Impacts of macrozoobenthic invasions on a temperate coastal food web

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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 3 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 poly-chaete *Marenzelleria viridis* appeared in 1989. Although *E. leei* and *M. viridis* reached similar peak biomasses in the 2000s (ca. 1700 and 2000 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 relatively unoc-cupied, 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 sec-ondary 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 Wad-den 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.

KEY WORDS: Ecological network analysis · Invasive species · Decadal changes · Carbon flows · Balgzand · *Ensis leei* · *Magallana gigas* · *Marenzelleria viridis*

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 1 or more individuals, a small popula-tion of fully reproductive individuals follows, after which the invading species becomes established in its new environment. This may subsequently result in an exponential increase of the new local popula-tion, followed by a phase of adjustment with a reduc-tion in abundance and biomass (e.g. Mack et al. 2000, Essink & 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 one or a combination of several factors: 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/or changes in environmental conditions (e.g. temperature, salinity) (Ribera & Boudouresque 1995, Essink & Dekker 2002).

During this process of increase and establishment, the invasive species can change local species distribution, due amongst others 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 non-native (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 & Dekker 2002, Reise et al. 2017).

The American razor clam *E. leei* (formerly known as *E. directus*; Beukema & Dekker 2011) was first detected on the Balgzand intertidal in the western Dutch Wadden Sea in 1984 and remained at a 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 is 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 the previously unoccupied lower edges of the tidal flats where currents are too strong for native species to settle (Dekker & Beukema 2012).

In the same tidal flat system (Balgzand), the polychaete *M. viridis* (formerly also known as *M.* cf. *wireni*; Essink & 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 lifespan (Zettler 1997) plus its high tolerance for low oxygen conditions, which allows it to live in deeper sediments than 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 & 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 & Ruesink 2013) combined with a long lifespan (Cardoso et al. 2007), fast maturation (Kobayashi et al. 1997) and high fecundity (Helm et al. 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, lo-

cated in the western part of the Dutch Wadden Sea. Based on the availability of time series and the observed invasive development of these 3 species, we compared the carbon flows and several ecological network analysis (ENA)-based indices of the Balgzand food web for 4 decades, i.e. the 1980s, 1990s, 2000s and 2010s. These periods roughly coincided with different phases of the invasion: 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 3 species was still relatively low.

Carbon flows of the system are analysed by means of ENA (Ulanowicz 1986, 2004, Fath et al. 2007). This 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.

ENA has previously been 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. 2009a,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. 2009b, 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. 2009a,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.

2. MATERIALS AND METHODS

2.1. Study area

The Balgzand area, covering approximately 50 km^2 of intertidal area and 10 km^2 of subtidal area, represents approximately 8% of the Marsdiep tidal basin in the western Dutch Wadden Sea (Fig. 1, Table 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 approximately 2% (Beukema 1988). The central and eastern part of the Balgzand is a mixture of these 2 extremes (Beukema & Cadée 1997). Mean tidal range is about 1.40 m (roughly −80 to +60 cm to MSL; Beukema & Cadée 1997). During each tidal cycle, the tidal flats are exposed for 2 to 4 h and are submerged for 8 to 10 h (de Vlas 1979) and at high water, mean water depth varies between a few dm up to 1.4 m (Postma 1982).

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 northwestern 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 & Cadée 1997) dominate 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 and from the eastern (Kornwerderzand) and western (Den Oever) sluices of Lake IJssel (Fig. 1). The average freshwater discharge via the Helsdeur and Het Kuitje (also known as Oostoever) is relatively low, in total on average 18 m^3 s^{-1} (Postma 1982), compared to approximately 400 m^3 s^{-1} (with maximum values up to 3000 m^3 s^{-1} in winter) via the sluices of Lake IJssel (van Aken 2008). Recent hydrodynamic model studies have 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
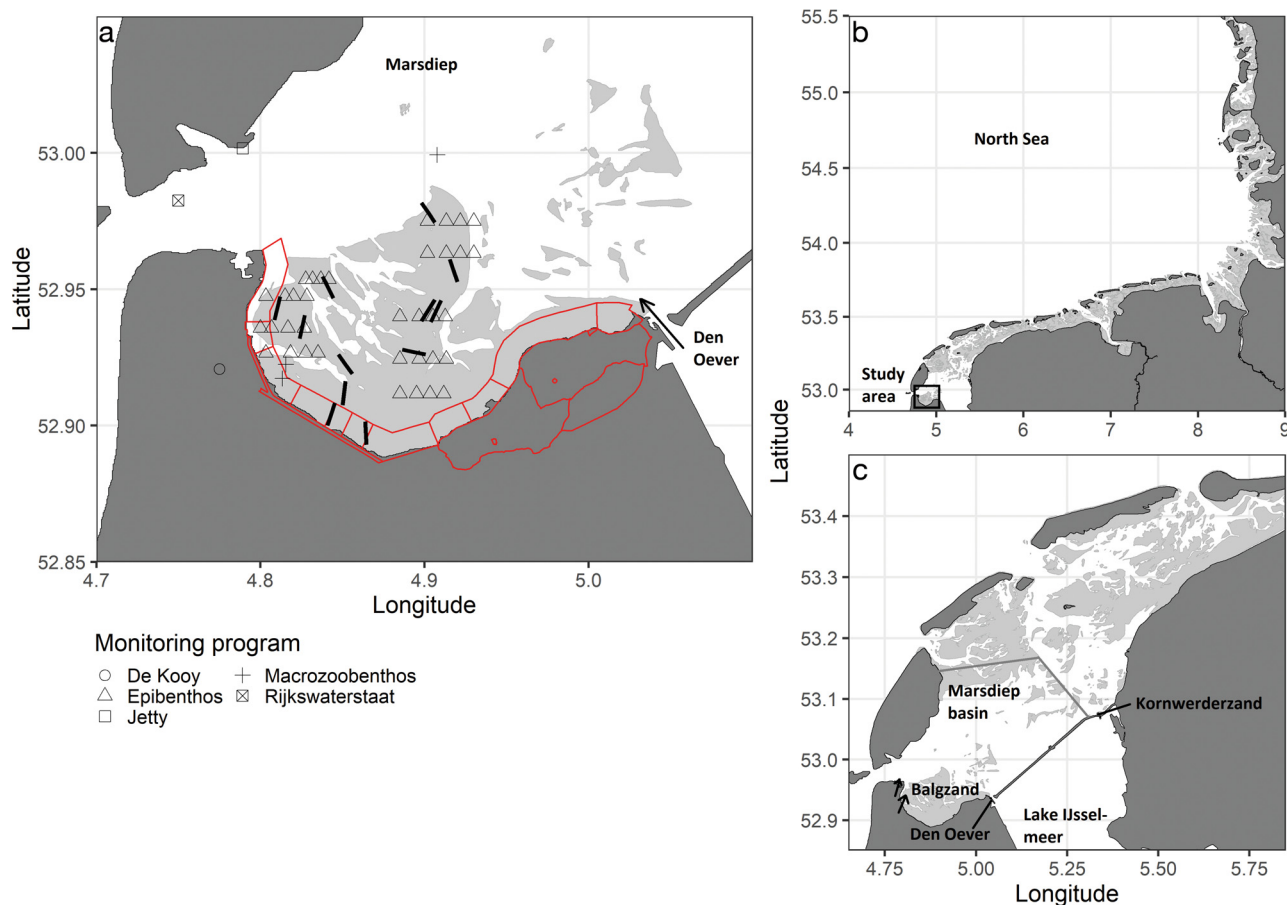
Fig. 1. (a) The Balgzand: (red lines) borders of the Sovon bird counting areas (www.sovon.nl); (O) closest weather station (De Kooy); (black lines) sampling transects and (+) stations for the NIOZ macrozoobenthic sampling program (www.nioz.nl); (△) stations for NIOZ epibenthic sampling; (⊠) RWS water quality station (Marsdiep Noord) (rijkswaterstaat.nl); (□) NIOZ water quality station (Jetty). (b) The trilateral Wadden Sea. (c) The western Dutch Wadden Sea. The locations of the 2 freshwater discharge sluices close to the Balgzand (Helsdeur in the north and Het Kuitje, also known as Oostoever, in the south) are indicated by arrows

freshwater input (van Aken 2008). 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 3 tidal periods (Zimmerman 1978).

2.2. ENA

2.2.1. Model construction

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, 1 for each decade (1980s, 1990s, 2000s and 2010s). These 4 networks consisted of living compartments, with some compartments representing a specific species whilst others comprised functional groups (e.g. phyto-

Table 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

plankton and zooplankton) and 3 non-living compartments susPOC (suspended particulate organic carbon), sedPOC (sediment particulate organic carbon) and DOC (dissolved organic carbon). The first 2 networks (BZ1980s, BZ1990s) comprised a total of 54 living compartments, including the invasive macrozoobenthic species *Ensis leei* and *Marenzelleria viridis*. The other 2 networks (BZ2000s, BZ2010s) consisted of 55 living compartments since they also include the invasive Pacific oyster *Magallana gigas* (see Table 3).

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

2.2.2. 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) mg C m^{-2} and all flows were expressed in terms of mg C m^{-2} d^{-1}. Missing data and information were collected from other sources (see Table 4; for a detailed description on data sources and data handling, see Text S1 in the Supplement at www.int-res.com/articles/suppl/m653p019_supp.pdf). Resulting data on uptake, dissipation, respiration, growth and egestion rates are supplied in Table S1, the applied ratios can be found in Table S2, both in the Supplement.

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 (Table S3 in the Supplement). Small changes in these diet matrices compared to Baird et al. (2004) were made based on regional prey selections for bivalves (Jung et al. 2019), the shore crab *Carcinus maenas* (Baeta et al. 2006), the brown shrimp *Crangon crangon* (del Norte-Campos & Temming 1994), fish (Kühl & 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* (Table S3).

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. 2019a,b). The external import of DOC (mg C m^{-2} d^{-1}) mainly originates from Lake IJssel and was calculated by multiplying the concentrations in Lake IJssel (mg DOC m^{-3}) by the freshwater discharge (m^3 d^{-1}) and the fraction of this discharge reaching the study area (unitless). This fraction was calculated from the mean Balgzand salinity and the system's flushing time.

The import of susPOC (mg POC m^{-2} d^{-1}) was assumed to be imported as and together with suspended sediment into the Marsdiep tidal basin (see Text S1). 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$_{ex}$; m^3 m^{-2} d^{-1}) was calculated as:

$$FW_{ex} = (V \times f) / (F \times A) \qquad (1)$$

where V is the tidal-averaged water volume of the Balgzand tidal flat system (30×10^6 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 d; Zimmerman 1978); and A is the total surface area of the Balgzand tidal system (50 km^2 = 50×10^6 m^2).

After conversion of chlorophyll *a* concentrations of freshwater algae in Lake IJssel (Rijkswaterstaat data; waterinfo.rws.nl) to carbon concentrations, the average daily import of carbon for each decade (mg C m^{-2} d^{-1}) was calculated by multiplying the daily exchange of freshwater (FW$_{ex}$; m^3 m^{-2} d^{-1}) by the average concentration of freshwater algae in Lake IJssel (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 susPOC was assigned to the benthic pool of particulate organic carbon (sedPOC). The excess of the pelagic pool of 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 (following de Jonge et al. 2019a,b) and that the final (balanced) flow matrices therefore represent steady-state conditions.

2.2.3. 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 (Table S4). 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) and Lau et al. (2017). The indicators used in this work are those most appropriate for describing the impact of invasions (Miehls et al. 2009a,b, Baird et al. 2012) (Table 2).

3. RESULTS

3.1. Biomasses

At Balgzand, the invasive species were observed for the first time between 1984 (*Ensis leei*) and 2001 (*Magallana gigas*), and all 3 species peaked in the mid-2000s (Fig. 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. 2).

When comparing the 4 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 3). 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 2 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 3, Fig. 2). The largest contribution to the total macrozoobenthic biomass of, respectively, 22–35% and 9–20% was made by 2 bivalve species (*Mya arenaria* and *Cerastoderma edule*). 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 and 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 3 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 3). The invasive *M. gigas* was absent during the first 2 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 3 decades of the study period.

Epibenthos biomass varied between 162 mg C m^{-2} in the 2000s and 467 mg C m^{-2} in the 1980s (Table 3). In the 1980s, the epibenthos biomass was dominated by plaice *Pleuronectes platessa*, which contributed over 70% of the total epibenthic biomass (Table 3). 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 the 1980s to more than 65% from the 1990s.

The total bird biomass was on average 99.5 mg C m^{-2}, and varied between 90 mg C m^{-2} in the 1980s and 110 mg C m^{-2} in the 1990s (Tables 3 & 4). 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.

Table 2. Overview of ENA metrics and indicators, and expected change in values resulting from invasions, as addressed in this study

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Network indices/metrics

FCI (Finn cycling index)

Unit	%
Definition	The total system throughflow of carbon generated by cycling (TST_c), as a proportion of the total system throughflow as the sum of the flows of all compartments (TST_{flow})
Indicator	Denotes how many times further than the straight throughflow path length an average unit of inflow travels because of cycling ($FCI = TST_c / TST_{flow}$)
Meaning and expected change for the indicator in case of invasive species	FCI is expected to decrease as the total throughflow speeds up during invasions
Reference	Finn (1976)

D/H (detritivory/herbivory ratio)

Unit	–
Definition	The ratio between detritivory and 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 in suspension-feeding invasive species such as *Magallana gigas* and *Ensis leei* as a result of an increase in herbivory flows
Reference	Ulanowicz & 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 as the system matures
Meaning and expected change for the indicator in case of invasive species	The value decreases as the system matures (i.e. from Phase III to Phase IV)
References	Christensen (1995), Odum (1969)

Trophic aggregations

LTA (Lindeman trophic analysis)

Unit	%; 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 result in possible shifts (e.g. increase in grazing by secondary producers) and shunts (e.g. reduction in 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 goes 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)

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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 are (1) directly affected due to predation by invaders and (2) 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 & Puccia (1990), Horn et al. (2019)
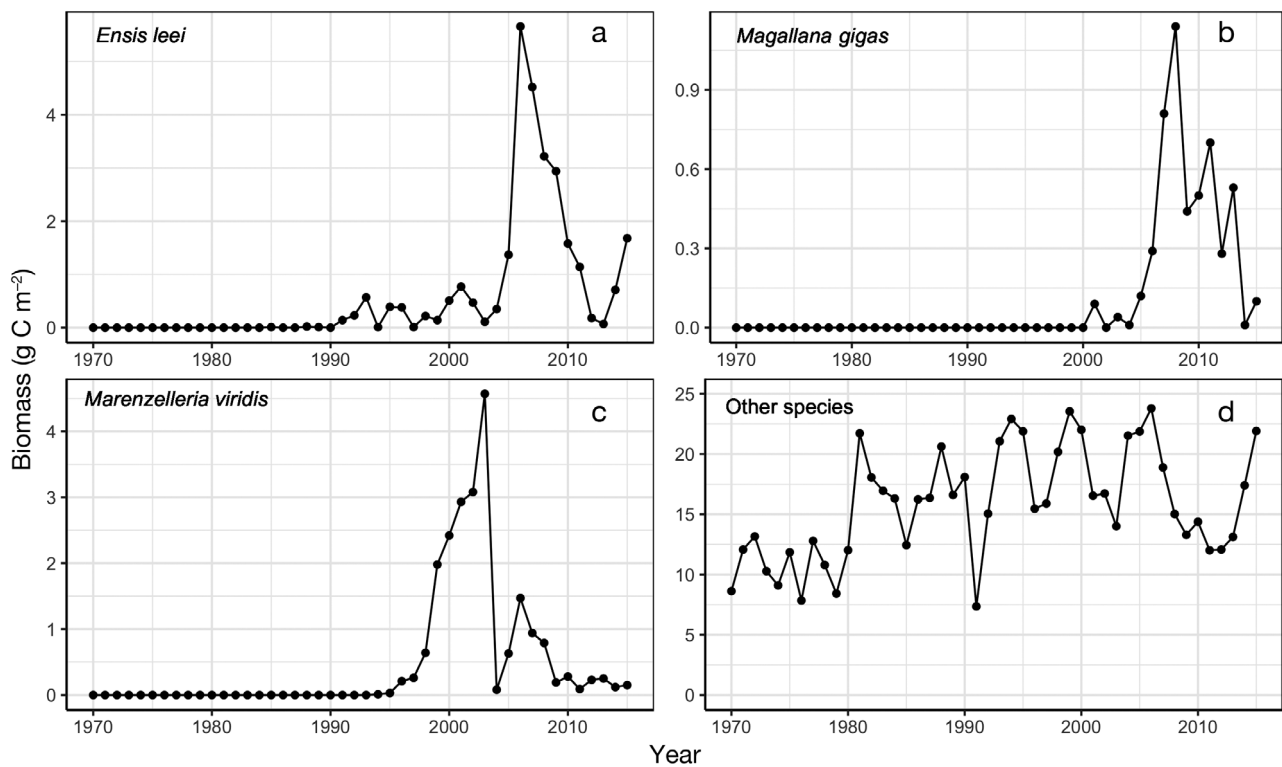
Fig. 2. Biomass (g C m^{-2}) of 3 recent invaders (a) *Ensis leei*, (b) *Magallana gigas* and (c) *Marenzelleria viridis* and (d) the sum of the other macrozoobenthic species of the Balgzand system from 1970 to 2015 (data courtesy: Jan Beukema & Rob Dekker, NIOZ)

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 a lowest value of 42.32 × 10^3 mg C m^{-2} in the 1990s and highest value of 45.45 × 10^3 mg C m^{-2} in the 1980s (Table 4). 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.

3.2. Carbon flows

Gross primary production rates ranged between 502 mg C m^{-2} d^{-1} in the 1990s and 561 mg C m^{-2} d^{-1} in the 2000s (Table 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.

The production of the other living components was dominated by benthic bacteria, which accounted for approximately 50% in the 2000s and 60% in the other

3 decades of the total (non-autotrophic) production (Table S3). 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) (Table S3). In the 2000s, the summed production of the other living components had increased by 20% compared to the 1980s (Table S3). The absolute increase in overall production between the 1980s and 2000s (+53 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 mg C m^{-2} d^{-1}) during that same time (Table S3).

From the 1980s to the 2000s, the consumption rate of the overall system (mg C m^{-2} d^{-1}) more than doubled, with the increase in overall consumption between these 2 decades (ca. +1250 mg C m^{-2} d^{-1}) being more or less equal to the consumption rates of *E. leei* (ca. 1100 mg C m^{-2} d^{-1}) and *M. viridis* (ca. 185 mg C m^{-2} d^{-1}) together during that decade (Table 5). In the 2000s, the consumption rates of *E. leei* and *M. viridis* were, respectively, 47 and 8% of the total consumption rate.

During the first 3 decades of the study period, the egestion and respiration rates of the overall system

Table 3. Mean biomass (mg C m^{-2}) per compartment per decade as used in the 4 respective networks (BZ1980s, BZ1990s, BZ2000s and BZ2010s). Sources and conversions are described in Text S1 in the Supplement. POC: particulate organic carbon; DOC: dissolved organic carbon

Compartment no. 1980/ 1990	Compartment no. 2000/ 2010	Compartment name	Biomass BZ1980s	Biomass BZ1990s	Biomass BZ2000s	Biomass BZ2010s
1	1	Phytoplankton	226.429	225.184	205.207	162.931
2	2	Microphytobenthos	5848.941	6964.981	8114.840	7679.415
3	3	Freshwater algae	388.036	384.935	330.210	335.410
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	1000.000	1000.000	1000.000	1000.000
7	7	Meiofauna	375.230	136.161	125.524	123.076
8	8	*Peringia ulvae*	352.292	530.410	555.350	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* sp.	38.743	102.439	261.886	282.257
14	14	*Heteromastus filiformis*	747.034	1091.920	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	163.450	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	209.270	1992.793	891.624
23	24	*Limecola balthica*	2185.742	1715.895	407.009	469.065
24	25	*Mya arenaria*	4481.915	5354.189	7962.460	3711.787
25	26	*Mytilus edulis*	1340.479	1291.409	968.240	971.200
26	27	*Scrobicularia plana*	170.387	214.565	109.672	127.890
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*	23.560	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	0.100	0.089	0.112
40	41	*Anas acuta*	1.003	1.743	4.269	4.810
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*	6.740	6.337	2.413	1.659
46	47	*Larus canus*	0.573	0.860	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	2042.900	1913.971	1748.554	1833.979
56	57	Sediment POC	39060.000	39060.000	39060.000	39060.000
57	58	Suspended POC	4348.671	1333.635	2122.980	2382.705

Table 4. 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. Sources (S) depict the types of sources of the values. A: long-term annual field observations within that period; B: empirical relationships based upon local field observations; C: incidental field observations during that period; D: assumptions from one period for the others. See Text S1 in the Supplement for more detail on data sources and calculations, and Table 3 for more detailed values for macrozoobenthos, epibenthos and birds

	Code	No.		1980s Bio	S	1990s Bio	S	2000s Bio	S	2010s 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	Epibenthos	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**	

Table 5. Overview of biomass (mg C m^{-2}) and carbon flows (mg C m^{-2} d^{-1}) of the sum of all compartments (living and non-living) and of the 3 invasive species within the Balgzand food web. GPP: gross primary production; NPP: net primary production

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

strongly increased, particularly respiration, which rose from just over 500 mg C m^{-2} d^{-1} in the 1980s to almost 1200 mg C m^{-2} d^{-1} in the 2000s (Table 5). In the 2000s, the bivalve *E. leei* and *M. viridis* contributed 50 and 6%, respectively, to the overall respiration. Overall respiration decreased from the 2000s to the 2010s, as did 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 approximately 1500 mg C m^{-2} d^{-1} in the 1980s to more than 2200 mg C m^{-2} d^{-1} in the 2000s, and decreased to less than 1950 mg C m^{-2} d^{-1} in the 2010s (Table 5). Variation in export, however, was less than that of import, showing an increase from just over 1000 mg C m^{-2} d^{-1} in the 1980s to approximately 1150 mg C m^{-2} d^{-1} in the 2010s (Table 5).

3.3. Network descriptors

The Finn cycling index (FCI; TST$_c$/TST$_{flow}$ ratio) decreased from 12% in the 1980s and 11% in the 1990s to 10% in the 2000s and 2010s (Table 6, see Table S4 in the Supplement). This decrease was in contrast with the relatively high value (more than 630 mg C m^{-2} d^{-1}) of the total cycled part (TST$_c$) of the system throughflow in the 2000s compared to the values of the other 3 decades (476 ± 35 mg C m^{-2} d^{-1}) (Table 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 through-

flow (TST$_{flow}$) in the 2000s/2010s (ca. 5770 mg C m^{-2} d^{-1}) compared to the those in the 1980s/1990s (ca. 3900 mg C m^{-2} d^{-1}) (Table 6). This increase in TST$_{flow}$ of almost 1900 mg C m^{-2} d^{-1} is partly caused by an increase in both consumption (ca. +775 mg C m^{-2} d^{-1}) and import (ca. + 530 mg C m^{-2} d^{-1}) (Table 5).

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 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 2 decades of the study period (Table 5). Although detritivory also increased, the difference between the first and second half of the study period was less than 20% (Table 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 3, Fig. 3). During the 1990s, the contribution of different bird species became evident (Table 3, Fig. 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 3, Fig. 3). During the 2010s, higher trophic levels were dominated by fish, in particular by the gobies *Pomatoschistus minutus* and *P. microps* (Table 3, Fig. 3). Within trophic level V, the contribution of the epibenthic crustaceans *C. crangon* and *Carcinus maenas* to the total biomass increased over time (Table 3, Fig. 3).

The trophic aggregation analysis indicated 9 trophic levels for the 1980s and 8 for the remaining decades (Fig. 4). According to the Lindeman spines, the carbon transfer efficiencies varied among the 4 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, to 48% in the 1990s, 87% in the 2000s and 68% in the 2010s (Fig. 4). For the second to the third trophic level (including bivalve-eating fish and birds), this transfer was 61, 43, 16

Table 6. Overview of outcomes of network indicators (see Table 2) for the Balgzand food web during different phases of invasions by *Ensis leei*, *Magallana gigas* and *Marenzelleria viridis*. TE: trophic efficiency

Indicator	Unit	BZ1980s Phase I	BZ1990s Phase II	BZ2000s Phase III	BZ2010s Phase IV
Metrics					
TST$_{flow}$	mg C m^{-2} d^{-1}	3698	4103	6503	5032
TST$_c$	mg C m^{-2} d^{-1}	451	460	633	516
FCI	%	12.2	11.2	9.7	10.3
Detritivory (D)	mg C m^{-2} d^{-1}	697	706	975	693
Herbivory (H)	mg C m^{-2} d^{-1}	270	377	1173	665
D/H ratio	–	2.58	1.87	0.83	1.04
P$_{GPP}$/B ratio	–	0.020	0.018	0.017	0.019
P$_{NPP}$/H ratio	%	135	95	34	56
Lindeman spines					
TL1 TE	%	36.6	48.0	86.6	68.3
TL1 detritus	mg C m^{-2} d^{-1}	292	266	23	159
TL2 TE	%	60.8	43.2	16.1	27.4
TL2 detritus	mg C m^{-2} d^{-1}	477	573	1035	666

and 27% for the respective decades (Fig. 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. 5) with a negative impact on its food sources (see Table S3), 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 Table S3). Meiofauna (feeding predominantly on benthic bacteria and benthic POC; see Table S3) was the only compartment that appeared to have been positively impacted by *E. leei* (+0.04). The other 2 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. 5). The invasive species also had an impact on each other (Fig. 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 relies on a wide variety of food sources including *C. edule* (24%), *Peringia ulvae* (12%) and *L. balthica* (11%) (see Table S3), 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 Table S3). 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*) (Table S3). *C. crangon* had a positive impact, however, on several fish species, in particular on *Myoxocephalus scorpius* (+0.42) and *Osmerus eper-*
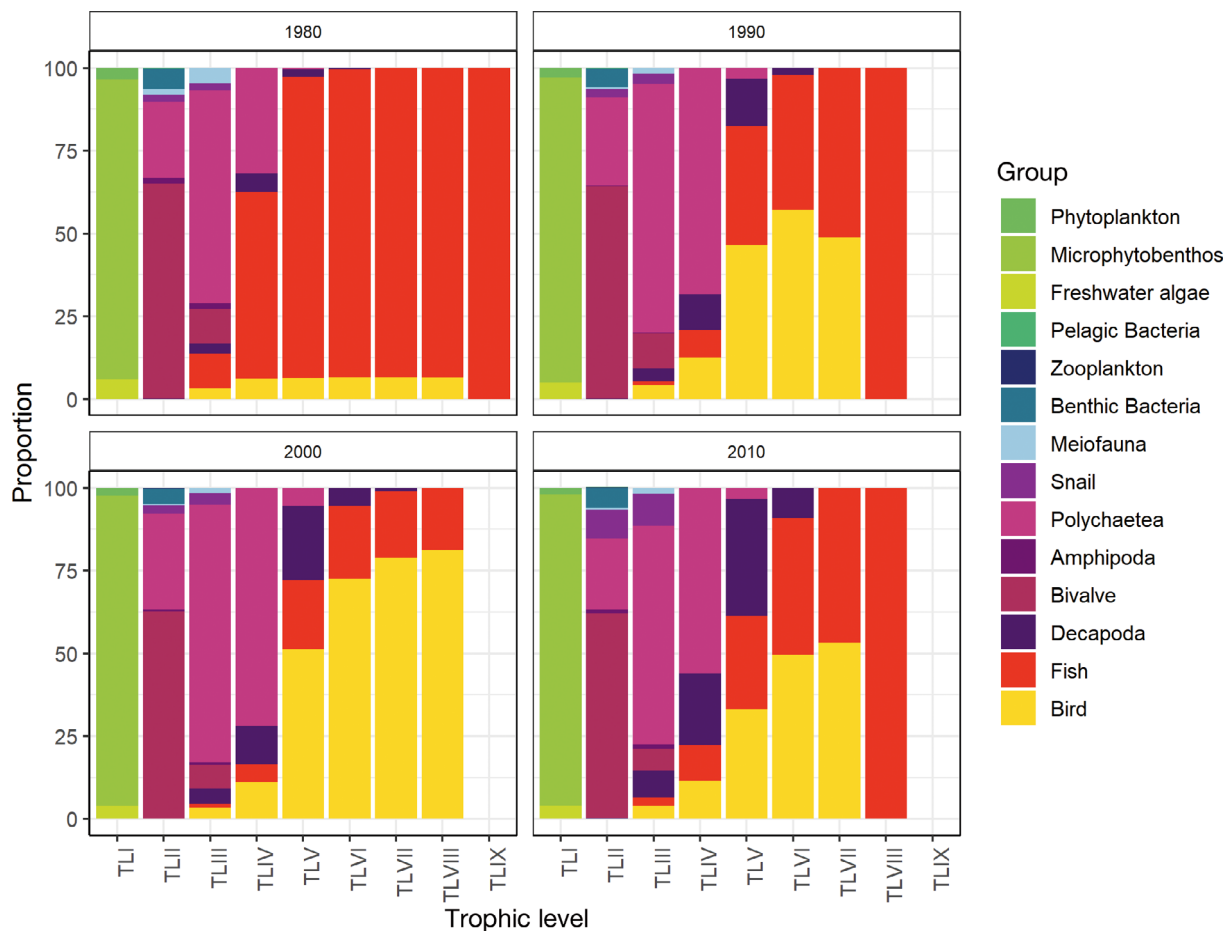

Fig. 3. Proportional composition of biomass of the different trophic levels (TL) of functional groups in each decade
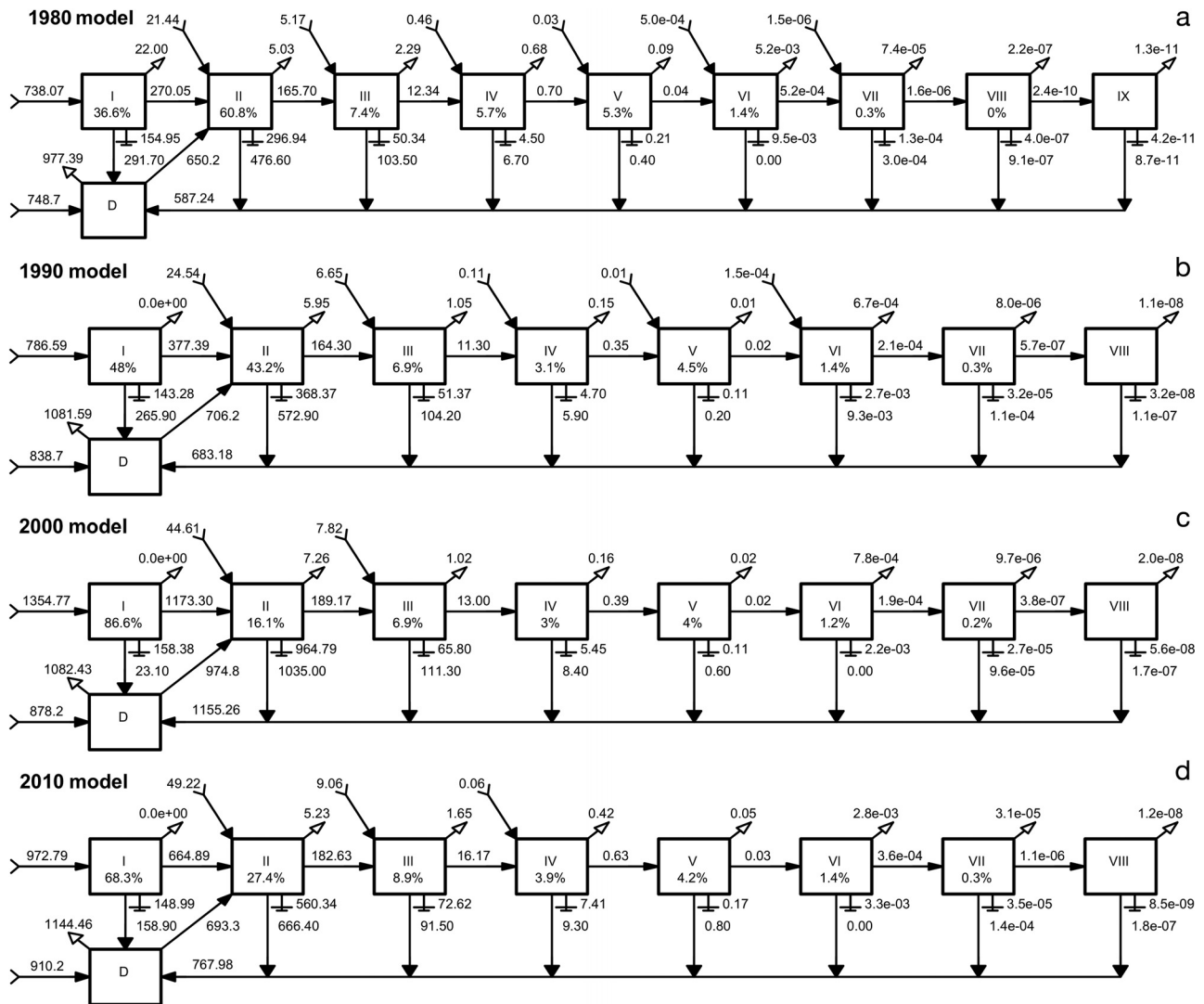
Fig. 4. Lindeman spines depicting carbon transfer (mg C m^{-2} d^{-1}) within the Balgzand tidal system during 4 decades (1980s, 1990s, 2000s, 2010s). The boxes indicated as 'D' refer to the detrital pool and the Roman numerals in the boxes of the spine to discrete trophic levels. Percent values in spine boxes refer to the efficiency of carbon transfer to the next trophic level. External input as well as export and loss due to respiration are indicated for each trophic level (mg C m^{-2} d^{-1})

lanus (+0.42) (Fig. 5). Both fish species largely rely on shrimps as a food source (45 and 50%, respectively, see Table S3).

4. DISCUSSION

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. ENA 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. (2009a,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 & 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 vari-
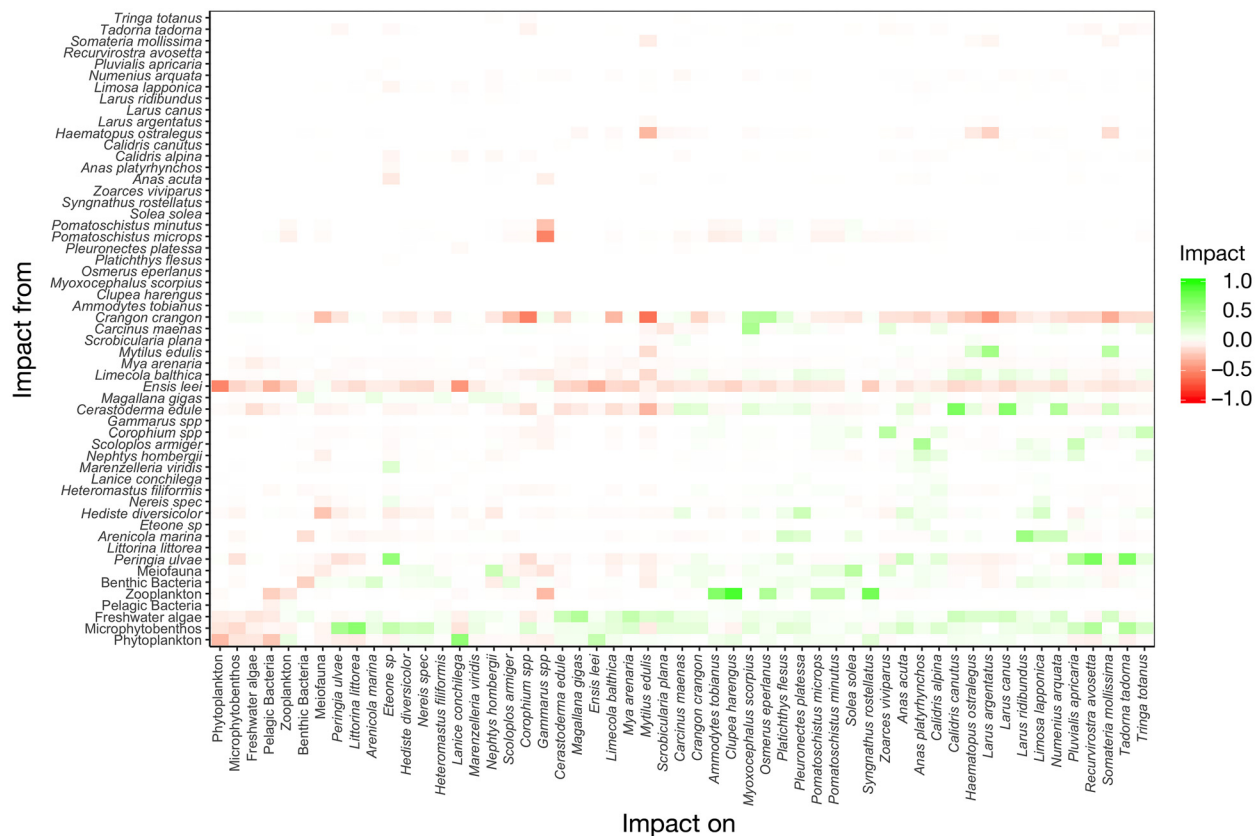
Fig. 5. Direct or indirect trophic impact of each living compartment ('Impact from') on each living compartment ('Impact on') of the food web of the Balgzand tidal system in the 2000s, based upon the mixed trophic impact (MTI) analysis

ous compartments was internally hand-balanced to achieve this condition (following de Jonge et al. 2019a,b). In reality, systems will not be in steady state but, for example, continuously responding to environmental conditions including (for our system) those of the 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 functioning of the system (Saint-Béat et al. 2015, de Jonge et al. 2019b). 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 im-

pact of salinity and its fluctuations on, specifically, the primary production of the freshwater borne phytoplankton was not considered due to a lack of information about the possible role of resuspended microphytobenthos in the functioning of the food web (de Jonge et al. 2019a). 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 4 decades revealed that all 3 species experienced a wax and wane in biomass which indicates that they followed all 4 phases of the typical pattern for invasions.

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*).

Starting in the mid-1980s, a period of eutrophication followed by a decline of nutrient supply occurred (Cadée 1984, de Jonge et al. 1993, Philippart et al. 2010, Jung et al. 2017a), and this was subsequently followed by a decrease in biomass and production of marine phytoplankton (Cadée 1984, Jacobs et al. 2020), microphytobenthos (MPB, Cadée & Hegeman 1977) and macrozoobenthos (Beukema & Cadée 1996). Because MPB data for Balgzand was only available up until 1981 (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 of MPB values affected the accuracy of import estimates (needed to meet the requirements of 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 biomass and production values of pelagic microalgae.

The Balgzand area also experienced a complete removal of mussel (*Mytilus edulis*) beds during the early 1990s (Beukema & Cadée 1996). The decrease in suspension-feeding by mussels during the early 1990s was most probably compensated for by the increase in 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, it is possible that the biomass of these suspension-feeding bivalves has been underestimated. However, in the case of the blue mussel, Beukema & Dekker (2007) found 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 *P. platessa* declined whilst that of predatory shrimp *C. crangon* increased, possibly as the result of changes in large-scale environmental conditions including increasing temperatures and distributional shifts in their predators (Jung et al. 2017b). Because these predators prefer different prey species (Table S3), their shift is expected to have had cascading effects on carbon flow networks (Jung et al. 2017b). The

increase in predatory shrimps, for example, appears to have had a negative impact on other small crustaceans (*Corophium* and *Gammarus*), possibly resulting from competition between these 3 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. 2009a,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. 2009b). The Sylt-Rømø Bight experienced a strong increase in seagrass (*Zostera noltii*) beds, 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.

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) halves 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 & Dekker 2011). However, with respect to the 3 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 & Dekker 1995). American razor clams are very efficient suspension-feeding bivalves (Kamermans et al. 2013) and they might take phytoplankton entering the tidal flats before other macrobenthos can take advantage of that food source, 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 recently been shown by Schwemmer et al. (2019).

In the 2000s, the overall consumption by *E. leei* (1096 mg C m^{-2} d^{-1}) was higher than the available primary production (561 mg C m^{-2} d^{-1}) (Table 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 the observations of van Raaphorst & van der Veer (1990).

Our results indicate 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 less material was being transported along the food chain in comparison to the other decades: the transport from the first to the second trophic level was highest in this decade as were the absolute values of the trophic transfers in the lower trophic levels (up to trophic level V) (Fig. 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 in carbon flow to higher trophic levels. This is in contrast to the situation within razor clam fields in the northeastern 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 2 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). These showed high biomass values and thereby increased the total biomass of bivalves. They 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 3 invasive species are still present and might therefore be considered established in the area. After their peak, the biomass of the 3 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 & 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 & 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.

4.4. Comparison with invasions in the NE Wadden Sea

The 3 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 of the extent to which the impact of invasive species is species-specific and/or area-specific, especially since, on average, the carbon budgets of the Balgzand and SRB systems were more or less similar with respect to overall biomass, and rates of consumption, import and export (Tables 7 & 8). However, biomass at Balgzand was dominated by non-living organic material, whilst the biomass of SRB was dominated by living compartments.

As *E. leei* and *M. viridis* were not included in 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 was zero in 1995 (invasion Phase I), more than 15000 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 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.

Table 7. Overview of biomass (mg C m^{-2}) and carbon flows (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 was 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	mg C m^{-2}	35110	61369	52457
	Other	mg C m^{-2}	19230	13333	19239
Primary production	GPP	mg C m^{-2} d^{-1}	559	658	973
	NPP	mg C m^{-2} d^{-1}	313	340	498
Consumption		mg C m^{-2} d^{-1}	2210	2492	2351
Egestion		mg C m^{-2} d^{-1}	NA	NA	NA
Respiration		mg C m^{-2} d^{-1}	987	1272	1248
Import		mg C m^{-2} d^{-1}	1938	2304	2178
Export		mg C m^{-2} d^{-1}	956	1034	910
Magallana gigas					
Biomass		mg C m^{-2}	0	15050	550
Production		mg C m^{-2} d^{-1}	0	15	1
Consumption		mg C m^{-2} d^{-1}	0	250	9
Egestion		mg C m^{-2} d^{-1}	0	0	0
Respiration		mg C m^{-2} d^{-1}	0	81	3

Table 8. Overview of outcomes of network indicators (see Table 2) 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 was conducted during Phase II of the invasion

Indicator	Unit	SRB1995 Phase I	SRB2007 Phase III	SRB2009 Phase IV
Metrics				
TST$_{flow}$	mg C m^{-2} d^{-1}	19146	22702	21558
TST$_c$	mg C m^{-2} d^{-1}	3178	3814	4656
FCI	%	16.6	16.8	21.6
D	mg C m^{-2} d^{-1}	1398	1256	1382
H	mg C m^{-2} d^{-1}	1119	1295	1088
D/H ratio	–	1.25	0.97	1.27
P$_{GPP}$/B ratio	–	0.016	0.011	0.019
P$_{NPP}$/H ratio	%	28	26	46
Lindeman spines				
TL1 TE	%	47.2	54.0	54.0
TL1 detritus	mg C m^{-2} d^{-1}	524	376	332
TL2 TE	%	15.8	16.7	18.4
TL2 detritus	mg C m^{-2} d^{-1}	868	979	936

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 6) but only +54% at SRB (Table 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 2 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.

4.5. Short- and long-term impacts

The success of the bivalve *E. leei* was most probably due to fulfilling at least 2, if not all 3, 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 relatively unoccupied in the western Dutch Wadden Sea (Dekker & Beukema 2012). Whether the third factor, a high number of individuals at the initial invasion, was 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 primary production utilization in the system increased, leading to higher herbivory in the system.

In addition (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 (Jung et al. 2017b). The invasion of *M. gigas* at SRB coincided with an extension of seagrass beds, which 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 yr, the historical invasive bivalve *M. arenaria* is still present in the Wadden Sea, with a recent (average) biomass of more than 5000 mg C m^{-2} at Balgzand (this paper) and almost 2000 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 mg C m^{-2} at Balgzand and less than 25 mg C m^{-2} at the SRB (Baird et al. 2012). The invasive success of *M. arenaria* is favoured by its high fecundity, a high tolerance towards variable 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 for 2 decades already, this species is likely to become established as an important member of the macrozoobenthic community.

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