010s
1	1	Phytoplankton	226.429	225.184	205.207	162.931
2	2	Microphytobenthos	5848.941	6964.981	8114.84	7679.415
3	3	Freshwater algae	388.036	384.935	330.21	335.41
4	4	Pelagic Bacteria	35.344	35.226	31.805	26.447
5	5	Zooplankton	13.937	17.804	21.019	20.182
6	6	Benthic Bacteria	1000	1000	1000	1000
7	7	Meiofauna	375.23	136.161	125.524	123.076
8	8	*Peringia ulvae*	352.292	530.41	555.35	1509.334
9	9	*Littorina littorea*	38.309	24.405	90.985	165.435
10	10	*Arenicola marina*	2988.212	2840.997	2322.123	2447.194
11	11	*Eteone sp*	13.363	20.277	30.839	28.256
12	12	*Hediste diversicolor*	1029.042	1433.284	1544.378	1328.094
13	13	*Nereis spp.*	38.743	102.439	261.886	282.257
14	14	*Heteromastus filiformis*	747.034	1091.92	1483.263	436.179
15	15	*Lanice conchilega*	147.455	385.344	496.445	98.629
16	16	*Marenzelleria viridis*	0.174	348.992	1709.799	186.634
17	17	*Nephtys hombergii*	131.846	162.609	163.45	71.978
18	18	*Scoloplos armiger*	251.679	196.313	177.028	220.932
19	19	*Corophium spp.*	317.887	64.999	141.357	217.104
20	20	*Gammarus spp.*	1.392	1.927	2.053	2.001
21	21	*Cerastoderma edule*	2591.144	3058.694	1910.172	3410.439
	22	*Magallana gigas*	-	-	369.068	355.704
22	23	*Ensis leei*	7.528	209.27	1992.793	891.624
23	24	*Limecola balthica*	2185.742	1715.895	407.009	469.065
24	25	*Mya arenaria*	4481.915	5354.189	7962.46	3711.787
25	26	*Mytilus edulis*	1340.479	1291.409	968.24	971.2
26	27	*Scrobicularia plana*	170.387	214.565	109.672	127.89
27	28	*Carcinus maenas*	7.844	9.161	14.719	41.611
28	29	*Crangon crangon*	90.709	114.421	129.925	207.319
29	30	*Ammodytes tobianus*	0.261	0.415	0.458	0.381
30	31	*Clupea harengus*	0.799	2.146	4.214	1.451
31	32	*Myoxocephalus scorpius*	0.091	0.027	0.007	0.134
32	33	*Osmerus eperlanus*	0.818	0.282	0.306	0.549
33	34	*Platichthys flesus*	23.56	9.177	4.237	1.953
34	35	*Pleuronectes platessa*	335.733	7.398	4.281	4.231
35	36	*Pomatoschistus microps*	0.945	7.548	9.588	40.303
36	37	*Pomatoschistus minutus*	3.591	10.668	8.389	16.428
37	38	*Solea solea*	1.238	0.451	0.432	0.132
38	39	*Syngnathus rostellatus*	0.135	0.211	0.238	1.848
39	40	*Zoarces viviparus*	0.932	0.1	0.089	0.112
40	41	*Anas acuta*	1.003	1.743	4.269	4.81
41	42	*Anas platyrhynchos*	2.691	4.255	5.198	2.049
42	43	*Calidris alpina*	1.415	2.916	3.459	4.059
43	44	*Calidris canutus*	5.481	5.608	2.724	3.564
44	45	*Haematopus ostralegus*	32.439	31.489	22.199	21.233
45	46	*Larus argentatus*	6.74	6.337	2.413	1.659
46	47	*Larus canus*	0.573	0.86	1.391	2.132
47	48	*Larus ridibundus*	3.881	4.286	4.293	4.484
48	49	*Limosa lapponica*	2.063	2.377	2.738	3.936
49	50	*Numenius arquata*	11.784	20.071	24.657	26.581
50	51	*Pluvialis apricaria*	0.333	1.481	1.079	0.706
51	52	*Recurvirostra avosetta*	0.696	1.127	0.848	0.574
52	53	*Somateria mollissima*	6.036	8.995	3.291	2.554
53	54	*Tadorna tadorna*	14.457	17.549	17.428	22.129
54	55	*Tringa totanus*	0.834	1.003	1.311	0.982
55	56	DOC	2042.9	1913.971	1748.554	1833.979
56	57	Sediment POC	39060	39060	39060	39060
57	58	Suspended POC	4348.671	1333.635	2122.98	2382.705

Appendix K for a detailed description on data sources and data handling). Resulting data on uptake, dissipation, respiration, growth, and egestion rates are supplied in Appendix L, the applied ratios can be found in Appendix M.

Table 8.3: Overview of the biomass (Bio; mg C m^{-2}) of various components used as input for the Balgzand ENA (Ecological Network Analysis) models for the 1980s, 1990s, 2000s and 2010s. Type of SourceCodes (S) depict the types of sources of the values, with A referring to long-term annual field observations within that period, B to empirical relationships based upon local field observations, C to incidental field observations during that period, and D to assumptions from one period for the others. See Appendix K for more detail on data sources and calculations, and Table 8.2 for more detailed values for macrozoobenthos, epifauna and birds.

				1980s		**1990s**		**2000s**		**2010s**	
	Code	**Nr**		**Bio**	**S**	**Bio**	**S**	**Bio**	**S**	**Bio**	**S**
Microalgae	C_{PHYT}	1	Marine phytoplankton	226	A	225	A	205	A	163	A
	C_{FWTR}	1	Freshwater phytoplankton	388	A	385	A	330	A	335	A
	C_{MPB}	1	Microphytobenthos	5849	B	6965	B	8115	B	7679	B
Bacteria	C_{PBAC}	1	Pelagic bacteria	35	A	35	A	32	A	26	A
	C_{BBAC}	1	Benthic bacteria	1000	C	1000	D	1000	D	1000	D
Zooplankton	C_{ZOO}	1	Zooplankton	14	B	18	B	21	B	20	B
Benthic fauna	C_{MEIO}	1	Meiofauna	375	C	136	B	126	B	123	B
	$C_{MZBSPEC}$	20-21	Macrozoobenthos	16835	A	19048	A	22698	A	16932	A
	C_{EPI}	13	Epifauna	467	C	162	C	177	C	316	C
Birds	$C_{BIRDSPEC}$	15	Birds	90	A	110	A	97	A	101	A
Organic carbon	DOC	1	Dissolved OC	2043	B	1914	B	1749	B	1834	B
	susPOC	1	Suspended particulate OC	4349	B	1334	B	2123	B	2383	B
	sedPOC	1	Sediment particulate OC	39060	B	39060	B	39060	B	39060	B
SUM		58-59		**70731**		**70392**		**75733**		**69974**	

For all species considered, the diet was assumed to be stable over time. The main diet matrices were constructed based on Baird et al. (2004) under the assumption that the main food connections within the Wadden Sea did not differ among the various areas (Appendix N). Small changes in these diet matrices compared to Baird et al. (2004) were made based on regional prey selections for bivalves (Chapter 7), the shore crab *Carcinus maenas* (Baeta et al., 2006), the brown shrimp *Crangon crangon* (del Norte-Campos and Temming, 1994), fish (Kühl and Kuipers, 1978), and birds (Ens et al., 2016). Furthermore, the occurrence of the invasive *M. gigas* required additions in the diet matrix for the BZ2000s and BZ2010s compared to that for the BZ1980s and the BZ1990s, with respect to the diet of this bivalve and its sole predator *Haematopus ostralegus* (Appendix N).

Additional carbon fluxes originate from external sources (import of organic carbon to the Balgzand area through dissolved and particulate fluxes and by means of freshwater algae) and by internal hand-balancing of the flow matrix of the various compartments to achieve steady-state conditions (following de Jonge et al., 2019*b*,*a*). The external import of dissolved organic carbon (DOC; $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) mainly originates from Lake IJssel and was calculated by multiplying the concentrations in Lake IJssel ($\mathrm{mg\,DOC\,m^{-3}}$) by the freshwater discharge ($\mathrm{m^3\,d^{-1}}$) and the fraction of this discharge reaching the study area (unitless). This fraction (unitless) was calculated from the mean Balgzand salinity and the system's flushing time.

The import of suspended particulate organic carbon (susPOC; $\mathrm{mg\,POC\,m^{-2}\,d^{-1}}$) was assumed to be imported as and together with suspended sediment into the Marsdiep tidal basin (see Appendix K). The import of freshwater algae was assumed to originate only from freshwater discharge of Lake IJssel. For each study period, the average daily amount of freshwater exchanged between the Marsdiep and the Balgzand (FW_{ex}; $\mathrm{m^3\,m^{-2}\,d^{-1}}$) was calculated as:

$$FW_{ex} = (V * f)/(F * A)$$

where: V is the tidal-averaged water volume of the Balgzand tidal flat system ($30 \times 10^6\,\mathrm{m^3}$); f is the fraction of freshwater at the Balgzand (0.19 in the 1980s/1990s and 0.16 in the 2000s/2010s, respectively); F is the average flushing time of the Balgzand into the Marsdiep (1.625 days; Zimmerman (1978)); A is the total surface area of the Balgzand tidal system ($50\,\mathrm{km^2} = 50 \times 10^6\,\mathrm{m^2}$).

After conversion of chlorophyll-a concentrations of freshwater algae in Lake IJssel (Rijkswaterstaat data; `http://waterinfo.rws.nl/`) to carbon concentrations, the average daily import of carbon for each decade ($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) was calculated by multiplying the daily exchange of freshwater (FW_{ex}; $\mathrm{m^3\,m^{-2}\,d^{-1}}$) by the average concentration of freshwater algae in Lake IJssel ($\mathrm{mg\,C\,m^{-3}}$).

The unused carbon production of microphytobenthos and macrozoobenthic species (e.g. production not consumed by herbivores, predators and bacteria), together with the total carbon egestion by macrozoobenthos, birds and half the carbon egestion by the fish, were assigned to the benthic pool of particulate organic carbon ("sedPOC"). Unused carbon production of fish and birds was assumed to be exported from the system due to migration. The unused carbon production of marine phytoplankton, freshwater algae, pelagic bacteria, zooplankton and (the other) half of the carbon egestion of fish was assigned to the pelagic pool of particulate organic carbon ("susPOC").

The excess of the pelagic pool of particulate organic carbon ("susPOC") was assigned to benthic pool of particulate organic carbon ("sedPOC"). The excess of the pelagic pool of dissolved organic carbon ("DOC") and of the benthic pool of particulate organic carbon ("sedPOC") was assumed to be exported from the system. This means that we double hand-balanced the flow matrix of the models de Jonge et al. (following 2019*b*,*a*) and that the final (balanced) flow matrices therefore represent steady-state conditions.

Output parameters

For each of the 4 reconstructed Balgzand food webs, a number of ENA network fluxes and indicators was calculated based upon the carbon flows between compartments (Appendix O). These different indicators have been developed over time and are extensively described by e.g. Baird et al. (2004, 2007, 2012); Scharler (2008); Fath (2015); Lau et al. (2017). The indicators used in this work are those most appropriate for describing the impact of invasions (Miehls et al., 2009*a*,*b*; Baird et al., 2012) (Table 8.4).

Table 8.4: Overview of ENA metrics and indicators, and expected change in values resulting from invasions, as addressed in this study.

NETWORK INDICES/METRICS	
FCI (Finn Cycling Index)	
Unit	%
Definition	The proportion of total system throughflow of carbon that is generated by cycling of the total system throughflow as the sum of the flows of all compartments
Indicator	Denotes how many times further than the straight throughflow path length an average unit of inflow travels because of cycling (FCI = TSTcycled / TSTflow)
Meaning and expected change for the indicator in case of invasive species	Finn Cycling Index is expected to decrease as the total throughflow speeds up during invasions.
References	Finn (1976)
D/H (Detrivory/Herbivory ratio)	
Unit	-
Definition	The ratio between detrivory versus herbivory
Indicator	Indicator of the importance of detritus to that of primary production for the food web
Meaning and expected change for the indicator in case of invasive species	A higher value means a more important role of detritus versus primary production as energy source for the ecosystem. D/H ratio is expected to decrease due to an increase of suspension feeding invasive species such as *Magallana gigas* and *Ensis leei* as a result of an increase of herbivory flows.
References	Ulanowicz and Kay (1991)
P_{GPP}/B (Gross primary production / biomass ratio)	
Unit	-
Definition	The gross primary production over the total living biomass
Indicator	This ratio is a function of the system's maturity. It is expected that biomass is accumulated when the system matures.
Meaning and expected change for the indicator in case of invasive species	The value decreases when the system matures (i.e. from Phase III to Phase IV).
References	Christensen (1995); Odum (1969)
TROPHIC AGGREGATIONS	
LTA (Lindeman trophic analysis)	
Unit	%; $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$
Definition	Simplified food chain in which the compartments are abstract discrete steps
Indicator	Aggregates a trophic network into a linear food chain consisting of a number of integer trophic levels, the so-called Lindeman spine
Meaning and expected change for the indicator in case of invasive species	It is expected that the invasion will illustrate possible shifts (e.g. increase in grazing by secondary producers) and shunts (e.g. reduction of carbon transfer to higher trophic levels due to enhanced returns to the detrital pool) in the food web. Specifically, the efficiency for TL I is expected to increase due to invasion of suspension feeders as more carbon going into the grazing food chain (decrease in primary production) while less is lost to the detritus pool.
References	Lindeman (1942); Ulanowicz (1995)
TROPHIC INTERACTIONS	
MTI (Mixed trophic impact)	
Unit	-
Definition	The mixed trophic impact (MTI) analysis is based on the concept that in a food web, all compartments are linked to, and thus influence each other.
Indicator	MTI quantifies the relative impact (positive or negative) that any one compartment can have on any other in the food web. The resulting matrix takes into account direct connections (predator-prey interactions) and indirect connections (cascading effects, competition).
Meaning and expected change for the indicator in case of invasive species	Negative effects are expected on compartments that were i) directly affected due to predation by invaders and ii) indirectly affected due to competition with invaders for food resources. Furthermore, different invaders might also impact each other negatively due to similar diet preferences. In contrast, positive effects are expected on those organisms not eaten by invaders.
References	Ulanowicz and Puccia (1990); Horn et al. (2019)

8.3 RESULTS

8.3.1 *Biomasses*

At Balgzand, the invasive species were observed for the first time between 1984 (*Ensis leei*) and 2001 (*Magallana gigas*), and all three species peaked in the mid-2000s (Fig. 8.2). While *E. leei* and *Marenzelleria viridis* reached similar peak biomasses of around 5000 mg C m^{-2}, the biomass of *M. gigas* remained relatively low. The biomass of the other macrozoobenthic species was relatively low in the 1970s and, on average, higher and more or less stable during the study period (Fig. 8.2).

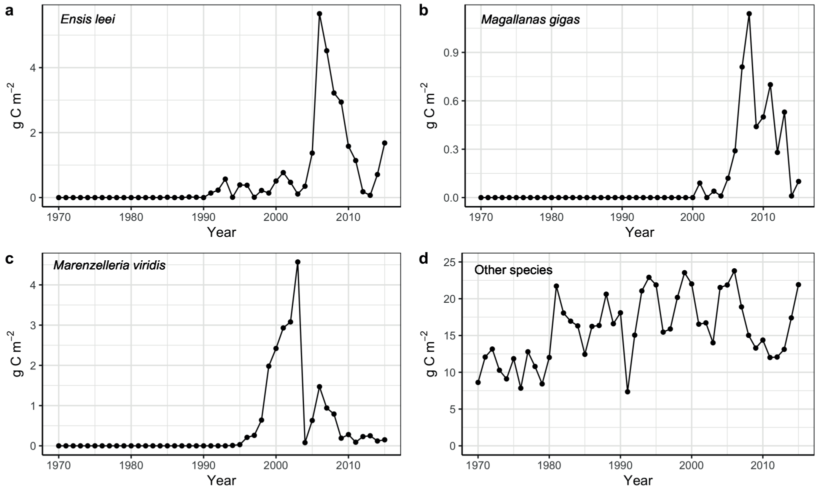


Figure 8.2: Biomass (g C m^{-2}) of three recent invaders (a) *Ensis leei*, (b) *Magallanas gigas* and (c) *Marenzelleria viridis* and (d) the sum of the other macrozoobenthic species of the Balgzand system from 1970 to 2015 (data courtesy: Jan Beukema & Rob Dekker, NIOZ).

When comparing the four decades, the total biomass of microalgae (marine phytoplankton, freshwater algae and microphytobenthos) was on average 7.72×10^3 mg C m^{-2}, varying between 6.46×10^3 mg C m^{-2} in the 1980s and 8.65×10^3 mg C m^{-2} in the 2000s (Table 8.2). The variation in microalgal biomass between decades was mainly due to the variation in biomass of microphytobenthos (contributing 90% or more to the total biomass of these primary producers), with the lowest value in the 1980s (5.85×10^3 mg C m^{-2}) and the highest value in the 2000s (8.12×10^3 mg C m^{-2}). The other two groups of primary producers displayed the highest values in the 1980s (i.e. 226 mg C m^{-2} for phytoplankton and 388 mg C m^{-2} for freshwater algae).

The mean biomass of total macrozoobenthos over all decades was 18.88×10^3 mg C m^{-2} and varied between 16.84×10^3 mg C m^{-2} in the 1980s and 22.70×10^3 mg C m^{-2} in the 2000s (Table 8.2, Fig. 8.2). The largest contribution was by two bivalve species (*M. arenaria* and *Cerastoderma edule*) of respectively 22-35

% and 9-20 % to the total macrozoobenthic biomass. The biomass of *M. arenaria* increased over time, reaching a maximum during the 2000s, whereas the biomass of *C. edule* showed no clear trend but was at its lowest value during the 2000s while it attained its maximum during the 2010s. The bivalve species *Limecola balthica* showed a decline over time, decreasing from 13 % of the total macrozoobenthic biomass in the 1980s to 3 % in the 2010s. The contribution of the lugworm *Arenicola marina* to the total macrozoobenthic biomass varied between 10 % in the 2000s and 18 % in the 1980s.

Biomass values of the three invasive species (*E. leei*, *M. viridis* and *M. gigas*) were highest during the 2000s (respectively 9 %, 8 % and 2 % of the total macrozoobenthos biomass; Table 8.2). The invasive *M. gigas* was absent during the first two decades of the study period, whilst the biomass of both *E. leei* and *M. viridis* were lowest during the 1980s (<1 % of the total macrozoobenthos biomass) compared to the following three decades of the study period.

Epibenthos biomass varied between $162\,\mathrm{mg\,C\,m^{-2}}$ in the 2000s and 467 $\mathrm{mg\,C\,m^{-2}}$ in the 1980s (Table 8.2). In the 1980s, the epibenthos biomass was dominated by plaice (*Pleuronectes platessa*) contributing to over 70% of the total epibenthic biomass (Table 8.2). Thereafter, the contribution of plaice declined to less than 5 % in the 1990s and to less than 1 % in the 2010s. From the 1990s onwards, the biomass of the epibenthos was dominated by the brown shrimp (*Crangon crangon*) that increased from 19 % in 1980s to more than 65 % since the 1990s.

The total bird biomass was on average $99.5\,\mathrm{mg\,C\,m^{-2}}$, and varied between $90\,\mathrm{mg\,C\,m^{-2}}$ in the 1980s and $110\,\mathrm{mg\,C\,m^{-2}}$ in the 1990s (Tables 8.2 and 8.3). In the 1980s, the biomass was dominated by the oystercatcher (*Haematopus ostralegus*) which declined from 33 % of the total bird biomass in the 1980s to 18 % in the 2010s. The contribution of the Eurasian curlew (*Numenius arquata*) to the total bird biomass increased from 12 % in the 1980s to 23 % in the 2010s and this was the dominating bird species in the 2000s.

The non-living compartments (DOC, susPOC and sedPOC) jointly comprised more than 50 % of the organic carbon of the ecosystem (living and non-living compartments), with lowest values of $42.32 \times 10^3\,\mathrm{mg\,C\,m^{-2}}$ in the 1990s and highest values of $45.45 \times 10^3\,\mathrm{mg\,C\,m^{-2}}$ in the 1980s (Table 8.3). These high values are mainly due to the amounts of sedPOC which contributed more than 85 % to the organic carbon within the non-living compartments.

8.3.2 *Carbon flows*

Gross primary production rates ranged between $502\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ in the 1990s and $561\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ in the 2000s (Table 8.5). Microphytobenthos was the dominant primary producer during the study period, with contributions increasing from approximately 62 % in the 1980s to 76 % in the 1990s and 80 % in the 2000s and 2010s. The contribution of phytoplankton decreased over time, from approximately 34 % in the 1980s to 20 % in the 1990s and 17 % in the 2000s and 2010s.

Table 8.5: Overview of biomass ($\mathrm{mg\,C\,m^{-2}}$) and carbon flows ($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) of the sum of all compartments (living and non-living) and of the three invasive species within the Balgzand food web.

Compartment		Unit	BZ1980s Phase I	BZ1990s Phase II	BZ2000s Phase III	BZ2010s Phase IV
Compartments	Living	(-)	55	55	56	56
	Other	(-)	3	3	3	3
Biomass	Living	($\mathrm{mg\,C\,m^{-2}}$)	25280	28084	32801	26697
	Other	($\mathrm{mg\,C\,m^{-2}}$)	45452	42308	42932	43277
Primary production	GPP	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	518	502	561	517
	NPP	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	364	359	403	372
Consumption		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	1099	1260	2351	1558
Egestion		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	484	564	999	649
Respiration		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	506	568	1195	790
Import		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	1514	1657	2285	1941
Export		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	1007	1089	1091	1152
Ensis leei						
Biomass		($\mathrm{mg\,C\,m^{-2}}$)	8	209	1993	892
Production		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	4	40	18
Consumption		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	4	115	1096	490
Egestion		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	2	48	458	205
Respiration		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	2	63	598	267
Magallana gigas						
Biomass		($\mathrm{mg\,C\,m^{-2}}$)	0	0	369	356
Production		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	0	0	0
Consumption		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	0	6	5
Egestion		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	0	0	0
Respiration		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	0	5	5
Marenzelleria viridis						
Biomass		($\mathrm{mg\,C\,m^{-2}}$)	0	349	1710	187
Production		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	5	24	3
Consumption		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	38	184	20
Egestion		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	19	92	10
Respiration		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	14	68	7

The production of the other living components was dominated by benthic bacteria, which accounted for approximately 50 % in the 2000s to 60 % in the other three decades of the total (non-autotrophic) production (Appendix O). Other producers that contributed 5 % or more to the total production included *A. marina* (all decades), *C. edule* (1980s, 1990s and 2010s), *E. leei* (2000s, 2010s), *L. balthica* (1980s, 1990s), *M. viridis* (2000s) and *M. arenaria* (2000s) (Appendix O). In the 2000s compared to the 1980s, the summed production of the other living components had increased by 20 % (Appendix O). The absolute increase in overall production between the 1980s and 2000s (+53 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) was more or less equal to the summed increase of the species-specific production by the invasive species *E. leei*, *M. gigas* and *M. viridis* (respectively 40+0+24 = 64 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) during that same time (Appendix O).

From the 1980s to the 2000s, the overall systems' consumption rate ($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) more than doubled, with the increase in overall consumption between these two decades (ca. +1250 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) being more or less equal to the consumption rates of *E. leei* (ca. 1100 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) and *M. viridis* (ca. 185 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) together during that decade (Table 8.5). In the 2000s, the consumption rate of *E. leei* and *M. viridis* was respectively 47 % and 8 % of the total consumption rate.

During the first three decades of the study period, the overall systems' egestion and respiration rates strongly increased, in particular respiration which rose from just over 500 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ in the 1980s to almost 1200 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ in the 2000s (Table 8.5). In the 2000s, the bivalve *E. leei* and *M. viridis* contributed 50 % and 6 %, respectively, to the overall systems respiration. Overall respiration decreased from the 2000s to the 2010s, as well as that of the absolute values and relative contribution of respiration of the invasive species. Import of carbon to the Balgzand tidal system increased by more than 50 %, from ca. 1500 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ in the 1980s to more than 2200 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ in the 2000s, and decreased to less than 1950 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ in the 2010s (Table 8.5). Variation in export, however, was less than that of import, showing an increase from just over 1000 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ in the 1980s to ca. 1150 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ in the 2010s (Table 8.5).

8.3.3 *Network descriptors*

The Finn cycling index (FCI; $\mathrm{TST_c/TST_{flow}}$ ratio) decreased from 12 % in the 1980s and 11 % in the 1990s to 10 % in the 2000s and 2010s (Table 8.6, Appendix O). This decrease was in contrast withthe relatively high value (more than 630 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) of the total cycled part ($\mathrm{TST_c}$) of the system throughflow in the 2010s compared to the values of the other three decades ((476 ± 35) $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) (Table 8.6). In addition, the low values of FCI during the second half of the study period resulted from relatively high values of the total system throughflow ($\mathrm{TST_{flow}}$) in the 2000s/2010s (ca. 5770 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) compared to the those in the 1980s/1990s (ca. 3900 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) (Table 8.6). This increase in total system throughflow ($\mathrm{TST_{flow}}$) of more than 1900 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$

is partly caused by an increase in both consumption (ca. +775 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) and import (ca. + 530 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) (Table 8.6).

Table 8.6: Overview of outcomes of network indicators for the Balgzand food web during different phases of invasions by *Ensis leei*, *Magallana gigas* and *Marenzelleria viridis*.

Indicator	Unit	BZ1980s Phase I	BZ1990s Phase II	BZ2000s Phase III	BZ2010s Phase IV
METRICS					
TST_{flow}	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	3698	4103	6503	5032
TST_{cycled}	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	451	460	633	516
FCI	(%)	12.20	11.20	9.70	10.30
P_{GPP}/B ratio	(-)	0.020	0.018	0.017	0.019
P_{NPP}/H ratio	(%)	135	95	34	56
D	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	697	706	975	693
H	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	270	377	1173	665
DH ratio	(-)	2.58	1.87	0.83	1.04
LINDEMAN SPINES					
TL1 TE	(%)	36.6	48.0	86.6	68.3
TL1 detritus	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	292	266	23	159
TL2 TE	(%)	60.8	43.2	16.1	27.4
TL2 detritus	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	477	573	1035	666

The D/H ratio (ratio between detritivory and herbivory) decreased from approximately 2 during the 1980s and 1990s to approximately 1 for the 2000s and 2010s (Table 8.6). This shift was mainly due to an increase in herbivory, which was more than 280 % higher for the second half of the study period (in particular the 2000s) than during the first two decades of the study period (Table 8.5). Although detritivory also increased, the difference between the first and second half of the study period was less than 20 % (Table 8.6).

The higher trophic levels were dominated in the 1980s by demersal fish species, mainly plaice (*P. platessa*) that made up over 80 % of the trophic levels V to IX (Table 8.2, Fig. 8.3). During the 1990s, the contribution of different bird species became evident (Table 8.2, Fig. 8.3) with a further increase during the 2000s. During the same decade, the trophic levels V to VIII were dominated by bird species (in particular *H. ostralegus*, *N. arquata* and *Tadorna tadorna*) with a contribution of over 50 % in trophic level V and over 70 % at the trophic levels VI, VII and VIII (Table 8.2, Fig. 8.3). During the 2010s, higher trophic levels were dominated by fish, in particular by the gobies *Pomatoschistus minutus* and *P. microps* (Table 8.2, Fig. 8.3). Within trophic level V, the contribution of the epibenthic crustaceans *C. crangon* and *Carcinus maenas* to the total biomass increased over time (Table 8.2, Fig. 8.3).

The trophic aggregation analysis indicated nine trophic levels for the 1980s and eight for the remaining decades (Fig. 8.4). According to the Lindeman spines, the carbon transfer efficiencies varied among the four decades, in particular at the base of the food web. Carbon transfer from the first to the second trophic level (from the microalgae as primary producers to primary consumers such as suspension-feeding bivalves) varied from 37 % in the 1980s, 48 % in the 1990s, 87 % in the 2000s to 68 % in the 2010s (Fig. 8.4). For the second

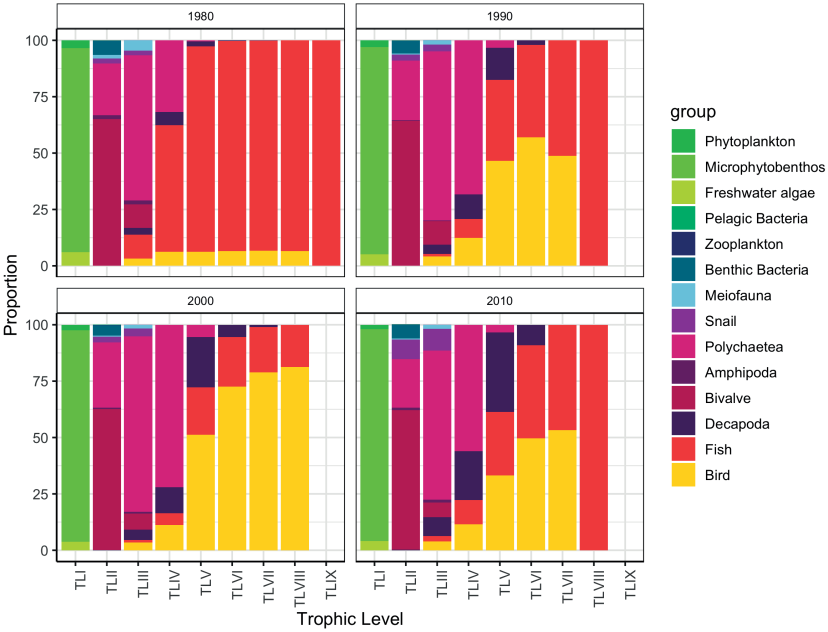


Figure 8.3: Proportional composition in biomass of the different trophic levels (TL) of functional groups in each decade.

to the third trophic level (including bivalve-eating fish and birds), this transfer was 61 %, 43 %, 16 % and 27 % for the respective decades (Fig. 8.4). This implies that during the 1980s, the relative trophic transfer between the primary producers and primary consumers was actually lower than that between the primary consumers and their predators.

During the 2000s, *E. leei* negatively impacted almost all compartments of the Balgzand food web (Fig. 8.5) with a negative impact on its food sources (see Appendix N), in particular on marine phytoplankton (-0.52) and pelagic bacteria (-0.25), which represented 53 % and 1 % of its diet during this decade, respectively. With respect to the impact on other (potentially competing) consumers, *E. leei* had the most negative impact on *Lanice conchilega* (-0.47), the species which relied most (85 % of its diet) on marine phytoplankton compared to all other species (see Appendix N). Meiofauna (feeding predominantly on benthic bacteria and benthic POC; see Appendix N) was the only compartment that appeared to have been positively impacted by *E. leei* (+0.04). The other two invasive species, *M. viridis* and *M. gigas*, generally had a low impact on other compartments, with values varying between -0.08 and +0.19 (Fig. 8.5). The invasive species also had an impact on each other (Fig. 8.5). *E. leei* had a negative impact on both *M. viridis* (-0.47) and *M. gigas* (-0.21), whilst *M. viridis* and *M. gigas* had a positive impact on each other (+0.16).

With respect to the native species, *C. crangon*, which relied on a wide variety of food sources including *C. edule* (24 %), *P. ulvae* (12 %) and *L. balthica* (11 %)

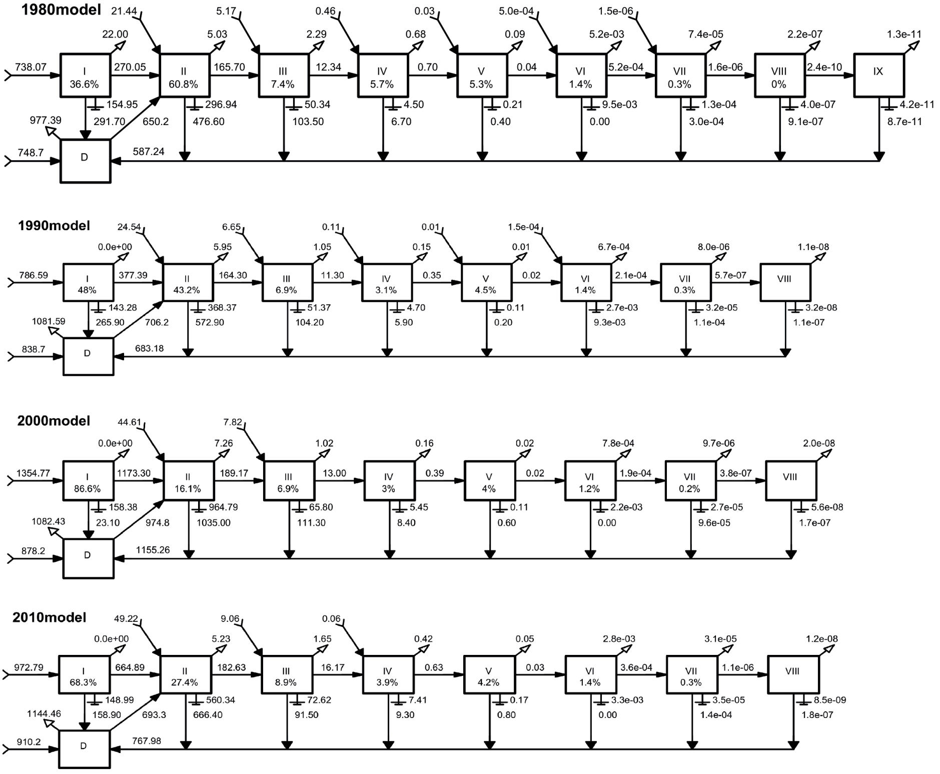


Figure 8.4: Lindeman spines on carbon transfer ($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) within the Balgzand tidal system during four decades (1980s, 1990s, 2000s, 2010s). The boxes indicated as "D" refer to the detrital pool and the Roman numerals in the boxes of the spine to discrete trophic levels. Percent values in spine boxes refer to the efficiency of carbon transfer to the next trophic level. External input as well as export and loss due to respiration have been indicated for each trophic level ($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$).

(see Appendix N), had a negative impact on several macrozoobenthic species including *Scoloplos armiger* (-0.24), which predominantly feeds on benthic bacteria (40 %) and benthic POC (40 %), and *Corophium spp.* (-0.55), which largely relies on microphytobenthos (65 %) as a food source (see Appendix N). In addition, *C. crangon* had a negative impact on all bird species, ranging from -0.04 for *Limosa lapponica* (which feeds on polychaetes, in particular on *A. marina* and *Hediste diversicolor*) to -0.30 for *Larus argentatus* (which relies for 60 % on the bivalve *M. edulis*) (Appendix N). *C. crangon* had a positive impact, however, on several fish species in particular on *Myoxocephalus scorpius* (+0.42) and *Osmerus eperlanus* (+0.42) (Fig. 8.5). Both fish species largely rely on shrimps as a food source (45 % and 50 %, respectively, see Appendix N).

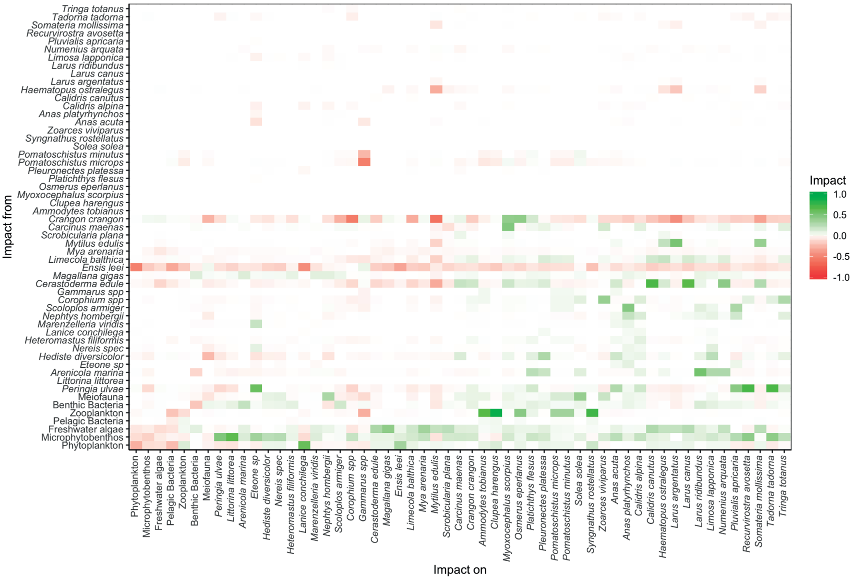


Figure 8.5: Direct or indirect trophic impact of each living compartment ("Impact from") on each living compartment ("Impact on") of the food web of the Balgzand tidal system in the 2000s, with positive values in green and negative values in red, based upon the mixed trophic impact (MTI) analysis.

8.4 DISCUSSION

8.4.1 *ENA as a tool to analyse the impact of invasive species*

Recently, Frost et al. (2019) stressed the limited ability at present to predict invasions and their impact due to the lack of theoretical frameworks. Ecological network analysis is such a framework for the analysis of the impact of invasive species on the food web via the construction of energy budgets, as has been demonstrated for freshwater lakes by Miehls et al. (2009*a*,*b*) and a coastal ecosystem by Baird et al. (2012). Application of ENA is particularly useful to examine if (and, if so, how) changes in local species composition (e.g. resulting from invasion) induce shifts in carbon flows among the fixed living compartments of a given ecosystem, the results of which can direct authorities to address the undesired consequences of such changes (de Jonge and Schückel, 2019). It should be kept in mind, however, that several factors may bias the temporal comparisons between networks of the same system during different phases of invasions. First, all budgets were considered to be in steady-state, and also the flow matrix of the various compartments was internally hand-balanced to achieve this condition (following de Jonge et al., 2019*b*,*a*). In reality, systems will not be in steady state but, for example, continuously responding to environmental conditions including (for our system) those in weather, tides, seasons and human pressures that vary within and between years. A second important factor that needs direct attention is the quality and quantity of the data on biomasses, diet matrices and external fluxes (import, export). Most biomass data were derived from monitoring data but for a few compartments, mostly at the basis of the food web (microphytobenthos, zooplankton, meiofauna, benthic and pelagic bacteria, and the sediment POC), values had to be estimated by using correlations or by taking values from other Wadden Sea areas into account. This may have impacted the output values representing the system functioning (Saint-Béat et al., 2015; de Jonge et al., 2019*b*). Here significant improvement is possible by further improving the Wadden Sea monitoring, by including all relevant parameters and by increasing the spatial and temporal resolution (see for example, de Jonge et al., 2006). In addition, the possible significant impact of salinity and its fluctuations on specifically the primary production of the freshwater borne phytoplankton was not considered due to lack on information as was the possible role of resuspended microphytobenthos in the food web functioning (de Jonge et al., 2019*a*). This means that due to missing data the complex functioning of the system at the bottom of the trophic chain could not be represented properly.

For Balgzand, the impact of invasive species was studied at a temporal scale of decades. With respect to the invasive species, this appears to be justified. Comparing the four decades revealed that all three species experienced a wax and wane in biomass which indicates that they followed all four phases of the typical pattern for invasions.

8.4.2 *Long-term changes in the Balgzand ecosystem*

The Balgzand area has experienced a number of large changes over the last decades such as the appearance of invasive species, a period of eutrophication, removal of intertidal mussel beds, and a shift in epibenthic predators from flatfish (plaice *Pleuronectes platessa*) to crustaceans (brown shrimp *Crangon crangon*).

A period of eutrophication followed by a decline of nutrient supply occurred since the mid-1980s (Cadée, 1984; de Jonge et al., 1993; Philippart et al., 2010, Chapter 2), and was subsequently followed by a decrease in biomass and production of marine phytoplankton (Cadée, 1984; Jacobs et al., 2020), microphytobenthos (MPB, Cadée and Hegeman, 1977) and macrozoobenthos (Beukema and Cadée, 1996). Because MPB data for Balgzand was only available until 1981 only (Cadée, 1984), our estimates for biomass and production of benthic microalgae were derived from a positive empirical relationship between air temperature and MPB biomass (de Jonge et al., 2012). The uncertainty in values of MPB affected the accuracy of import estimates (needed to fulfill the requirements by the primary consumers) and, subsequently, that of ENA indices such as the FCI. In addition, the lack of information on the fraction of MPB that resuspends and on the Production/Biomass ratio of the freshwater phytoplankton in an estuarine environment increased the uncertainty of the values of biomass and production of pelagic microalgae.

The Balgzand area also experienced a complete removal of mussel beds (*Mytilus edulis*) during the early 1990s (Beukema and Cadée, 1996). The decrease in suspension-feeding by mussels during the early 1990s was most probably compensated for by the increase of the invasive species *Ensis leei*, and to some extent of *Mya arenaria*. As the sampling program used for this study was not focused on sampling the Pacific oyster and blue mussel beds in the area, there is the possibility that the biomass of these suspension-feeding bivalves has been underestimated. However, in case of the blue mussel, Beukema and Dekker (2007) a linear relationship between mussel stock assessments by their sampling program and other monitoring programs on Balgzand (with biomass of other programs being approximately 7% higher), indicating that the present values were sufficient to represent the blue mussel biomass. It is unclear if this also holds for the oysters.

Over time, the biomass of predatory plaice (*Pleuronectes platessa*) declined whilst that of predatory shrimp (*Crangon crangon*) increased, possibly as the result of changes in large-scale environmental conditions including increasing temperatures and distributional shifts in their predators (Chapter 5). Because these predators prefer different prey species, (Appendix N), their shift is expected to have had cascading effects on carbon flow networks (Chapter 5). The increase of predatory shrimps, for example, appeared to have had a negative impact on other small crustaceans (Corophium and Gammarus), possibly resulting from competition between these three abundant species for food and space.

Long-term changes in ecosystems coinciding with but unrelated to invasions not only occurred at Balgzand but also in other systems, for instance during the invasions of zebra mussels in Oneida Lake (North-American lakes) and Pacific oyster in the Sylt-Rømø Bight (northeastern Wadden Sea) (Miehls et al., 2009*a*,*b*; Baird et al., 2012). In Oneida Lake, the biomass of double-crested cormorants (*Phalacrocorax auritus*) increased and with it the predation rate on fish (Miehls et al., 2009*a*). The Sylt-Rømø Bight experienced a strong increase in seagrass beds (*Zostera noltii*), with its cover of the entire intertidal area expanding from 8 % in 1995, to 19 % in 2007 and 33 % in 2010, which resulted in an increase in benthic primary productivity (Baird et al., 2012). Most probably, such coinciding changes influenced (in addition to the invasions) the rates of the carbon flows and the values of the network indices.

8.4.3 *Impact of invasive species at Balgzand on carbon flows*

The network indicators and the results of the trophic aggregations point to differences in the carbon transport pathways between the first (1980s, 1990s) and the second (2000s, 2010s) half of the study period. One of the differences between the 1980s/1990s models and the 2000s/2010s models is the addition of a compartment in the form of the macrozoobenthic species *Magallana gigas*, which invaded the Balgzand area around 2001 (Beukema and Dekker, 2011). However, with respect to the three invasive species (*E. leei*, *Marenzelleria viridis*, *M. gigas*), both the biomass and the impact matrix for the 2000s suggest that *E. leei* was the invasive species with the highest impact on the food web.

E. leei is mostly found in high numbers at the edges of the intertidal flats and low lying flat areas below mean sea level (Beukema and Dekker, 1995). American razor clams are very efficient suspension-feeding bivalves (Kamermans et al., 2013) and they might have taken phytoplankton entering the tidal flats before other macrobenthos could take advantage of that food source and thereby limiting the carbon flow to this group (which includes, not only suspension-feeders but possibly also deposit-feeding organisms living on the higher tidal flats).

In the 2000s, the highest negative impact of *E. leei* on other consumers was found for *Lanice conchilega*, most likely due to the aforementioned competition for the same food resources such as phytoplankton and non-living suspended particulate organic carbon. The partial overlap between the ecological niche of *E. leei* with that of *L. conchilega* within the Wadden Sea has been recently shown by Schwemmer et al. (2019).

In the 2000s, the overall consumption by *E. leei* ($1096\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) was higher than the available primary production ($561\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) (Table 8.5). To fulfil the carbon requirements of this consumer, an additional import of marine phytoplankton had to be assumed to balance the model. This implies that import of organic matter from external sources was needed to fulfil the food requirements, which is in accordance with van Raaphorst and van der Veer (1990).

Our results indicated that *E. leei* also had a negative effect on most predators; this was most likely an indirect effect because the competition for food resources reduces the amount of prey items for these predators. When taking only the relative values of the 2000s into account, it seems that there is less material transported along the food chain in comparison to the other decades; the transport from the first to the second trophic level is highest in this decade as are the absolute values of the trophic transfers in the lower trophic levels (up to trophic level V) (Fig. 8.4, above arrows from one trophic level to the next). The high mobility of the American razor clam may have helped them to escape predation (Swennen et al., 1985), subsequently resulting in the observed decrease of carbon flow to higher trophic levels. This is in contrast with the situation within razor clam fields in the NE Wadden Sea, where the energy in this habitat is transferred very efficiently from phytoplankton via razor clams to bivalve-eating gulls (Horn et al., 2017).

The impact of the other two invasive species, *M. gigas* and *M. viridis*, appeared to be minor at the scale of the Balgzand. There might, however, be other impacts of invasive species on the Balgzand system that are not covered by the food web analysis as performed here with ENA, for example the extensive reefs formed by *M. gigas* that especially influence the direct (physical) environment surrounding them (Jones et al., 1994; Gutiérrez et al., 2003). It showed high biomass values and thereby increased the total biomass of bivalves. It increased the herbivory of the system as expressed by the D/H ratio and impacted most of the other species (mostly through direct food competition).

A few decades after their introduction at Balgzand, the three invasive species are still present and might therefore be considered established in the area. After their peak, biomass of the three invasive species rapidly declined to relatively low values in the 2010s, implying that in terms of standing stock, the long-term impacts of these invasions were, at least locally, limited. Underlying mechanisms are unclear at present, despite their contrasting habitat requirements: both *M. gigas* and *M. viridis* are spread over the whole Balgzand area while the presence of *E. leei* is restricted to the (almost empty) lower edges of the tidal flats where current velocities are high (Dekker and Beukema, 2012). *M. viridis* might suffer from a high fish predation in line with other polychaetes (Poiesz et al., 2020). Natural mortality of *E. leei* can be high: after severe winters and storm events they are often washed ashore in vast numbers (Dannheim and Rumohr, 2012). Despite its low permanent biomass at present, the impact of *E. leei* on the Balgzand food web remains substantial due to its high filtration capacity.

8.4.4 *The impact of invasive species: is it species or area specific?*

The three species, *E. leei*, *M. viridis* and *M. gigas* were not only invasive at Balgzand but also in other parts of the Wadden Sea. In one of these areas, the Sylt-Rømø Bight (SRB), their impact has also been studied by ENA modelling (Baird et al., 2012). This allows for a first analysis ofto what extent the impact of invasive species is species-specific and/or area-specific, especially since on average, the carbon budgets of Balgzand and SRB systems were more or less similar with respect to overall biomass, and rates of consumption, imports and export (Table 8.7 & 8.8). However, biomass at Balgzand was dominated by non-living organic material, whilst the biomass of SRB was dominated by living compartments.

Because *Ensis leei* and *Marenzelleria viridis* were not included into the network analyses of SRB (Baird et al., 2012), both species most probably played a minor role in this food web. In the SRB, the biomass of the Pacific oyster

Table 8.7: Overview of biomass ($\mathrm{mg\,C\,m^{-2}}$) and carbon flows ($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) of the sum of all compartments (living and non-living) and of the invasive Pacific oyster (*Magallana gigas*) within the Sylt-Rømø Bight (SRB) food web (biomass and flux data derived from Baird et al. (2012), if not available then based upon conversions from Horn et al. (2017)). No study conducted during phase II of the invasion, NA: either not available or not possible to be reconstructed from these sources.

Parameter		Unit	SRB1995 Phase I	SRB2007 Phase III	SRB2009 Phase IV
Compartments	Living	(-)	56	60	60
	Other	(-)	3	3	3
Biomass	Living	($\mathrm{mg\,C\,m^{-2}}$)	35110	61369	52457
	Other	($\mathrm{mg\,C\,m^{-2}}$)	19230	13333	19239
Primary production	GPP	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	559	658	973
	NPP	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	313	340	498
Consumption		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	2210	2492	2351
Egestion		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	NA	NA	NA
Respiration		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	987	1272	1248
Import		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	1938	2304	2178
Export		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	956	1034	910
Magallana gigas					
Biomass		($\mathrm{mg\,C\,m^{-2}}$)	0	15050	550
Production		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	15	1
Consumption		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	250	9
Egestion		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	0	0
Respiration		($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	0	81	3

Table 8.8: Overview of outcomes of network indicators for the Sylt-Rømø Bight (SRB) food web during different phases of invasions by *Magallana gigas* (data derived from Baird et al. (2012) and Horn et al. (2017)), no study conducted during phase II of the invasion.

Indicator	Unit	SRB1995 Phase I	SRB2007 Phase III	SRB2009 Phase IV
METRICS				
$\mathrm{TST_{flow}}$	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	19146	22702	21558
$\mathrm{TST_{cycled}}$	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	3178	3814	4656
FCI	(%)	16.6	16.8	21.6
$\mathrm{P_{GPP}/B}$ ratio	(-)	0.016	0.011	0.019
$\mathrm{P_{NPP}/H}$ ratio	(%)	28	26	46
D	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	1398	1256	1382
H	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	1119	1295	1088
DH ratio	(-)	1.25	0.97	1.27
LINDEMAN SPINES				
TL1 TE	(%)	47.2	54	54
TL1 detritus	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	524	376	332
TL2 TE	(%)	15.8	16.7	18.4
TL2 detritus	($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$)	868	979	936

was zero in 1995 (invasion Phase I), more than 15 000 mg C m^{-2} during its peak abundance in 2007 (invasion Phase III) and less than 600 mg C m^{-2} in 2010 (invasion Phase IV) (Table 8.7). During their peak abundances (invasion Phase III), consumption by *M. gigas* at SRB was more than 10 % of the total consumption within this area whilst consumption by *E. leei* at Balgzand was more than 45 % of the local total consumption.

The impact of the invasion of *E. leei* on the carbon flows at Balgzand appeared to be stronger than that of *M. gigas* on the flows at SRB. When moving from zero (Phase I) to peak (Phase III) biomass, the total herbivory at Balgzand increased by +334% (Table 8.6) whilst that at SRB by +54% (Table 8.8). Furthermore, the trophic transfer from primary to secondary producers increased by +137% at Balgzand and by +14% at SRB from Phase I to Phase III. To balance the increased consumption rates between these two phases, the import of carbon from external sources increased by +51 % at Balgzand and +19 % at SRB.

At Balgzand, where predation on *E. leei* was limited, the trophic transfer from secondary producers to higher trophic levels was strongly reduced (-74 %) between invasive Phases I and III. Although predation on *M. gigas* in the northeastern Wadden Sea was assumed to be absent (Baird et al., 2012; Horn et al., 2017), the increase in biomass of the Pacific oyster at SRB coincided with an increase (6 %) in trophic transfer from secondary producers to higher tropic levels. Apparently, this change in trophic transfer at SRB is dominated by changes in another prey species than *M. gigas* and/or their predators. At SRB, an increase in the trophic transfer from secondary producers to detritus (13 %) and detritivory (20 %) occurred at SRB from Phase I to Phase III, most probably due to the invasion by the suspension-feeding *M. gigas*, but this increase was less than that observed for Balgzand.

The impact of *E. leei* at Balgzand in the southwestern Wadden Sea had similar but stronger and longer-lasting effects on the ecosystem than that of *M. gigas* at the SRB in the northeastern Wadden Sea. In spite of the much higher maximum biomass of the Pacific oyster at SRB (more than 15 g C m^{-2}) compared to that of the American razor clam at Balgzand (less than 2 g C m^{-2}), the impact of *M. gigas* on carbon fluxes (consumption rates, carbon transfer between trophic levels) appeared much lower during its peak abundance. After the peak (Phase IV), the consumption by *M. gigas* at SRB was less than 1 % whilst consumption by *E. leei* at Balgzand was still more than 30 % of the total consumption.

8.4.5 *Short- and long-term impacts*

The success of bivalve *E. leei* was most probably due to fulfilling at least two, if not all three, of the major factors that strengthen the impact of an invader (Ruesink, 2018). It is well adapted to the environmental conditions in the Wadden Sea and it occupies an ecological niche that was empty before in the western Dutch Wadden Sea (Dekker and Beukema, 2012). Whether the third factor, a high number of individuals at the initial invasion, is fulfilled or not is difficult to determine. The fact that *E. leei* occupies a niche that was formerly unoccupied is also confirmed by the present study, as the efficiency of utilizing the primary production in the system increased, leading to higher herbivory in the system.

Additional (and most probably unrelated) to the impact of *E. leei* at Balgzand there was also a switch from juvenile flatfishes (mainly plaice) to crustaceans (mainly shrimps) over the study period, leading to a shorter food chain in the system because of a shift in predation pressure (Chapter 5). The invasion of *M. gigas* at SRB coincided with an extension of seagrass beds, that increased the primary production of this area. Observed changes in carbon fluxes during invasions reflected, therefore, not only the impacts of the invasive species under consideration but also coinciding shifts in the lower (SBR) and higher (Balgzand) trophic levels of the food web. Still, the observed enhanced consumption of primary producers, enhanced reliance on external import to fuel the food web and the enhanced transfer of carbon from secondary producers to the detritus pool appear to be predominantly caused by the invasions at both locations within the Wadden Sea.

After 600 years, the historical invasive bivalve, *M. arenaria*, is still present in the Wadden Sea, with recent (average) biomass of more than 5000 $\mathrm{mg\,C\,m^{-2}}$ at Balgzand (this paper) and almost 2000 $\mathrm{mg\,C\,m^{-2}}$ at the SRB (Baird et al., 2012). The present consumption by this suspension-feeding bivalve is relatively low, less than 80 $\mathrm{mg\,C\,m^{-2}}$ at Balgzand and less than 25 $\mathrm{mg\,C\,m^{-2}}$ at the SRB (Baird et al., 2012). The invasive success *M. arenaria* is favored by its high fecundity, a high tolerance towards environmental conditions, longevity, and large size (Strasser, 1998). In addition, it most likely evolved along with the changing conditions and the other living organisms in the area. Since *E. leei* possesses similar properties and has influenced the food web dynamics in the western Wadden Sea already for two decades, this species is likely to get established as an important member of the macrozoobenthic community.

8.5 ACKNOWLEDGMENTS

During the revision of the manuscript, Prof. dr Victor N. de Jonge passed away suddenly after a heart attack. We are most grateful for his inspiration and guidance to apply Ecological Network Analyses to study the impacts of the invasive species on the Balgzand. We would like to thank Harald and Ragnhild Asmus for initiating the program on the impacts of invasive species in the Wadden Sea (INFOWEB, funded by the German Federal Ministry of education and Research (Bundesministerium für Bildung und Forschung; BMBF) and the Dutch NWO Earth and Life Sciences (Nederlandse Organisatie voor Wetenschappelijk Onderzoek 839.11.001). Thanks to Sonja van Leeuwen for proofreading the manuscript. Furthermore, we acknowledge all persons and organizations involved in long-term monitoring within the World Heritage Wadden Sea, in

particular our NIOZ colleagues who work on the Balgzand intertidal program until the present day.

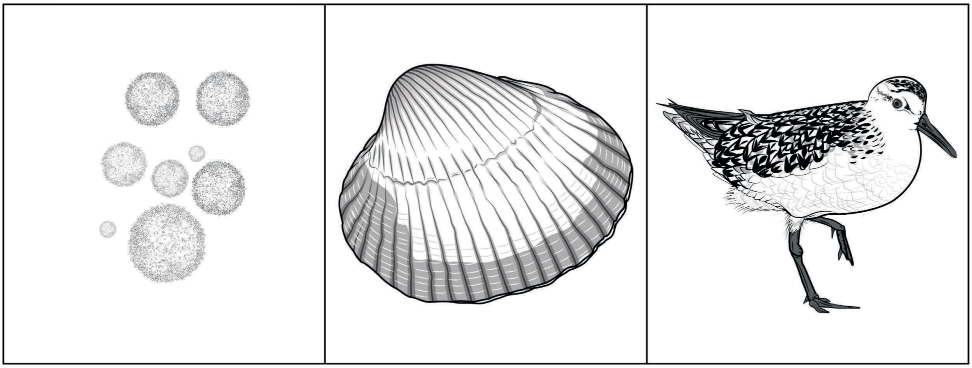
Part III

General Discussion

9

SYNTHESIS

A. S. Jung



9.1 INTRODUCTION

Assessment of the impact of invasive species on the coastal food web is not easy and single species analysis, where functioning or health of the whole system is explained by the analysis of a single species, are not a reasonable approach to look at these effects on the whole ecosystem (Levin and Lubchenco, 2008). Within natural ecosystems, introductions of invasive species generally occur within the same period as other changes in internal dynamics and external drivers that can affect the interactions within the food web. Such effects may add up, reduce or enhance the impacts of invasions. It is therefore essential to, when studying the impacts of invasive species, explore all other major changes that occurred within the ecosystem and take their impacts into account.

A holistic approach is needed and Ecological Network Analysis (ENA) is such a holistic approach to compare trophic interactions within food webs under different conditions, e.g. before and after an invasion. It looks at flows of one unit (e.g. carbon, nitrogen or phosphorus) through the system via connections over biological compartments. This also allows for an estimate of the impact that each compartment has on other compartments within the system. The ENA quantifies carbon transfer indices within a food web, enabling comparison between situations before and after the introduction of invasive species (Blossey, 1999).

Information on long-term changes in abiotic and biotic factors within an ecosystem is crucial in understanding and analyzing changes in species composition and energy flow as a consequence of invasive species. Prerequisite is that sufficient (long-term) data on species' biomass from all trophic levels (from bacteria to top predators) are available for the full study period. Furthermore, such an analysis would benefit from such an analysis and comparison in various subareas. As with any other model, to construct such a model, decisions and assumptions have to be made including the geographical boundaries of the ecosystem that is being described.

This thesis is part of the joint research project INFOWEB (The impact of biological <u>in</u>vasions on the <u>fo</u>od <u>web</u> of the Wadden Sea) that focuses on the impact of invasive species on the functioning of the Wadden Sea ecosystem by description and comparison of the ecosystem at the level of tidal basins. This study focuses on the Balgzand intertidal in the Marsdiep tidal basin in the western Dutch Wadden Sea. Other research groups from the Alfred Wegener Institute (AWI) and the Senckenberg Institute have focused on the impacts of invasive species in the Jade Bay in the central Wadden Sea (Schückel et al., 2015; de la Vega et al., 2018) and the Sylt-Rømø tidal basin in the north-eastern part of the Wadden Sea (de la Vega, 2016; Horn, 2016; de la Vega et al., 2018). The project was financed within the framework of a transnational sea and coastal research program set up by Dutch Netherlands Organization for Sciences (NWO) and the German Bundesministerium für Bildung und Forschung (BFMF) to study the impacts of invasive species on the Wadden Sea ecosystem.

The Balgzand area is a tidal flats system located in the westernmost part of the Dutch Wadden Sea. During the last 40 years, the Balgzand tidal flats were invaded by two bivalves (*Ensis leei* in 1982, *Magallana gigas* in 2001) and one polychaete (*Marenzelleria viridis* in 1989). Local long-term time series on nutrients, phytoplankton, macrozoobenthos, crustaceans, fish and birds (complemented with incidental studies, e.g. on bacteria and zooplankton) allowed for studying the possible impacts of these invasive species in relation to other changes within this ecosystem.

The study is limited to the intertidal parts. This implies that seals (although present in the western Wadden Sea) were not included into the food web analysis because they forage mainly in the gullies of the Wadden Sea and in the adjacent North Sea (Aarts et al., 2019).

At the beginning of this study, the following three main research questions were formulated:

1. Which changes in the food web, including the invasions, happened on the Balgzand tidal flats over the course of the last decades?
2. Did those changes happen concurrently to each other and, if so, how did they interact?
3. How did these changes influence the trophic interactions between different native and invasive species?

To discriminate between local and generic impacts, results for the Balgzand system will subsequently be compared with those found in the other areas studied within the INFOWEB project.

First, the long-term changes in the western Dutch Wadden Sea will be described (section 9.2). Next, the cumulative effects of these changes will be explored (section 9.4), the impacts of the invasive species at the Balgzand area will be analysed by means of ENA model (section 9.3), and subsequently the results will be compared with the impact of invasions in other areas (section 9.5). Finally, suggestions for future research directions will be given (section 9.6).

9.2 CONCURRING LONG-TERM CHANGES IN THE WESTERN DUTCH WADDEN SEA

Analyses of long-term data sets and their potential impacts on the Balgzand food web are often an update of previous analyses of ongoing field observations (among others van Raaphorst and van der Veer, 1990; Beukema, 1992; Beukema and Cadée, 1997; Philippart et al., 2000; van Beusekom and de Jonge, 2002; Baretta-Bekker et al., 2009; van der Veer et al., 2011). In several cases, the new analyses of a now longer data set confirmed an original hypothesis, in other cases the results lead to new conclusions then have been drawn in the past.

The western Dutch Wadden Sea has a strong exchange with the surrounding North Sea (van Raaphorst and van der Veer, 1990; Philippart et al., 2000, Chapter 2, Chapter 3) and as a consequence the changes in the North Sea can also influence the Wadden Sea. However, abiotic conditions in the Wadden Sea can also differ from the conditions in the North Sea meaning that results from studies focusing on the North Sea cannot be used directly on the Wadden Sea. In Chapter 3 long-term data from higher order phytoplankton compositions were used to estimate the area of the coastal North Sea that still influences the Wadden Sea. This area has been set to be between 10 to 100 km of the coastline of the Netherlands (Chapter 3).

9.2.1 *Abiotic conditions*

Temperature changes in the western Dutch Wadden Sea have been observed in the four decades of this study and beyond (van Aken, 2008*b*). A warming of 1.5 °C has been found between 1980 and 2005 (van Aken, 2008*b*). The variability of the temperature in the western Dutch Wadden Sea is strongly correlated with the North Atlantic Oscillation Index and has a delay of only a few days to the surrounding air temperature (van Aken, 2008*b*).

The changes in salinity within the western Dutch Wadden Sea are strongly correlated to the freshwater supply from the Lake IJssel (van Aken, 2008*a*). After the closure of the Afsluitdijk in 1932 the variability of the salinity more than doubled, this was most likely caused by the reduction of the buffer volume between the river IJssel and the Marsdiep tidal basin (van Aken, 2008*a*). The water discharge from the lake in turn is dependent on the precipitation in the catchment area of the rivers Rhine and IJssel. Over the course of our study period the freshwater discharge showed annual variability, most likely connected to precipitation, but the overall trend in discharge stayed constant (Jager and Bartelds, 2002).

9.2.2 *Nutrients*

In Chapter 2, the compilation of the nutrient budgets of the western part of the Dutch Wadden Sea for the period 1974-1993, done by Philippart et al. (2000), is updated. Philippart et al. (2000) observed a shift in the most limiting nutrient for phytoplankton growth in 1976/1978 (from N to P) and in 1987/1988 (from P to N) during a period of eutrophication followed by nutrient reduction. The residual flux of the nitrogen budget was negative after 1978, which was explained as the result of enhanced benthic denitrification through increased deposition of phytoplankton biomass, whilst the residual flux of phosphorus was positive (additional import) during the full study period. Based upon the information on nutrient budgets and phytoplankton species composition, Philippart et al. (2000) divided the study period (1974-1993) into three periods:

- 1974-1976 (low phytoplankton biomass; P-limited phytoplankton growth),
- 1978-1987 (high phytoplankton biomass; N-limited phytoplankton growth) and
- 1988-1993 (high phytoplankton biomass; P-limited phytoplankton growth).

The updated time series, covering the period between 1976 and 2012, revealed that the budget of phosphorus (P) was closed from 1992 onwards by a net loss (additional export) instead of a net gain (Chapter 2). This finding led to the hypothesis that the recent net loss in P is caused by depletion of P previously stored in the sediment during a period of eutrophication and enhanced sediment import into the Wadden Sea to fill in former gullies. Based upon the information on nutrient budgets, it was concluded that the study period (1976-2012) could be divided differently into three periods, namely:

- 1976-1980 (net import of both phosphorus and nitrogen; storage of phosphorus and, to a lesser degree, nitrogen into the sediment),
- 1981-1991 (net import of phosphorus and net export of nitrogen; release of phosphorus and nitrogen from the sediment), and
- 1992-2012 (net export of both phosphorus and nitrogen; depletion of P-stores and continuation of denitrification).

9.2.3 *Primary production*

Since the subdivision of the Zuiderzee by the Afsluitdijk into a freshwater basin (Lake IJssel) and a coastal intertidal area (the western part of the Dutch Wadden Sea), the freshwater inflow into the coastal system is regulated by sluices which discharge only around low water (van Aken, 2008*a*). This inflow not only supplies the system with freshwater but also with nutrients (Chapter 2) and organic material (Cadée, 1982).

The observed long-term changes in the nutrient budgets will have an impact on the productivity of the system as nutrients are direct drivers for primary production of phytoplankton (Cadée and Hegeman, 1974*a*; Cadée and Hegeman, 1974*b*; Philippart et al., 2000; Cadée and Hegeman, 2002). Studies on long-term changes in pelagic and benthic microalgae showed that biomass and primary production generally increased when nutrient inputs increased and decreased when external nutrient supplies were reduced (Philippart et al., 2000; Cadée and Hegeman, 2002; Philippart et al., 2010; Jacobs et al., 2020). The decrease in phytoplankton biomass and production, however, did not directly follow the decrease in nutrients (Cadée and Hegeman, 2002; Jacobs et al., 2020), which might now be explained by storage and release of nutrients in the sediment keeping local nutrient concentrations relatively high when nutrient inputs were lowered (Chapter 2).

In the 1980s and 1990s, the enhanced supply of nutrients into the system led to an enhanced primary production of marine phytoplankton. This enhanced primary production of marine phytoplankton may have led to a food supply that was sufficient to support the local secondary production. In recent years, lower biomass and production of phytoplankton blooms in spring and especially in autumn (Philippart et al., 2010; Jacobs et al., 2020) may have indicated a lower food supply by marine algae. There are studies suggesting that estuaries can be fueled by freshwater microalgae transported along rivers (Fry, 2006;

Antonio et al., 2010) and that this may also play a major role within the western Dutch Wadden Sea (Cadée, 1982), however, the import and use of freshwater microalgae are so far mostly ignored when exploring the importance of various food sources for macrozoobenthos including suspension-feeding bivalves (Hummel, 1985; Kamermans, 1994; Christianen et al., 2017).

Stable isotope analysis of bivalves and of the various food sources indicated that freshwater algae in the form of suspended organic matter (SPOM) are used by the bivalve species of the Balgzand (Chapter 7). The highest import of chlorophyll a from Lake IJssel into the western Wadden Sea was in autumn in 2014, supplying the system with an alternative food source in a time were the production of marine phytoplankton was reduced. This means that there is a possibility that bivalves hardly fed on freshwater algae in former years, which would explain why freshwater algae were barely found in bivalve stomach contents at that time (Hummel, 1985; Kamermans, 1994).

9.2.4 *Macrozoobenthos*

Between 1975 and 2014, several taxonomic groups of the macrozoobenthic community changed in biomass and abundance (Chapter 5). Polychaetes almost tripled in biomass from the mid-1970s to the early/mid-2000s, predominantly due to the invasion of *M. viridis* in 1982, and decreased again after this peak. Bivalve biomass almost doubled in the early 1980s and remained generally high hereafter (but strongly variable) until a decrease in the early 2000s. The unprecedented low bivalve biomass in the early 1990s is considered to result from a combination of overfishing and low recruitment of blue mussels and cockles (Dankers and Zuidema, 1995; Beukema and Cadée, 1996; Dankers et al., 2003). Observed changes in bivalve biomass can also party be attributed to historical and more recent invasions by relatively large and long-lived species (*M. arenaria* in the 13th or 14th century, *E. leei* in 1982, *M. gigas* in 2001) which are responsible for the peak in biomass in the mid-2000s (Chapter 5). After an initially high biomass of these invaders, they all decreased in biomass in recent years (Rob Dekker, NIOZ; pers. com.), which corresponds with the normal pattern of typical invasions (Reise et al., 2006). Based upon the biomass of the invasive bivalves and polychaete, the long-term dynamics within macrozoobenthic community at Balgzand can be roughly split up into four decades, namely:

- the 1980s, when *E. leei* (1982) and *M. viridis* (1989) were introduced, but their biomass was still low;
- 1990s, when biomass of the invaders was increasing (*E. leei*, *M. viridis*);
- the 2000s, when *M. gigas* (2001) was introduced and all three of invaders reached their peak biomass;
- the 2010s, characterized by a decline in the biomass of the macrozoobenthos as the three invaders reached their lag-phase.

9.2.5 *Fish and epibenthic community*

With respect of the fish community, a shift from cold water to warm water species was found between 1960 and 2011, as well as an increase in some rare fish species (Chapter 4). Simultaneously, a 10-fold decrease in total fish biomass from the 1980s to 2014 could be observed. This is in accordance with other observations on fish dynamics within the Wadden Sea (Tulp et al., 2008). This decrease in biomass was also observed for the juvenile plaice (Pleuronectes platessa) and flounder (*Platichthys flesus*, Chapter 5), that were using the Balgzand as a nursery area (van der Veer et al., 2011). In recent years, this nursery function seemed to have shifted to other areas such as deeper gullies (van der Veer et al., 2011). Simultaneously with the decrease in fish biomass and abundance, an increase in crustacean biomass could be observed, especially for the brown shrimp *Crangon crangon* (Chapter 5). This increase was also observed for subtidal areas and the North Sea coast (Tulp et al., 2012; Temming and Hufnagl, 2015). Whilst in the Balgzand intertidal the epibenthos was characterized by a high biomass of juvenile plaice and flounder in the 1980s, nowadays (2010) the brown shrimp and gobies dominate this community.

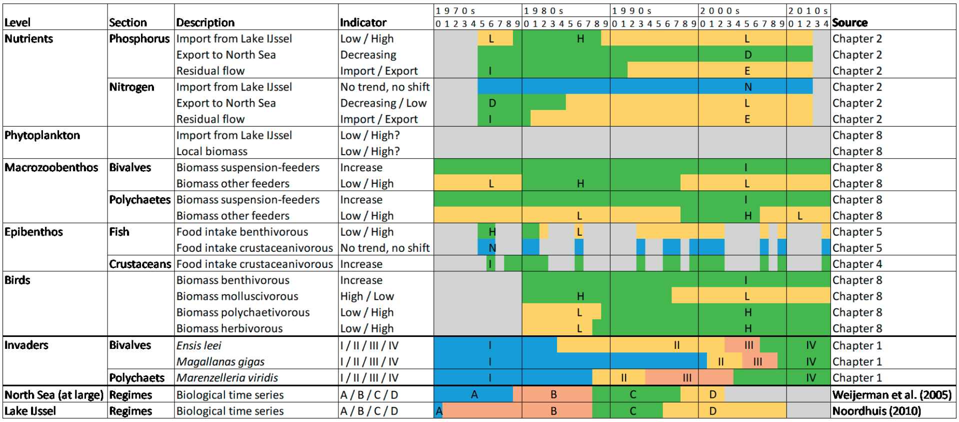
9.2.6 *Birds*

Long-term changes in wading birds were not explicitly studied in a separate chapter of this thesis, however as a main predator on the intertidal mudflats they are an important component of the ecosystem. Their abundance and distribution is highly dependent on the availability of food resources in the Wadden Sea (van der Zee et al., 2012; de Fouw et al., 2020). The long-term trends of the wading birds indicated a decline of many shellfish eating species in the early 1990s (e.g. Common Eider - *Somateria mollissima*, Oystercatcher - *Haematopus ostralegus*, Knot - *Calidris canutus*, and Herring Gull- *Larus argentatus*; van Roomen et al., 2005), most likely due to the disappearing of blue mussel and cockle beds in the early 1990s (Beukema and Cadée, 1996). However, most bird species feeding in the Wadden Sea are migratory species and they might not be affected by the events in the Wadden Sea as much as species that are feeding in the area all year around. This would be due to lower competition in other areas within their migratory route (Rakhimberdiev et al., 2015). The decrease in numbers of shellfish eating birds was contrasted by the positive trends in worm-eating species (e.g. Avocet - *Recurvirostra avosetta*, Dunlin - *Calidris alpina*, and Bar-tailed Godwit - *Limosa lapponica*, Leopold et al., 2004; van Roomen et al., 2005). Even after the shellfish population increased again after 1990, most shellfish-eating birds remained declining in numbers in the western Wadden Sea (Ens et al., 2009). On the other hand, species with a worm-dominated diet continued to increase in numbers after 1990, for species with a mixed diet contrasting trends have been found (Ens et al., 2009).

9.2.7 *Invasive species at Balgzand*

The Balgzand ecosystem was already subject to major changes in external drivers before *E. leei*, *M. gigas* and *M. viridis* were detected and became invasive (see also Fig. 9.1), such as enhanced riverine nutrient import in the 1980s (Chapter 2) and habitat destruction (Chapter 4). Biological changes in the North Sea ecosystem (1970-2002) at large scale (including the Wadden Sea) in 1978/'79, 1987/'88 and 1997/'98 were attributed to shifts in environmental conditions (e.g. salinity, temperature and weather) that occurred one year earlier than the biological shifts (Weijerman et al., 2005). Biological shifts in the adjacent Lake IJssel (1959-2009) were attributed to an increase in phosphate and a reduction in fisheries (1970/'71), a decrease in phosphate and a shift in climate (1987/'88), 1995/'96 (an increase of fisheries and more frequent occurrence of climate extremes) and 2000/'04 (decrease in fish stocks and further reduction of phosphate concentrations Weijerman et al., 2005; Noordhuis, 2010).

The Pacific oyster (*M. gigas*) combines several traits that are considered important factors for a successful invader. They have a long lifespan (up to 10 years, Cardoso et al., 2007), a high fecundity with over 50 million eggs per spawning (Helm, 2004), and mature after about one year (Kobayashi et al., 1997). Additionally they have a wide tolerance for environmental conditions. They can survive in salinities between 10 and 30 PSU, can tolerate temperatures between -5 and $40\,^{\circ}\mathrm{C}$ (Shamseldin et al., 1997). Due to their hard shell, big size and attachment to hard substrate they are also considered to lack natural predators (Troost, 2010).



Level	Section	Description	Indicator	1970s	1980s	1990s	2000s	2010s	Source
				0 1 2 3 4 5 6 7 8 9	0 1 2 3 4 5 6 7 8 9	0 1 2 3 4 5 6 7 8 9	0 1 2 3 4 5 6 7 8 9	0 1 2 3 4	
Nutrients	Phosphorus	Import from Lake IJssel	Low / High	L	H		L		Chapter 2
		Export to North Sea	Decreasing				D		Chapter 2
		Residual flow	Import / Export	I			E		Chapter 2
	Nitrogen	Import from Lake IJssel	No trend, no shift				N		Chapter 2
		Export to North Sea	Decreasing / Low	D			L		Chapter 2
		Residual flow	Import / Export	I			E		Chapter 2
Phytoplankton		Import from Lake IJssel	Low / High?						Chapter 8
		Local biomass	Low / High?						Chapter 8
Macrozoobenthos	Bivalves	Biomass suspension-feeders	Increase				I		Chapter 8
		Biomass other feeders	Low / High	L	H		L		Chapter 8
	Polychaetes	Biomass suspension-feeders	Increase				I		Chapter 8
		Biomass other feeders	Low / High		L		H	L	Chapter 8
Epibenthos	Fish	Food intake benthivorous	Low / High	H	L				Chapter 5
		Food intake crustaceanivorous	No trend, no shift	N					Chapter 5
	Crustaceans	Food intake crustaceanivorous	Increase	I					Chapter 4
Birds		Biomass benthivorous	Increase				I		Chapter 8
		Biomass molluscivorous	High / Low		H		L		Chapter 8
		Biomass polychaetivorous	Low / High		L		H		Chapter 8
		Biomass herbivorous	Low / High		L		H		Chapter 8
Invaders	Bivalves	*Ensis leei*	I / II / III / IV	I		II	III	IV	Chapter 1
		Magallanas gigas	I / II / III / IV	I			II III	IV	Chapter 1
	Polychaets	*Marenzelleria viridis*	I / II / III / IV	I		II III		IV	Chapter 1
North Sea (at large)	Regimes	Biological time series	A / B / C / D	A	B	C	D		**Weijerman et al. (2005)**
Lake IJssel	Regimes	Biological time series	A / B / C / D	A	B	C	D		**Noordhuis (2010)**

Figure 9.1: Overview of food web dynamics at the Balgzand tidal flats and adjacent systems (North Sea, Lake IJssel) between 1970 and 2014 as described in different chapters of this PhD thesis (see Figure 9.2 for more detail on the invasive macrozoobenthic species). Information on regime shifts in other waters is taken from Weijerman et al. (2005); Noordhuis (2010). First letters of indicators were used to mark periods were necessary.

The Pacific oyster was first found on the Balgzand in 2001, started to exponentially increase in 2005, reached peak biomass in 2008, after which the biomass declined again (Fig. 9.2). In the early days of the invasion by the Pacific oyster, it was feared that they might replace the traditional beds of blue mussels in the Wadden Sea (Fey et al., 2010). Nowadays, both species occupy the same reefs and thereby form a new unique community (Eschweiler and Christensen, 2011).

Similar to the Pacific oyster the American razor clam (*E. leei*) shows several, although a bit different, traits that make it a successful invader. It is a long living (up to 20 years, von Cosel, 2009) bivalve, that reproduces twice a year (Cardoso et al., 2009). It can withstand salinities between 7 and 32 PSU (Maurer et al., 1974) and prefers living along the edges of tidal flats. These areas are often associated with high currents which razor clams can deal with as they are highly mobile (Dekker and Beukema, 2012). The border between subtidal and intertidal was not really occupied before the invasion of *E. leei*, it therefore seems to occupy an ecological niche not fully occupied before in the western Dutch Wadden Sea (Dekker and Beukema, 2012). The American razor clam was first detected in 1984 on the Balgzand and was then first found in relative low biomass in the area until a rapid increase started 2005 followed by a peak in 2008 where after the biomass decreased again (Fig. 9.2). The American razor clam became the dominant species in the transition zone between the subtidal and intertidal at the northern border of the Balgzand (Dekker and Beukema, 2012). Because this area is only occasionally falling dry during low tide, it is less accessible as as foraging ground for wading birds reducing the probability of predation on these clams (Freudendahl et al., 2010).

The polychaete *M. viridis* is considered to be a brackish species and has a salinity tolerance between 0 and 32 PSU with an optimum between 3.5 and 25 PSU (George, 1966; Bochert et al., 1996; Daunys et al., 2000; Kauppi et al., 2015). It can live in a wide temperature range (0 to 30 °C, George, 1966; Bochert et al., 1996) and has a high tolerance for low oxygen conditions, which allows it to live in deeper sediments then other species on the tidal flats (Bochert et al., 1997; Daunys et al., 2000). This might also affect their availability as a food source for other predators such as fish and birds (Bochert et al., 1997; Zettler, 1997). As the other two invasive species *M. viridis* has a high fecundity (10000 - 46000 eggs per female per spawning period), for a polychaete it has a relatively long life span of 2 to 3 years (Zettler, 1997). Within the Balgzand tidal flat system, the polychaete *M. viridis* was first found in 1989, showing a consistent increase from 1993 (although really low in the first few years) to a maximum in 2003, after which it decreased again (Fig. 9.2).

In recent years there have been records of another invasive bivalve, the dwarf surf clam (*Mulinia lateralis*), that has been found within the Wadden Sea and also on the Balgzand it self (Klunder et al., 2019). This species has only been found occasionally so far but due to its biological traits it has the potential to be the next successful invader in the system (Craeymeersch et al., 2019; Klunder et al., 2019). One of the main differences between the dwarf surf clam and the two invasive bivalves included in this study is that it has a relativly small maximum size and therefore could be considered as a potential food source for birds in the system during its whole life cycle (Craeymeersch et al., 2019). This could hamper the invasive success of the species.

9.3 IMPACT OF INVASIVE SPECIES BY MEANS OF ECOLOGICAL NETWORK ANALYSIS

Based upon the availability of the data sets, in combination with the observations with respect to changes (shifts) in the time series and the timing of the phases of the invasive species under consideration, it was decided to use decades as a marker to separate the different ENA models. Although most changes seem to switch stages close to the change in decades, this was not always the case but it considered to be close enough in most of the cases to justify this decision. At least one major change happening at the change of each decade and the three main invaders in the area show the different stages of invasions within the different decades.

The way ENA models are constructed allows to estimate the impact that one species has on the other compartments in the model by means of the carbon flow in the system. The results in the model of the 2000s, when this invasive species was first found and reached its peak biomass, indicated that *M. gigas* enhanced the carbon flow to benthic bacteria and benthic detritus feeders such as *Arenicola marina*, *Heteromastus filiformis* and *Scoloplos armiger* (Chapter 8).

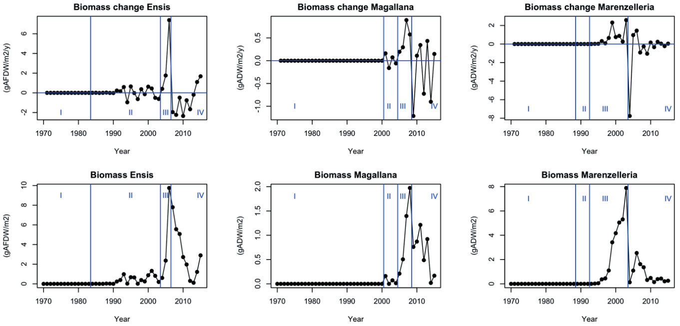


Figure 9.2: Change in biomass (top panels) and total biomass (lower panels) of three common macrozoobenthic invaders at the Balgzand intertidal in winter from 1970 to 2014 (unpublished data from R. Dekker). Roman numbers indicate phases of invasive species (c.f. Reise et al., 2006), being (I) before arrival (or before detection), (II) after arrival & during establishment, (III) consistent (exponential) increase in biomass, and (IV) adjustment with a decline after the peak (see Chapter 1)

For the Pacific oyster, the results of the Lindeman spine indicate that the carbon transfer efficiency from trophic level I (primary producers) to trophic level II (grazers) is the highest (86.8%) in the 2000s compared to the other decades, whilst it is the lowest (16.1%) in that decade for the carbon transfer efficiency from trophic level II to III (Chapter 8). These findings indicate that the relatively high amount of carbon that is being grazed (amongst others by the three invasive species) is not efficiently transferred further up the food chain (e.g. benthic feeding fish and birds). As the Pacific oyster barely had any predators in the Wadden Sea after settling (Cadée, 2001, 2008; Troost, 2010), the carbon produced and used by this species is mostly either exported (when the animals are fished) or transferred back into detritus pool (when the animal dies locally) instead of being transported further along the food chain (when the animal is eaten by local predators). Although the impact calculated by the ENA model was not that high (positive or negative), the Pacific oyster might still have changed the ecosystem and food web in a way that is not considered in the ENA models because the sampling program on macrozoobenthos used for this study does not focus on reef-forming bivalves (Beukema and Dekker, 2007). Furthermore, the extensive reefs formed by *M. gigas* influence especially the direct environment surrounding these reefs (Jones et al., 1994; Gutiérrez et al., 2003).

E. leei had a negative impact on almost all other compartments included in the ENA model, in particular on pelagic coastal microalgae and pelagic bacteria (Chapter 8). With respect to the impact on other primary consumers (tropic level II), this species had the most negative impact on the suspension-feeding *Lanice conchilega*. Together with the suspension-feeding Pacific oyster, it appeared to have enhanced the uptake of (pelagic) primary producers resulting into a high carbon transfer efficiency from trophic level I to trophic level II (grazers) in the 2000s. With respect to *M. viridis*, the species positively impacted on benthic predators such as *Eteone spp.* and negatively on benthic bacteria and meiofauna due to predator-prey relationships within the 2000s.

9.4 CUMULATIVE EFFECTS OF INVASIVE SPECIES AND OTHER LONG-TERM CHANGES

In principle, concurrent changes in biomass of invasive species and other long-term changes within the Balgzand system may be due to common drivers (e.g. temperature, habitat destruction), food web dynamics (e.g. food availability, competition with other suspension-feeding organisms, predation pressure), habitat dynamics (e.g. bioturbation, habitat provisioning reefs) or coincidental.

When studying causes and consequences of long-term ecosystem changes should, one should take note of actual baselines and not (only) focus on those occurring during the study period, the so-called "shifting baseline syndrome" (Pauly, 1995). Results strongly suggest, for example, that the closure of the former Zuiderzee in the early 1930s impacted the phosphorus budget and subsequently food web dynamics until the early 1990s (Chapter 2). Furthermore, the two introductions of the bivalve *M. arenaria* (more than 1 million and more than 700 years ago) made it the most dominant suspension-feeding bivalve species in recent times, occupying a niche that can obviously not be taken by any other benthic organism (Chapter 8).

The coinciding changes in the western Wadden Sea and adjacent waters (North Sea, Lake IJssel) during the last decades, however, strongly suggest that environmental conditions with respect to salinity, nutrient availability and temperature played a role in shaping the Balgzand ecosystem and subsequently the potential of new species to become invasive. For example, the average increase in water temperatures since the late-1980s might have promoted the recruitment success of the warm-water Pacific oyster (Troost, 2010). If the increase in water temperatures enhanced the occurrence of hypoxia in time and space, this might have promoted the survival of *M. viridis* which is able to withstand stressful environmental conditions such as low oxygen (Bochert et al., 1997).

Within the study period, the Balgzand area was impacted by eutrophication with enhanced imports of nutrients (in particularly phosphorus) from Lake IJssel and the North Sea coastal zone in the 1970s and 1980s (Chapter 2). This nutrient increase resulted in a doubling of biomass and primary production by estuarine phytoplankton (de Jonge, 1990). After nutrient imports were reduced in the late 1980s, phytoplankton biomass and production stayed relatively high (de Jonge, 1997; Jacobs et al., 2020). This ongoing enhanced local biomass production by estuarine microalgae until the mid-1990s was probably nourished by the release of nutrients previously stored into the sediment of the western Wadden Sea (Chapter 2, van Beusekom et al., 2019). Nutrient burial was likely enhanced by the relatively high sediment import from the North Sea needed to fill in the former gullies of the Zuiderzee (Chapter 2) until net sedimentation changed into net erosion after 2000 (Elias et al., 2012).

The occurrence of the expansion phases of the invaders happened after this period of eutrophication, i.e. when the import of nutrients from external sources (Lake IJssel, North Sea) and the release from the sediment were relatively low again (Chapter 2; Fig. 9.3). No longer fueled by enhanced nutrient supply, local biomass and production of estuarine phytoplankton went down (Jacobs et al., 2020) as most probably that of microphytobenthos did as well. From 1987 to 2008, summer phytoplankton biomass in Lake IJssel stayed more or less the same in spite of the reduction in phosphate concentrations (Noordhuis, 2010). If freshwater discharge from Lake IJssel was more or less constant in time (Jager and Bartelds, 2002), than freshwater algae must have become relatively more important as a potential food source for estuarine herbivore macrozoobenthos. This suggestion is in line with findings that the estuarine food web was strongly supported by freshwater algae in 2014, whilst there was no indication for this from previous studies on bivalve diets (Chapter 7).

The success of the invasive suspension-feeders may be explained if they are better competitors for freshwater algae than the native suspension-feeding bivalves (Figure 9.3). The Pacific oyster was indeed found to have the highest proportion of freshwater algae in its diet during all seasons compared to three native suspension-feeding bivalve species (Chapter 7). The success of the American razor clam might be partly due to the fact that its highest densities are found at the transition zone between the subtidal and intertidal at the northern border of the Balgzand (Dekker and Beukema, 2012), where freshwater algae will be transported to first (Duran-Matute et al., 2014). Because *M. viridis* is relatively tolerant to brackish waters (Blank et al., 2004), it may continue feeding when other benthic organisms close down their filtering activities when freshwater patches pass, and subsequently take more advantage from freshwater algae as a food source.

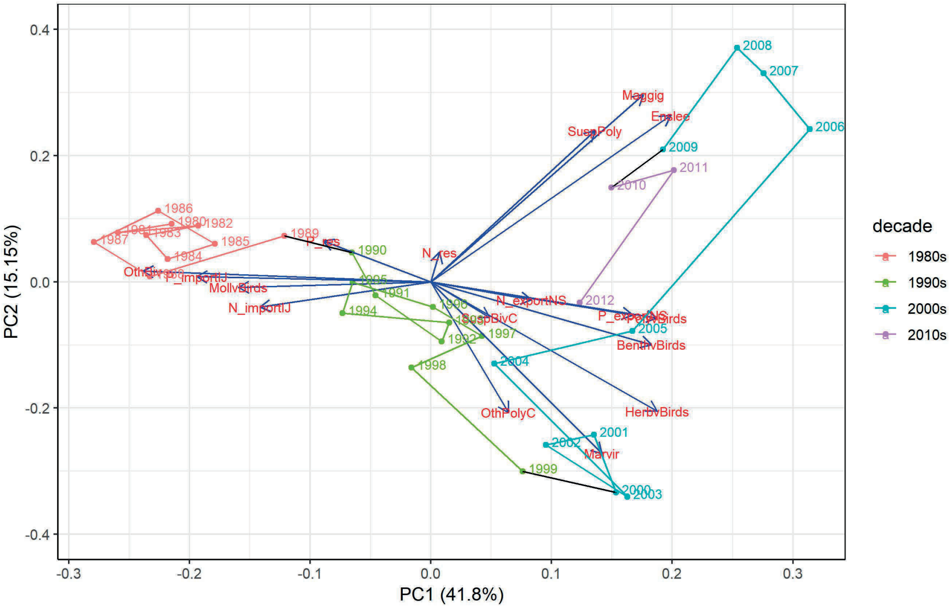


Figure 9.3: PCA of normalized time series on nutrient dynamics (Chapter 2), biomass of macrozoobenthic feeding guilds, biomass of invasive species and bird biomass (Chapter 8) from 1980 to 2012

Potential invasive success of introduced species may be hampered if predation pressure is high. Within the western Wadden Sea between 1975 and 2014, a shift in macrozoobenthic and epibenthic predators was observed from juvenile flatfish that feed mainly on small macrozoobenthos (including small bivalves and polychaetes) to gobies and shrimps that feed mainly on small crustaceans (Chapter 5; Fig. 9.3). This change occurred more or less simultaneously with an increase in food availability for juvenile flatfish, partly due to the increase in the invasive *M. viridis* (Chapter 5). This suggests that the decline in juvenile flatfish abundance and biomass was not primarily due to food limitation and that the increase in *M. viridis* may be partly explained by a release in predation pressure. However, the observed reduction of summer growth in the remaining juvenile plaice was attributed limited macrozoobenthic prey availability, although most probably due to reduced activity of lugworms (reducing the accessibility of their tails as prey items) than the abundance of polychaetes (Chapter 6).

With respect to waders (birds that feed on the tidal flats during low tide), predation pressure on invasive bivalves may be limited if they are too strongly attached to each other (*M. gigas*), burrowed too deep in the sediment to be reached (*E. leei*) and/or of a size too big to be ingested (both species). The most dominant bird species that generally decreased (Oystercatcher) or increased (Eurasian curlew) over time are not considered to be important predators on the invasive bivalves and polychaete, respectively (Chapter 8).

As indicated in 9.2, however, the 2000s (when peaks in invasive species occurred) were characterized by a relative low trophic transfer from primary to secondary consumers which might be due to a relative low predation pressure on the invasive species resulting from low abundance of their predators such as juvenile flatfish and/or low accessibility for their predators such as waders (Chapter 8).

In this study, several organisms and trophic guilds appeared to effect each other in the long-term but it should be noted that these time series are only a selection of the full Balgzand ecosystem. The majority of the food web is studied less intensely, such as the sediment particulate organic carbon (POC), bacteria and meiofauna. A few studies have been conducted in the 1980s, but since then they have been mostly ignored. Also the smaller part of the pelagic food web, the zooplankton, has not been included in any long-term studies. This implies that potentially important information about our food web is missing, and even some major changes may not be represented in our study.

9.5 COMPARISON WITH INVASIONS IN OTHER AREAS

The three invasive species studied in this project were mostly also invaders in the rest of the Wadden Sea (Essink, 1998; Troost, 2010; Tulp et al., 2010; Reise et al., 2017) although with different timings. The introduction of the Pacific oyster took place in the late 1970s early 1980s, however they were often first detected in the 1990s at different sites (Troost, 2010). In the Sylt-Rømø Bight the Pacific oyster was first found in 1991 and had a lag phase of about 15 years (Reise et al., 2017) which is about 10 years longer than what we observed for the Balgzand. The reason for this difference is not fully clear, however it might be that especially climate conditions (high summer temperature, mild winters) were favorable at the Balgzand in the early years of the invasion (Beukema and Dekker, 2011), additionally the surrounding area has been invaded for a longer time (Troost, 2010), both these factors could be responsible for shortening the lag phase in this area. The timing of the exponential phase in the Sylt-Rømø Bight was more or less the same as we found for the Balgzand, although slightly longer (from 2001 to 2007). Although a subsequent decrease in numbers has been observed for the years 2007 till 2010, a second exponential growth has been found for the Sylt-Rømø Bight in the years 2011 till 2017 (Reise et al., 2017). For the Balgzand the decrease after the peak in 2008 was not followed by a second exponential growth but year to year variation in biomass has still been present.

Although the American razor clam is subject to many studies (Freudendahl et al., 2010; Dannheim and Rumohr, 2012; Schwemmer et al., 2019), long-term data set about population dynamics are rare (Tulp et al., 2010). The population dynamics found for the rest of the Dutch coastline in the years 1995 to 2008 follow a similar pattern as the ones found for the Balgzand (Tulp et al., 2010). However, this series ends before the peak of the population at Balgzand was reached making a comparison difficult.

The polychaete *M. viridis* has been found in the North Sea, the Wadden Sea, including the Ems-Dollard and the Baltic Sea in the early 1980s (McLusky et al., 1993; Essink, 1998). Within the Ems-Dollard the first occurrence was in 1983 (Essink, 1998). Here it showed a lag phase of about 6 years, followed by an exponential growth of another 6 years, making it a total of 12 years till peak densities have been reached (Essink and Dekker, 2002). On the Balgzand we found a shorter lag phase of 3 years followed by a steady increase after this for 11 years. Although in the beginning this increase was rather low (increase $<1\,\mathrm{g\,AFDM\,m^{-2}}$) and it might be up for discussion if these years count into the exponential growth or not. However, this results in a total of 14 years till peak densities were reached, which is similar to what has been found for the Ems-Dollard (Essink and Dekker, 2002). Within the Baltic Sea the population had a longer lag phase of 15 years, followed by a 3 year exponential increase with peak densities in 2009 (Kauppi et al., 2015).

Within the Wadden Sea several ENA models have been constructed for different areas (Baird et al., 2004, 2007, 2008, 2011, 2012; Schückel et al., 2015; de la Vega, 2016; Horn, 2016; de la Vega et al., 2018; de Jonge et al., 2019*b*,*a*), however direct comparison of ENA models is only possible if they were constructed in a similar way. This is especially true for the construction and selection of the compartment structure and the selection of which species/compartments to include. As a consequence many of the published studies are difficult to compare to the results in Chapter 8. The only studies of the ones listed above that can be used for comparison as it was constructed in a very similar way is the one by Baird et al. (2012). The models of Horn (2016); Schückel et al. (2015) are missing the epibenthic compartments, the one form de la Vega (2016) includes seals and more of the pelagic food web than the models constructed in this study. In a comparison paper new models for these areas have been constructed to make them more comparable. These new models however have summarized many species into higher order compartments for this purpose (de la Vega et al., 2018). Even though this means we can not directly compare the ENA indices of the Balgzand models with the other ENA models form the Wadden Sea we can still compare the main trends within the biomass of the different species and how invasive species developed in the different areas. The invasive species *M. gigas* and *E. leei* had a higher biomass in the Sylt-Rømø-Bight than in the Jade Bay, leading to a more specialized system, vulnerable to disturbances in the Sylt-Rømø-Bight (Schückel et al., 2015; de la Vega, 2016).

The results of our study line up with some of the results of the study by Baird et al. (2012). They also found an increase in trophic efficiency of trophic level I in the presence of two of the invasive species we looked at in Chapter 8.

9.6 FUTURE PERSPECTIVES

Overall the results of this thesis cover a huge part of the Balgzand food web and the development that happened over the last decades. But as the natural world is complex and the included parts do not cover everything there are still open questions and areas for improvement.

As pointed out above we are missing some important parts of the food web in the extensive list of long-term series conducted on the Balgzand. To close these open areas the long-term series should be extended to these parts of the food web to make sure that future models will be able to include measured values instead of estimations. However, financial resources are limited and measuring everything is not feasible. Therefore it is important to carefully consider the questions that could be answered by obtaining certain information. The missing information for building the full ENA models are mainly at the basis of the food web, including bacteria, meiofauna and zooplankton. All three of these are considered to be part of the diet of at least one of the three invasive species included in this study. This means we can only partly explain the patterns we see in the population dynamics of the invasive species as we are missing essential information about their food availability. For most cases it is still unclear what exactly triggered the onset of the exponential growth and the subsequent decline in biomass of the three invasive species Essink and Dekker (2002); Reise et al. (2017) and food availability might be an important factor for this. But not only are the missing parts of the food web an important part for future studies. Also the comparison of models from different areas should be tried to achieve. For this the construction of ENA models should follow a defined set of steps to make different models more comparable to each other.

Because the natural habitat of the Pacific oyster has much higher water temperatures, the recruitment of the Pacific oyster is higher in mild winters and warm summers than in cold ones (Fey et al., 2010). This could be important in lights of climate change and the potential occurrence of higher temperatures in the future. In the light of climate change, temperature and the tolerance and reproductive capacity in higher temperatures might start to be more and more important. This might allow the three invasive species included in this study to increase again and further dominate the system. However, it might also lead to more invasions (supported by global trading) and disappearance of species that are not as tolerant to warm temperatures. Additional a warm climate might also lead to more rain that could lead to lower salinities in coastal areas, further promoting the abundance of invasive species tolerant to low salinities such as *M. viridis*.

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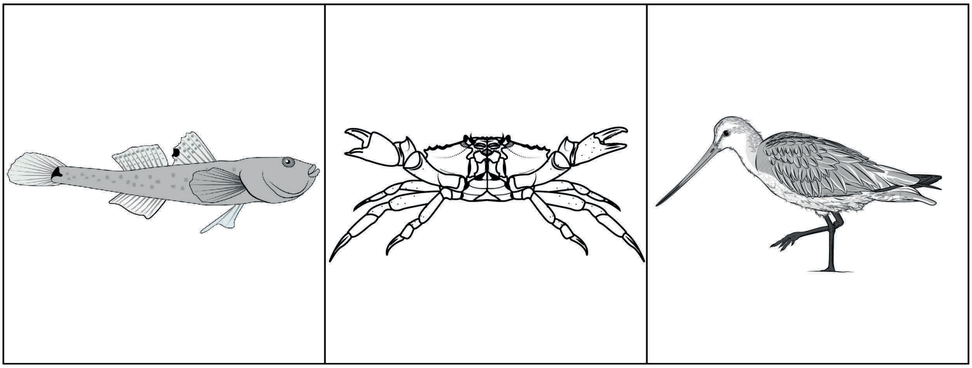

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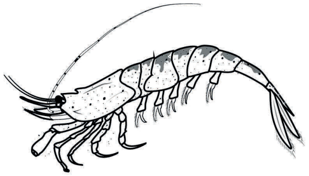
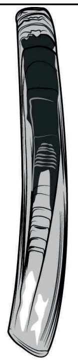
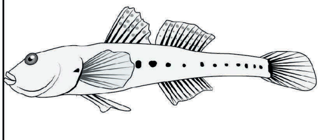
APPENDICES

A

PREDICTION OF PHOSPHOROUS AND NITROGEN DATA FOR MISSING STATIONS

In Chapter 2 we estimated phosphorus concentrations at several stations by applying models, the results and validations for phosphorous and nitrogen are shown within this supplementary material.

Table A.1: Model summary of the GAM model used to predict monthly values for the measurement stations Station b and c as well as Noordwijk and Vrouwezand

	Phosphorous	Nitrogen
(Intercept)	3.12 (0.07)***	69.75 (1.49)***
LocatieNOORDWK2	−0.16 (0.11)	−1.84 (2.16)
LocatieVLIESM	−0.60 (0.11)***	−10.60 (2.27)***
LocatieVROUWZD	2.48 (0.10)***	178.59 (2.24)***
EDF: s(Year):LocatieMARSDND	4.52 (4.89)***	4.06 (4.61)***
EDF: s(Year):LocatieNOORDWK2	4.45 (4.84)***	1.00 (1.00)***
EDF: s(Year):LocatieVLIESM	3.87 (4.46)***	4.20 (4.71)***
EDF: s(Year):LocatieVROUWZD	4.97 (5.00)***	4.65 (4.93)***
EDF: s(yday):LocatieMARSDND	2.09 (8.00)***	3.26 (8.00)***
EDF: s(yday):LocatieNOORDWK2	2.57 (8.00)***	3.24 (8.00)***
EDF: s(yday):LocatieVLIESM	3.75 (8.00)***	4.94 (8.00)***
EDF: s(yday):LocatieVROUWZD	7.08 (8.00)***	7.05 (8.00)***
AIC	8595.50	21961.46
BIC	8813.60	22174.33
Log Likelihood	−4259.45	−10943.32
Deviance	6213.56	2830326.71
Deviance explained	0.62	0.88
Dispersion	2.88	1315.46
R^2	0.61	0.88
GCV score	2.93	1337.71
Num. obs.	2197	2188
Num. smooth terms	8	8

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Table A.2: Model summary of the phosphorous predictions for Station a from Noordwijk and Stations d and e from Vrouwezand

	Stat. a	Stat. d	Stat. e
(Intercept)	2.96 (1.14)*	3.57 (0.72)***	3.53 (0.82)***
NOORDWK2	0.82 (0.17)***		
factor(Month)2	−2.03 (1.03)	0.75 (0.87)	−1.34 (1.01)
factor(Month)3	−2.94 (1.06)**	−0.34 (0.75)	−1.08 (0.87)
factor(Month)4	−2.67 (1.22)*	−1.22 (0.75)	−2.07 (0.84)*
factor(Month)5	−3.07 (1.00)**	−1.60 (0.75)*	−2.51 (0.86)**
factor(Month)6	−3.86 (1.06)***	−0.61 (0.74)	−1.17 (0.87)
factor(Month)7	−3.32 (1.03)**	−0.70 (0.72)	−2.01 (0.83)*
factor(Month)8	−3.12 (1.06)**	0.60 (0.72)	−1.16 (0.83)
factor(Month)9	−3.00 (1.09)**	0.81 (0.74)	−0.62 (0.85)
factor(Month)10	−3.04 (1.04)**	−0.15 (0.73)	−0.45 (0.85)
factor(Month)11	−1.46 (1.14)	−1.52 (0.75)*	−1.90 (0.88)*
factor(Month)12	−3.15 (1.33)*	−1.30 (0.73)	−2.54 (0.85)**
VROUWZD		0.44 (0.04)***	0.53 (0.05)***
R^2	0.48	0.54	0.54
Adj. R^2	0.39	0.51	0.51
Num. obs.	80	183	189

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Table A.3: Model summary of the nitrogen predictions for Station a from Noordwijk and Stations d and e from Vrouwezand

	Stat. a	Stat. d	Stat. e
(Intercept)	10.57 (14.50)	204.42 (26.74)***	164.07 (26.65)***
NOORDWK2	0.78 (0.11)***		
factor(Month)2	−1.77 (11.60)	32.65 (19.74)	14.52 (20.19)
factor(Month)3	−17.98 (12.47)	61.83 (17.74)***	48.12 (18.11)**
factor(Month)4	−9.45 (14.45)	31.90 (16.05)*	31.02 (16.28)
factor(Month)5	−16.10 (11.96)	−0.96 (16.47)	2.38 (16.48)
factor(Month)6	−26.86 (12.66)*	−35.83 (17.54)*	−21.70 (17.87)
factor(Month)7	−16.29 (12.57)	−51.41 (18.23)**	−42.86 (18.49)*
factor(Month)8	−15.70 (13.12)	−80.85 (20.55)***	−69.17 (20.05)***
factor(Month)9	−18.76 (13.46)	−93.18 (20.32)***	−86.15 (20.50)***
factor(Month)10	−16.96 (12.25)	−99.54 (19.50)***	−66.43 (19.74)***
factor(Month)11	6.09 (13.62)	−112.89 (18.38)***	−93.29 (18.87)***
factor(Month)12	−19.01 (15.49)	−70.96 (17.17)***	−72.26 (17.52)***
VROUWZD		0.36 (0.06)***	0.45 (0.06)***
R^2	0.61	0.84	0.83
Adj. R^2	0.54	0.83	0.82
Num. obs.	80	163	170

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

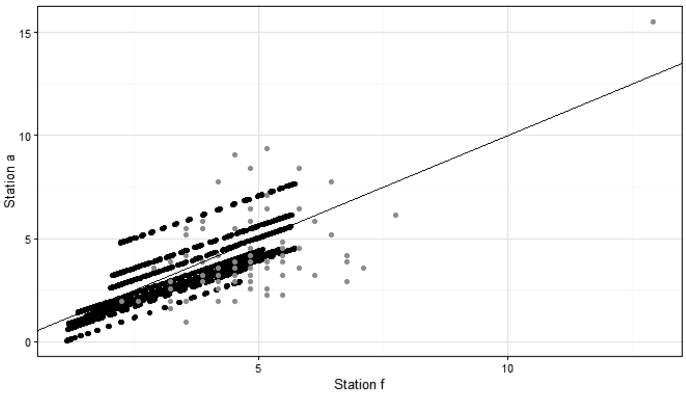


Figure A.1: Observed (grey) and predicted (black) of phosphorous concentrations (mmol P m^{-3}) at Station a and f in years measured at both stations.

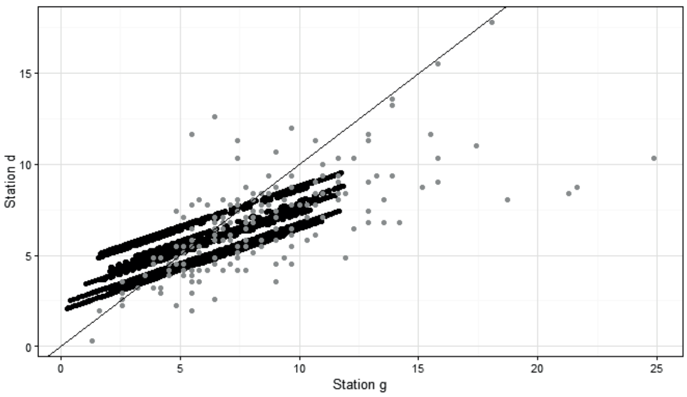


Figure A.2: Observed (grey) and predicted (black) of phosphorous concentrations (mmol P m^{-3}) at Station d and g in years measured at both stations.

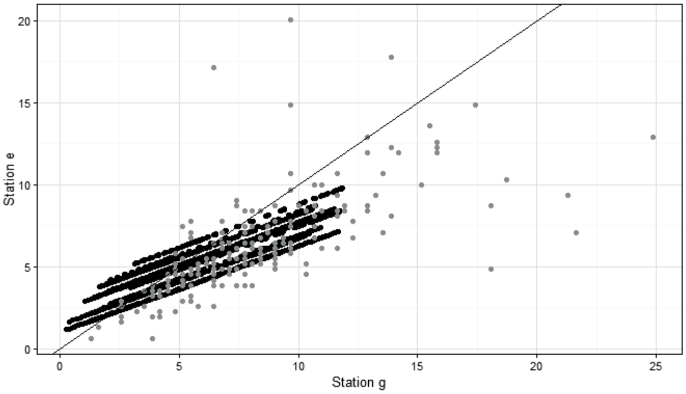


Figure A.3: Observed (grey) and predicted (black) of phosphorous concentrations (mmol P m^{-3}) at Station e and g in years measured at both stations.

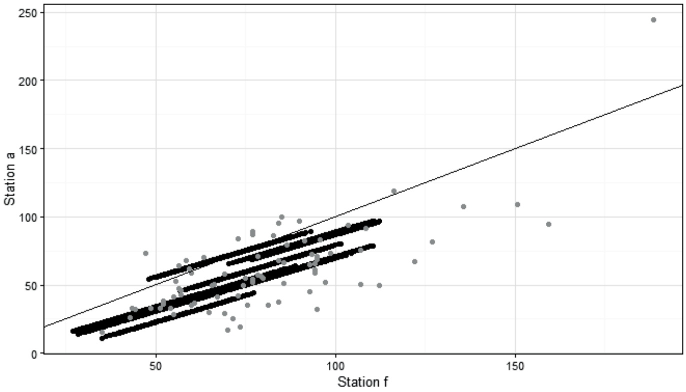


Figure A.4: Observed (grey) and predicted (black) of nitrogen concentrations (mmol N m^{-3}) at Station a and f in years measured at both stations.

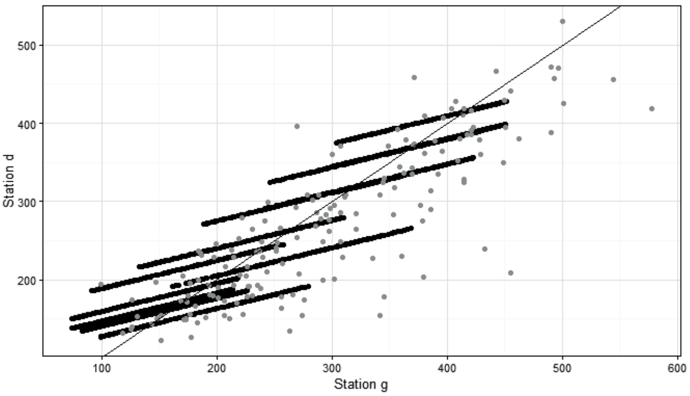


Figure A.5: Observed (grey) and predicted (black) of nitrogen concentrations (mmol N m^{-3}) at Station d and g in years measured at both stations.

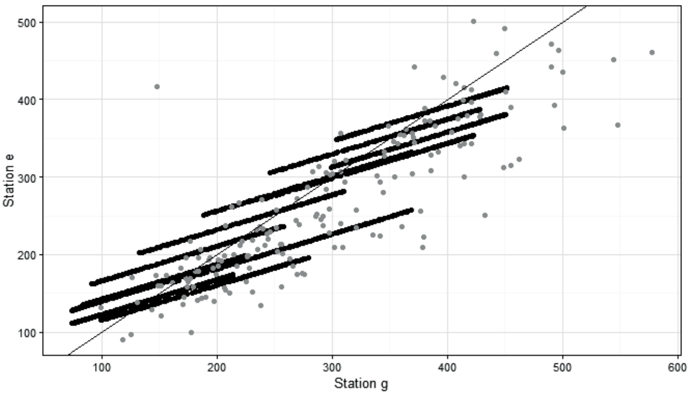


Figure A.6: Observed (grey) and predicted (black) of nitrogen concentrations (mmol N m^{-3}) at Station e and g in years measured at both stations.

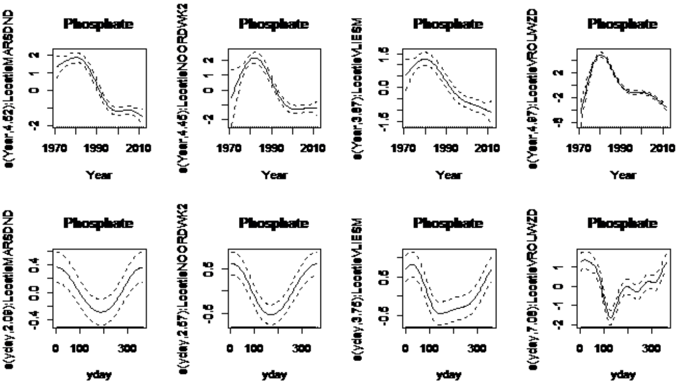


Figure A.7: Modelled year and seasonal trend in phosphorus at different locations.

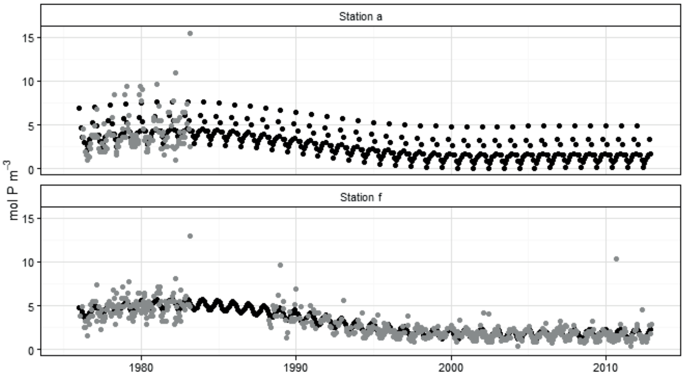


Figure A.8: Observed (grey) and predicted (black) values of phosphorous concentration (mmol P m^{-3}) at Station a and f at the full time series.

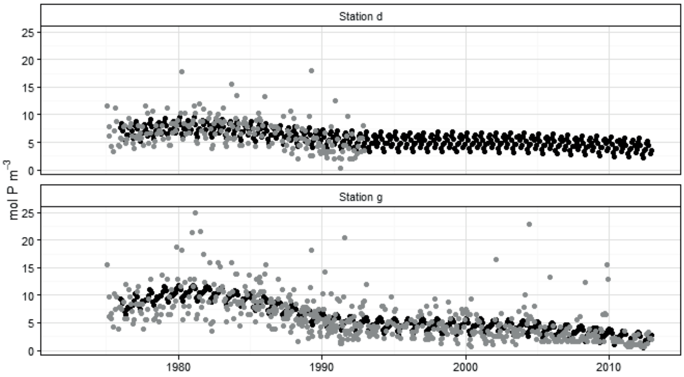


Figure A.9: Observed (grey) and predicted (black) values of phosphorous concentration (mmol P m^{-3}) at Station d and g at the full time series.

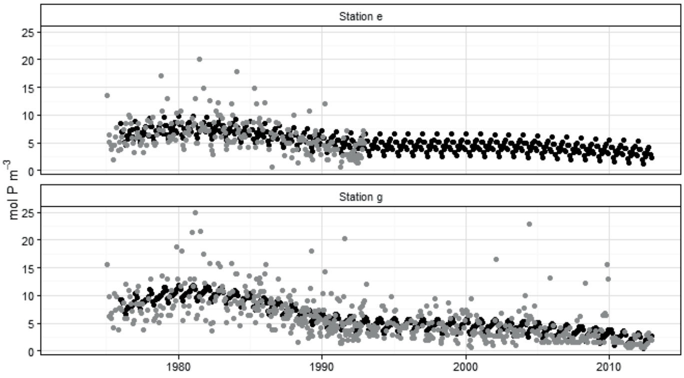


Figure A.10: Observed (grey) and predicted (black) values of phosphorous concentration (mmol P m^{-3}) at Station e and g at the full time series.

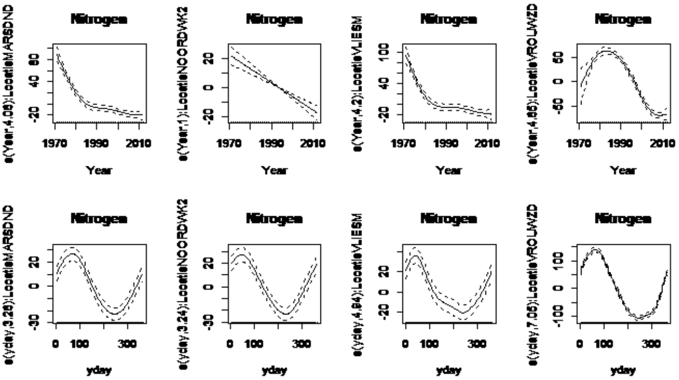


Figure A.11: Modelled year and seasonal trend in nitrogen at different locations.

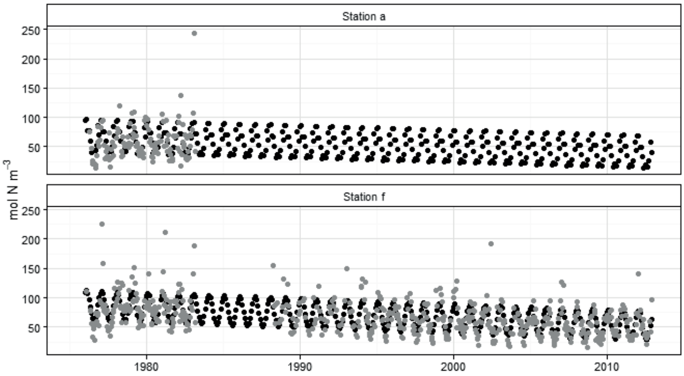


Figure A.12: Observed (grey) and predicted (black) values of nitrogen concentration (mmol N m^{-3}) at Station a and f at the full time series.

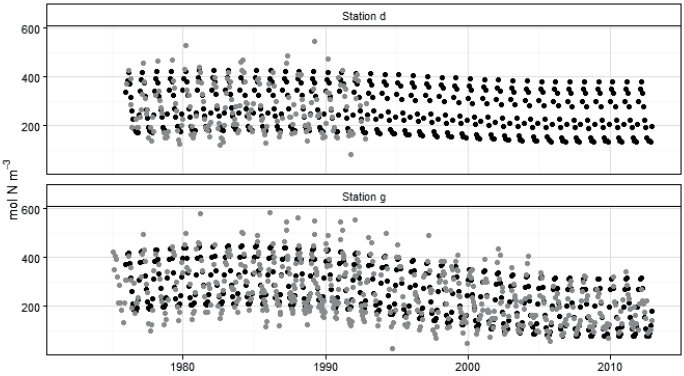


Figure A.13: Observed (grey) and predicted (black) values of nitrogen concentration (mmol N m^{-3}) at Station d and g at the full time series.

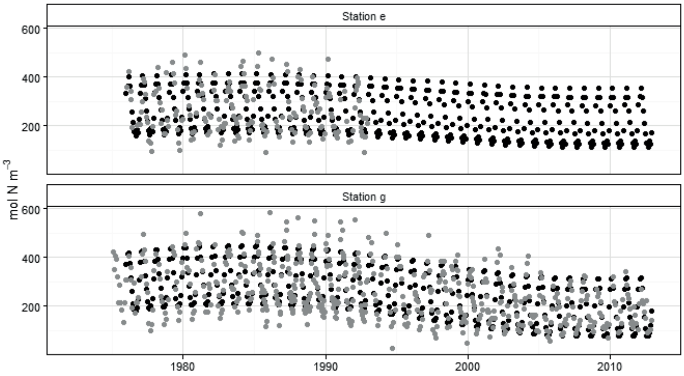


Figure A.14: Observed (grey) and predicted (black) values of nitrogen concentration (mmol N m^{-3}) at Station e and g at the full time series.

B

PRESENCE AND ABSENCE OF PHYTOPLANKTON ORDERS

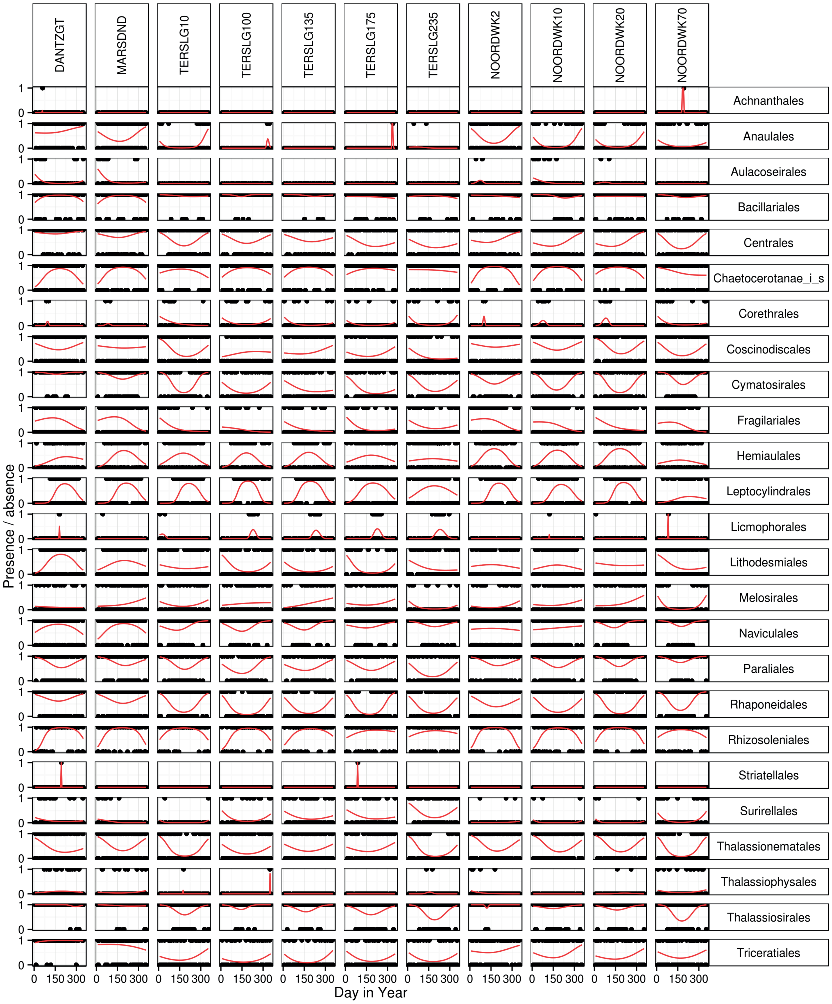


Figure B.1: Presence and absence of diatom orders at different stations of the Dutch coastal zone.

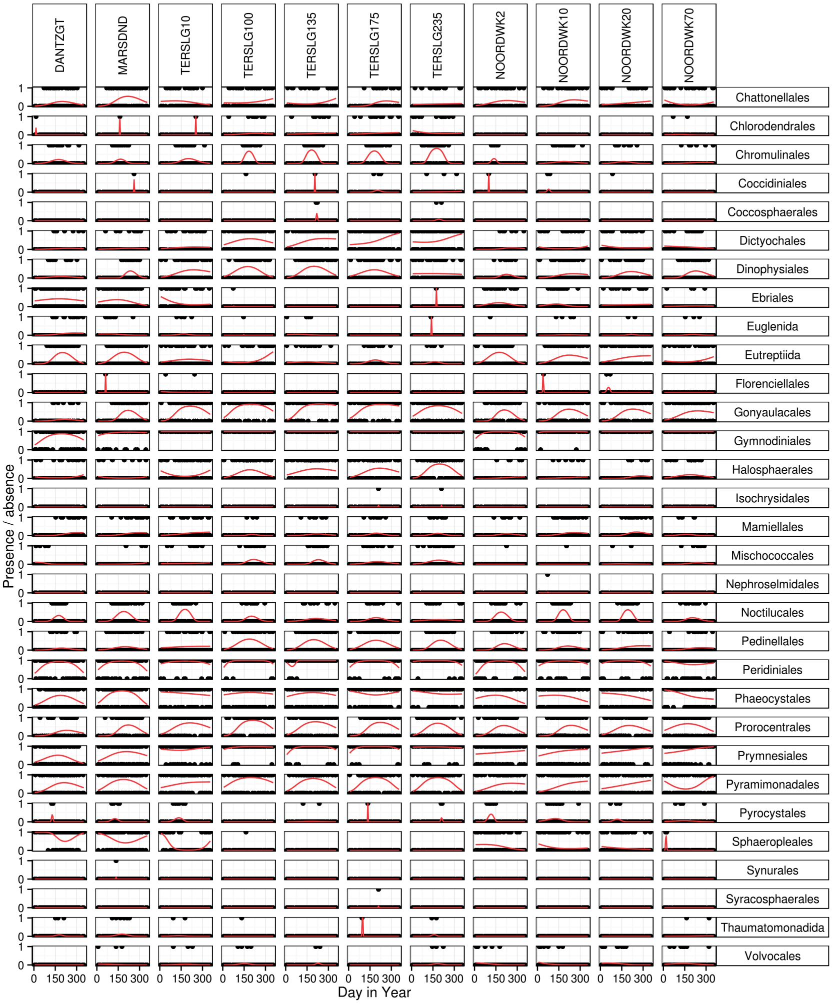


Figure B.2: Presence and absence of flagellate orders at different stations of the Dutch coastal zone.

C

SPECIES OF PHYTOPLANKTON IN THE DUTCH COASTAL ZONE

Table C.1: Species list with taxonomical information of Order and functional group of each species found in the study period.

Scientific name of species or group	Order	Functional group
Cocconeis spp.	Achnanthales	Diatom
Eunotogramma dubium	Anaulales	Diatom
Aulacoseira spp.	Aulacoseirales	Diatom
Bacillaria paxillifer	Bacillariales	Diatom
Cylindrotheca closterium	Bacillariales	Diatom
Cylindrotheca gracilis	Bacillariales	Diatom
Fragilariopsis spp.	Bacillariales	Diatom
Nitzschia spp.	Bacillariales	Diatom
Nitzschia coarctata	Bacillariales	Diatom
Nitzschia reversa	Bacillariales	Diatom
Nitzschia sigma	Bacillariales	Diatom
Pseudo-nitzschia spp.	Bacillariales	Diatom
Pseudo-nitzschia australis	Bacillariales	Diatom
Pseudo-nitzschia delicatissima	Bacillariales	Diatom
Pseudo-nitzschia fraudulenta	Bacillariales	Diatom
Pseudo-nitzschia granii	Bacillariales	Diatom
Pseudo-nitzschia heimii	Bacillariales	Diatom
Pseudo-nitzschia pseudodelicatissima	Bacillariales	Diatom
Pseudo-nitzschia pungens	Bacillariales	Diatom
Pseudo-nitzschia seriata f. obtusa	Bacillariales	Diatom
Pseudo-nitzschia seriata f. seriata	Bacillariales	Diatom
Pseudo-nitzschia subpacifica	Bacillariales	Diatom
Pseudo-nitzschia turgidula	Bacillariales	Diatom
Centrales	Centrales	Diatom
Attheya spp.	Chaetocerotanae_incertae_sedis	Diatom
Bacteriastrum hyalinum	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros spp.	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros affinis	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros anastomosans	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros atlanticus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros borealis	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros brevis	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros bulbosus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros ceratosporus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros compressus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros concavicornis	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros constrictus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros contortus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros convolutus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros coronatus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros costatus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros curvisetus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros danicus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros debilis	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros decipiens	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros densus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros diadema	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros dichaeta	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros didymus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros eibenii	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros lauderi	Chaetocerotanae_incertae_sedis	Diatom

Continued on next page

Table C.1 – *Continued from previous page*

Scientific name of species or group	Order	Functional group
Chaetoceros lorenzianus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros peruvianus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros pseudocurvisetus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros radicans	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros seiracanthus	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros septentrionalis	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros similis	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros simplex	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros simplex var. calcitrans	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros socialis	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros subtilis	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros teres	Chaetocerotanae_incertae_sedis	Diatom
Chaetoceros tortissimus	Chaetocerotanae_incertae_sedis	Diatom
Corethron criophilum	Corethrales	Diatom
Actinocyclus spp.	Coscinodiscales	Diatom
Actinocyclus normanii	Coscinodiscales	Diatom
Actinocyclus octonarius	Coscinodiscales	Diatom
Actinocyclus roperi	Coscinodiscales	Diatom
Actinoptychus senarius	Coscinodiscales	Diatom
Actinoptychus splendens	Coscinodiscales	Diatom
Aulacodiscus argus	Coscinodiscales	Diatom
Coscinodiscus spp.	Coscinodiscales	Diatom
Coscinodiscus centralis	Coscinodiscales	Diatom
Coscinodiscus concinnus	Coscinodiscales	Diatom
Coscinodiscus granii	Coscinodiscales	Diatom
Coscinodiscus perforatus var. pavillardii	Coscinodiscales	Diatom
Coscinodiscus radiatus	Coscinodiscales	Diatom
Coscinodiscus wailesii	Coscinodiscales	Diatom
Roperia tesselata	Coscinodiscales	Diatom
Brockmanniella brockmannii	Cymatosirales	Diatom
Campylosira cymbelliformis	Cymatosirales	Diatom
Cymatosira belgica	Cymatosirales	Diatom
Lennoxia faveolata	Cymatosirales	Diatom
Minutocellus polymorphus	Cymatosirales	Diatom
Minutocellus scriptus	Cymatosirales	Diatom
Plagiogrammopsis vanheurckii	Cymatosirales	Diatom
Asterionella formosa	Fragilariales	Diatom
Asterionella glacialis	Fragilariales	Diatom
Asterionella kariana	Fragilariales	Diatom
Diatoma tenuis	Fragilariales	Diatom
Fragilaria spp.	Fragilariales	Diatom
Fragilaria oblonga	Fragilariales	Diatom
Fragilaria ulna	Fragilariales	Diatom
Bellerochea malleus	Hemiaulales	Diatom
Cerataulina pelagica	Hemiaulales	Diatom
Eucampia groenlandica	Hemiaulales	Diatom
Eucampia zodiacus	Hemiaulales	Diatom
Subsilicea fragilarioides	Hemiaulales	Diatom
Leptocylindrus danicus	Leptocylindrales	Diatom
Leptocylindrus mediterraneus	Leptocylindrales	Diatom
Leptocylindrus minimus	Leptocylindrales	Diatom
Licmophora spp.	Licmophorales	Diatom
Ditylum brightwellii	Lithodesmiales	Diatom
Helicotheca tamesis	Lithodesmiales	Diatom
Lithodesmium undulatum	Lithodesmiales	Diatom
Tropidoneis spp.	Lithodesmiales	Diatom
Melosira spp.	Melosirales	Diatom
Melosira moniliformis	Melosirales	Diatom
Melosira nummuloides	Melosirales	Diatom
Melosira westii	Melosirales	Diatom
Podosira stelligera	Melosirales	Diatom
Stephanopyxis palmeriana	Melosirales	Diatom
Stephanopyxis turris	Melosirales	Diatom
Diploneis spp.	Naviculales	Diatom

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Table C.1 – *Continued from previous page*

Scientific name of species or group	Order	Functional group
Gyrosigma spp.	Naviculales	Diatom
Gyrosigma balticum	Naviculales	Diatom
Gyrosigma fasciola	Naviculales	Diatom
Gyrosigma tenuissimum	Naviculales	Diatom
Haslea spp.	Naviculales	Diatom
Membraneis challengeri	Naviculales	Diatom
Navicula spp.	Naviculales	Diatom
Navicula distans	Naviculales	Diatom
Pleurosigma spp.	Naviculales	Diatom
Pleurosigma aestuarii	Naviculales	Diatom
Pleurosigma affine	Naviculales	Diatom
Pleurosigma angulatum	Naviculales	Diatom
Pleurosigma planctonicum	Naviculales	Diatom
Stauroneis membranacea	Naviculales	Diatom
Trachyneis aspera	Naviculales	Diatom
Paralia marina	Paraliales	Diatom
Delphineis minutissima	Rhaponeidales	Diatom
Delphineis surirella	Rhaponeidales	Diatom
Rhaphoneis spp.	Rhaponeidales	Diatom
Rhaphoneis amphiceros	Rhaponeidales	Diatom
Dactyliosolen blavyanus	Rhizosoleniales	Diatom
Dactyliosolen phuketensis	Rhizosoleniales	Diatom
Guinardia flaccida	Rhizosoleniales	Diatom
Rhizosolenia spp.	Rhizosoleniales	Diatom
Rhizosolenia alata	Rhizosoleniales	Diatom
Rhizosolenia delicatula	Rhizosoleniales	Diatom
Rhizosolenia fragilissima	Rhizosoleniales	Diatom
Rhizosolenia hebetata f. hiemalis	Rhizosoleniales	Diatom
Rhizosolenia hebetata f. semispina	Rhizosoleniales	Diatom
Rhizosolenia indica	Rhizosoleniales	Diatom
Rhizosolenia pungens	Rhizosoleniales	Diatom
Rhizosolenia robusta	Rhizosoleniales	Diatom
Rhizosolenia setigera	Rhizosoleniales	Diatom
Rhizosolenia shrubsolei	Rhizosoleniales	Diatom
Rhizosolenia stolterfothii	Rhizosoleniales	Diatom
Rhizosolenia styliformis	Rhizosoleniales	Diatom
Grammatophora marina	Striatellales	Diatom
Striatella unipunctata	Striatellales	Diatom
Campylodiscus spp.	Surirellales	Diatom
Entomoneis spp.	Surirellales	Diatom
Surirella spp.	Surirellales	Diatom
Thalassionema spp.	Thalassionematales	Diatom
Thalassionema nitzschioides	Thalassionematales	Diatom
Thalassiothrix longissima	Thalassionematales	Diatom
Amphora spp.	Thalassiophysales	Diatom
Cyclostephanos dubius	Thalassiosirales	Diatom
Cyclotella spp.	Thalassiosirales	Diatom
Cyclotella meneghiniana	Thalassiosirales	Diatom
Detonula pumila	Thalassiosirales	Diatom
Lauderia annulata	Thalassiosirales	Diatom
Porosira glacialis	Thalassiosirales	Diatom
Skeletonema costatum	Thalassiosirales	Diatom
Skeletonema potamos	Thalassiosirales	Diatom
Skeletonema subsalsum	Thalassiosirales	Diatom
Stephanodiscus spp.	Thalassiosirales	Diatom
Thalassiosira spp.	Thalassiosirales	Diatom
Thalassiosira angstii	Thalassiosirales	Diatom
Thalassiosira anguste-lineata	Thalassiosirales	Diatom
Thalassiosira eccentrica	Thalassiosirales	Diatom
Thalassiosira hendeyi	Thalassiosirales	Diatom
Thalassiosira lacustris	Thalassiosirales	Diatom
Thalassiosira levanderi	Thalassiosirales	Diatom
Thalassiosira nodulolineata	Thalassiosirales	Diatom
Thalassiosira nordenskioeldii	Thalassiosirales	Diatom

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Table C.1 – *Continued from previous page*

Scientific name of species or group	Order	Functional group
Thalassiosira rotula	Thalassiosirales	Diatom
Auliscus sculptus	Triceratiales	Diatom
Cerataulus radiatus	Triceratiales	Diatom
Cerataulus turgidus	Triceratiales	Diatom
Odontella aurita	Triceratiales	Diatom
Odontella aurita var. minima	Triceratiales	Diatom
Odontella granulata	Triceratiales	Diatom
Odontella mobiliensis	Triceratiales	Diatom
Odontella regia	Triceratiales	Diatom
Odontella rhombus	Triceratiales	Diatom
Odontella sinensis	Triceratiales	Diatom
Odontella subaequa	Triceratiales	Diatom
Triceratium alternans	Triceratiales	Diatom
Chattonella spp.	Chattonellales	Flagellate
Chattonella antiqua	Chattonellales	Flagellate
Fibrocapsa japonica	Chattonellales	Flagellate
Heterosigma akashiwo	Chattonellales	Flagellate
Halosphaeraceae	Chlorodendrales	Flagellate
Tetraselmis spp.	Chlorodendrales	Flagellate
Dinobryon spp.	Chromulinales	Flagellate
Dinobryon faculiferum	Chromulinales	Flagellate
Dinobryon petiolatum	Chromulinales	Flagellate
Paulsenella spp.	Coccidiniales	Flagellate
Paulsenella chaetoceratis	Coccidiniales	Flagellate
Braarudosphaera bigelowii	Coccosphaerales	Flagellate
Dictyocha spp.	Dictyochales	Flagellate
Dictyocha fibula	Dictyochales	Flagellate
Dictyocha speculum	Dictyochales	Flagellate
Dinophysis spp.	Dinophysiales	Flagellate
Dinophysis acuminata	Dinophysiales	Flagellate
Dinophysis acuta	Dinophysiales	Flagellate
Dinophysis norvegica	Dinophysiales	Flagellate
Dinophysis ovum	Dinophysiales	Flagellate
Dinophysis rotundata	Dinophysiales	Flagellate
Sinophysis stenosoma	Dinophysiales	Flagellate
Ebria tripartita	Ebriales	Flagellate
Euglena spp.	Euglenida	Flagellate
Euglenaceae	Euglenida	Flagellate
Phacus spp.	Euglenida	Flagellate
Trachelomonas spp.	Euglenida	Flagellate
Eutreptiella spp.	Eutreptiida	Flagellate
Pseudochattonella spp.	Florenciellales	Flagellate
Alexandrium spp.	Gonyaulacales	Flagellate
Alexandrium leei	Gonyaulacales	Flagellate
Alexandrium margalefii	Gonyaulacales	Flagellate
Alexandrium minutum	Gonyaulacales	Flagellate
Alexandrium ostenfeldii	Gonyaulacales	Flagellate
Alexandrium peruvianum	Gonyaulacales	Flagellate
Alexandrium tamarense	Gonyaulacales	Flagellate
Amphidoma spp.	Gonyaulacales	Flagellate
Ceratium spp.	Gonyaulacales	Flagellate
Ceratium furca	Gonyaulacales	Flagellate
Ceratium fusus	Gonyaulacales	Flagellate
Ceratium horridum	Gonyaulacales	Flagellate
Ceratium inflatum	Gonyaulacales	Flagellate
Ceratium lineatum	Gonyaulacales	Flagellate
Ceratium longipes	Gonyaulacales	Flagellate
Ceratium macroceros	Gonyaulacales	Flagellate
Ceratium pentagonum	Gonyaulacales	Flagellate
Ceratium tripos	Gonyaulacales	Flagellate
Fragilidium subglobosum	Gonyaulacales	Flagellate
Gonyaulax spp.	Gonyaulacales	Flagellate
Gonyaulax digitale	Gonyaulacales	Flagellate
Gonyaulax rugosum	Gonyaulacales	Flagellate

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Table C.1 – *Continued from previous page*

Scientific name of species or group	Order	Functional group
Gonyaulax spinifera	Gonyaulacales	Flagellate
Gonyaulax triacantha	Gonyaulacales	Flagellate
Gonyaulax verior	Gonyaulacales	Flagellate
Micracanthodinium spp.	Gonyaulacales	Flagellate
Protoceratium reticulatum	Gonyaulacales	Flagellate
Pyrophacus horologium	Gonyaulacales	Flagellate
Amphidinium spp.	Gymnodiniales	Flagellate
Amphidinium sphenoides	Gymnodiniales	Flagellate
Cochlodinium spp.	Gymnodiniales	Flagellate
Gymnodiniaceae spp.	Gymnodiniales	Flagellate
Gymnodinium elongatum	Gymnodiniales	Flagellate
Gymnodinium lebouriae	Gymnodiniales	Flagellate
Gymnodinium mikimotoi	Gymnodiniales	Flagellate
Gymnodinium sanguineum	Gymnodiniales	Flagellate
Gymnodinium simplex	Gymnodiniales	Flagellate
Gyrodinium spp.	Gymnodiniales	Flagellate
Gyrodinium britannicum	Gymnodiniales	Flagellate
Gyrodinium calyptoglyphe	Gymnodiniales	Flagellate
Gyrodinium spirale	Gymnodiniales	Flagellate
Herdmania litoralis	Gymnodiniales	Flagellate
Katodinium asymmetricum	Gymnodiniales	Flagellate
Katodinium glaucum	Gymnodiniales	Flagellate
Nematodinium armatum	Gymnodiniales	Flagellate
Polykrikos spp.	Gymnodiniales	Flagellate
Polykrikos schwarzii	Gymnodiniales	Flagellate
Torodinium robustum	Gymnodiniales	Flagellate
Warnowia spp.	Gymnodiniales	Flagellate
Pterosperma spp.	Halosphaerales	Flagellate
Pterosperma parallelum	Halosphaerales	Flagellate
Pterosperma undulatum	Halosphaerales	Flagellate
Pterosperma vanhoeffenii	Halosphaerales	Flagellate
Emiliania huxleyi	Isochrysidales	Flagellate
Micromonas spp.	Mamiellales	Flagellate
Meringosphaera spp.	Mischococcales	Flagellate
Nephroselmis spp.	Nephroselmidales	Flagellate
Kofoidinium velleloides	Noctilucales	Flagellate
Noctiluca scintillans	Noctilucales	Flagellate
Pronoctiluca pelagica	Noctilucales	Flagellate
Spatulodinium pseudonoctiluca	Noctilucales	Flagellate
Apedinella spinifera	Pedinellales	Flagellate
Pseudopedinella spp.	Pedinellales	Flagellate
Azadinium spinosum	Peridiniales	Flagellate
Boreadinium pisiforme	Peridiniales	Flagellate
Cachonina niei	Peridiniales	Flagellate
Diplopsalis lenticula	Peridiniales	Flagellate
Diplopsalopsis asymmetricum	Peridiniales	Flagellate
Diplopsalopsis orbicularis	Peridiniales	Flagellate
Ensiculifera spp.	Peridiniales	Flagellate
Glenodinium danicum	Peridiniales	Flagellate
Glenodinium foliaceum	Peridiniales	Flagellate
Heterocapsa spp.	Peridiniales	Flagellate
Heterocapsa minima	Peridiniales	Flagellate
Heterocapsa triquetra	Peridiniales	Flagellate
Islandium tricingulatum	Peridiniales	Flagellate
Lebouraia minuta	Peridiniales	Flagellate
Oblea rotunda	Peridiniales	Flagellate
Oxytoxum spp.	Peridiniales	Flagellate
Peridiniaceae	Peridiniales	Flagellate
Peridinium quinquecorne	Peridiniales	Flagellate
Preperidinium meunieri	Peridiniales	Flagellate
Preperidinium pseudooblea	Peridiniales	Flagellate
Protoperidiniaceae	Peridiniales	Flagellate
Protoperidinium spp.	Peridiniales	Flagellate
Protoperidinium achromaticum	Peridiniales	Flagellate

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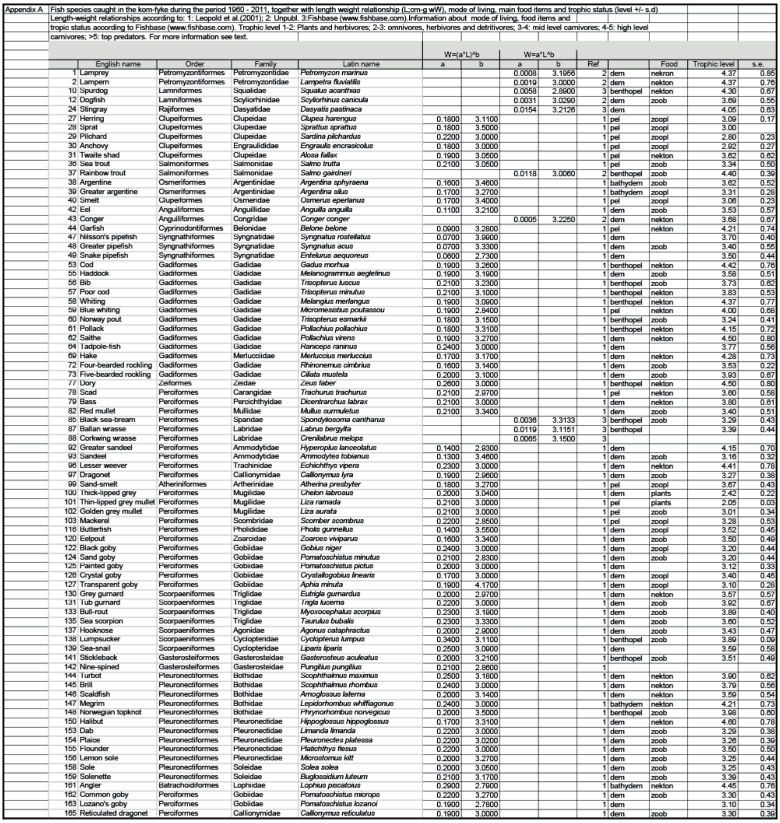
Table C.1 – *Continued from previous page*

Scientific name of species or group	Order	Functional group
Protoperidinium bipes	Peridiniales	Flagellate
Protoperidinium brevipes	Peridiniales	Flagellate
Protoperidinium cerasus	Peridiniales	Flagellate
Protoperidinium claudicans	Peridiniales	Flagellate
Protoperidinium conicoides	Peridiniales	Flagellate
Protoperidinium conicum	Peridiniales	Flagellate
Protoperidinium curtipes	Peridiniales	Flagellate
Protoperidinium curvipes	Peridiniales	Flagellate
Protoperidinium denticulatum	Peridiniales	Flagellate
Protoperidinium depressum	Peridiniales	Flagellate
Protoperidinium diabolus	Peridiniales	Flagellate
Protoperidinium divergens	Peridiniales	Flagellate
Protoperidinium excentricum	Peridiniales	Flagellate
Protoperidinium granii	Peridiniales	Flagellate
Protoperidinium leonis	Peridiniales	Flagellate
Protoperidinium marie-lebouriae	Peridiniales	Flagellate
Protoperidinium minutum	Peridiniales	Flagellate
Protoperidinium mite	Peridiniales	Flagellate
Protoperidinium oblongum	Peridiniales	Flagellate
Protoperidinium obtusum	Peridiniales	Flagellate
Protoperidinium ovatum	Peridiniales	Flagellate
Protoperidinium pallidum	Peridiniales	Flagellate
Protoperidinium pellucidum	Peridiniales	Flagellate
Protoperidinium pentagonum	Peridiniales	Flagellate
Protoperidinium punctulatum	Peridiniales	Flagellate
Protoperidinium pyriforme	Peridiniales	Flagellate
Protoperidinium steinii	Peridiniales	Flagellate
Protoperidinium subinerme	Peridiniales	Flagellate
Protoperidinium thorianum	Peridiniales	Flagellate
Protoperidinium thulesense	Peridiniales	Flagellate
Scrippsiella spp.	Peridiniales	Flagellate
Scrippsiella faeroense	Peridiniales	Flagellate
Scrippsiella trochoidea	Peridiniales	Flagellate
Thecadinium spp.	Peridiniales	Flagellate
Thecadinium yashimaense	Peridiniales	Flagellate
Phaeocystis spp.	Phaeocystales	Flagellate
Mesoporos perforatus	Prorocentrales	Flagellate
Prorocentrum spp.	Prorocentrales	Flagellate
Prorocentrum balticum	Prorocentrales	Flagellate
Prorocentrum compressum	Prorocentrales	Flagellate
Prorocentrum lima	Prorocentrales	Flagellate
Prorocentrum micans	Prorocentrales	Flagellate
Prorocentrum minimum	Prorocentrales	Flagellate
Prorocentrum triestinum	Prorocentrales	Flagellate
Chrysochromulina spp.	Prymnesiales	Flagellate
Corymbellus aureus	Prymnesiales	Flagellate
Prymnesiaceae	Prymnesiales	Flagellate
Prymnesium spp.	Prymnesiales	Flagellate
Pyramimonas spp.	Pyramimonadales	Flagellate
Pyramimonas longicauda	Pyramimonadales	Flagellate
Dissodinium pseudolunula	Pyrocystales	Flagellate
Pyrocystis hamulus	Pyrocystales	Flagellate
Pediastrum spp.	Sphaeropleales	Flagellate
Mallomonas spp.	Synurales	Flagellate
Acanthoica spp.	Syracosphaerales	Flagellate
Acanthoica quattrospina	Syracosphaerales	Flagellate
Protaspis glans	Thaumatomonadida	Flagellate
Brachiomonas spp.	Volvocales	Flagellate
Chlamydomonas spp.	Volvocales	Flagellate
Pteromonas spp.	Volvocales	Flagellate

D

SPECIES INFORMATION FOR SPECIES CAUGHT WITH THE KOM-FYKE



Appendix A Fish species caught in the kom-fyke during the period 1960 - 2011, together with length weight relationship (L;cm-g wW), mode of living, main food items and trophic status (level +/- s.d)
Length-weight relationships according to: 1: Leopold et al.(2001); 2: Unpubl. 3:Fishbase (www.fishbase.com).Information about mode of living, food items and tropic status according to Fishbase (www.fishbase.com). Trophic level 1-2: Plants and herbivores; 2-3: omnivores, herbivores and detritivores; 3-4: mid level carnivores; 4-5: high level carnivores; >5: top predators. For more information see text.

					W=(a*L)^b		W=a*L^b						
	English name	Order	Family	Latin name	a	b	a	b	Ref		Food	Trophic level	s.e.
1	Lamprey	Petromyzontiformes	Petromyzontidae	*Petromyzon marinus*			0.0008	3.1956	2	dem	nekron	4.37	0.85
2	Lampern	Petromyzontiformes	Petromyzontidae	*Lampetra fluviatilis*			0.0019	3.0000	2	dem	nekton	4.37	0.76
10	Spurdog	Lamniformes	Squalidae	*Squalus acanthias*			0.0058	2.8900	3	benthopel	nekton	4.30	0.67
12	Dogfish	Lamniformes	Scyliorhinidae	*Scyliorhinus canicula*			0.0031	3.0290	2	dem	zoob	3.69	0.55
24	Stingray	Rajiformes	Dasyatidae	*Dasyatis pastinaca*			0.0154	3.2126	3	dem		4.05	0.63
27	Herring	Clupeiformes	Clupeidae	*Clupea harengus*	0.1800	3.1100			1	pel	zoopl	3.09	0.17
28	Sprat	Clupeiformes	Clupeidae	*Sprattus sprattus*	0.1800	3.5000			1	pel	zoopl	3.00	
29	Pilchard	Clupeiformes	Clupeidae	*Sardina pilchardus*	0.2200	3.0000			1	pel	zoopl	2.80	0.23
30	Anchovy	Clupeiformes	Engraulididae	*Engraulis encrasicolus*	0.1800	3.0000			1	pel	zoopl	2.92	0.27
31	Twaite shad	Clupeiformes	Clupeidae	*Alosa fallax*	0.1900	3.0500			1	pel	nekton	3.62	0.62
36	Sea trout	Salmoniformes	Salmonidae	*Salmo trutta*	0.2100	3.0500			1	pel	zoob	3.34	0.50
37	Rainbow trout	Salmoniformes	Salmonidae	*Salmo gairdneri*			0.0118	3.0060	2	benthopel	zoob	4.40	0.39
38	Argentine	Osmeriformes	Argentinidae	*Argentina sphyraena*	0.1600	3.4600			1	bathydem	zoob	3.62	0.52
39	Greater argentine	Osmeriformes	Argentinidae	*Argentina silus*	0.1700	3.2700			1	bathydem	zoopl	3.31	0.28
40	Smelt	Clupeiformes	Osmeridae	*Osmerus eperlanus*	0.1700	3.4000			1	pel	zoopl	3.06	0.23
42	Eel	Anguiliformes	Anguillidae	*Anguilla anguilla*	0.1100	3.2100			1	dem	zoob	3.53	0.57
43	Conger	Anguiliformes	Congridae	*Conger conger*			0.0005	3.2250	2	dem	nekton	3.68	0.67
44	Garfish	Cyprinodontiformes	Belonidae	*Belone belone*	0.0900	3.2800			1	pel	nekton	4.21	0.74
47	Nilsson's pipefish	Syngnathiformes	Syngnatidae	*Syngnatus rostellatus*	0.0700	3.9900			1	dem		3.70	0.40
48	Greater pipefish	Syngnathiformes	Syngnatidae	*Syngnatus acus*	0.0700	3.3300			1	dem	zoob	3.40	0.55
49	Snake pipefish	Syngnathiformes	Syngnatidae	*Entelurus aequoreus*	0.0600	2.7300			1	dem		3.50	0.44
53	Cod	Gadiformes	Gadidae	*Gadus morhua*	0.1900	3.2600			1	benthopel	nekton	4.42	0.76
55	Haddock	Gadiformes	Gadidae	*Melanogrammus aeglefinus*	0.1900	3.1900			1	dem	zoob	3.58	0.51
56	Bib	Gadiformes	Gadidae	*Trisopterus luscus*	0.2100	3.2300			1	benthopel	zoob	3.73	0.62
57	Poor cod	Gadiformes	Gadidae	*Trisopterus minutus*	0.2100	3.1000			1	benthopel	nekton	3.83	0.53
58	Whiting	Gadiformes	Gadidae	*Melangius merlangus*	0.1900	3.0900			1	benthopel	nekton	4.37	0.77
59	Blue whiting	Gadiformes	Gadidae	*Micromesistius poutassou*	0.1900	2.8400			1	pel	nekton	4.00	0.68
60	Norway pout	Gadiformes	Gadidae	*Trisopterus esmarkii*	0.1800	3.1500			1	benthopel	zoob	3.24	0.41
61	Pollack	Gadiformes	Gadidae	*Pollachius pollachius*	0.1800	3.3100			1	benthopel	nekton	4.15	0.72
62	Saithe	Gadiformes	Gadidae	*Pollachius virens*	0.1900	3.2700			1	dem	nekton	4.50	0.80
64	Tadpole-fish	Gadiformes	Gadidae	*Raniceps raninus*	0.2400	3.0000			1	dem		3.77	0.56
69	Hake	Gadiformes	Merlucciidae	*Merluccius merluccius*	0.1700	3.1700			1	dem	nekton	4.28	0.73
72	Four-bearded rockling	Gadiformes	Gadidae	*Rhinonemus cimbrius*	0.1600	3.1400			1	dem	zoob	3.53	0.22
73	Five-bearded rockling	Gadiformes	Gadidae	*Ciliata mustela*	0.2000	3.1000			1	dem	zoob	3.93	0.67
77	Dory	Zeiformes	Zeidae	*Zeus faber*	0.2600	3.0000			1	benthopel	nekton	4.50	0.80
78	Scad	Perciformes	Carangidae	*Trachurus trachurus*	0.2100	2.9700			1	pel	nekton	3.60	0.58
79	Bass	Perciformes	Percichthyidae	*Dicentrarchus labrax*	0.2100	3.0000			1	dem	nekton	3.80	0.61
82	Red mullet	Perciformes	Mullidae	*Mullus surmuletus*	0.2100	3.3400			1	dem	zoob	3.40	0.51
85	Black sea-bream	Perciformes	Sparidae	*Spondyliosoma cantharus*			0.0036	3.3133	3	benthopel	zoob	3.29	0.43
87	Ballan wrasse	Perciformes	Labridae	*Labrus bergylta*			0.0119	3.1151	3	benthopel		3.39	0.44
88	Corkwing wrasse	Perciformes	Labridae	*Crenilabrus melops*			0.0065	3.1500	3				
92	Greater sandeel	Perciformes	Ammodytidae	*Hyperoplus lanceolatus*	0.1400	2.9300			1	dem		4.15	0.70
93	Sandeel	Perciformes	Ammodytidae	*Ammodytes tobianus*	0.1300	3.4600			1	dem	zoob	3.16	0.32
96	Lesser weever	Perciformes	Trachinidae	*Echiichthys vipera*	0.2300	3.0000			1	dem	nekton	4.41	0.78
97	Dragonet	Perciformes	Callionymidae	*Callionymus lyra*	0.1900	2.9600			1	dem	zoob	3.27	0.38
99	Sand-smelt	Atheriniformes	Artherinidae	*Atherina presbyter*	0.1800	3.2700			1	pel	zoopl	3.67	0.43
100	Thick-lipped grey	Perciformes	Mugilidae	*Chelon labrosus*	0.2000	3.0400			1	dem	plants	2.42	0.22
101	Thin-lipped grey mullet	Perciformes	Mugilidae	*Liza ramada*	0.2100	3.0000			1	pel	plants	2.05	0.03
102	Golden grey mullet	Perciformes	Mugilidae	*Liza aurata*	0.2100	3.0000			1	pel	zoob	3.01	0.34
103	Mackerel	Perciformes	Scombridae	*Scomber scombrus*	0.2200	2.8500			1	pel	zoopl	3.28	0.53
116	Butterfish	Perciformes	Pholididae	*Pholis gunnellus*	0.1400	3.5500			1	dem	zoopl	3.52	0.45
120	Eelpout	Perciformes	Zoarcidae	*Zoarces viviparus*	0.1600	3.3400			1	dem	zoob	3.50	0.49
122	Black goby	Perciformes	Gobiidae	*Gobius niger*	0.2400	3.0000			1	dem	zoopl	3.20	0.44
124	Sand goby	Perciformes	Gobiidae	*Pomatoschistus minutus*	0.2100	2.8300			1	dem	zoob	3.20	0.44
125	Painted goby	Perciformes	Gobiidae	*Pomatoschistus pictus*	0.2000	3.0000			1	dem		3.12	0.33
126	Crystal goby	Perciformes	Gobiidae	*Crystallogobius linearis*	0.1700	3.0000			1	dem	zoopl	3.40	0.45
127	Transparent goby	Perciformes	Gobiidae	*Aphia minuta*	0.1900	4.1700			1	dem	zoopl	3.10	0.28
130	Grey gurnard	Scorpaeniformes	Triglidae	*Eutrigla gurnardus*	0.2000	2.9700			1	dem	nekton	3.57	0.57
131	Tub gurnard	Scorpaeniformes	Triglidae	*Trigla lucerna*	0.2200	3.0000			1	dem	zoob	3.92	0.67
133	Bull-rout	Scorpaeniformes	Triglidae	*Myoxocephalus scorpius*	0.2300	3.1900			1	dem	zoob	3.89	0.40
135	Sea scorpion	Scorpaeniformes	Triglidae	*Taurulus bubalis*	0.2300	3.3300			1	dem	zoob	3.60	0.52
137	Hooknose	Scorpaeniformes	Agonidae	*Agonus cataphractus*	0.2000	2.9000			1	dem	zoob	3.43	0.47
138	Lumpsucker	Scorpaeniformes	Cyclopteridae	*Cyclopterus lumpus*	0.3400	3.1100			1	benthopel	zoob	3.89	0.09
139	Sea-snail	Scorpaeniformes	Cyclopteridae	*Liparis liparis*	0.2500	3.0900			1	dem		3.59	0.58
141	Stickleback	Gasterosteiformes	Gasterosteidae	*Gasterosteus aculeatus*	0.2000	3.2100			1	benthopel	zoob	3.51	0.49
142	Nine-spined	Gasterosteiformes	Gasterosteidae	*Pungitius pungitius*	0.2100	2.8600			1				
144	Turbot	Pleuronectiformes	Bothidae	*Scophthalmus maximus*	0.2500	3.1800			1	dem	nekton	3.90	0.62
145	Brill	Pleuronectiformes	Bothidae	*Scophthalmus rhombus*	0.2400	3.0000			1	dem	nekton	3.79	0.56
146	Scaldfish	Pleuronectiformes	Bothidae	*Arnoglossus laterna*	0.2000	3.1400			1	dem	nekton	3.59	0.54
147	Megrim	Pleuronectiformes	Bothidae	*Lepidorhombus whiffiagonus*	0.2400	3.0000			1	bathydem	nekton	4.21	0.73
148	Norwegian topknot	Pleuronectiformes	Bothidae	*Phrynorhombus norvegicus*	0.2000	3.5000			1	benthopel	zoob	3.98	0.60
150	Halibut	Pleuronectiformes	Pleuronectidae	*Hippoglossus hippoglossus*	0.1700	3.3100			1	dem	nekton	4.60	0.78
153	Dab	Pleuronectiformes	Pleuronectidae	*Limanda limanda*	0.2200	3.0000			1	dem	zoob	3.29	0.38
154	Plaice	Pleuronectiformes	Pleuronectidae	*Pleuronectes platessa*	0.2200	3.0200			1	dem	zoob	3.26	0.39
155	Flounder	Pleuronectiformes	Pleuronectidae	*Platichthys flesus*	0.2200	3.0000			1	dem	zoob	3.50	0.50
156	Lemon sole	Pleuronectiformes	Pleuronectidae	*Microstomus kitt*	0.2000	3.2700			1	dem	zoob	3.25	0.44
158	Sole	Pleuronectiformes	Soleidae	*Solea solea*	0.2000	3.0500			1	dem	zoob	3.25	0.43
159	Solenette	Pleuronectiformes	Soleidae	*Buglossidium luteum*	0.2100	3.1700			1	dem	zoob	3.39	0.43
161	Angler	Batrachoidiformes	Lophiidae	*Lophius piscatoius*	0.2900	2.7900			1	bathydem	nekton	4.45	0.76
162	Common goby	Perciformes	Gobiidae	*Pomatoschistus microps*	0.2200	3.2700			1	dem	zoob	3.30	0.43
163	Lozano's goby	Perciformes	Gobiidae	*Pomatoschistus lozanoi*	0.1900	2.7800			1	dem		3.10	0.34
165	Reticulated dragonet	Perciformes	Callionymidae	*Callionymus reticulatus*	0.1900	3.0000			1	dem	zoob	3.30	0.39

E

MEAN DAILY CATCHES IN KOM-FYKE

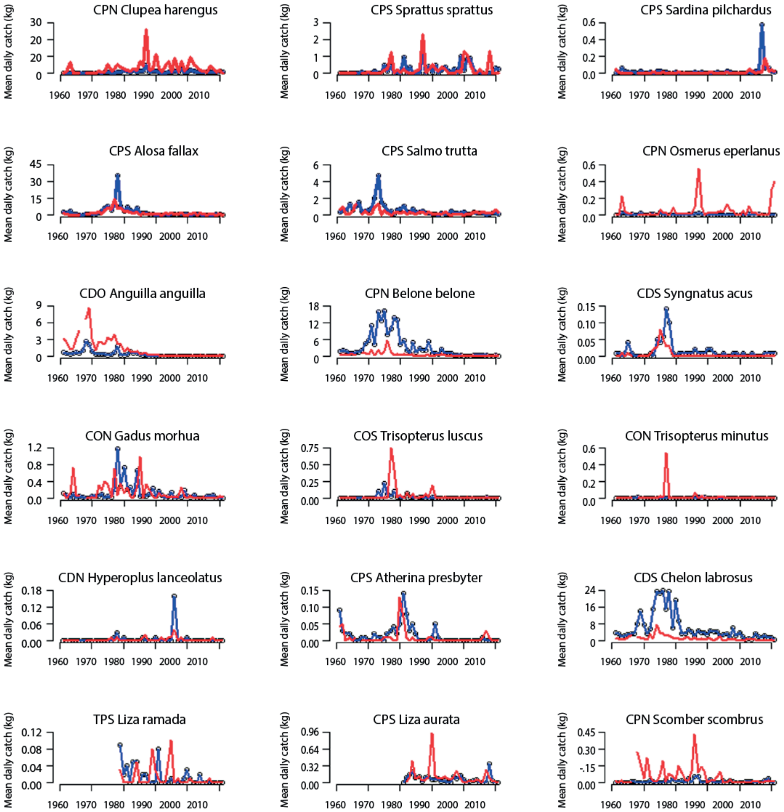


Figure E.1: Mean daily catch (kg d-1) of the fish species that occurred in the kom-fyke in at least 10 years for spring (blue) and autumn (red). Coding: First letter: C: core species, T: transient species; Second letter: P: pelagic species; D: demersal species; O: benthopelagic species; Third letter: N: northern species; S: southern species; O: in between NS species.

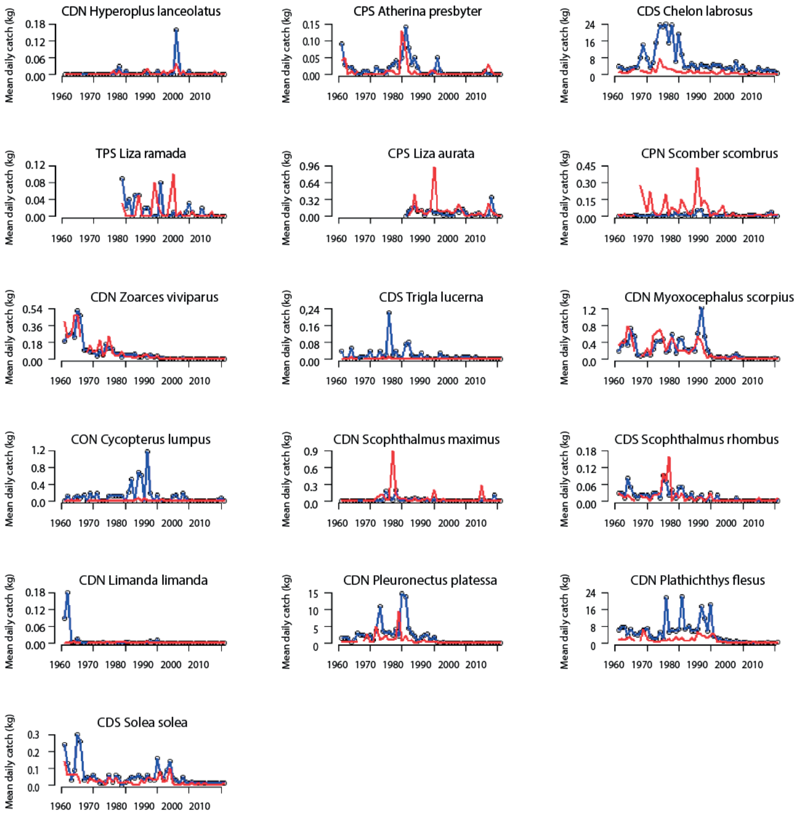


Figure E.2: Mean daily catch (kg d-1) of the fish species that occurred in the kom-fyke in at least 10 years for spring (blue) and autumn (red). Coding: First letter: C: core species, T: transient species; Second letter: P: pelagic species; D: demersal species; O: benthopelagic species; Third letter: N: northern species; S: southern species; O: in between NS species.

F

SAMPLING DATES EPIBENTHIC SURVEY

Table F.1: Species list with taxonomical information of Order and functional group of each species found in the study period.

Cruiseid	Date	Cruiseid	Date	Cruiseid	Date
197501	02.04.1975	197809	04.09.1978	198211	09.08.1982
197502	17.04.1975	197810	02.10.1978	198301	31.05.1983
197503	02.05.1975	197901	02.04.1979	198601	21.01.1986
197504	15.05.1975	197902	18.04.1979	198602	19.03.1986
197505	29.05.1975	197903	01.05.1979	198603	17.04.1986
197506	14.06.1975	197904	14.05.1979	198604	22.05.1986
197507	01.07.1975	197905	29.05.1979	198605	25.06.1986
197508	11.07.1975	197906	12.06.1979	198606	18.09.1986
197509	29.07.1975	197907	25.07.1979	198607	09.10.1986
197510	12.08.1975	197908	10.09.1979	198608	05.11.1986
197511	28.08.1975	198001	19.02.1980	199101	21.05.1991
197512	08.09.1975	198002	06.03.1980	199102	25.06.1991
197513	11.09.1975	198003	24.03.1980	199301	15.03.1993
197514	24.09.1975	198004	10.04.1980	199302	14.04.1993
197515	08.10.1975	198005	21.04.1980	199303	27.04.1993
197516	24.10.1975	198006	06.05.1980	199304	10.05.1993
197517	07.11.1975	198007	19.05.1980	199305	25.05.1993
197601	03.04.1976	198008	01.06.1980	199306	08.06.1993
197602	05.05.1976	198009	13.06.1980	199307	21.06.1993
197603	19.05.1976	198010	02.07.1980	199308	19.07.1993
197604	02.06.1976	198011	14.07.1980	199309	18.08.1993
197605	16.06.1976	198101	09.02.1981	199401	15.03.1994
197606	01.07.1976	198102	24.02.1981	199402	30.04.1994
197607	02.08.1976	198103	09.03.1981	199403	18.04.1994
197608	08.09.1976	198104	23.03.1981	199404	02.05.1994
197609	13.10.1976	198105	07.04.1981	199405	17.05.1994
197610	10.11.1976	198106	21.04.1981	199406	31.05.1994
197701	29.03.1977	198107	06.05.1981	199407	13.06.1994
197702	05.05.1977	198108	18.05.1981	199408	27.06.1994
197703	02.06.1977	198109	03.06.1981	199409	25.07.1994
197704	04.07.1977	198110	19.06.1981	199410	22.08.1994
197705	01.08.1977	198111	08.07.1981	199501	07.03.1995
197706	20.09.1977	198201	20.03.1982	199502	21.03.1995
197707	20.10.1977	198202	06.04.1982	199503	03.04.1995
197801	30.03.1978	198203	14.04.1982	199504	19.04.1995

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Table F.1 – *Continued from previous page*

Cruiseid	Date	Cruiseid	Date	Cruiseid	Date
197802	13.04.1978	198204	28.04.1982	199505	02.05.1995
197803	25.04.1978	198205	10.05.1982	199506	16.05.1995
197804	10.05.1978	198206	24.05.1982	199507	31.05.1995
197805	29.05.1978	198207	08.06.1982	199508	15.06.1995
197806	07.06.1978	198208	21.06.1982	199509	29.06.1995
197807	27.06.1978	198209	06.07.1982	199510	13.07.1995
197808	26.07.1978	198210	21.07.1982	199511	14.08.1995
199601	28.02.1996	200011	17.07.2000	201410	25.08.2014
199602	27.03.1996	200012	02.08.2000	201411	23.09.2014
199603	09.04.1996	200013	03.10.2000	201412	21.10.2014
199604	22.04.1996	200101	26.02.2001	201413	10.11.2014
199605	06.05.1996	200102	12.03.2001	201414	15.12.2014
199606	20.05.1996	200103	26.03.2001		
199607	03.06.1996	200104	10.04.2001		
199608	17.06.1996	200105	24.04.2001		
199609	04.07.1996	200106	07.05.2001		
199610	31.07.1996	200107	28.05.2001		
199611	28.08.1996	200108	13.06.2001		
199701	27.02.1997	200109	20.07.2001		
199702	10.03.1997	200110	21.08.2001		
199703	26.03.1997	200201	18.02.2002		
199704	08.04.1997	200202	04.03.2002		
199705	22.04.1997	200203	20.03.2002		
199706	13.05.1997	200204	02.04.2002		
199707	26.05.1997	200205	17.04.2002		
199708	09.06.1997	200206	09.05.2002		
199709	24.06.1997	200701	19.02.2007		
199710	07.07.1997	200702	07.03.2007		
199711	04.08.1997	200703	26.03.2007		
199712	11.09.1997	200704	10.04.2007		
199801	17.03.1998	200705	23.04.2007		
199802	01.04.1998	200706	07.05.2007		
199803	17.04.1998	200707	22.05.2007		
199804	29.04.1998	200708	04.06.2007		
199805	12.05.1998	200709	19.06.2007		
199806	26.05.1998	200710	19.07.2007		
199807	11.06.1998	200711	23.08.2007		
199808	25.06.1998	200712	11.10.2007		
199809	16.07.1998	200901	03.03.2009		
199810	28.07.1998	200902	31.03.2009		
199811	11.08.1998	200903	15.04.2009		
199901	25.02.1999	200904	19.05.2009		
199902	08.03.1999	200905	02.06.2009		

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Table F.1 – *Continued from previous page*

Cruiseid	Date	Cruiseid	Date	Cruiseid	Date
199903	24.03.1999	200906	15.06.2009		
199904	19.04.1999	200907	29.06.2009		
199905	03.05.1999	200908	27.07.2009		
199906	10.05.1999	200909	25.08.2009		
200001	13.01.2000	200910	23.09.2009		
200002	14.02.2000	201401	21.01.2014		
200003	24.02.2000	201402	24.02.2014		
200004	13.03.2000	201403	21.03.2014		
200005	04.04.2000	201404	03.04.2014		
200006	18.04.2000	201405	14.04.2014		
200007	02.05.2000	201406	01.05.2014		
200008	14.05.2000	201407	02.06.2014		
200009	06.06.2000	201408	30.06.2014		
200010	19.06.2000	201409	28.07.2014		

G

CALCULATIONS OF DENSITIES AND BIOMASS OF EPIBENTHIC SPECIES

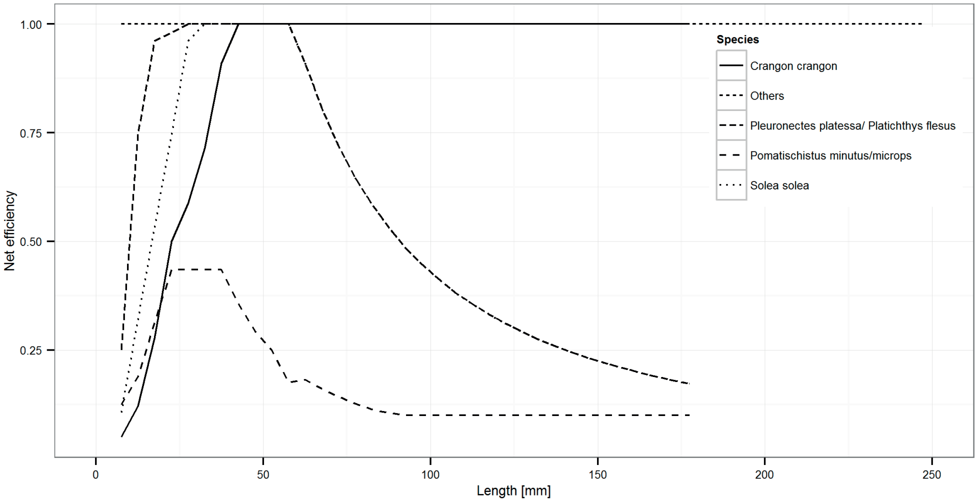


Figure G.1: Net efficiency for different species and animal length.

Table G.1: Specific species coefficients a and b of the length (L; cm) wet mass (W; g) relationships $W = (a \times L)^b$ after Leopold et al. (2001).

Species	a	b
Clupea harengus	0.18	3.11
Osmerus eperlanus	0.17	3.4
Syngnatus rostellatus	0.07	3.99
Ammodytes tobianus	0.13	3.46
Zoarces viviparus	0.16	3.34
Pomatoschistus minutus	0.21	2.83
Myoxocephalus scorpius	0.23	3.19
Gasterosteus aculeatus	0.2	3.21
Pleuronectes platessa	0.22	3.02
Platichthys flesus	0.22	3
Solea solea	0.2	3.05
Pomatoschistus microps	0.22	3.27
Carcinus maenas	0.38	2.81
Crangon crangon	0.17	3.18

H

FOOD REQUIREMENTS

Table H.1: Annual food requirement [g AFDM m^{-2} y^{-1}] by epibenthos at the Balgzand intertidal over the period 1975-2014. Empty cells indicate that the species was not counted in these years, in bold years all analysed species have been sampled over a sufficient period.

	Pleuronectes platessa			*Platichthys flesus*			*Solea solea*		*Pomatoschistus microps*		*Pomatoschistus minutus*		*Carcinus maenas*	*Crangon crangon*	Total
Year	0-group	I-group	II-group	0-group	I-group	II-group	0-group	I-group	0-group	I-group	0-group	I-group	All ages	All ages	
1975	0.907	1.498	2.655				0.071	0	0.321	0.066	0.377	0.012			
1976	**0.924**	**2.907**	**0.58**	**0.094**	**0.874**	**1.445**	**0.027**	**0**	**0.345**	**0.057**	**0.519**	**0.017**	**0.311**	**12.921**	**21.02**
1977	1.129	4.182	1.226										0.311	7.611	
1978	1.848	2.777	1.804										0.868	18.174	
1979	2.259			0.096			0.047	0					0.548	22.662	
1980	**0.464**	**9.177**	**8.493**	**0.015**	**0.171**	**0.524**	**0.023**	**0.154**	**0.111**	**0.07**	**0.089**	**0.007**	**0.475**	**21.521**	**41.29**
1981	**0.631**	**5.249**	**3.721**	**0.043**	**0.076**	**0.931**	**0.007**	**0**	**0.072**	**0.039**	**0.008**	**0.001**	**0.316**	**20.345**	**31.44**
1982	1.091	0	0	0.016	0.004	0	0.014	0.055							
1986	**1.035**	**1.109**	**0.163**	**0.001**	**0.099**	**0.59**	**0.006**	**0**	**0.087**	**0.05**	**0**	**0**	**0.133**	**16.554**	**19.83**
1993	**0.283**	**0.1**	**0.027**	**0.03**	**0.09**	**0.975**	**0.009**	**0**	**0.895**	**0.023**	**0.214**	**0.023**	**0.633**	**33.798**	**37.1**
1994	0.411	0.034	0	0.065	0.053	0.001	0.026	0							
1995	0.347	0.042	0.017	0.082	0.112	0.01	0.041	0							
1996	**0.374**	**0.042**	**0**	**0.031**	**0.197**	**0.062**	**0.009**	**0**	**0.733**	**0.038**	**0.224**	**0.008**	**0.584**	**26.711**	**29.01**
1997	**0.302**	**0.047**	**0**	**0.003**	**0.03**	**0.021**	**0.002**	**0.003**	**0.297**	**0.043**	**0.925**	**0.009**	**0.886**	**20.511**	**23.08**
1998	0.178	0.037	0.002	0.011	0.01	0.1	0.001	0							
1999	0.22	0.002	0	0.02	0.012	0.003			0	0.013	0	0.014	0.274	4.324	
2000	**0.402**	**0.004**	**0.001**	**0.01**	**0.042**	**0.126**	**0.01**	**0**	**0.569**	**0.031**	**0.669**	**0.035**	**0.683**	**25.003**	**27.59**
2001	**0.477**	**0.004**	**0**	**0.108**	**0.014**	**0.012**	**0.002**	**0**	**0**	**0.027**	**0.001**	**0.02**	**1.096**	**11.473**	**13.23**
2002	0.284	0.038	0	0.009	0.027	0.016	0.007	0.015	0	0.02	0	0.015	0.325	11.474	
2007	**0.149**	**0.008**	**0**	**0.039**	**0.003**	**0.028**	**0.049**	**0.035**	**0.47**	**0.008**	**0.116**	**0.052**	**0.912**	**39.463**	**41.33**
2009	**0.149**	**0.006**	**0**	**0.048**	**0.042**	**0.062**	**0.006**	**0.001**	**0.974**	**0.017**	**0.624**	**0.031**	**2.25**	**32.27**	**36.48**
2014	**0.324**	**0**	**0**	**0.039**	**0.014**	**0.001**	**0.007**	**0**	**0.97**	**0.047**	**1.338**	**0.102**	**2.282**	**34.38**	**39.5**
Average	0.64	1.3	0.89	0.04	0.1	0.27	0.02	0.01	0.39	0.04	0.34	0.02	0.76	21.13	30.08
sd	0.54	2.33	1.97	0.03	0.19	0.42	0.02	0.04	0.35	0.02	0.39	0.02	0.61	9.69	8.95

I

MATRIX PLOTS FROM SIMMR RUNS OF BIVALVE STABLE ISOTOPE MIXING MODELS

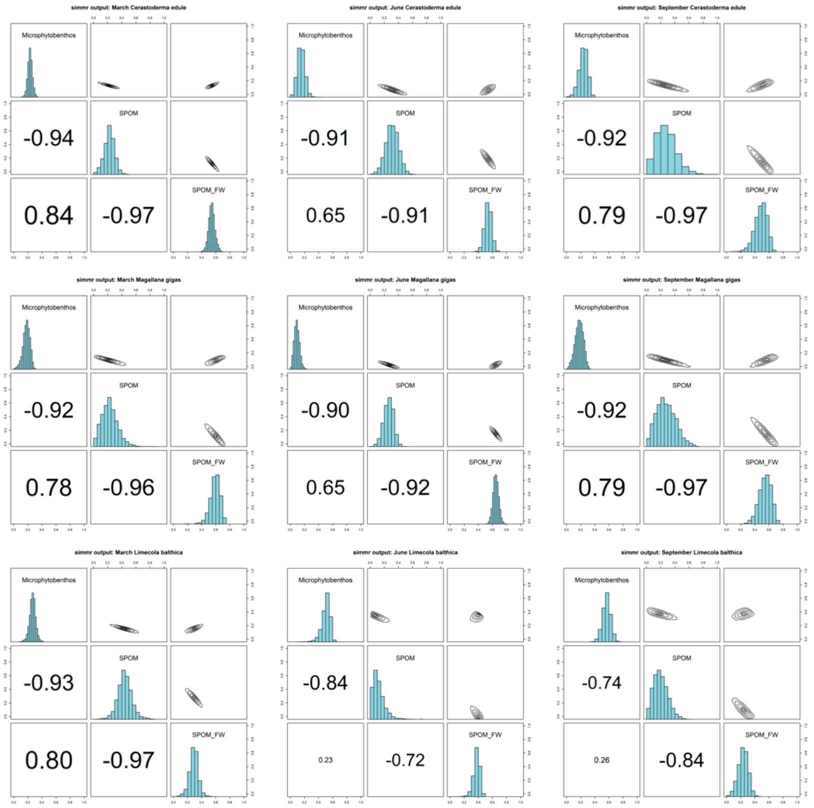


Figure I.1: Season-specific matrix plots of food sources (microphytobenthos, estuarine SPOM and freshwater SPOM) for estuarine bivalves in March, June and September 2014.

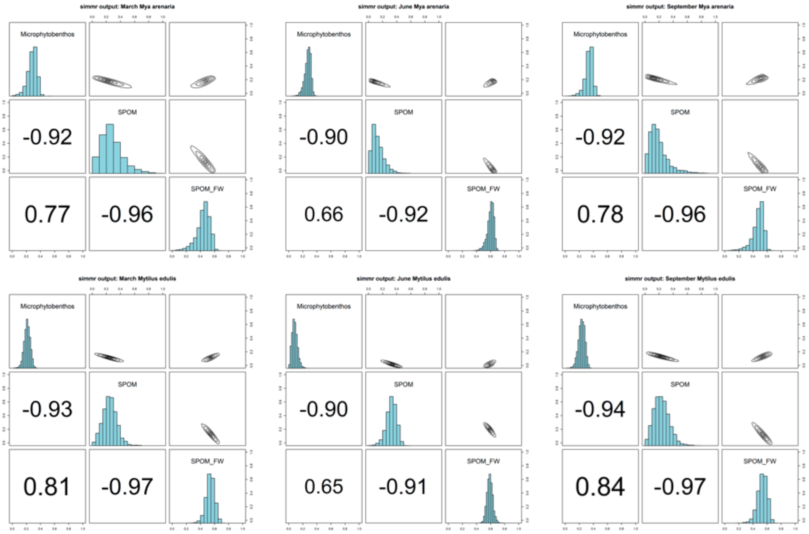


Figure I.2: Season-specific matrix plots of food sources (microphytobenthos, estuarine SPOM and freshwater SPOM) for estuarine bivalves in March, June and September 2014.

J

MODEL RESULTS FROM STABLE ISOTOPES VS LENGTH IN BIVALVES

Table J.1: Summary of the linear models (with fixed slope) of the relationship of $\delta^{13}C$ with shell length (mm) and season (in comparison to June for *S. plana*, and to March for all other species) for the different bivalve species as sampled in March, June, September and December 2014 at the Balgzand tidal flats.

	Dependent variable:					
	$\delta^{13}C$					
	Cerastoderma edule	*Limecola balthica*	*Magallana gigas*	*Mya arenaria*	*Mytilus edulis*	*Scrobicularia plana*
	(1)	(2)	(3)	(4)	(5)	(6)
Length	0.004	-0.083^{*}	-0.002	-0.019^{***}	0.016^{**}	0.018
	(0.017)	(0.046)	(0.003)	(0.006)	(0.006)	(0.039)
June	0.621^{**}	2.040^{***}	0.434^{*}	0.094	0.153	
	(0.306)	(0.476)	(0.238)	(0.295)	(0.224)	
September	1.115^{***}	3.155^{***}	1.080^{***}	1.091^{***}	1.160^{***}	1.680^{***}
	(0.280)	(0.469)	(0.250)	(0.286)	(0.224)	(0.396)
December	1.504^{***}		0.728^{**}		0.806^{***}	
	(0.368)		(0.299)		(0.251)	
Constant	-19.706^{***}	-16.437^{***}	-20.229^{***}	-17.710^{***}	-20.417^{***}	-17.754^{***}
	(0.420)	(0.732)	(0.290)	(0.319)	(0.276)	(1.353)
Observations	60	59	39	30	57	10
R^2	0.349	0.515	0.386	0.473	0.409	0.774
Adjusted R^2	0.302	0.489	0.313	0.412	0.364	0.710
Residual Std. Error	0.802 (df = 55)	1.447 (df = 55)	0.576 (df = 34)	0.642 (df = 26)	0.625 (df = 52)	0.558 (df = 7)
F Statistic	7.371^{***} (df = 4; 55)	19.488^{***} (df = 3; 55)	5.334^{***} (df = 4; 34)	7.763^{***} (df = 3; 26)	9.001^{***} (df = 4; 52)	12.006^{***} (df = 2; 7)
Note:						$^{*}p<0.1$; $^{**}p<0.05$; $^{***}p<0.01$

Table J.2: Summary of the linear models (with fixed slope) of the relationship of $\delta^{15}N$ with shell length (mm) and season (in comparison to June for *S. plana*, and to March for all other species) for the different bivalve species as sampled in March, June, September and December 2014 at the Balgzand tidal flats.

	Dependent variable:					
	$\delta^{15}N$					
	Cerastoderma edule	*Limecola balthica*	*Magallana gigas*	*Mya arenaria*	*Mytilus edulis*	*Scrobicularia plana*
	(1)	(2)	(3)	(4)	(5)	(6)
Length	0.061^{***}	-0.029	0.006^{***}	0.017^{***}	0.027^{***}	-0.058^{**}
	(0.010)	(0.021)	(0.002)	(0.004)	(0.004)	(0.024)
June	0.364^{*}	0.928^{***}	0.375^{**}	0.073	0.902^{***}	
	(0.183)	(0.215)	(0.176)	(0.224)	(0.146)	
September	1.130^{***}	0.791^{***}	0.625^{***}	0.440^{*}	1.035^{***}	1.532^{***}
	(0.167)	(0.211)	(0.184)	(0.218)	(0.146)	(0.238)
December	-0.537^{**}		0.017		0.154	
	(0.220)		(0.221)		(0.164)	
Constant	9.507^{***}	11.394^{***}	10.273^{***}	9.925^{***}	9.449^{***}	12.491^{***}
	(0.251)	(0.330)	(0.214)	(0.242)	(0.180)	(0.814)
Observations	60	59	39	30	57	10
R^2	0.577	0.342	0.443	0.483	0.637	0.855
Adjusted R^2	0.546	0.306	0.378	0.423	0.610	0.814
Residual Std. Error	0.479 (df = 55)	0.652 (df = 55)	0.425 (df = 34)	0.488 (df = 26)	0.407 (df = 52)	0.336 (df = 7)
F Statistic	18.740^{***} (df = 4; 55)	9.518^{***} (df = 3; 55)	6.764^{***} (df = 4; 34)	8.095^{***} (df = 3; 26)	22.862^{***} (df = 4; 52)	20.687^{***} (df = 2; 7)

Note: $^{*}p<0.1$; $^{**}p<0.05$; $^{***}p<0.01$

K

SOURCES AND CONSTRUCTIONS OF STANDING STOCK BIOMASS DATA

K.1 MICROALGAE

For the Balgzand tidal flat system, it was assumed that the main primary producers fueling the food web were marine phytoplankton, freshwater phytoplankton and microphytobenthos (Chapter 7).

K.1.1 *Marine phytoplankton (C_{PHYT}; $\mathrm{mg\,C\,m^{-2}}$)*

The biomass of marine phytoplankton (B_{PHYT}; $\mathrm{mg\,Chl-a\,m^{-3}}$) has been monitored as chlorophyll-a concentrations at the NIOZ Jetty, a station located close to the research area (Fig. 8.1), since the 1970s. Measurements at this station were always taken at high tide, therefore more likely representing the phytoplankton population of the coastal North Sea than that of the central Wadden Sea. Results from Duran-Matute et al. (2014) indicate that the water of Balgzand contains a considerable amount of freshwater originating from lake IJsselmeer (Fig. 8.1). In addition, freshwater might also have been imported via the discharge from the Balgzand channel (Fig. 8.1). The percentage of (additional) freshwater on the Balgzand (compared to that of the coastal North Sea) was estimated via the salinity of the water of the Balgzand area as compared to the salinity measured at the Jetty. The results led to estimations of the coastal water fractions (84% and 81% in the 1980s/1990s and 2000s/2010s, respectively), the biomass of coastal waters ($\mathrm{mg\,Chl-a\,m^{-3}}$) and the average water depth of the Balgzand (Table 8.1) were then used to estimate the local chlorophyll-a mass ($\mathrm{mg\,Chl-a\,m^{-2}}$), which was subsequently converted to carbon mass ($\mathrm{mg\,C\,m^{-2}}$) by applying a fixed conversion factor of $38\,\mathrm{mg\,C\,mg^{-1}\,Chl-a}$ (de Jonge, 1980; Riemann et al., 1989).

K.1.2 *Freshwater phytoplankton (C_{FWTR}; $\mathrm{mg\,C\,m^{-2}}$)*

As indicated in the previous paragraph, the total biomass of freshwater microalgae (B_{FWTR}; $\mathrm{mg\,Chl-a\,m^{-3}}$) in the study area was assumed to be the sum of the supply from lake IJsselmeer and the Balgzand channel. Biomass of freshwater microalgae was calculated by multiplying the long-term chlorophyll-a concentrations in the water of lake IJsselmeer at Den Oever (52.934 566 5 ° N, 5.103 873 34° E) as measured by the Rijkswaterstaat (`http://waterinfo.rws.nl/`; $\mathrm{mg\,Chl-a\,m^{-3}}$) by the estimated fraction of freshwater on the Balgzand (16% and 19%, see the above section of marine phytoplankton). We assumed that freshwater algae were not affected during their transfer from their main sources to the brackish waters of the Balgzand tidal flat system. These chlorophyll-a concentrations, the average depth of the Balgzand (Table 8.1) and a fixed conversion factor of $38\,\mathrm{mg\,C\,mg^{-1}\,Chl-a}$ (de Jonge, 1980; Riemann et al., 1989) were subsequently used to estimate the local carbon mass (C_{FWTR}; $\mathrm{mg\,C\,m^{-2}}$) of freshwater microalgae.

K.1.3 *Microphytobenthos (C_{MPB}; $\mathrm{mg\,C\,m^{-2}}$)*

Since no long-term data on microphytobenthos were available, biomass of these benthic microalgae in the top 0.5 cm of the sediment ($B_{MPB0.5}$; $\mathrm{mg\,Chl-a\,m^{-2}}$) was derived from an empirical relationship with average annual air temperature (AT; °C) as was found for the Ems estuary by (de Jonge et al., 2012):
$B_{MPB0.5}$ = 26176*AT - 15499
For the Balgzand tidal flat area, mean air temperature (°C) values were obtained from the KNMI meteorological station at the airport of Den Helder ("De Kooy", see Royal Netherlands Meteorological Institute, `https://www.knmi.nl/nederland-nu/klimatologie/maandgegevens`). Assuming that microphytobenthos occurred to depth of 2 cm instead of 0.5 cm in the sediment of the tidal flats (Revsbech and Jørgensen, 1986; de Jonge et al., 2019*a*), microphytobenthos biomass at 0.5 cm ($B_{MPB0.5}$; $\mathrm{mg\,Chl-a\,m^{-2}}$) was multiplied by 1.7 to derive at total microphytobenthic biomass (B_{MPB}; $\mathrm{mg\,Chl-a\,m^{-2}}$) in the sediment (de Jonge and Colijn, 1994). Subsequently, total benthic biomass (B_{MPB}; $\mathrm{mg\,Chl-a\,m^{-2}}$) was converted to total carbon (C_{MPB}; $\mathrm{mg\,C\,m^{-2}}$) by using a ratio of $38\,\mathrm{mg\,C\,mg^{-1}\,Chl-a}$ (de Jonge, 1980; Riemann et al., 1989).

K.2 BACTERIA

K.2.1 *Pelagic bacteria (C_{PBAC}; $\mathrm{mg\,C\,m^{-2}}$)*

Since no data were available, annual averages of biomass of pelagic bacteria were derived from the annual averages in chlorophyll-a concentration of phytoplankton as measured in the Marsdiep tidal inlet. Hereto, CHLa concentration of phytoplankton (B_{PHYT}; $\mathrm{mg\,Chl-a\,m^{-3}}$) was first converted to bacterial density (N_{BACT}; cells $\mathrm{mL^{-1}}$) according to Bird and Kalff (1984):
$Log_{10}N_{BACT} = 5.87 + 0.78 * log_{10}B_{PHYT}$
Bacterial cell densities were subsequently converted to biovolume (V_{BACT}; $\mathrm{\mu m^3\,mL^{-1}}$) by using a mean volume of $0.11\,\mathrm{\mu m^3}$ per cell (van Duyl and Kop, 1988). Biovolume was finally converted to carbon concentration (C_{PBAC}; $\mathrm{mg\,C\,m^{-2}}$) by applying a carbon to volume ratio of $10^{-13}\,\mathrm{mg\,C\,\mu m^{-3}}$ (Rublee et al., 1978) and taking the mean water depth (0.67 m) of the Balgzand area into account.

K.2.2 *Benthic bacteria (C_{BBAC}; $\mathrm{mg\,C\,m^{-2}}$)*

In the 1980s, biomass of benthic bacteria concentration in the upper 3 mm of the sediment (C_{BBAC3}; $\mathrm{mg\,C\,m^{-2}}$) at the Balgzand tidal flats was, on average, 150 mg C m^{-2} (van Duyl and Kop, 1990). Assuming that the top 2 cm should be considered as being biologically important (Revsbech and Jørgensen, 1986; de Jonge et al., 2019*a*) and that benthic bacteria are homogeneously distributed up to this depth, then total biomass of benthic bacteria (C_{BBAC}) was 1000 mg C m^{-2}. This value fits well with those found for other estuaries (Austin and Findlay, 1989). Due to a lack of data for other periods, the biomass of benthic bacteria was considered to be similar during all other periods.

K.3 ZOOPLANKTON (C_{ZOO}; mg C m^{-2})

Because no zooplankton data were available, annual averages of biomass of zooplankton (C_{ZOO}; mg C m^{-2}) were based upon an empirical relationship between zooplankton densities (N_{ZOO}; n m^{-3}) and sea surface temperature in the first half year (January till May; SST; °C) as found in the north-eastern part of the Wadden Sea (Martens and Beusekom, 2008), according to:
$N_{ZOO} = 6.0068 * SST - 14.099$
Sea surface temperatures (SST; °C) were taken from the long-term field observations at the NIOZ Jetty as annual average values from January till May between 1982 and 2010. Zooplankton densities (N_{ZOO}; numbers m^{-3}) were subsequently converted to zooplankton mass (C_{ZOO}; mg C m^{-2}) by assuming a carbon content of 0.01 mg C per individual (Löder et al., 2011) and taking the average depth (0.67 m) of the study area into account.

K.4 BENTHIC FAUNA

K.4.1 *Meiofauna (C_{MEIO}; mg C m^{-2})*

In the 1970s, the density of meiofauna (N_{MEIO}; n m^{-2}) at the Balgzand tidal flats was 2.44×10^6 individuals m^{-2} and the community consisted of Nematodes, Harpacticoids, Turbellaria and Annelida (see Witte and Zijlstra, 1984, Table 2). Assuming a mean carbon content of 0.153 846 µg C per individual (Bouwman et al., 1984), this density represented a mean biomass of meiofauna (C_{MEIO}; mg C m^{-2}) of 375.23 mg C m^{-2}. For the 1980s, we assumed that meiofauna biomass was equal to that in the 1970s. For the 1990s, 2000s and 2010s, meiofauna biomass (C_{MEIO}; mg C m^{-2}) was derived from an empirical relationship with median grain size (µm) and silt content (%) of the top layer (2 cm) of the sediment of the tidal flats according to (Schückel et al., unpublished):
Meiofauna (n m^{-2}) = median grain size (µm) * silt content (%)
Data on median grain size and silt content of the Balgzand were obtained from Beukema and Cadée (1997) and unpublished data of the Royal Netherlands Institute for Sea Research (NIOZ) data base.

K.4.2 *Macrozoobenthos* ($C_{MZBSPEC}$; mg C m^{-2})

The ecosystem network analysis approach includes 20 species of macrozoobenthos, grouped into four feeding guilds (Baird et al., 2012). Biomass of each of these macrozoobenthic species ($B_{MZBSPEC}$; mg AFDM m^{-2}) used in the analysis was obtained from the NIOZ long-term monitoring program (Beukema and Cadée, 1997, and unpublished data). Although sampling nowadays takes place in late summer (July/August) and late winter (February/March), only winter samples are available for the full study period. Samples were taken during low tide with a core along 12 transects and at 3 quadrats to a depth of about 30 cm, and sieved over a 1 mm sieve (see Beukema and Cadée, 1997, for a detailed description of sampling methods). Biomass was originally determined as ash-free dry mass (mg AFDM m^{-2}) and converted here into carbon content ($C_{MZBSPEC}$; mg C m^{-2}) by using a conversion factor of 0.58 mg C mg AFDM^{-1} (Asmus and Asmus, 1998) for all species.

K.4.3 *Epibenthos* (C_{EPI}; mg C m^{-2})

At the Balgzand tidal flats, the epibenthic community was sampled in 1975-1983, 1986, 1991, 1993-2002, 2007, 2009 and 2014 (see 5 for more details). The biomass of the epibenthic species, originally determined as wet mass (mg WM m^{-2}), was converted to ash-free dry mass (BEPI; mg AFDM m^{-2}) by using a conversion factor of 0.17 mg AFDM mg WM^{-1} (de Vlas, 1979), and subsequently to carbon mass (C_{EPI}; mg C m^{-2}) by using a conversion factor of 0.58 mg C mg AFDM^{-1} (Asmus and Asmus, 1998).

K.5 BIRDS ($C_{BIRDSPEC}$; mg C m^{-2})

Since 1975, bird counting took place during high tide on a monthly basis (van Roomen et al., 2005). Data for numbers of birds present on the tidal roosts at high tide were obtained from SOVON (Foundation of bird research in the Netherlands, `https://www.sovon.nl/`). Assuming that these birds were evenly distributed over the tidal flats during low tide, bird densities ($N_{BIRDSPEC}$; n m^{-2}) were calculated by dividing the total bird numbers at the tidal roosts bordering the submerged area during high tide by the total surface area of the exposed tidal flats during low tide. For each of these bird species, densities ($N_{BIRDSPEC}$; n m^{-2}) were converted to biomass ($C_{BIRDSPEC}$; mg C m^{-2}) by using a species-specific wet body mass (mg WM) taken from Dunning Jr (1992), and a conversion of 0.2 mg C mg WM^{-1} for all species (Horn and de la Vega, 2016).

K.6 ORGANIC MATTER

K.6.1 *Dissolved Organic Carbon* (C_{DOC}; mg C m^{-2})

The DOC standing stock estimations were obtained by using measured DOC concentrations (`http://waterinfo.rws.nl/`) at two stations in lake IJsselmeer, being "Vrouwezand" (52.810 350° N, 5.393 138° E) and "Den Oever" (52.934 566 5 ° N, 5.103 873 34° E), and one station in the Marsdiep tidal basin, being "Marsdiep Noord" (52.982 540° N, 4.749 931° E) (indicated as Rijkswaterstaat in Fig. 8.1). The salinity at "Marsdiep Noord" was used to calculate the DOC concentrations (C_{DOC}; mg C m^{-3}) of the Balgzand water (see also the procedure followed for the freshwater algae) and was then converted to mg C m^{-2} using the water depth of the area (0.67 m).

K.6.2 *Suspended Particulate Organic Carbon* (C_{SUSPOC}; mg C m^{-2})

The basis for all calculations on susPOC is the Rijkswaterstaat (RWS) monitoring data on suspended particulate organic carbon and suspended particulate matter (SPM) at the station "Marsdiep Noord" (`http://waterinfo.rws.nl/`). Standing stock of susPOC as measured by RWS (here indicated as ALL susPOC) contains also carbon coming from compartments already integrated into our model (such as phytoplankton, zooplankton, and pelagic bacteria). To avoid double counting, these categories were excluded from the susPOC values. Over the years the fraction of ALL susPOC in comparison to the SPM at the station was 0.0543 (calculated from the Rijkswaterstaat data `http://waterinfo.rws.nl/`). In addition to the measurements at "Marsdiep Noord", SPM measurements for the Amsteldiep tidal channel at the eastern border of the Balgzand area (Fig. 8.1) for the period 1973-1975 were used as reference for the correctness of the calculations based on station "Marsdiep Noord". On average, the 1973-1975 value of the "Amsteldiep" station was a factor 2.36 times higher than the SPM values at station "Marsdiep Noord" during the same years. We assumed that this ratio was constant over time. Since measured ALL susPOC values were available for all years at station "Marsdiep Noord", these SPM values were multiplied by the factor 2.36 to get the values for Balgzand. The SPM values were then used to calculate the ALL susPOC values with the factor mentioned above. Finally, the detritus susPOC concentrations (C_{SUSPOC}; mg C m^{-3}) was calculated as the ALL susPOC values minus the biomass of phytoplankton (C_{PHYT}), zooplankton (C_{ZOO}), and pelagic bacteria (C_{PBAC}).

K.6.3 *Sediment Particulate Organic Carbon* (C_{SEDPOC}; mg C m^{-2})

Particulate organic matter in the sediment is not part of any monitoring program. For this study values published by van Duyl and Kop (1990) and originating from Etcheber et al. (1988) as measured in 1986 were used. They report a value of 1.953 g organic carbon per liter wet sediment. Assuming that the volume of a 2 cm slice of one square meter equals 20 L of sediment ($2 * 100 * 100 = 20.000 cm^3 = 20 dm^3 = 20 L$), we arrive at a concentration of POC in the sediment (C_{SEDPOC}) of 39 060 mg C m^{-2} (1.953 g C L^{-1}* 20 L). Due to the lack of data in this area, no statement on the variability of the sediment carbon over time can be made. POC was therefore assumed to be similar for all periods.

L

ENA ENERGETICS

Table L.1: Mean biomass (mg C m^{-2}) and the daily input, output, consumption, production, respiration and egestion (mg C m^{-2} d-1) per compartment per decade as used in the four respective networks (BZ1980s, BZ1990s, BZ2000s and BZ2100s).

Compartment nr		mg m^{-2} or mg m^{-2} d^{-1}	BIOMASS				INPUT				OUTPUT				PRODUCTION				RESPIRATION				CONSUMPTION				EGESTION			
1980s/ 1990s	2000s/ 2010s	Compartment Name	1980s	1990s	2000s	2010s	1980s	1990s	2000s	2010s	1980s	1990s	2000s	2010s	1980s	1990s	2000s	2010s	1980s	1990s	2000s	2010s	1980s	1990s	2000s	2010s	1980s	1990s	2000s	2010s
1	1	Phytoplankton	226.43	225.18	205.21	162.93	176.67	165.94	672.51	343.24	21.55	0.00	0.00	0.00	176.67	99.30	97.43	88.55	62.54	35.15	34.49	31.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	2	Microphytobenthos	5848.94	6964.98	8114.84	7679.42	322.28	383.77	479.05	423.14	0.00	0.00	0.00	0.00	322.28	383.77	447.13	423.14	85.08	101.32	118.04	111.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	3	Freshwater algae	388.04	384.93	330.21	335.41	238.79	236.88	203.21	206.41	0.00	0.00	0.00	0.00	19.40	19.25	16.51	16.77	6.87	6.81	5.84	5.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	4	Pelagic Bacteria	35.34	35.23	31.81	26.45	0.00	0.00	5.01	0.35	0.00	0.00	0.00	0.00	10.60	10.57	9.54	7.93	10.60	10.57	9.54	7.93	21.21	21.14	19.08	15.87	0.00	0.00	0.00	0.00
5	5	Zooplankton	13.94	17.80	21.02	20.18	0.00	0.00	0.00	0.00	5.33	6.30	7.68	5.54	8.32	10.62	12.54	12.04	9.87	12.60	14.88	14.29	27.72	35.42	41.81	40.15	9.54	12.19	14.39	13.82
6	6	Benthic Bacteria	1000.00	1000.00	1000.00	1000.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	156.80	156.80	156.80	156.80	174.40	174.40	174.40	174.40	392.00	392.00	392.00	392.00	60.80	60.80	60.80	60.80
7	7	Meiofauna	375.23	136.16	125.52	123.08	4.34	13.09	16.69	16.29	0.00	0.00	0.00	0.00	8.22	2.98	2.75	2.70	31.27	11.35	10.46	10.26	53.74	19.50	17.98	17.63	14.26	5.17	4.77	4.68
8	8	*Peringia ulvae*	352.29	530.41	555.35	1509.33	8.97	10.31	11.95	11.75	0.00	0.00	0.00	0.00	1.41	2.12	2.22	6.04	2.17	3.27	3.42	9.30	14.09	21.22	22.21	60.37	10.51	15.83	16.57	45.03
9	9	*Littorina littorea*	38.31	24.41	90.99	165.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.05	0.18	0.33	0.23	0.15	0.55	0.99	0.77	0.49	1.82	3.31	0.46	0.29	1.09	1.98
10	10	*Arenicola marina*	2988.21	2841.00	2322.12	2447.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.92	19.89	16.25	17.13	19.46	18.50	15.12	15.94	139.45	132.58	108.37	114.20	99.07	94.19	76.99	81.14
11	11	*Eteone sp*	13.36	20.28	30.84	28.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.06	0.09	0.08	0.44	0.67	1.02	0.93	0.54	0.82	1.25	1.15	0.06	0.09	0.14	0.13
12	12	*Hediste diversicolor*	1029.04	1433.28	1544.38	1328.09	3.47	0.00	0.00	1.73	0.00	0.00	0.00	0.00	3.09	4.30	4.63	3.98	12.50	17.41	18.76	16.13	48.24	67.19	72.39	62.25	32.65	45.48	49.00	42.14
13	13	*Nereis spec.*	38.74	102.44	261.89	282.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.31	0.79	0.85	0.47	1.24	3.18	3.43	1.82	4.80	12.28	13.23	1.23	3.25	8.31	8.96
14	14	*Heteromastus filiformis*	747.03	1091.92	1483.26	436.18	0.00	0.00	0.00	1.62	0.00	0.00	0.00	0.00	3.74	5.46	7.42	2.18	7.11	10.40	14.13	4.15	58.36	85.31	115.88	34.08	47.51	69.45	94.34	27.74
15	15	*Lanice conchilega*	147.46	385.34	496.45	98.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.81	2.12	2.73	0.54	1.55	4.05	5.22	1.04	3.04	7.94	10.23	2.03	0.68	1.77	2.28	0.45
16	16	*Marenzelleria viridis*	0.17	348.99	1709.80	186.63	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.89	23.94	2.61	0.01	13.96	68.39	7.47	0.02	37.58	184.13	20.10	0.01	18.74	91.80	10.02
17	17	*Nephtys hombergii*	131.85	162.61	163.45	71.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	1.79	1.80	0.79	1.38	1.70	1.71	0.75	7.84	9.67	9.72	4.28	5.01	6.18	6.21	2.74
18	18	*Scoloplos armiger*	251.68	196.31	177.03	220.93	1.43	1.72	1.92	2.88	0.00	0.00	0.00	0.00	0.25	0.20	0.18	0.22	1.92	1.50	1.35	1.69	7.19	5.61	5.06	6.31	5.02	3.91	3.53	4.40
19	19	*Corophium spp*	317.89	65.00	141.36	217.10	1.54	2.85	2.85	4.35	0.00	0.00	0.00	0.00	1.27	0.26	0.57	0.87	5.97	1.22	2.65	4.08	8.71	1.78	3.87	5.95	1.47	0.30	0.65	1.00
20	20	*Gammarus spp.*	1.39	1.93	2.05	2.00	0.01	0.07	0.06	0.25	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.04	0.05	0.05	0.05	0.06	0.08	0.08	0.08	0.01	0.02	0.02	0.02
21	21	*Cerastoderma edule*	2591.14	3058.69	1910.17	3410.44	3.78	1.15	7.61	8.41	0.00	0.00	0.00	0.00	12.96	15.29	9.55	17.05	4.06	4.80	2.99	5.35	64.78	76.47	47.75	85.26	47.76	56.38	35.21	62.86
	22	*Magallana gigas*	0	0	369.07	355.70	0	0	0.00	0.00	0	0	0.00	0.00	0	0	0.37	0.36	0	0	4.80	4.62	0	0	5.54	5.34	0	0	0.37	0.36
22	23	*Ensis leei*	7.53	209.27	1992.79	891.62	0.27	0.00	4.61	8.15	0.00	0.00	0.00	0.00	0.15	4.19	39.86	17.83	2.26	62.78	597.84	267.49	4.14	115.10	1096.04	490.39	1.73	48.13	458.34	205.07
23	24	*Limecola balthica*	2185.74	1715.90	407.01	469.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.49	13.73	3.26	3.75	3.26	2.56	0.61	0.70	112.81	88.56	21.01	24.21	92.07	72.28	17.14	19.76
24	25	*Mya arenaria*	4481.92	5354.19	7962.46	3711.79	0.00	0.00	1.22	1.80	0.00	0.00	0.00	0.00	8.96	10.71	15.92	7.42	20.85	24.90	37.03	17.26	44.82	53.54	79.62	37.12	15.01	17.93	26.66	12.43
25	26	*Mytilus edulis*	1340.48	1291.41	968.24	971.20	1.31	1.57	0.00	0.00	0.00	0.00	0.00	0.00	1.34	1.29	0.97	0.97	7.37	7.10	5.32	5.34	9.93	9.57	7.17	7.19	1.22	1.18	0.88	0.89
26	27	*Scrobicularia plana*	170.39	214.57	109.67	127.89	0.00	0.00	0.50	0.78	0.00	0.00	0.00	0.00	0.85	1.07	0.55	0.64	0.66	0.83	0.42	0.49	4.26	5.36	2.74	3.20	2.75	3.47	1.77	2.07
27	28	*Carcinus maenas*	7.84	9.16	14.72	41.61	1.36	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.04	0.06	0.17	0.05	0.06	0.09	0.26	0.72	1.41	2.46	5.64	0.64	1.32	2.31	5.22
28	29	*Crangon crangon*	90.71	114.42	129.93	207.32	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.26	1.43	2.28	26.31	33.18	37.68	60.12	46.90	49.56	55.78	86.31	19.59	15.12	16.67	23.91
29	30	*Ammodytes tobianus*	0.26	0.41	0.46	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	31	*Clupea harengus*	0.80	2.15	4.21	1.45	0.00	0.00	0.00	0.00	0.01	0.02	0.00	0.00	0.01	0.02	0.03	0.01	0.01	0.03	0.07	0.02	0.03	0.07	0.13	0.05	0.01	0.02	0.03	0.01
31	32	*Myoxocephalus scorpius*	0.09	0.03	0.01	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
32	33	*Osmerus eperlanus*	0.82	0.28	0.31	0.55	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.04	0.01	0.01	0.03	0.02	0.01	0.01	0.01
33	34	*Platichthys flesus*	23.56	9.18	4.24	1.95	0.00	0.00	0.00	0.00	0.07	0.03	0.03	0.03	0.07	0.03	0.01	0.01	0.15	0.06	0.03	0.01	0.58	0.34	0.22	0.15	0.36	0.26	0.18	0.13
34	35	*Pleuronectes platessa*	335.73	7.40	4.28	4.23	0.00	0.00	0.00	0.00	2.35	0.05	0.23	1.09	2.35	0.05	0.03	0.03	3.52	0.08	0.04	0.04	13.09	0.81	0.73	0.80	7.22	0.68	0.66	0.72
35	36	*Pomatoschistus microps*	0.95	7.55	9.59	40.30	0.01	0.00	0.00	0.00	0.00	0.19	0.19	0.37	0.03	0.23	0.29	1.21	0.03	0.23	0.29	1.21	0.08	0.81	0.72	4.02	0.02	0.36	0.15	1.60
36	37	*Pomatoschistus minutus*	3.59	10.67	8.39	16.43	0.00	0.00	0.00	0.00	0.07	0.28	0.00	0.00	0.11	0.32	0.25	0.49	0.11	0.32	0.25	0.49	0.27	0.89	0.57	1.95	0.05	0.25	0.07	0.96
37	38	*Solea solea*	1.24	0.45	0.43	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.05	0.01	0.02	0.01	0.13	0.04	0.06	0.02	0.07	0.02	0.03	0.01
38	39	*Syngnathus rostellatus*	0.13	0.21	0.24	1.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.04	0.00	0.00	0.00	0.02
39	40	*Zoarces viviparus*	0.93	0.10	0.09	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
40	41	*Anas acuta*	1.00	1.74	4.27	4.81	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.01	0.01	0.06	0.11	0.26	0.29	0.10	0.17	0.42	0.47	0.03	0.06	0.15	0.17
41	42	*Anas platyrhynchos*	2.69	4.25	5.20	2.05	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.06	0.09	0.11	0.04	0.09	0.15	0.18	0.07	0.03	0.05	0.06	0.03
42	43	*Calidris alpina*	1.42	2.92	3.46	4.06	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.01	0.01	0.01	0.02	0.05	0.06	0.07	0.29	0.61	0.72	0.84	0.27	0.55	0.65	0.76
43	44	*Calidris canutus*	5.48	5.61	2.72	3.56	0.00	0.00	0.00	0.00	0.02	0.02	0.06	0.06	0.02	0.02	0.01	0.01	1.08	1.10	0.53	0.70	1.38	1.41	0.69	0.90	0.28	0.29	0.14	0.18
44	45	*Haematopus ostralegus*	32.44	31.49	22.20	21.23	0.00	0.00	0.00	0.00	0.09	0.09	0.00	0.00	0.09	0.09	0.06	0.06	0.88	0.85	0.60	0.57	4.17	4.05	2.85	2.73	3.21	3.11	2.19	2.10
45	46	*Larus argentatus*	6.74	6.34	2.41	1.66	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.30	0.29	0.11	0.07	0.40	0.37	0.14	0.10	0.08	0.08	0.03	0.02
46	47	*Larus canus*	0.57	0.86	1.39	2.13	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.02	0.03	0.05	0.08	0.03	0.04	0.07	0.11	0.01	0.01	0.01	0.02
47	48	*Larus ridibundus*	3.88	4.29	4.29	4.48	0.00	0.00	0.00	0.00	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.21	0.23	0.23	0.24	0.39	0.43	0.43	0.45	0.16	0.18	0.18	0.19
48	49	*Limosa lapponica*	2.06	2.38	2.74	3.94	0.00	0.00	0.00	0.00	0.01	0.01	0.07	0.07	0.01	0.01	0.01	0.01	0.33	0.38	0.44	0.63	0.42	0.48	0.56	0.80	0.08	0.10	0.11	0.16
49	50	*Numenius arquata*	11.78	20.07	24.66	26.58	0.00	0.00	0.00	0.00	0.03	0.05	0.00	0.00	0.03	0.05	0.07	0.07	0.39	0.66	0.81	0.88	1.22	2.08	2.56	2.76	0.80	1.37	1.68	1.81
50	51	*Pluvialis apricaria*	0.33	1.48	1.08	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.02	0.02	0.01	0.04	0.03	0.02	0.00	0.01	0.01	0.00
51	52	*Recurvirostra avosetta*	0.70	1.13	0.85	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.05	0.07	0.06	0.04	0.07	0.11	0.08	0.06	0.02	0.04	0.03	0.02
52	53	*Somateria mollissima*	6.04	8.99	3.29	2.55	0.00	0.00	0.00	0.00	0.02	0.02	0.05	0.06	0.02	0.02	0.01	0.01	0.15	0.23	0.08	0.07	0.82	1.22	0.45	0.35	0.65	0.97	0.35	0.27
53	54	*Tadorna tadorna*	14.46	17.55	17.43	22.13	0.00	0.00	0.00	0.00	0.04	0.05	0.00	0.00	0.04	0.05	0.05	0.06	0.38	0.46	0.45	0.58	1.95	2.37	2.35	2.99	1.54	1.87	1.85	2.35
54	55	*Tringa totanus*	0.83	1.00	1.31	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.28	0.34	0.44	0.33	0.27	0.33	0.43	0.32
55	56	DOC	2042.90	1913.97	1748.55	1833.98	444.92	424.83	372.56	361.45	452.53	398.95	323.56	356.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
56	57	Sediment POC	39060.00	39060.00	39060.00	39060.00	0.00	0.00	0.00	0.00	318.89	445.12	70.08	180.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
57	58	Suspended POC	4348.67	1333.64	2122.98	2382.71	303.75	413.85	505.65	548.76	205.97	237.53	688.79	606.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

M

ENA RATIOS

Table M.1: Ratios between production and biomass (P/B; d^{-1}), production and respiration (P/R; -) and production and consumption (P/C; -) for each ENA compartment per decade as used in the four networks (BZ1980s, BZ1990s, BZ2000s and BZ2010s). Sources (with numbers in square brackets referring to compartment numbers in 2000/2010): [20] Baird et al. 2004. Mar Ecol Prog Ser 279:45-61; [6-14, 17-19, 21, 24-27, 29] Schückel et al. 2015. Mar Ecol Prog Ser 536:25-38; [1-5, 15-16, 28, 30-40, 43, 45, 48, 50-55] unpublished data supplied by Ulricke Schückel (Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Wadden Sea Station Sylt Hafenstr. 43, D-25992, List/ Sylt, Germany); [22-23, 41-42, 44, 46-47, 49] unpublished data supplied by Sabine Horn (Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Wadden Sea Station Sylt Hafenstr. 43, D-25992, List/ Sylt, Germany).

Compartment nr			P/B				P/R				P/C			
1980/ 1990	2000/ 2010	Compartment name	1980	1990	2000	2010	1980	1990	2000	2010	1980	1990	2000	2010
1	1	Phytoplankton	0.780	0.441	0.475	0.543	2.825	2.825	2.825	2.825				
2	2	Microphytobenthos	0.055	0.055	0.055	0.055	3.788	3.788	3.788	3.788				
3	3	Freshwater algae	0.050	0.050	0.050	0.050	2.825	2.825	2.825	2.825				
4	4	Pelagic Bacteria	0.300	0.300	0.300	0.300	1.000	1.000	1.000	1.000	0.500	0.500	0.500	0.500
5	5	Zooplankton	0.597	0.597	0.597	0.597	0.843	0.843	0.843	0.843	0.300	0.300	0.300	0.300
6	6	Benthic Bacteria	0.157	0.157	0.157	0.157	0.899	0.899	0.899	0.899	0.400	0.400	0.400	0.400
7	7	Meiofauna	0.022	0.022	0.022	0.022	0.263	0.263	0.263	0.263	0.153	0.153	0.153	0.153
8	8	*Peringia ulvae*	0.004	0.004	0.004	0.004	0.649	0.649	0.649	0.649	0.100	0.100	0.100	0.100
9	9	*Littorina littorea*	0.002	0.002	0.002	0.002	0.333	0.333	0.333	0.333	0.100	0.100	0.100	0.100
10	10	*Arenicola marina*	0.007	0.007	0.007	0.007	1.075	1.075	1.075	1.075	0.150	0.150	0.150	0.150
11	11	*Eteone sp*	0.003	0.003	0.003	0.003	0.091	0.091	0.091	0.091	0.074	0.074	0.074	0.074
12	12	*Hediste diversicolor*	0.003	0.003	0.003	0.003	0.247	0.247	0.247	0.247	0.064	0.064	0.064	0.064
13	13	*Nereis spec.*	0.003	0.003	0.003	0.003	0.247	0.247	0.247	0.247	0.064	0.064	0.064	0.064
14	14	*Heteromastus filiformis*	0.005	0.005	0.005	0.005	0.525	0.525	0.525	0.525	0.064	0.064	0.064	0.064
15	15	*Lanice conchilega*	0.005	0.005	0.006	0.006	0.523	0.523	0.523	0.523	0.267	0.267	0.267	0.267
16	16	*Marenzelleria viridis*	0.014	0.014	0.014	0.014	0.351	0.350	0.350	0.350	0.130	0.130	0.130	0.130
17	17	*Nephtys hombergii*	0.011	0.011	0.011	0.011	1.053	1.053	1.053	1.053	0.185	0.185	0.185	0.185
18	18	*Scoloplos armiger*	0.001	0.001	0.001	0.001	0.131	0.131	0.131	0.131	0.035	0.035	0.035	0.035
19	19	*Corophium spp*	0.004	0.004	0.004	0.004	0.213	0.213	0.213	0.213	0.146	0.146	0.146	0.146
20	20	*Gammarus spp.*	0.004	0.004	0.004	0.004	0.167	0.167	0.167	0.167	0.111	0.111	0.111	0.111
21	21	*Cerastoderma edule*	0.005	0.005	0.005	0.005	3.189	3.189	3.189	3.189	0.200	0.200	0.200	0.200
	22	*Magallana gigas*			0.001	0.001			0.077	0.077			0.067	0.067
22	23	*Ensis leei*	0.020	0.020	0.020	0.020	0.067	0.067	0.067	0.067	0.036	0.036	0.036	0.036
23	24	*Limecola balthica*	0.008	0.008	0.008	0.008	5.371	5.371	5.371	5.371	0.155	0.155	0.155	0.155
24	25	*Mya arenaria*	0.002	0.002	0.002	0.002	0.430	0.430	0.430	0.430	0.200	0.200	0.200	0.200
25	26	*Mytilus edulis*	0.001	0.001	0.001	0.001	0.182	0.182	0.182	0.182	0.135	0.135	0.135	0.135
26	27	*Scrobicularia plana*	0.005	0.005	0.005	0.005	1.300	1.300	1.300	1.300	0.200	0.200	0.200	0.200
27	28	*Carcinus maenas*	0.004	0.004	0.004	0.004	0.640	0.640	0.640	0.640	0.044	0.026	0.024	0.029
28	29	*Crangon crangon*	0.011	0.011	0.011	0.011	0.038	0.038	0.038	0.038	0.021	0.025	0.026	0.026
29	30	*Ammodytes tobianus*	0.006	0.006	0.006	0.006	7.087	7.194	7.150	7.212	0.625	0.624	0.624	0.625
30	31	*Clupea harengus*	0.008	0.008	0.008	0.008	0.500	0.500	0.500	0.500	0.250	0.250	0.250	0.250
31	32	*Myoxocephalus scorpius*	0.004	0.004	0.004	0.004	1.842	1.833	3.000	1.857	0.385	0.407	0.429	0.388
32	33	*Osmerus eperlanus*	0.010	0.010	0.010	0.010	0.704	0.703	0.703	0.704	0.208	0.208	0.208	0.208
33	34	*Platichthys flesus*	0.003	0.003	0.003	0.003	0.479	0.479	0.479	0.479	0.121	0.080	0.057	0.039
34	35	*Pleuronectes platessa*	0.007	0.007	0.007	0.007	0.667	0.667	0.667	0.667	0.179	0.064	0.041	0.037
35	36	*Pomatoschistus microps*	0.030	0.030	0.030	0.030	1.000	1.000	1.000	1.000	0.359	0.278	0.398	0.301
36	37	*Pomatoschistus minutus*	0.030	0.030	0.030	0.030	1.000	1.000	1.000	1.000	0.406	0.359	0.438	0.253
37	38	*Solea solea*	0.002	0.002	0.002	0.002	0.056	0.073	0.042	0.046	0.022	0.028	0.016	0.018
38	39	*Syngnathus rostellatus*	0.003	0.004	0.003	0.004	0.461	0.463	0.461	0.462	0.149	0.150	0.150	0.150
39	40	*Zoarces viviparus*	0.004	0.004	0.004	0.004	1.806	1.810	1.789	1.792	0.380	0.380	0.382	0.384
40	41	*Anas acuta*	0.003	0.003	0.003	0.003	0.048	0.048	0.048	0.048	0.029	0.029	0.029	0.029
41	42	*Anas platyrhynchos*	0.001	0.001	0.001	0.001	0.027	0.027	0.027	0.027	0.017	0.017	0.017	0.017
42	43	*Calidris alpina*	0.003	0.003	0.003	0.003	0.159	0.159	0.159	0.159	0.013	0.013	0.013	0.013
43	44	*Calidris canutus*	0.004	0.004	0.004	0.004	0.019	0.019	0.019	0.019	0.015	0.015	0.015	0.015
44	45	*Haematopus ostralegus*	0.003	0.003	0.003	0.003	0.100	0.100	0.100	0.100	0.021	0.021	0.021	0.021
45	46	*Larus argentatus*	0.002	0.002	0.002	0.002	0.033	0.033	0.033	0.033	0.026	0.026	0.026	0.026
46	47	*Larus canus*	0.002	0.002	0.002	0.002	0.046	0.045	0.046	0.045	0.035	0.034	0.035	0.034
47	48	*Larus ridibundus*	0.005	0.005	0.005	0.005	0.094	0.094	0.094	0.094	0.050	0.050	0.050	0.050
48	49	*Limosa lapponica*	0.004	0.004	0.004	0.004	0.023	0.023	0.023	0.023	0.018	0.018	0.018	0.018
49	50	*Numenius arquata*	0.003	0.003	0.003	0.003	0.082	0.082	0.082	0.082	0.026	0.026	0.026	0.026
50	51	*Pluvialis apricaria*	0.001	0.001	0.001	0.001	0.036	0.036	0.036	0.036	0.027	0.027	0.027	0.027
51	52	*Recurvirostra avosetta*	0.003	0.003	0.003	0.003	0.041	0.041	0.041	0.041	0.027	0.027	0.027	0.027
52	53	*Somateria mollissima*	0.003	0.003	0.003	0.003	0.106	0.106	0.106	0.106	0.020	0.020	0.020	0.020
53	54	*Tadorna tadorna*	0.003	0.003	0.003	0.003	0.104	0.104	0.104	0.104	0.020	0.020	0.020	0.020
54	55	*Tringa totanus*	0.003	0.003	0.003	0.003	0.270	0.270	0.270	0.270	0.008	0.008	0.008	0.008

N

DIET MATRICES

Table N.1: Diet matrices of the models for each predator compartment in percent (%) of the total diet. Diet matrices for the BZ1980s and BZ1990s networks are the same, as well as the ones for the BZ2000s and BZ2010s networks.

COMPARTMENT	Pelagic Bacteria	Zooplankton	Benthic Bacteria	Meiofauna	*Peringia ulvae*	*Littorina littorea*	*Arenicola marina*	*Eteone sp*	*Hediste diversicolor*	*Nereis spec.*	*Heteromastus filiformis*	*Lanice conchilega*	*Marenzelleria viridis*	*Nephtys hombergii*	*Scoloplos armiger*
PERIOD	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades
Phytoplankton	0	0.24975	0	0	0	0	0	0	0.14985	0.14985	0	0.84915	0	0	0
Microphytobenthos	0	0	0	0.18	0.75	0.73	0.1	0	0.3	0.3	0.05	0	0.1	0	0.1
Freshwater algae	0	0.00025	0	0	0	0	0	0	0.00015	0.00015	0	0.00085	0	0	0
Pelagic Bacteria	0	0.05	0	0	0	0	0	0	0	0	0	0.01	0	0	0
Zooplankton	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0
Benthic Bacteria	0	0	0	0.3	0.125	0.14	0.35	0	0.1	0.1	0.2	0	0.1	0	0.4
Meiofauna	0	0	0	0	0	0	0	0	0.1	0.1	0	0	0.01	0.33	0
Peringia ulvae	0	0	0	0	0	0	0	0.7	0.05	0.05	0	0	0	0	0
Littorina littorea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arenicola marina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eteone sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hediste diversicolor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nereis spec.	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0
Heteromastus filiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0
Lanice conchilega	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marenzelleria viridis	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0
Nephtys hombergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scoloplos armiger	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0
Corophium spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gammarus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cerastoderma edule	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magallana gigas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ensis leei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limecola balthica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mya arenaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilus edulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scrobicularia plana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carcinus maenas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crangon crangon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ammodytes tobianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clupea harengus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myoxocephalus scorpius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmerus eperlanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platichthys flesus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuronectes platessa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pomatoschistus microps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pomatoschistus minutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solea solea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syngnathus rostellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zoarces viviparus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anas acuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anas platyrhynchos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calidris alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calidris canutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haematopus ostralegus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus argentatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus canus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus ridibundus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limosa lapponica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Numenius arquata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pluvialis apricaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Recurvirostra avosetta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Somateria mollissima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tadorna tadorna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tringa totanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOC	1	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0
Sediment POC	0	0	1	0.42	0.125	0.13	0.55	0	0.15	0.15	0.45	0	0.6	0.64	0.4
Suspended POC	0	0.6	0	0.1	0	0	0	0	0.15	0.15	0	0.14	0.19	0	0.1

Table N.1: Continued

COMPARTMENT	*Corophium spp*	*Gammarus spp.*	*Cerastoderma edule*	*Magallana gigas*	*Magallana gigas*	*Ensis leei*	*Limecola balthica*	*Mya arenaria*	*Mytilus edulis*	*Scrobicularia plana*	*Carcinus maenas*	*Crangon crangon*	*Ammodytes tobianus*	*Clupea harengus*	*Myoxocephalus scorpius*
PERIOD	All decades	All decades	All decades	1980s/1990s	2000s/2010s	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades
Phytoplankton	0	0	0.2	0	0.19	0.527	0.2	0.15	0.2	0.15	0	0	0	0	0
Microphytobenthos	0.65	0.35	0.21	0	0.15	0.21	0.3	0.3	0.18	0.29	0.08	0.05	0	0	0
Freshwater algae	0	0	0.416	0	0.488	0.1	0.248	0.41	0.456	0.344	0	0	0	0	0
Pelagic Bacteria	0	0	0.01	0	0.01	0.01	0	0.01	0.01	0	0	0	0	0	0
Zooplankton	0	0	0	0	0	0	0	0	0	0	0	0	0.75	1	0
Benthic Bacteria	0.13	0.29	0	0	0	0	0.075	0	0	0.05	0.02	0.1	0	0	0
Meiofauna	0	0	0	0	0	0	0	0	0	0	0.05	0.1	0.1	0	0
Peringia ulvae	0	0	0	0	0	0	0	0	0	0	0	0.12	0.02	0	0
Littorina littorea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arenicola marina	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0
Eteone sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hediste diversicolor	0	0	0	0	0	0	0	0	0	0	0.15	0.04	0.01	0	0
Nereis spec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heteromastus filiformis	0	0	0	0	0	0	0	0	0	0	0	0.04	0.01	0	0
Lanice conchilega	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Marenzelleria viridis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtys hombergii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scoloplos armiger	0	0	0	0	0	0	0	0	0	0	0	0.03	0	0	0
Corophium spp	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0	0
Gammarus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0
Cerastoderma edule	0	0	0	0	0	0	0	0	0	0	0.23	0.24	0	0	0
Magallana gigas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ensis leei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limecola balthica	0	0	0	0	0	0	0	0	0	0	0.05	0.11	0	0	0
Mya arenaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilus edulis	0	0	0	0	0	0	0	0	0	0	0.02	0.02	0	0	0
Scrobicularia plana	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0	0
Carcinus maenas	0	0	0	0	0	0	0	0	0	0	0.03	0	0	0	0.497
Crangon crangon	0	0	0	0	0	0	0	0	0	0	0.17	0	0	0	0.45
Ammodytes tobianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clupea harengus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myoxocephalus scorpius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmerus eperlanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platichthys flesus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuronectes platessa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pomatoschistus microps	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0.046
Pomatoschistus minutus	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0.007
Solea solea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syngnathus rostellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zoarces viviparus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anas acuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anas platyrhynchos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calidris alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calidris canutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haematopus ostralegus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus argentatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus canus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus ridibundus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limosa lapponica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Numenius arquata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pluvialis apricaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Recurvirostra avosetta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Somateria mollissima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tadorna tadorna	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tringa totanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sediment POC	0.13	0.36	0	0	0	0	0.075	0	0	0.05	0.1	0.1	0	0	0
Suspended POC	0.09	0	0.164	0	0.162	0.153	0.102	0.13	0.154	0.116	0	0	0	0	0

Table N.1: Continued

COMPARTMENT	*Osmerus eperlanus*	*Platichthys flesus*	*Pleuronectes platessa*	*Pomatoschistus microps*	*Pomatoschistus minutus*	*Solea solea*	*Syngnathus rostellatus*	*Zoarces viviparus*	*Anas acuta*	*Anas platyrhynchos*	*Calidris alpina*	*Calidris canutus*	*Haematopus ostralegus*	*Haematopus ostralegus*
PERIOD	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	1980s/1990s	2000s/2010s
Phytoplankton	0	0	0	0	0	0	0.0999	0	0	0	0	0	0	0
Microphytobenthos	0	0	0	0	0	0	0.02	0	0	0	0	0	0	0
Freshwater algae	0	0	0	0	0	0	0.0001	0	0	0	0	0	0	0
Pelagic Bacteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zooplankton	0.5	0.05	0	0.4	0.4	0	0.8	0	0	0	0	0	0	0
Benthic Bacteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meiofauna	0	0	0.01	0.15	0.15	0.4	0	0.2	0	0	0	0	0	0
Peringia ulvae	0	0.15	0	0	0	0.05	0.02	0	0.3	0	0.2	0	0	0
Littorina littorea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arenicola marina	0	0.25	0.2	0	0	0.11	0	0	0	0	0.09	0	0.05	0.05
Eteone sp	0	0.01	0	0	0	0	0	0	0.04	0.09	0.01	0	0	0
Hediste diversicolor	0	0.1	0.3	0.06	0.06	0.11	0	0	0.2	0.08	0.09	0	0.04	0.04
Nereis spec.	0	0	0	0.01	0.01	0	0	0	0	0.05	0.04	0	0	0
Heteromastus filiformis	0	0.04	0	0.03	0.03	0	0	0	0.04	0.03	0.09	0	0	0
Lanice conchilega	0	0	0.03	0	0	0	0	0	0	0.03	0.04	0	0	0
Marenzelleria viridis	0	0	0	0	0	0	0	0	0.04	0.05	0.01	0	0	0
Nephtys hombergii	0	0	0	0	0	0	0	0	0.04	0.21	0.125	0	0	0
Scoloplos armiger	0	0	0	0.05	0.05	0	0	0	0	0.46	0	0	0	0
Corophium spp	0	0	0	0.05	0.05	0.1	0	0.4	0	0	0.125	0	0.02	0.02
Gammarus spp.	0	0	0	0.04	0.04	0.01	0	0	0.04	0	0	0	0	0
Cerastoderma edule	0	0.05	0.14	0	0	0	0	0	0.21	0	0.01	0.81	0.28	0.28
Magallana gigas	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
Ensis leei	0	0.03	0.03	0	0	0.02	0	0	0	0	0	0	0	0
Limecola balthica	0	0	0.13	0.1	0.1	0	0	0.05	0.04	0	0.04	0.19	0.25	0.25
Mya arenaria	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0.01
Mytilus edulis	0	0	0	0	0	0	0	0	0.04	0	0	0	0.26	0.25
Scrobicularia plana	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05
Carcinus maenas	0	0.05	0.08	0.06	0.06	0	0	0.15	0.005	0	0.09	0	0.02	0.02
Crangon crangon	0.5	0.22	0.08	0.05	0.05	0.1	0.02	0.2	0.005	0	0.04	0	0.02	0.02
Ammodytes tobianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clupea harengus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myoxocephalus scorpius	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmerus eperlanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platichthys flesus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuronectes platessa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pomatoschistus microps	0	0.025	0	0	0	0.05	0.02	0	0	0	0	0	0	0
Pomatoschistus minutus	0	0.025	0	0	0	0.05	0.02	0	0	0	0	0	0	0
Solea solea	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syngnathus rostellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zoarces viviparus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anas acuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anas platyrhynchos	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calidris alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calidris canutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haematopus ostralegus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus argentatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus canus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larus ridibundus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limosa lapponica	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Numenius arquata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pluvialis apricaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Recurvirostra avosetta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Somateria mollissima	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tadorna tadorna	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tringa totanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DOC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sediment POC	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Suspended POC	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table N.1: Continued

COMPARTMENT	*Larus argentatus*	*Larus canus*	*Larus ridibundus*	*Limosa lapponica*	*Numenius arquata*	*Pluvialis apricaria*	*Recurvirostra avosetta*	*Somateria mollissima*	*Tadorna tadorna*	*Tringa totanus*
PERIOD	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades	All decades
Phytoplankton	0	0	0	0	0	0	0	0	0	0
Microphytobenthos	0	0	0	0	0	0	0	0	0	0
Freshwater algae	0	0	0	0	0	0	0	0	0	0
Pelagic Bacteria	0	0	0	0	0	0	0	0	0	0
Zooplankton	0	0	0	0	0	0	0	0	0	0
Benthic Bacteria	0	0	0	0	0	0	0	0	0	0
Meiofauna	0	0	0	0	0	0	0	0	0	0
Peringia ulvae	0	0	0	0.01	0	0.48	0.81	0	0.8	0.2
Littorina littorea	0.004	0	0	0.01	0	0	0	0.002	0	0
Arenicola marina	0	0	0.55	0.3	0.29	0	0	0	0	0
Eteone sp	0	0	0	0.01	0	0.06	0	0	0	0
Hediste diversicolor	0.01	0.0129	0.08	0.25	0	0	0.08	0	0.08	0.1
Nereis spec.	0	0.0012	0	0.1	0	0	0	0	0	0
Heteromastus filiformis	0	0	0.01	0.02	0	0	0	0	0	0
Lanice conchilega	0	0	0.01	0.02	0	0	0	0.002	0	0
Marenzelleria viridis	0	0	0	0	0	0	0	0	0	0
Nephtys hombergii	0.011	0.032	0.05	0.08	0.019	0.16	0	0	0	0.1
Scoloplos armiger	0	0	0.1	0.05	0	0.3	0	0	0	0
Corophium spp	0.015	0.017	0	0	0	0	0.11	0	0.11	0.3
Gammarus spp.	0	0	0	0	0.001	0	0	0	0	0
Cerastoderma edule	0.19	0.76	0.1	0.02	0.5	0	0	0.45	0.01	0
Magallana gigas	0	0	0	0	0	0	0	0	0	0
Ensis leei	0	0	0	0.02	0	0	0	0	0	0
Limecola balthica	0.15	0.1769	0.1	0.05	0.13	0	0	0.026	0	0.1
Mya arenaria	0	0	0	0	0	0	0	0	0	0
Mytilus edulis	0.6	0	0	0.02	0	0	0	0.45	0	0
Scrobicularia plana	0	0	0	0	0	0	0	0	0	0
Carcinus maenas	0.02	0	0	0.02	0.05	0	0	0.07	0	0.1
Crangon crangon	0	0	0	0.02	0.01	0	0	0	0	0.1
Ammodytes tobianus	0	0	0	0	0	0	0	0	0	0
Clupea harengus	0	0	0	0	0	0	0	0	0	0
Myoxocephalus scorpius	0	0	0	0	0	0	0	0	0	0
Osmerus eperlanus	0	0	0	0	0	0	0	0	0	0
Platichthys flesus	0	0	0	0	0	0	0	0	0	0
Pleuronectes platessa	0	0	0	0	0	0	0	0	0	0
Pomatoschistus microps	0	0	0	0	0	0	0	0	0	0
Pomatoschistus minutus	0	0	0	0	0	0	0	0	0	0
Solea solea	0	0	0	0	0	0	0	0	0	0
Syngnathus rostellatus	0	0	0	0	0	0	0	0	0	0
Zoarces viviparus	0	0	0	0	0	0	0	0	0	0
Anas acuta	0	0	0	0	0	0	0	0	0	0
Anas platyrhynchos	0	0	0	0	0	0	0	0	0	0
Calidris alpina	0	0	0	0	0	0	0	0	0	0
Calidris canutus	0	0	0	0	0	0	0	0	0	0
Haematopus ostralegus	0	0	0	0	0	0	0	0	0	0
Larus argentatus	0	0	0	0	0	0	0	0	0	0
Larus canus	0	0	0	0	0	0	0	0	0	0
Larus ridibundus	0	0	0	0	0	0	0	0	0	0
Limosa lapponica	0	0	0	0	0	0	0	0	0	0
Numenius arquata	0	0	0	0	0	0	0	0	0	0
Pluvialis apricaria	0	0	0	0	0	0	0	0	0	0
Recurvirostra avosetta	0	0	0	0	0	0	0	0	0	0
Somateria mollissima	0	0	0	0	0	0	0	0	0	0
Tadorna tadorna	0	0	0	0	0	0	0	0	0	0
Tringa totanus	0	0	0	0	0	0	0	0	0	0
DOC	0	0	0	0	0	0	0	0	0	0
Sediment POC	0	0	0	0	0	0	0	0	0	0
Suspended POC	0	0	0	0	0	0	0	0	0	0

O

ENA OUTPUT

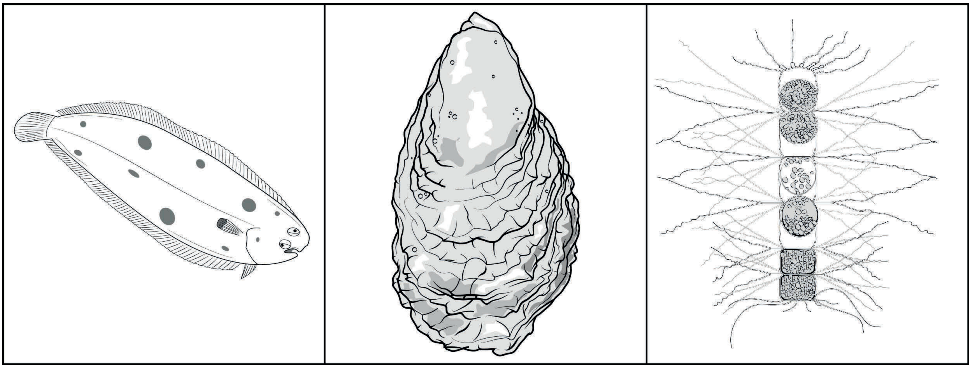
Table O.1: Complete ENA network output of all four models, for explanations or definitions see documentation of the enaR package (Lau et al., 2017; Borrett and Lau, 2014; Fath et al., 2019).

enaR variable	**Full name**	**BZ1980s**	**BZ1990s**	**BZ2000s**	**BZ2010s**
Boundary	Boundary (sum of all inputs or sum of all outputs)	1513.84	1656.59	2285.41	1941.34
TST	Total systems throughflow	3697.7	4102.78	6503.27	5032.74
TSTp	Total system throughput	5212.13	5759.37	8788.68	6974.08
APL	Average path length	2.44	2.48	2.85	2.59
FCI	Finn cycling index	0.12	0.11	0.07	0.07
BFI	Boundary flow intensity	0.41	0.4	0.35	0.39
DFI	Direct flow intensity	0.21	0.23	0.34	0.3
IFI	Indirect flow intensity	0.38	0.36	0.31	0.31
ID.F	Ratio of indirect to direct flow	1.77	1.57	0.93	1.03
ID.F.I	Input-oriented ratio of indirect to direct flow intensity	1.6	1.52	1.31	1.32
ID.F.O	Output-oriented ratio of indirect to direct flow intensity	1.68	1.48	1.19	0.9
HMG.I	Input-oriented network homogenization ratio	1.6	1.59	1.55	1.55
HMG.O	Output-oriented network homogenization ratio	1.68	1.65	1.54	1.61
AMP.I	Input-oriented network amplification ratio	9	6	3	3
AMP.O	Output-oriented network amplification ratio	17	16	59	47
mode0.F	Boundary input	1513.84	1656.59	2285.41	1941.34
mode1.F	Internal first passage flow	1731.89	1985.15	3752.65	2717.21
mode2.F	Cycled flow	452.1	461.04	465.21	374.18
mode3.F	Dissipative equivalent to mode1.F	1731.89	1985.15	3752.65	2717.21
mode4.F	Dissipative equivalent to mode0.F	1513.84	1656.59	2285.41	1941.34
sumInputs	Sum of all inputs	1513.84	1656.59	2285.41	1941.34
sumOutputs	Sum of all outputs	1514.43	1656.59	2285.41	1941.34
H	Flow diversity	5.34	5.43	5.17	5.29
AMI	Average mutual information	1.76	1.78	1.97	1.85
Hr	Residual mutual information	3.58	3.65	3.21	3.44

Table O.1: Continued

enaR variable	Full name	BZ1980s	BZ1990s	BZ2000s	BZ2010s
CAP	Capacity	27838.74	31246.78	45475.24	36897
ASC	Ascendency	9166.16	10230.15	17294.51	12901.21
OH	Overhead	18672.58	21016.63	28180.73	23995.79
ASC.CAP	Ascendency-to-capacity ratio	0.33	0.33	0.38	0.35
OH.CAP	Overhead-to-capacity ratio	0.67	0.67	0.62	0.65
robustness	Robustness	0.37	0.37	0.37	0.37
ELD	Effective link density of the network	3.46	3.54	3.04	3.3
TD	Trophic depth of the network	3.38	3.43	3.91	3.6
A.input	Ascendency of just the imports	2366.55	2709.53	4263.9	3255.04
A.internal	Ascendency of just the internal flows	4329.56	4787.15	8516.4	6139.23
A.export	Ascendency of just the export flows	1540.22	1708.22	2089.89	1877.2
A.respiration	Ascendency of just the respiration flows	929.83	1025.26	2424.32	1629.74
OH.input	Overhead of the imports alone	3961.05	4201.39	5653.32	5122.06
OH.internal	Overhead of the internal flows	9707	11340.47	15730.21	12755.5
OH.export	Overhead of the exports alone	2560.37	2640.81	2561	2826
OH.respiration	Respiration portion of system overhead	2444.15	2833.96	4236.19	3292.24
CAP.input	Input portion of system capacity	6327.61	6910.92	9917.22	8377.1
CAP.internal	Internal portion of system capacity	14036.56	16127.62	24246.61	18894.73
CAP.export	Export portion of system capacity	4100.59	4349.03	4650.89	4703.19
CAP.respiration	Respiration portion of system capacity	3373.99	3859.22	6660.51	4921.98
ATL	Average trophic level	2.58	2.58	2.57	2.57
Detritivory	Detritivory, flow from the detrital pool (non-living nodes) to the second trophic level	650.17	706.2	974.85	693.33
DetritalInput	Exogenous inputs to the detrital pool	748.67	838.69	878.22	910.21
DetritalCirc	Internal circulation within the detrital pool	205.97	237.53	688.79	606.83
NCYCS	Number of cycles	4	4	4	4
NNEX	Number of disjoint nexuses	4	4	4	4
CI	Cycling Index	0	0	0	0
Herbivory	Sum of herbivory flows	270.05	377.39	1173.3	664.89
DH	Detritivory Herbivory ratio	2.41	1.87	0.83	1.04
MTL	Mean Trophic Level	2.15	2.12	2.11	2.13
RED_CAP	Redundancy-to-capacity ratio	0.35	0.36	0.35	0.35

SUMMARY



The international Wadden Sea is one of the largest intertidal systems in the world; it is located in the south-eastern part of the North Sea following the coastlines of Denmark, Germany and the Netherlands. With its intertidal as well as shallow subtidal flats, drainage gullies and deeper inlets and channels it forms an unique system that, due to its outstanding universal values, became a UNESCO world heritage site in 2009 for the German and Dutch part, and in 2014 for the Danish part. The north-eastern and south-western part of the Wadden Sea are micro-tidal regions ($<1.5\,\mathrm{m}$ tidal amplitude) and differ from the macro-tidal central Wadden Sea ($>3\,\mathrm{m}$ tidal amplitude), which is also strongly influenced by the large freshwater runoff ($>850\,\mathrm{m}^3\,\mathrm{s}^{-1}$) of the river Elbe.

In addition to influences of tides, geomorphology and freshwater runoff, the Wadden Sea also experiences the impacts of human behavior. Food collection (hunting whales, seals and birds, collecting shellfish and fishing) started as early as the prehistoric times, but has increased in the last 2000 years. Embankment of inhabited salt-marshes started at least 1000 years ago. Impacts of pollution (including those of nutrients) are acknowledged since the 1970s. Since the mid-1980s, the Wadden Sea started to experience the consequences of climate change, including the increase in water temperatures. Relative recently, the introduction of invasive species is being considered as a potential threat for the natural values of the Wadden Sea.

This PhD is part of a larger NWO-BMBF project called "INFOWEB" (Impact of invasive species on the Wadden Sea food web). The main goals of the project was to investigate the impact of invasions on the Wadden Sea ecosystem, which can only be understood if the changes in the food web are looked upon in the light of all major changes within these systems. Therefore, multiple PhD and post-doctoral researchers have focused on different regions and systems in the Wadden Sea: the micro-tidal Balgzand system in the south-western Wadden Sea and the macro-tidal Jade bight in the central Wadden Sea, and the micro-tidal Sylt-Rømø bight system in the north-eastern part. This study is focused on the Balgzand intertidal area in the western Dutch Wadden Sea.

The aim of this study is to identify the effects of the invasion of three macrozoobenthic species (*Ensis leei*, *Magallana gigas*, and *Marenzelleria viridis*) on the system in terms of multi-annual and seasonal changes and variability of several aspects of the Balgzand ecosystem such as nutrients, changes in biodiversity, and changes in trophic interactions. One of the main goal was to be able to construct ENA food web models of several decades and examine the changes in the system in terms of trophic structure, cycling and other system properties.

The aims stated above lead to the following research questions:

1. Which changes in the food web, including the invasions, occurred at the Balgzand tidal flats over the course of the last decades?

2. Did those changes happened concurrently to each other and, if so, how did they interact?

3. How did these changes influence the trophic interactions between different native and invasive species?

To answer these questions several studies have been conducted. The first section (Chapter 2 to 4) considers studies on long-term changes within the western Dutch Wadden Sea and coastal zone from the bottom (nutrients) to the top (single trophic levels) of the food web. The second section (Chapter 5 to 8) takes a closer look at the food web interactions of the Balgzand intertidal. The last section contains the synthesis.

PART 1: LONG-TERM CHANGES IN THE WESTERN DUTCH WADDEN SEA AND COASTAL ZONE

Sources and (temporal) sinks of nutrients in the western Wadden Sea (1976-2012)

The trophic state of the Balgzand ecosystem is strongly influenced by nutrient dynamics in the western part of the Dutch Wadden Sea, which was dominated by eutrophication of coastal waters in the mid-1980s. In **Chapter 2** long-term field observations of nitrogen [N] and phosphorus [P] concentrations were used to construct nutrient budgets for the western Dutch Wadden Sea between 1976 and 2012. Nutrients enter into the western Dutch Wadden Sea via river runoff, through exchange with the coastal zone of the North Sea, neighbouring tidal basins and through atmospheric deposition (for N). The highest concentrations in phosphorus and nitrogen were observed 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 western Wadden Sea. The budgets suggested that the period of the initial net import of phosphorus and nitrogen switched to a net export in 1981 for nitrogen and in 1992 for phosphorus. Such different behaviour in nutrient budgets during the rise and fall of external nutrient concentrations might be the result of different sediment-water exchange dynamics for P and N. It was hypothesized that during the period of increasing eutrophication (1976-1981) P, and to a lesser degree N, were stored in sediments as organic and inorganic nutrients. In the following period (1981-1992) external nutrient concentrations (especially in the North Sea) decreased, but P concentrations in the Wadden Sea remained high due to prolonged sediment release, while denitrification removed substantial amounts of N. From 1992 onwards, P and N budgets were closed by net loss, most probably because P stores were then depleted and denitrification continued. Under the present conditions (lower rates of sediment import and depleted P stores), nutrient concentrations in this area are expected to be more strongly influenced by wind-driven exchange with the North Sea and precipitation-driven discharge from Lake IJssel. This implies that the consequences of climate change will be more important in determining the present and future trophic state of the Balgzand, than during the 1970s and 1980s when nutrient dynamics were dominated by variations in nutrient concentrations of the riverine runoff.

Geographical variation in phytoplankton dynamics in the coastal zone (2001-2009)

The exchange of particulate matter between western Dutch Wadden Sea and the North Sea coastal zone is considered to be important, but the size of the exchange zone is still an unresolved issue. In **Chapter 3**, phytoplankton order richness was applied as an innovative marine tracer to identify the geographical position of a coastal exchange zone in the SE North Sea, including its variability in time and space. Previous observations on dynamics of suspended particulate matter accumulation resulted in a hypothesized boundary between coastal waters (including the Wadden Sea) and open North Sea waters, the so-called "line-of-no-return". Our study along two transects (Terschelling, Noordwijk) in the Dutch coastal zone showed seasonality patterns in phytoplankton order richness, both for diatoms and flagellates. The coastal Wadden Sea was found to be clearly different from the open North Sea, implying that seasonality in Wadden Sea phytoplankton was 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". Our findings indicated 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.

Long-term changes of fish community in the western Wadden Sea (1960-2011)

Most coastal ecological time series are too short to give a long historical perspective and to identify large-scale consecutive impacts of human behaviour on coastal systems. In **Chapter 4**, catches of the ongoing daily sampling program of the fish fauna in the western Dutch Wadden Sea using fixed gear were analysed for the years 1960-2011 (52 years). The total daily catch during spring (mainly immigrating fish from the coastal zone) and autumn (mainly emigrating young-of-the-year) 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. Mean individual biomass decreased in spring between 1980 and the present from about 150 to 20 g wet mass. No trend was found in autumn mean individual biomass which fluctuated around 20 g wet mass. The trophic position of pelagic fish in spring fell from about 3.9 to 3.1 from 1980 to 2011. 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 was argued that the most likely explanatory variables were 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 concluded 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 corroborated that ecological change in coastal ecosystems has not only occurred in the past but still continues.

PART 2: FOOD WEB INTERACTIONS AT BALGZAND, WESTERN WADDEN SEA

Shifts in predators and epibenthic predation pressure at Balgzand, western Wadden Sea (1975-2014)

Coinciding changes in top predators may dampen or amplify the impacts of invasive species on trophic interactions within coastal food webs. In **Chapter 5**, the long-term changes (1975 to 2014) in predator–prey interactions following concurrent changes in predatory epibenthic fish and crustaceans in the western Wadden Sea were explored. Historical and recent invasions had resulted in an increase in relatively large and long-lived bivalves (*Mya arenaria*, *Ensis leei*, *Magallana gigas*) which have found a size refuge from epibenthic predators in the Wadden Sea. While bivalves dominated the macrozoobenthic biomass, polychaetes were the main food source of epibenthic predators, with the invasive polychaete *Marenzelleria viridis* probably becoming an important food source during the early 2000s. Food requirements of epibenthic crustaceans, mainly *Crangon crangon*, almost doubled from 5 to 10 g ash-free dry mass (AFDM) $m^{-2}\,y^{-1}$, and requirements of epibenthic fish decreased by more than 80%, mainly due to the local disappearance of juveniles of the flatfish *Pleuronectes platessa*. While the overall food requirements of the epibenthic predators stayed more or less constant, 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} thereafter, resulting from changes in native (*Nereis diversicolor* and *Heteromastus filiformis*) and invasive (*M. viridis*) polychaetes. These findings illustrate that coinciding species-specific changes and interactions of both predators and prey should be taken into account to determine the impact of invasions on the food web structure and functioning of coastal systems.

Causes and consequences of growth reduction of plaice at Balgzand, western Wadden Sea (1975-2019)

Long-term changes in performance of predator species can have consequences for predator-prey interactions within the coastal food web and subsequently for the impacts of invasive species. In **Chapter 6**, the potential mechanisms for the observed decrease in summer growth of plaice *Pleuronectes platessa* L. in the western Dutch Wadden Sea was studied by analysing published and unpublished information from long-term investigations (1986-2019). Observed growth variability could be explained by differences induced by environmental variability (water temperature), and by non-genetic irreversible adaptation and sex. Dynamic Energy Budget analysis indicated that especially sexually-dimorphic growth in combination with variability in sex ratio could explain most of the variability in growth and the increase in the range of the size of individuals within the population over time. Summer growth reduction was not only observed among 0-group plaice in the intertidal, but also in the subtidal and tidal gullies as well as among I-and II-group plaice. Intraspecific competition for food was not detected but some support for interspecific competition with other predators was found. Also resource competition with the other abundant epibenthic species (0-, I- and II-group flounder *Platichthys flesus*; the brown shrimp *Crangon crangon*; the shore crab *Carcinus maenas*; the goby species *Pomatoschistus minutus* and *P. microps*) could not explain the summer growth reduction. The observed growth reduction coincided with a decrease in stomach content, especially of regenerating body parts of benthic prey items. It was hypothesised that macrozoobenthos becomes less active after the spring phytoplankton bloom, reducing prey availability for juvenile plaice in summer, causing a reduction in food intake and hence in growth.

The importance of freshwater algae import in the western Wadden Sea for the Balgzand food web (2014)

Estuarine food webs are generally considered to be supported by marine pelagic and benthic primary producers and by the import of dead organic matter from the coastal zone. Although estuaries receive considerable amounts of freshwater phytoplankton and organic compounds from adjacent rivers, the potential contribution of these living and dead matter to estuarine food webs is often assumed to be negligible and, therefore, not examined. Based on stable isotope analyses, **Chapter 7** reported the importance of freshwater suspended particulate organic matter for fueling estuarine food webs in comparison to estuarine suspended organic matter and microphytobenthos. This previously neglected food source contributed 50-60 % (annual average) of food intake of suspension-feeding bivalves such as cockles (*Cerastoderma edule*), mussels (*Mytilus edulis*) and Pacific oysters (*Magallana gigas*) at the estuarine Balgzand tidal flats (12-32 psu). For these species, this proportion was particularly high in autumn during strong run-off of suspended organic matter-rich freshwater, whilst estuarine suspended organic matter (20 %-25 %) and microphytobenthos (15 %-30 %) were relatively important in summer when the freshwater run-off was very low. These findings have implications for our understanding of the trophic interactions within coastal food webs and potentially for freshwater management of estuarine ecosystems.

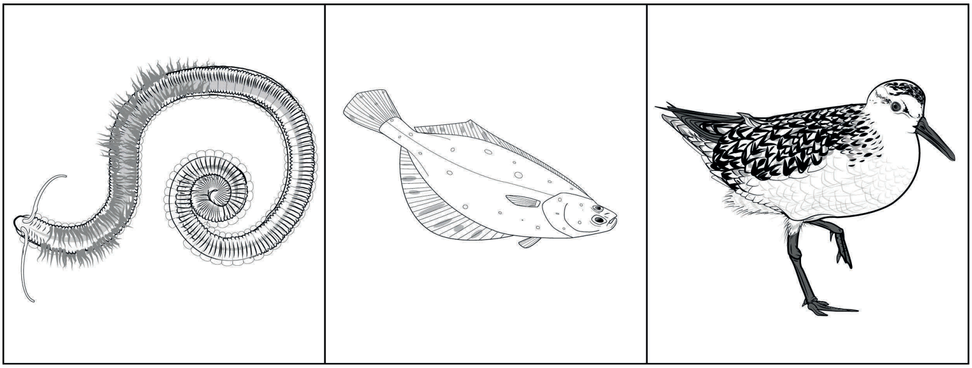
Impacts of macrozoobenthic invasions on carbon flows at Balgzand western Wadden Sea (1980s-2010s)

If invasions coincided with other changes affecting the food web dynamics, then the impacts of the invasive species can only be identified by taking the full dynamics of the system into account. In **Chapter 8**, a carbon flow model of the Balgzand was constructed at different time frames and analyzed for the impacts of the invasive species on carbon flows by using Ecological Network Analysis (ENA). The bivalves *Ensis leei* and *Magallana gigas* were observed for the first time in 1984 and 2001, respectively, the polychaete *Marenzelleria viridis* in 1989. Although *E. leei* and *M. viridis* reached a more or less similarly high biomass during their peak in the 2000s (ca. 1700 and 2000 $\mathrm{mg\,C\,m^{-2}}$, respectively), the consumption by bivalves was higher (>45% of total consumption) than that of the polychaete (<10%). Biomass and impact of *M. gigas* remained low. *E. leei*occupied an ecological niche that was partially empty, which led to competitive advantage with respect to other suspension feeders. Increasing biomass of *E. leei* coincided with a 70% increase of trophic transfer from primary to secondary producers and an 80% increase from secondary producers to detritus. Carbon flows from secondary producers to higher trophic levels were reduced by more than 60%. These shifts in trophic transfer were stronger than observed during the invasion of *M. gigas* in the Sylt-Rømø bight in the north-eastern Wadden Sea. At Balgzand, biomass of *M. gigas* and *M. viridis*, rapidly declined to low values in the 2010s, implying a limited and temporally impact. In the 2010s, however, *E. leei* was still responsible for 30% of the total consumption in the 2010s, indicating a long-term impact.

PART 3: SYNTHESIS

In **Chapter 9** the different aspects of the chapters in this thesis are summarized and discussed with respect to the concurrent changes and their cumulative effects on the system. There is a strong suggestion that changes within a system are indeed happening concurrent to each other and might even influence each other. The western Wadden Sea suffered from several long-term changes in many different areas of the food web, influencing those in species composition and trophic interactions. Changes that were found within this thesis were changes in nutrient concentrations, macrozoobenthic, fish, and epibenthic abundance and composition. Other studies also found changes in temperature, salinity, pythoplankton concentrations, microphytobenthos concentrations and bird abundance and composition. There is a strong suggestion that these changes within the system are indeed happening concurrent to each other and might even influence each other. Changes in the composition and concentration of primary producers can influence the food availability of higher trophic levels and therefor also influence the species composition of the rest of the food chain. Changes in abiotic factors such as salinity, nutrient availability and temperature played a role in shaping the Balgzand ecosystem and subsequently the potential of new species to become invasive. In the light of climate change, temperature and the tolerance and reproductive capacity at higher temperatures might become more and more important. This will enable warmwater species that are already introduced to further establish themselves, and will be setting the stage for inescapable invasions of new species entering the Wadden Sea as the result of temperature-driven poleward migration. Such changes may interfere with effectiveness of management (e.g. protection and restoration of natural values such as the Outstanding Unique Values). This is particularly true when current laws and regulations aim for conservation and enhancement of specific species and habitats and not that of the ecosystem's functions including nursery function for juvenile fish and the fueling capacity for migratory birds. Trilateral governments could or should take proactive measures to ensure sustained ecosystem functioning, taking the consequences of future invasions due to global warming explicitly into account.

SAMENVATTING



De internationale Waddenzee is het grootste aaneengesloten intergetijdegebied ter wereld. Het gebied is gelegen in het zuidoostelijke deel van de Noordzee langs de kusten van Denemarken, Duitsland en Nederland. Het samenspel van wadplaten, permanent ondergedoken zandbanken, prielen, geulen en zeegaten vormt een uniek ecosysteem dat, vanwege haar onvervangbare unieke natuurwaarde, op de werelderfgoedlijst van UNESCO is geplaatst (het Duitse en Nederlandse deel in 2009 en het Deense deel in 2014). Het noordoostelijke en zuidwestelijke deel van de Waddenzee zijn zogenaamde microgetijdengebieden ($<1.5\,\mathrm{m}$ getijamplitude), het centrale deel is een macrogetijdegebied ($<3\,\mathrm{m}$ getijamplitude) en staat onder een sterke beïnvloeding van toevoer van zoetwater ($>850\,\mathrm{m}^3\,\mathrm{s}^{-1}$) uit de Elbe rivier.

Naast de invloed van getij, geomorfologie en zoetwaterafvoer, ondervindt de Waddenzee ook de effecten van menselijk handelen. Het verzamelen van voedsel (jagen op walvissen, zeehonden en vogels, het verzamelen van schaaldieren en vissen) is begonnen in de prehistorie en is in de afgelopen 2000 jaar toegenomen. De aanleg van bewoonde kwelders begon ruim 1000 jaar geleden. De gevolgen van vervuiling (inclusief die met nutriënten) worden sinds de jaren zeventig onderkend. Sinds medio jaren tachtig worden de effecten van klimaatverandering op Waddenzee, waaronder die van de stijging van de watertemperatuur, meer en meer zichtbaar. Relatief recent wordt de introductie van invasieve soorten beschouwd als een potentiële bedreiging voor de natuurwaarden van de Waddenzee.

Dit proefschrift is een onderdeel van het "INFOWEB" project, waarin door een Nederlands-Duits onderzoekconsortium de invloed van invasieve soorten op het voedselweb van de trilaterale Waddenzee is onderzocht. Het project is gesubsidieerd door het Nederlandse (NWO) en het Duitse (BMBF) ministerie van onderwijs en wetenschappen. Het doel van dit onderzoek was om de invloed van de invasies op het voedselweb van de Waddenzee zo goed mogelijk in kaart te brengen, daarbij rekening houdend met alle andere grote veranderingen in dit gebied.

Meerdere promovendi en postdoctorale onderzoekers hebben hiervoor naar verschillende deelgebieden van de Waddenzee gekeken: het Balgzand (een microgetijdegebied in de zuidwestelijke Waddenzee), de Jadebocht (een macrogetijdegebied in de centrale Waddenzee) en het Sylt-Rømø getijdenbekken (een microgetijdegebied in het noordoostelijke deel van de Waddenzee, op de grens van Duitsland en Denemarken). Dit proefschrift beschrijft de resultaten van het onderzoek dat zich richtte op het intergetijdengebied van het Balgzand in de westelijke Nederlandse Waddenzee.

Het onderzoek aan het Balgzand richtte zich vooral op de gevolgen van recentelijke invasies van een aantal soorten bodemdieren [de schelpen *Ensis leei* (Amerikaanse zwaardschede) en *Magallana gigas* (Japanse oester) en de borstelworm *Marenzelleria viridis*] op het lokale voedselweb. Net als voor de andere studiegebieden, is ook voor het Balgzand de invloed van de invasieve soorten op het voedselweb vertaald in veranderingen in de koolstofstromen tussen de verschillende trofische niveaus aan de hand van een ecologische netwerkanalyse (ENA). Zowel de meerjarige en seizoeneffecten van de invasies op andere soorten en op hun interacties zijn bestudeerd, in samenhang met andere veranderingen in dit gebied zoals die in de toevoer van voedingsstoffen, in de biodiversiteit en in de trofische interacties.

Samengevat worden in dit proefschrift de volgende onderzoeksvragen behandeld:

1. Welke veranderingen in het voedselweb, inclusief die als gevolg van de invasies, hebben in de afgelopen decennia plaatsgevonden op de wadplaten van Balgzand?
2. Hebben veranderingen gelijktijdig plaatsgevonden en, zo ja, is er sprake geweest van interacties tussen de invasies en andere veranderingen?
3. Hoe hebben eventuele veranderingen de trofische interacties tussen de inheemse en invasieve soorten in het lokale voedselweb beïnvloed?

Het eerste deel (Hoofdstuk 2 tot 4) van dit proefschrift beschrijft een aantal studies naar lange-termijn veranderingen van het westelijke deel van de Waddenzee en de nabijgelegen kustzone van de Noordzee in verschillende compartimenten van het voedselweb (van nutriënten tot predatoren). Het tweede deel (Hoofdstuk 5 tot 8) gaat dieper in op de gevolgen van deze veranderingen voor de trofische interacties in het lokale voedselweb van het Balgzand. Het laatste deel (Hoofdstuk 9) bespreekt de samenhang tussen de diverse resultaten.

SECTIE 1: LANGE-TERMIJN VERANDERINGEN IN DE WESTELIJKE WADDENZEE EN DE NEDERLANDSE KUSTZONE

Bronnen en (tijdelijke) opslag van nutriënten in de westelijke Waddenzee (1976-2012)

De basis van het voedselweb van het Balgzand wordt beïnvloed door de beschikbaarheid van nutriënten, met name stikstof (N) en fosfor (P), in het westelijke deel van de Nederlandse Waddenzee. Hoofdstuk 2 beschrijft nutriëntenbudgetten voor de westelijke Nederlandse Waddenzee aan de hand van de door Rijkswaterstaat gemeten concentraties van N en P tussen 1976 en 2012. Deze nutriënten komen de westelijke Nederlandse Waddenzee binnen via de afvoer van zoetwater door spui, door uitwisseling met de kustzone van de Noordzee, door uitwisseling met aangrenzende getijbekkens, en door atmosferische depositie (alleen voor N). De hoogste concentraties van N en P zijn waargenomen halverwege de jaren tachtig. Hierna namen de concentraties weer af door o.a. een verbeterde fosforverwijdering bij de zuivering van het afvalwater, een reductie van stikstofbemesting in de landbouw en een verwijdering van fosfaten uit wasmiddelen.

Volgens deze nutriëntenbudgetten veranderde de aanvankelijke netto import van fosfor en stikstof in een netto export, voor stikstof gebeurde dit in 1981 en voor fosfor in 1992. Deze verschuiving is vermoedelijk het gevolg van een verschillende uitwisseling tussen bodem en water ten tijde van toenemende eutrofiering (meer externe toevoer van nutriënten) en de-eutrofiering (minder externe toevoer van nutrienten). Mogelijk dat een deel van P (en, in mindere mate, van N) in anorganische en organisch vorm werd opgeslagen in het sediment van de wadbodem tijdens de periode van toenemende eutrofiëring (1976-1981). Dit proces kan versterkt zijn door de aanwezigheid van oude geulen die zich na de afsluiting van de Zuiderzee opvulden met nutriëntenrijk bodemmateriaal afkomstig uit de Noordzee. In de daaropvolgende periode (1981-1992) nam de externe toevoer van nutrienten vanuit de rivieren af, zoals onder meer zichtbaar in de afnemende concentraties van N en P in de Noordzee. In de Waddenzee bleven de concentraties van P echter hoog, waarschijnlijk als gevolg van een langdurige afgifte van het eerder opgeslagen P uit het sediment. Mogelijk dat ook het eerder opgeslagen N toen uit de wadbodem vrijkwam, maar dit leidde niet tot relatief hoge concentraties van N in het water omdat aanzienlijke hoeveelheden meteen naar de atmosfeer verdwenen als gevolg van denitrificatie. Na 1992 was de sluitpost van beide budgetten negatief, wat er op wijst dat er voor P waarschijnlijk geen langjarige afgifte vanuit de wadbodem meer plaatsvond en dat er voor N nog steeds een deel naar de atmosfeer verdween.

Onder de huidige omstandigheden is de aanvoer van nutriëntenrijk materiaal vanuit de Noordzee relatief laag (de oude geulen zijn inmiddels grotendeels opgevuld) en bevat de wadbodem geen voorraad aan N en P meer. Door het wegvallen van deze eerder sturende factoren mag verwacht worden dat de huidige nutriëntendynamiek gevoeliger zal zijn voor veranderingen in de sterkte van de windgedreven uitwisseling van het water met de Noordzee en de hoeveelheid van de neerslag-gedreven afvoer van zoetwater uit het IJsselmeer. De huidige beschikbaarheid van nutriënten voor het voedselweb van het Balgzand staat hierdoor, meer dan in de jaren tachtiger, onder invloed van veranderingen in wind en neerslagpatronen bijvoorbeeld als gevolg van klimaatverandering.

Geografische variatie in de seizoendynamiek van fytoplankton in de kustzone (2001-2009)

Zoals hierboven beschreven wordt de beschikbaarheid van nutriënten voor het voedselweb van het Balgzand voor een belangrijk deel bepaald door de uitwisseling van zwevend materiaal tussen de westelijke Waddenzee en de aangrenzende kustzone van de Noordzee. In Hoofdstuk 3 is aan de hand van de seizoendynamiek in fytoplankton (zwevende algen) onderzocht hoe ver deze uitwisselingzone zich geografisch uitstrekt. Het studiegebied was gebaseerd op een eerder geformuleerde hypothetische grens tussen kustwateren (inclusief de Waddenzee) en het water van de open Noordzee, de zogenaamde "line-of-no-return".

De aanwezigheid van een dergelijke scheidingslijn is aangescherpt aan de hand van de seizoenvariatie in de rijkdom van fytoplanktonordes (een innovatieve mariene tracer, waarbij algensoorten op de taxonomische rang van ordes zijn geclusterd). Hiervoor is gebruik gemaakt van gegevens van diatomeeën (kiezelwieren) en flagellaten (zwevende algen met zweepharen) zoals tussen 2001 en 2009 zoals door Rijkswaterstaat verzameld op meetstations in de westelijke Waddenzee en langs twee raaien (Terschelling en Noordwijk) in de kustzone van de Noordzee.

De seizoendynamiek in de algengroepen van Waddenzee bleek duidelijk te verschillen van die in de open Noordzee. Dit impliceert dat de seizoendynamiek in het fytoplankton mede wordt bepaald door lokale omgevingsfactoren die anders zijn dan in de Noordzee en de Waddenzee. Langs de raaien in de Noordzee leek er op basis van de seizoendynamiek in diatomeeën, een scheiding te bestaan tussen stations tot van 10 km (Terschelling) tot 20 km (Noordwijk) uit de kust en de stations die verder op zee lagen, wat de aanwezigheid van de "line-of-no-return" onderbouwt. De nieuw ontwikkelde tracer (seizoenpatronen in rijkdom van fytoplankton ordes) kan mogelijk, naast bovenstaande toepassing, ook ingezet worden om andere relaties tussen fytoplankton en milieufactoren te bestuderen.

Lange-termijn veranderingen in vissen in de westelijke Waddenzee (1960-2011)

Veel van de ecologische tijdreeksen zijn te kort om een lang historisch beeld te schetsen van opeenvolgende effecten op kustsystemen van langjarige menselijk activiteiten, waaronder visserij, toevoer van nutriënten en veranderingen in het klimaat. Het bemonsteringsprogramma van de visfauna met behulp van een vast vistuig (fuik) in de westelijke Nederlandse Waddenzee, gestart in 1960, vormt hierop een uitzondering. Hoofdstuk 4 beschrijft de resultaten van de analyse van deze vangsten voor de periode van 1960 tot en met 2011 (52 jaar).

In de lente trekt vis vanuit de kustzone van de Noordzee de Waddenzee in en in de herfst migreert vis met ook opgegroeide jonge vis vanuit de Waddenzee weer naar de Noordzee. De visvangst in de lente en die in de herfst (in kg per dag) was het grootst aan het eind van de jaren zeventig. Tussen 1980 en 2011 namen de vangsten met 90% af, zowel van pelagische (vooral in de waterkolom voorkomend) als van demersale (aan de bodem gebonden) soorten. In het voorjaar daalde in deze periode het gemiddelde gewicht van de vissen van ongeveer 150 gram tot 20 g natgewicht. Het gemiddelde gewicht in het najaar bleef tussen 1980 en 2011 ongeveer gelijk. Verder daalde voor de pelagische vissen het gemiddelde trofische niveau van ongeveer 3.9 naar 3.1.

De vangstpatronen van de verschillende soorten lieten een tweetal gemeenschappelijke trends zien. De eerste en meest belangrijke trend voor zowel voor- als najaar was een afname in het totale dagelijkse gewicht van vangsten vanaf de jaren 1960, gevolgd door stabilisatie vanaf het midden van de jaren negentig. Deze trend was sterk gecorreleerd met een toename in watertemperatuur, een fysieke verstoring van leefgebieden in de kustzone (als gevolg van baggeren, zandsuppleties en visserij) en een verhoogde predatiedruk door toppredatoren. De tweede trend was een stijging van de vangsten met een maximum rond 1980, gevolgd door een gestage daling in de lente tot aan 2011 en een aanvankelijke daling gevolgd door een stabilisatie vanaf 2000 in de herfst. Deze secundaire trend was het sterkst gecorreleerd met veranderingen in de grootschalige hydrodynamische circulatie op de Noordzee en verder.

Samengevat lijkt sinds de jaren tachtig de trofische structuur van de visfauna in de kustzone veranderd en de kinderkamerfunctie van de Waddenzee verminderd. Dergelijke ecologische veranderingen in kustecosystemen hebben blijkbaar niet alleen in het verleden plaatsgevonden, maar zijn nog steeds gaande.

SECTIE 2: VOEDSELWEB-INTERACTIES OP HET BALGZAND (WESTELIJKE WADDENZEE)

Lange-termijn veranderingen in prooi-predator interacties op het Balgzand (1975-2014)

De invloed van invasieve soorten op trofische interacties in het voedselweb van wadplaten kan versterkt of verzwakt worden door gelijktijdige veranderingen in epibenthische predatoren, zoals roofvissen en garnalen. In Hoofdstuk 5 worden de consequenties van de veranderingen in predatoren tussen 1975 en 2014 (een verschuiving van dichtheden en groottes van roofvissen, garnalen en krabben) voor de interacties met hun prooien onderzocht.

De invasies van de strandgaper (*Mya arenaria*), Amerikaanse zwaardschede (*Ensis leei*) en Japanse oester (*Magallana gigas*) leidden tot een dominantie van deze schelpdieren in de totale biomassa van bodemdieren van de wadplaten van het Balgzand. Deze langlevende schelpdieren kunnen zo groot worden dat ze al snel niet of nauwelijks meer gegeten kunnen worden door hun belangrijkste predatoren, waaronder jonge platvissen en garnalen. Dit betekent dat deze predators daardoor steeds meer aangewezen raakten op wormen als prooi, waaronder de invasieve *Marenzelleria viridis* die waarschijnlijk aan het begin van deze eeuw als een belangrijke voedselbron functioneerde.

Door de verschuiving in dichtheden en groottes van predatoren tussen 1975 en 2014 nam de voedselbehoefte van de garnaal *Crangon crangon* van 5 tot 10 g asvrije droge stof (AVDS) $\mathrm{m}^{-2}\,\mathrm{jaar}^{-1}$ toe en die van met name jonge schol (*Pleuronectes platessa*) met meer dan 80% af. De totale voedselbehoefte van de epibenthische predatoren bleef min of meer gelijk (ca. $30\,\mathrm{g\,AVDS\,m^{-2}\,jaar^{-1}}$). De eetbare fractie van de bodemdieren nam toe van ca. 5 tot $20\,\mathrm{g\,AVDS\,m^{-2}}$ tussen 1975 en 2000 en vervolgens af tot $10\,\mathrm{g\,AVDS\,m^{-2}}$, vooral als gevolg van veranderingen in zowel inheemse wormen (*Nereis diversicolor* en *Heteromastus filiformis*) als in invasieve (*M. viridis*) soorten.

Gelijktijdige veranderingen (zoals verschuivingen in aantallen en groottes van predatoren) kunnen van invloed zijn op prooi-predator relaties, en daarmee op de ontwikkeling en rol van invasieve soorten op de structuur van het voedselweb op wadplaten en het functioneren van kustsystemen.

Groeireductie van schol gedurende de zomer op het Balgzand (1975-2009)

Zoals hiervoor beschreven kunnen lange-termijn veranderingen in predatiedruk gevolgen hebben voor predator-prooi interacties die vervolgens doorwerken op de invloed van invasieve soorten op het kust ecosysteem. In Hoofdstuk 6 worden de mogelijke oorzaken en gevolgen van een waargenomen variatie in de groei van de schol *Pleuronectes platessa* gedurende de zomer geanalyseerd

De waargenomen variatie in de afname van de groei van de schol gedurende de zomer kan deels worden verklaard door de variatie in omgevingsfactoren (temperatuur van het water), door niet-genetische onomkeerbare adaptatie en door geslacht. Energiebudgetten wijzen vooral in de richting van groeiverschillen tussen mannen en vrouwen in combinatie met verschillen in de geslachtsverhouding als belangrijkste onderliggende oorzaak van de waargenomen variaties tussen populaties. De afname van de groei in de zomer bleek niet beperkt tot jonge (0-jarige) schol in het intergetijdengebied, maar trad ook op bij oudere vissen (1- en 2-jarige schol) en ook in andere deelgebieden (permanent ondergedoken zandbanken en getijdengeulen).

De zomergroeireductie leek niet te worden veroorzaakt door onderlinge competitie voor voedsel, maar voedselcompetitie van jonge schol met andere predatoren kan niet worden uitgesloten. Er werd echter geen aanwijzing voor dergelijke concurrentie gevonden met veel voorkomende vissen, zoals 0-, 1- en 2-jarige bot (*Platichthys flesus*) en grondels (*Pomatoschistus minutus* en *P. microps*), en met schaaldieren zoals de garnaal (*Crangon crangon*) en de strandkrab (*Carcinus maenas*).

De zomergroei reductie bleek gepaard te gaan met een afname van de maaginhoud van de jonge schol, vooral in het aandeel van regenererende lichaamsdelen van bodemdieren, zoals de staarten van wadpieren. Een mogelijke verklaring hiervoor is dat bodemdieren minder actief worden na de voorjaarsbloei van fytoplankton, waardoor prooien zoals wormen minder actief worden en minder goed bereikbaar zijn als prooi. Uiteindelijk leidt deze afname in voedselaanbod tot een afname in voedselopname door de schol, een geringere maaginhoud en daarmee tot een reductie in de groei van deze predator in de zomer.

Het belang van zoetwateralgen voor het voedselweb van het Balgzand (2014)

Zoals eerder beschreven kunnen kustsystemen voor een belangrijk deel worden gevoed door uitwisseling van organisch materiaal met een aangrenzende zee. Estuaria worden ook gevoed door rivieren, die aanzienlijke hoeveelheden zoetwater (en daarmee dode en levende organische deeltjes) in estuaria lozen. De potentiële bijdrage van organisch materiaal aan het estuariëne voedselweb uit deze bron wordt vaak als verwaarloosbaar beschouwd en dan ook niet meegenomen in analyses. In Hoofdstuk 7 worden de mogelijke bijdragen van verschillende bronnen van organisch materiaal aan het voedselweb van de wadplaten van het Balgzand (met zoutgehalten variërend tussen 12 en 32 psu) beschreven op basis van de verhoudingen in stabiele isotopen in bodemdieren. Hierbij zijn de bijdragen van drie verschillende voedselbronnen, namelijk het mariene fytoplankton (zwevende algen), het microfytobenthos (de bodemalgen) en het organisch materiaal afkomstig uit het zoete water, aan het dieet van schelpdieren bepaald.

De jaarlijkse bijdrage van het organisch materiaal afkomstig uit het zoete water bleek een groot deel (50-60%) van het dieet te vertegenwoordigen van de schelpdieren die algen uit het water filteren zoals de kokkel (*Cerastoderma edule*), de mossel (*Mytilus edulis*) en de Japanse oester (*Magallana gigas*). Deze bijdrage was het grootst in de herfst bij een sterke afvoer van zoetwater rijk aan zwevend organisch materiaal. De overige voedselbronnen waren relatief belangrijk in de zomer tijdens lage zoetwaterafvoer. Een voedselweb in een estuarium kan dus wel degelijk en voor een belangrijk deel worden gevoed door organisch materiaal afkomstig uit rivieren. Dit betekent voor het Balgzand dat het spuisluisbeheer repercussies heeft voor het voedselaanbod voor primaire consumenten (zoals filtrerende schelpdieren).

Gevolgen van invasieve bodemdieren voor koolstofstromen van het Balgzand (1980s-2010s)

Bij veranderingen in een voedselweb dat gelijktijdig onder invloed staat van invasies en andere ontwikkelingen kan de bijdrage van de invasies aan die veranderingen alleen worden geïdentificeerd door rekening te houden met de volledige dynamiek van het systeem. Hoofdstuk 8 beschrijft de veranderingen in koolstofstromen van het Balgzand gedurende 4 decennia (voor, tijdens en na de piek in de invasies van 3 soorten bodemdieren) met behulp van Ecologische Netwerk Analyse (ENA), waarbij zoveel mogelijk beschikbare data voor alle componenten van het voedselweb (dus niet alleen die van de invasieve soorten) zijn meegenomen.

De invasieve Amerikaans zwaardschede (*Ensis leei*) en de Japanse oester (*Magallana gigas*) werden voor het eerst waargenomen in respectievelijk 1984 en 2001, de borstelworm *Marenzelleria viridis* in 1989. Hoewel *E. leei* en *M. viridis* een min of meer vergelijkbaar hoge biomassa bereikten tijdens hun piek in de jaren 2000 (respectievelijk ca. 1700 en 2000 $\mathrm{mg\,C\,m^{-2}}$), was de consumptie door de zwaardschede veel hoger (> 45% van de totale consumptie) dan de consumptie van de borstelworm (< 10%). De biomassa en de invloed van *M. gigas* op de koolstofstromen bleven gedurende al die jaren laag.

De Amerikaanse zwaardschede vestigde zich aan de waterrand van de wadplaten, een ecologische niche die voorheen gedeeltelijk leeg was. Hierdoor had dit schelpdier vooral met opkomend tij als eerste toegang tot het voorbij zwevende fytoplankton en ander organisch materiaal uit mariene en zoetwaterbronnen. De sterke toename biomassa van de zwaardschede ging gepaard met een sterke toename (van ca. 50% tot ca. 80%) van de koolstofstromen van primaire producenten (microalgen) naar secundaire producenten (algen-etende bodemdieren). Omdat de zwaardschede (die nu de bulk van het beschikbare algenvoedsel voor haar rekening namen) zelf niet of nauwelijks gegeten werd, halveerde de koolstofstroom van de secundaire producenten naar de hogere trofische niveaus en verdubbelde die van secundaire producenten naar detritus (dood organisch materiaal). De gevolgen van de invasie van de Amerikaanse zwaardschede voor het voedselweb van het Balgzand waren groter dan die van de invasie van de Japanse oester in het Sylt-Rømø getijdebekken (in de NO Waddenzee, op de grens van Duitsland en Denemarken).

Na de piek in totale biomassa van invasieve soorten op het Balgzand gedurende de eerste 10 jaar van deze eeuw daalden de biomassa van de Japanse oester *M. gigas* en de borstelworm en *M. viridis* weer vrij snel. De biomassa van de Amerikaanse zwaardschede bleef echter hoog en dit schelpdier nam nog 30% van de totale consumptie van het voedselweb voor haar rekening gedurende de afgelopen 10 jaar. Dit wijst niet alleen op een langjarige maar ook op een sterke invloed tijdens de aanwezigheid van deze invasieve soort op het voedselweb van het Balgzand.

SECTIE 3: SYNTHESE

Hoofdstuk 9 vat de verschillende aspecten van de hoofdstukken in dit proefschrift samen en relateert de bevindingen ten aanzien van de invloed van invasieve soorten aan die van andere gelijktijdige veranderingen en hun cumulatieve effecten op het ecosysteem van het Balgzand. Samengevat kan op basis van dit proefschrift de volgende conclusies m.b.t. de eerder gestelde onderzoeksvragen worden getrokken.

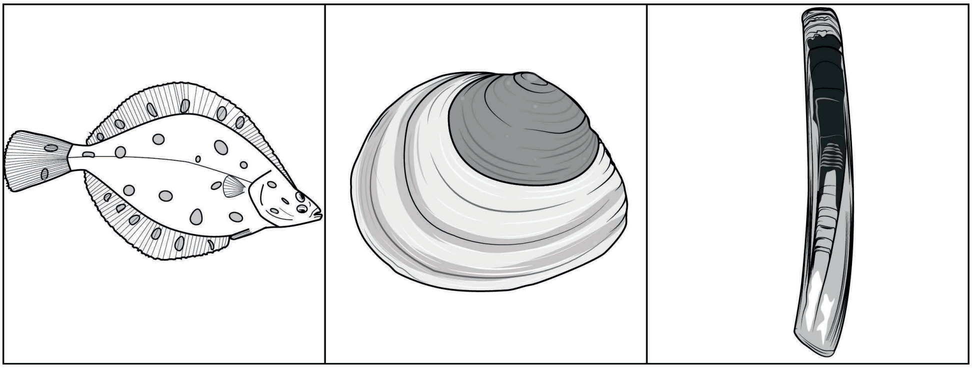
Gedurende afgelopen decennia onderging de westelijke Waddenzee verschillende veranderingen die de soortensamenstelling en trofische interacties van het voedselweb hebben beïnvloed. Dit proefschrift beschrijft een aantal van die veranderingen, waaronder een toename en afname in nutriëntconcentraties, en verschuivingen in de aantallen en soortensamenstelling van bodemdieren, vissen en schaaldieren (krabben en garnalen). Uit andere studies weten we dat er tegelijkertijd ook veranderingen hebben plaatsgevonden in de temperatuur, het zoutgehalte, de concentraties van microalgen (fytoplankton en microfytobenthos) en in aantallen vogels.

Er zijn sterke aanwijzingen dat deze gelijktijdige veranderingen elkaar inderdaad hebben beïnvloed. Zo hebben de veranderingen in de samenstelling en concentratie van primaire producenten gevolgen gehad voor de voedselbeschikbaarheid van hogere trofische niveaus en daarmee ook de soortensamenstelling van de rest van de voedselketen. Veranderingen in abiotische factoren zoals zoutgehalte, beschikbaarheid van voedingsstoffen en temperatuur speelden een rol bij de ontwikkeling van het ecosysteem van het Balgzand, waaronder de mogelijkheid van nieuwe soorten om al dan niet invasief te worden.

In het licht van de huidige klimaatverandering kan verwacht worden dat drempelwaarden in temperatuurtolerantie en het aanpassingsvermogen van soorten aan veranderende temperaturen steeds belangrijker worden voor de verdere ontwikkelingen van dit voedselweb. Hogere temperaturen bieden reeds geïntroduceerde warmwatersoorten de gelegenheid om zich verder uit te breiden en effenen de weg voor onontkoombare introducties van nieuwe soorten die de Waddenzee vanuit het zuiden zullen bereiken.

Dergelijke veranderingen in de leefomgeving zullen van invloed zijn op de effectiviteit van natuurbeheer. Dit geldt met name voor de wet- en regelgeving die gericht is op het behoud en de verbetering van specifieke soorten en leefgebieden (zoals de Natura 2000 instandhoudingsdoelstellingen) en minder voor het beheer dat zich richt op de functies van het ecosysteem, zoals de kinderkamerfunctie voor jonge vissen en de opvetcapaciteit voor trekvogels. Trilaterale regeringen zouden proactieve maatregelen kunnen of moeten nemen om het functioneren van ecosystemen duurzaam te waarborgen, waarbij ook expliciet rekening wordt gehouden met de gevolgen van toekomstige invasies als gevolg van de opwarming van de aarde.

CURRICULUM VITAE



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Work Experience

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2010	Student research assistant at the Institute of Hydrobiology and Fisheries Science, University Hamburg, Analyses of zooplankton abundances
2010	Student research assistant as a participant of a research cruise on FS Meteor cruise no. 79/3 to Senghor Seamount
2007	Student research assistant at the University of Hamburg as a course leader of a tutorial, Course "Zoological biodiversity"

LIST OF MY PUBLICATIONS

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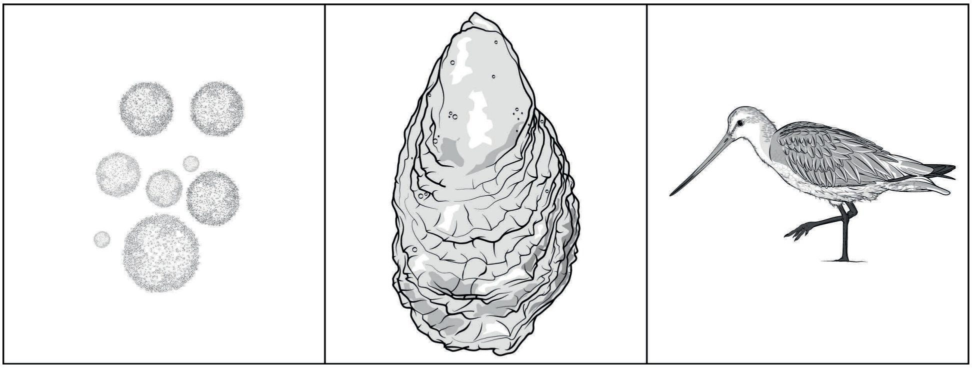

Doing a PhD is not easy and takes a lot of time and effort. Although the name on the front page is just a single one, doing the research to be able to write a PhD thesis and getting through the process of it all is not something that is done alone. This means there are some people I would like to thank for their support and help over the more than eight years period it took for me to finalize this thesis.

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Over the four years that I was located on Texel I did many field sampling campaigns on the Balgzand and the Wadden Sea. However these trips can’t be done alone and therefore I had help. First of all I wanted to thank the crew of the RV Stern and Navicula, especially Ewout, Bram, Klaas-Jan, Wim-Jan, and Hein, for their help, support and patience on these trips. I also wanted to thank Rob Dekker for taking me with him to his field sampling trips and teaching me a lot of small but important details about the Balgzand, as well as letting me use his data that he collected over the course of several decades. I was also able to profit from the decade long work done by others at the NIOZ such as Hans Witte, Jan Beukema, Gerhard Cadée, and Rob Dapper, whom I also want to thank for their dedication and help, as well as the possibility to use their data.

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Living on an island means you are sometimes limited in your activities as you either need to be able to do them on the island or you are depending on a ferry and its service times to leave and come back. This means it is a good idea to build a friends group that you can plan activities with. Living in "De Potvis" means you often have a lot of people around that are in a similar situation. Unfortunately, as it is often in the scientific world, people are often only visiting or having short stays. During my four years this means I had to welcome and say goodbye to many people over time. Some were there for longer, some for shorter periods but often deep friendships developed even in sometimes only a few months. I want to thank all the people I met during my time on Texel, for providing me with much needed down time, and showing me that doing a PhD is not only about research. The following names are in no particular order and might miss someone, please don't be mad if I forgot to include you, I am no less grateful and happy about everyone I met during my time! First there are the people I shared a house with over time, Olga, Pim, Robin, Sander, Saara and Vera thanks for the great evenings and the fun we had. Then there were so many students that I have in great memories, Rebecca, Bas, Floor, Boukje, Reinier, Robert, Wilbert, Matthijs, Rob, Shira, Yorick, Marcel, Krissy, Anne (all three of you ;)), Irene, Ineke, Jarco, Rachel, Milou, Hannah, David, Jason, Simone, Fadia, Tomek, Naomi, Monika, Helga, Lucia, Esther, Marloes, Arno, and many more. Thank you so, so much for all the great evenings in the Potvis bar and the friendships that developed after this. Then there is the PhD/assistants crew Andreas, Lodewijk, Freek, Anouk, Fokje, Kristina, Nate, Marin, Maaike, Joop, Niamh, Sjoerd, Dennis, Jessica, Tristan, Maram, Anja, Michiel, Eveline, Marc, and whomever I might have forgotten, thank you for the many running dinners and fun times we had. For the Jug Bros concerts we went to and the parties we celebrated. This group was often extended to more people and therefor I also want to thank Nikki, Leslie, Sofia, Vania, Linda, Lieke, Hans, Darci, Tanya, Ginny, Martina, Esmee, Sabine, Gabriella, Leandro, Sigrid, Inge, Sophie, Sandra, Nicole, Julie, Susanne, Daan, Esmee, Eva, Carola, Claudia, Paul, Cait, Lisa, and Eli for their friendships as well as lunch and coffee break conversations!

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Writing this thesis was often done by listening to music. Music plays a big role in my life and I love going to live concerts. I was really happy when I discovered that there are regular live performances on Texel by a local band. I want to thank the Jug Bros for the many great evenings we had, the conversations, friendship, and being able to join them on a recording in the studio. I also want to thank the many artists that I was able to see live over time for giving me a space to turn off my head and just live in the moment. To just name a few I want to thank Frank Turner, Brian Fallon, Dropkick Murphys, Flogging Molly, Tim Vantol, Bruce Springsteen, John Allen, Skinny Lister, Donots, Miu, Matze Rossi, Josh Lobley, Paul Henshaw, Will Varley, Nathan Gray, and many more for providing me with a soundtrack while writing.

After my contract on Texel ended I moved to Passau and during my time there I was allowed to use an office space in the faculty of mathematics and I wanted to thank Prof. Dr. Kreuzer for this oppertunity. I also want to thank Julia, Wolfgang, Thomas, Tobi, Tina, and the rest of the gang for welcoming me and the many lunch and coffee breaks we had together. I also want to thank Sonja for giving me a job that offered some change in my daily routine.

After two years in Passau it was time to move on and I finally found a full time job again and then it was in Hamburg, so back to where I started before I went on this journey. I want to thank Andre, Stephan and Ulf from initions for the trust they put into me and the opportunity to start a job as a data scientist even without a finished PhD. I really love working here and I am so happy I applied even though this meant that finishing this thesis took a bit longer after starting a full time job again. I also want to thank all my colleagues at initions for the great atmosphere at work. You make it fun to go to work every day (at least when you are not on maternity leave)!

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Euch allen möchte ich sagen, dass ich es nicht als selbstverständlich ansehe, dass es in Familien einen solchen Zusammenhalt gibt und, dass es immer so toll harmoniert wie es das bei uns meist tut. Ich bin froh, dass unsere Familie so ist!

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