

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 as well as their prey, 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 directus*, *Crassostrea 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 yr⁻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 g AFDM m⁻² until the 2000s and decreased to 10 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.

KEY WORDS: Long-term dynamics · Predation · Epibenthos · Intertidal · Wadden Sea · Fish · Crustaceans

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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 to 700 yr ago, Strasser 1998), *Ensis leei* (formerly known as *E. directus*; around 1982, Beukema & Dekker 2011) and *Crassostrea gigas* (around 2001, Beu-

kema & Dekker 2011) and the polychaete *Marenzelleria viridis* (formerly also known as *M. cf. wireni*, Essink & Dekker 2002; around 1989, Beukema & Dekker 2011), that increased to high biomass within the system (Beukema & Dekker 1995, 2011, Essink & Dekker 2002, Troost 2010). These invaders not only competed for food such as phytoplankton or microphytobenthos with native macrozoobenthic species (Essink & Dekker 2002, Troost 2010) but also changed the amount of attractive food sources for predators (Essink & 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 & Temming 1994, van der Veer et al. 2011). For example, shrimp feed on small bivalves and crustaceans (Pihl & 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 & 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 & Wanink 1989 and literature therein), which is often correlated to the size of the animal (Zwarts & Wanink 1989). Other factors influencing prey selection include thick shells (e.g. cockles, Bijleveld et al. 2015; mussels, Leonard et al. 1999, Smith & Jennings 2000) and clumping behaviour (e.g. mussels, Côté & Jenkinson 1999).

This means that for a new invasive species, success is influenced by whether it fits the native predator's prey spectra with regard to size and palatability and how well it can avoid predation by means of burrowing, aggregation or other behaviour (Stokesbury & Himmelman 1996, López et al. 2010). In the western Wadden Sea, for instance, the invasive bivalve species *M. arenaria* and *C. 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 & Wanink 1993) and that of *C. 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 (*C.*

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 (Tulp et al. 2012, Temming & Hufnagl 2015). This is most likely due to a decline in numbers and a shift in the distributional range of the shrimp's key predators (Temming & Hufnagl 2015) as well as an increase in small brown shrimp in the area, at least in spring (Beukema & 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.

MATERIALS AND METHODS

Sampling

Study area

All sampling took place at Balgzand, a tidal flat system of 50 km² bordering the Marsdiep tidal inlet in the western part of the Wadden Sea (Fig. 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 & 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 yr over the period 1975 to 2014 (1975–1983, 1986, 1991, 1993–2002, 2007, 2009 and 2014, Table S1 in the Supplement at www.int-res.com/articles/suppl/m579p037_supp.pdf). 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. 1); however, often not all stations could be visited due to prevailing weather conditions (water depth). In most years, sampling started in February and continued at frequent intervals (usually every 2 to 4 wk) 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 1 tickler chain, towed at a speed of about 35 m min⁻¹ following Riley & 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% formalin-seawater solution until 1990 and by deep-freezing after 1990.



Fig. 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

Samples were sorted to species level, and lengths 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 for a certain species were high ($\sim > 100$ ind.) the sample was subsampled and densities were corrected by this subsampling factor. For the most abundant species, except for the shore crab *Carcinus maenas*, information about catch efficiency was available (plaice, 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, Fig. S1 in the Supplement). For these species, the number of individuals caught was corrected 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 on 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.

Macrozoobenthic surveys

The macrozoobenthic community has been monitored since the 1970s, 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 to March) and once in late summer (August to September). For the present analyses, only data for late summer were used. However, from 1975 up to and including 1987, polychaetes were not, or were inadequately, sampled and quantified in summer. For this reason, polychaete data for this period were calculated from the winter data of the following year (~0.5 yr 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 to 2009 (R. Dekker unpubl.). This fixed factor predicted summer values with a standard deviation of ~20%. The 15 stations consisted of 12 fixed transects and 3 permanent quadrats. At each of the 12 transects, cores were taken to a depth of approximately 35 cm at equal intervals (20 m), covering 0.45 m^2 in summer. At the 3 permanent quadrats, 0.95 m^2 of sediment was taken, also to a depth of approximately 35 cm, which consisted of 18 randomly divided positioned cores (9 of ~0.1 m^2 and 9 of 0.009 m^2). For more information about sampling strategy, see Beukema (1976). Transect and quadrat cores were sieved in the field over 1 mm^2 mesh screens. All macrozoobenthic organisms retained were collected and sorted alive in the laboratory down to species and, if possible, year-class level (bivalves assessed by means of the number of year marks on the shell) within 1 or 2 d 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 a cup which was

dried for 3 d in a ventilated stove at 60°C, weighed, 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. The total biomass (all age classes combined) per surface area per station for each species i was calculated. The species-specific total mean biomass (g AFDM m^{-2}) at Balgzand was then calculated as the arithmetic mean of the above total biomass at all 15 stations sampled during a survey.

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 (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; g AFDM $m^{-2} d^{-1}$) and daily growth requirements (DGR; 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} ; 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:

$$W_{ijk} = (a L_{ijk})^b \quad (1)$$

where a (shape coefficient; g WM^{1/3} cm⁻¹) and b (unitless) are species-specific parameters (Table S2 in the Supplement). Second, the species-, age- and size-specific wet mass W_{ijk} (g WM) was converted into species-, age- and size-specific metabolic mass (M_{ijk} ; 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 of each age class was calculated to obtain the total metabolic wet mass of the age class of each species per square meter, so:

$$M_{ij} = \sum k (n_{ijk} M_{ijk}) \quad (2)$$

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

$$DMR_{ij} = c_i Q_{10i}^{0.1T} m_i M_{ij} \quad (3)$$

where c_i (g AFDM g WM⁻¹) is the species-specific conversion factor from wet mass to AFDM (de Vlas 1979; Table 1), T is temperature (°C), Q_{10i} is the species-specific increase in physiological rates with a temperature increase of 10°C (Table 1), m_i (WM^{-0.8} d⁻¹) is the maintenance coefficient (Table 1) and M_{ij} (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.

DGR_{ij} was based on the observed increase in length (L) 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. 1). Hereafter, instantaneous growth rate (g_{ijt} ; d⁻¹) between 2 sampling events (from t to $t+1$) was determined from the change in W_{ijt} g WM in the period t to $t+1$ between the 2 surveys (Δt ; d) according to:

$$g_{ijt} = (\ln W_{ijt+1} - \ln W_{ijt}) / \Delta t \quad (4)$$

Here, g_{ijt} (d⁻¹) was considered to represent the instantaneous growth rate at the midpoint in time (t^* ; day number) between the 2 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

Table 1. Adjusted coefficients for different species for calculating the food requirement. Q_{10i} values were taken from Freitas et al. (2010); wet weight ash-free dry mass conversion factor (c_i ; Brey et al. 2013; 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
<i>Solea solea</i>	2.79	0.2	0.02
<i>Pleuronectes platessa</i>	2.33	0.17	0.02
<i>Pomatoschistus microps</i>	1.53	0.19	0.01
<i>Pomatoschistus minutus</i>	1.53	0.19	0.01
<i>Platichthys flesus</i>	2.33	0.17	0.02
<i>Carcinus maenas</i>	2.16	0.14	0.01
<i>Crangon crangon</i>	2.90	0.19	0.02

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} for each sampling event (t) (DGR_{ijt} ; g WM d⁻¹ m⁻²) was calculated as the sum of the products of g_{ijt} and W_{ijkt} :

$$DGR_{ijt} = \sum k (g_{ijt} W_{ijkt}) \quad (5)$$

For the conversion from 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 3 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:

$$DFRG_{ijt} = c_i DGR_{ijt} / E_i \quad (6)$$

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:

$$DFI_{ijt} = DMR_{ijt} + DFRG_{ijt} \quad (7)$$

To estimate the total food requirement per year (DFI_{ij} ; g AFDM m⁻² yr⁻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 to 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, leading to a potential underestimation of the annual food requirement. Monthly total food requirement (DFI_{ijm} ; g AFDM m⁻² m⁻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 on the order of 20% (Brett & 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) and 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 of 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 & Temming (1994) for brown shrimp *Crangon crangon* and Kühl & Kuipers (1978) for various fish species. For predation on macrozoobenthos, this fraction (f ; unitless) ranged from 0.15 for gobies *Pomatoschistus microps* and *P. minutus* to 1.00 for sole *Solea solea* (Table 2). The annual food requirement of macrozoobenthos by a particular epibenthic predator species i of a particular age class j (DFI_{ij} ; g AFDM $m^{-2} yr^{-1}$) was subsequently calculated as this weight fraction multiplied by DFI_{ij} .

Available macrozoobenthic prey for epibenthos

For each of the individuals of each species that was encountered during the macrozoobenthic surveys, its potential as a food item for epibenthos was defined in line with the previous subsection (Table 2). 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 of all other polychaetes. All data were stored in a Microsoft Access 2010 database, which was directly accessed with the open source program R (R Development Core Team 2016) that was used for all calculations and estimations.

RESULTS

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 requirement 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 shrimp *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 newly recruited 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%.

Table 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 & Kuipers (1978), except for *Carcinus maenas* (Baeta et al. 2006) and *Crangon crangon* (del Norte-Campos & Temming 1994)

Prey	Age group:	<i>Pleuronectes platessa</i>			<i>Platichthys flesus</i>			<i>Solea solea</i>		<i>Pomatoschistus microps</i>		<i>Pomatoschistus minutus</i>		<i>Carcinus maenas</i>	<i>Crangon crangon</i>
		0	I	II	0	I	II	0	I	0	I	0	I	All	All
Macrozoobenthos		0.95	0.95	0.95	0.95	0.95	0.95	1	1	0.15	0.35	0.15	0.35	0.4	0.3
<i>Crangon crangon</i>										0.6	0.57	0.6	0.57		
Small crustaceans										0.26	0.06	0.26	0.06		0.35
Other		0.05	0.05	0.05	0.05	0.05	0.05				0.02		0.02	0.5	0.3
Cannibalism														0.1	0.05

Food requirements

During the study period (1975 to 2014), the total biomass (g WM m⁻²) of epibenthic predators at the Balgzand tidal flats was, on average, dominated by brown shrimp *C. crangon* and juvenile plaice *Pleuro-nectes platessa*. While the biomass of shrimp was higher at the end of the study period (Fig. 2), the biomass of juvenile plaice (of all age groups) was high in the 1970s and early 1980s but much lower thereafter (Fig. 3). Other relatively dominant fish with regard to biomass were the European flounder *Platichthys fle-sus* (in particular the II-group) and 2 goby species (*Pomatoschistus minutus* and *P. microps*, in particular the 0-group) (Fig. 3). Their biomass was, on average, comparable with that of the shore crab *Carcinus maenas* (Fig. 2). Other rarer fish species caught were

lesser sandeel *Ammodytes tobianus*, Atlantic herring *Clupea harengus*, three-spined stickleback *Gaster-osteus aculeatus*, shorthorn sculpin *Myoxocephalus scorpius*, European smelt *Osmerus eperlanus* and eelpout *Zoarces viviparus* (Fig. 2). Because of their generally low numbers, it was not possible to estimate their growth in time, and annual food require-ment could therefore not be calculated for these fish species.

The calculation of food requirements as total annual food requirement was restricted to (1) epiben-thic species with the highest biomass, including plaice, flounder, sole and both goby species as well as brown shrimp and shore crabs; (2) those years dur-ing which at least 5 cruises were conducted; (3) those years during which all these species were sorted; and (4) availability of information for all age classes of the

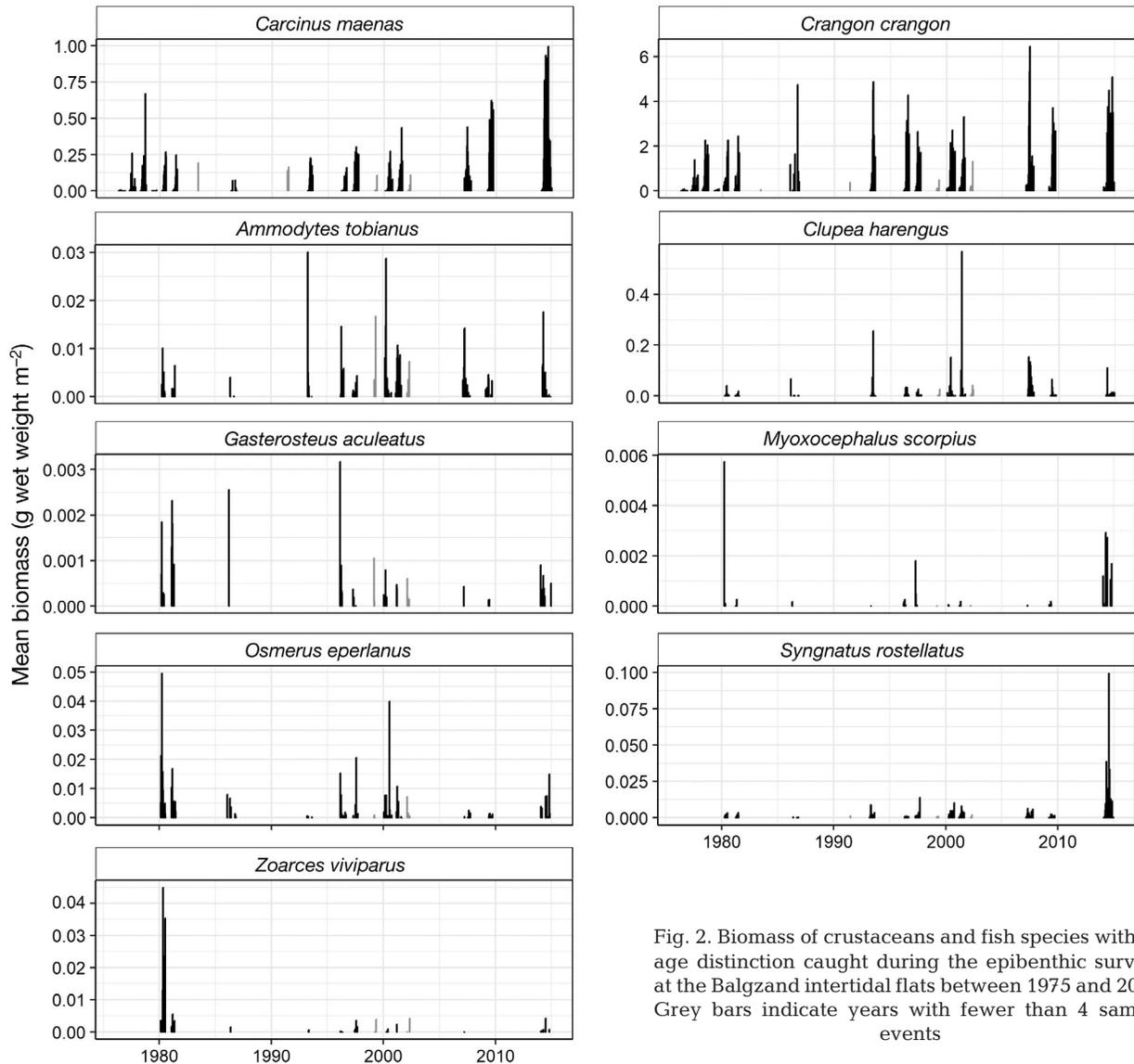


Fig. 2. Biomass of crustaceans and fish species without age distinction caught during the epibenthic surveys at the Balgzand intertidal flats between 1975 and 2014. Grey bars indicate years with fewer than 4 sample events

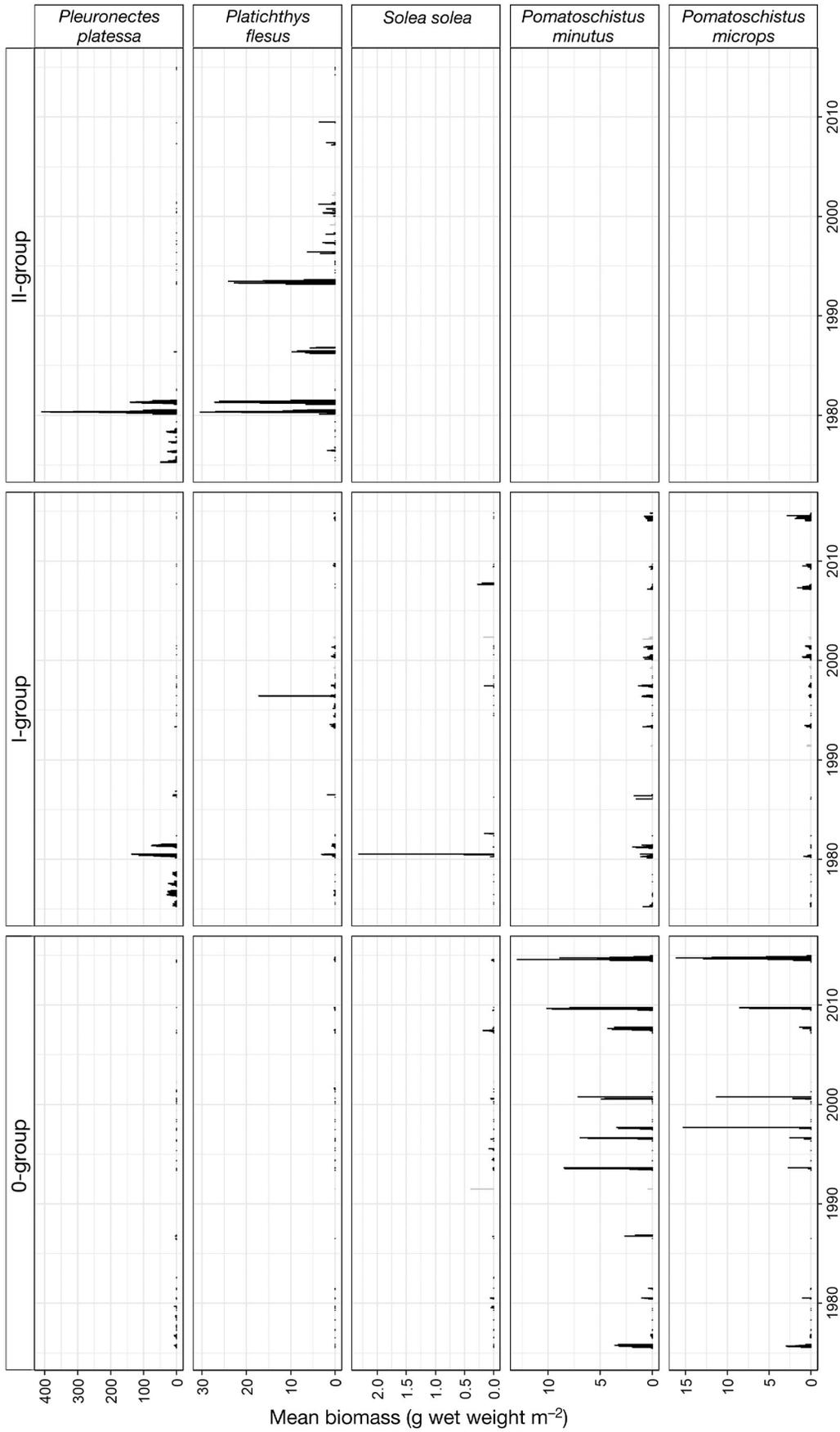


Fig. 3. Biomass (g wet wt m⁻²) of age classes of various flatfish and goby species caught during the epibenthic surveys at the Balgzand intertidal flats between 1975 and 2014. Grey bars indicate years with fewer than 4 sample events

selected fish species. This resulted in analyses of the annual food requirement for 5 fish species (divided into 2 or 3 year classes) and 2 crustaceans during 12 years between 1975 and 2014 (Table S3 in the Supplement at www.int-res.com/articles/suppl/m579/p037_supp.pdf).

Within this period, the sum of the total annual food requirement by these 7 epibenthic species ranged from less than 13 g AFDM m⁻² yr⁻¹ in 2001 to more than 40 g AFDM m⁻² yr⁻¹ in 1980 and 2007 (Table S3). On average, shrimp *C. crangon* contributed most, with their total food requirement ranging from less than 5 g AFDM m⁻² yr⁻¹ in 1999 to almost 40 g AFDM m⁻² yr⁻¹ in 2007 (Table S3, Fig. 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 yr⁻¹ in 2009 and 2014 (Table S3, Fig. 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 (Table S3, Fig. 4).

Overall, the summed total annual food requirement of crustaceans appeared to have increased, whereas that of fish decreased (Fig. 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 (Fig. 4).

Total food requirement by crustaceans (dominated by shrimp *C. crangon*) was relatively high (>2 g AFDM m⁻² mo⁻¹) from May to August compared to early spring (March) and late autumn (October) (Fig. 5). During the first years of the study period, specifically prior to 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). 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).

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 thereafter (Fig. 6). This trend was apparent in the biomass of both bivalves and polychaetes (Fig. 6) as well as in *Peringia ulvae*

and other groups. On average, the biomass consisted of more than 70 % of bivalves, whereas the potential macrozoobenthic prey items consisted of more than 80 % of polychaetes (Fig. 6), but in the most recent years, *P. ulvae* showed biomass values that were comparable with those found for polychaetes.

With respect to 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. 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. 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 considered as prey (Fig. 6, *Arenicola* tails and other polychaetes) generally increased from <5 g AFDM m⁻² in the 1970s to >20 g AFDM m⁻² in the early 2000s and <10 g AFDM m⁻² at the end of the study period. The biomass of the regenerating tails of the lugworms was relatively low (<5 g AFDM m⁻²) but higher in the 1980s and 1990s than before and after this period (Fig. 6).

DISCUSSION

Long-term changes in epibenthic predators

Despite the continuous and/or enhanced impacts of eutrophication, fisheries and climate change during the study period (Philippart & Cadée 2000, Lotze 2005, Wolff 2013, Jung et al. 2017), 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 observed 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 (van der Veer et al. 2015). 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 in-

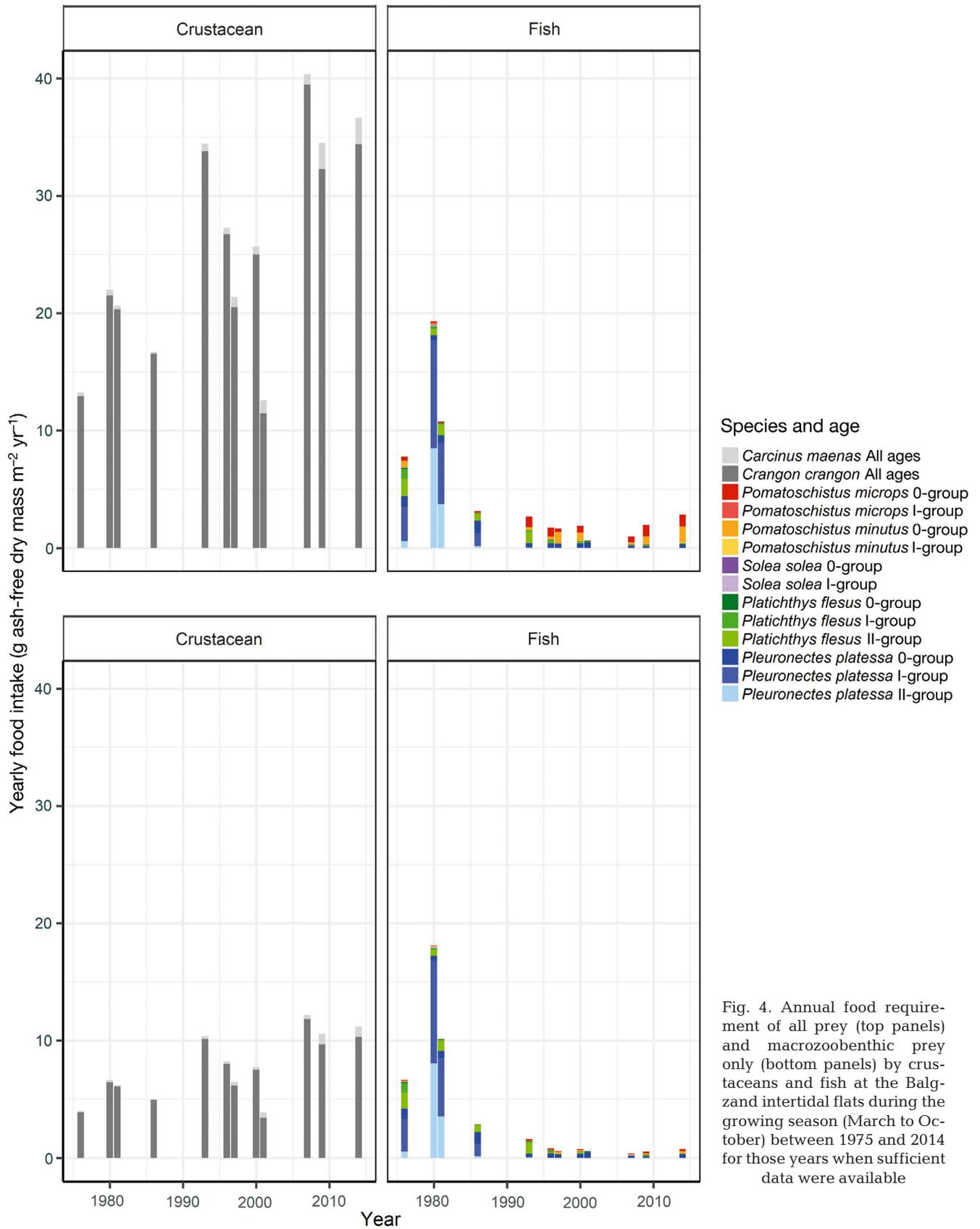


Fig. 4. Annual food requirement of all prey (top panels) and macrozoobenthic prey only (bottom panels) by crustaceans and fish at the Balgzand intertidal flats during the growing season (March to October) between 1975 and 2014 for those years when sufficient data were available

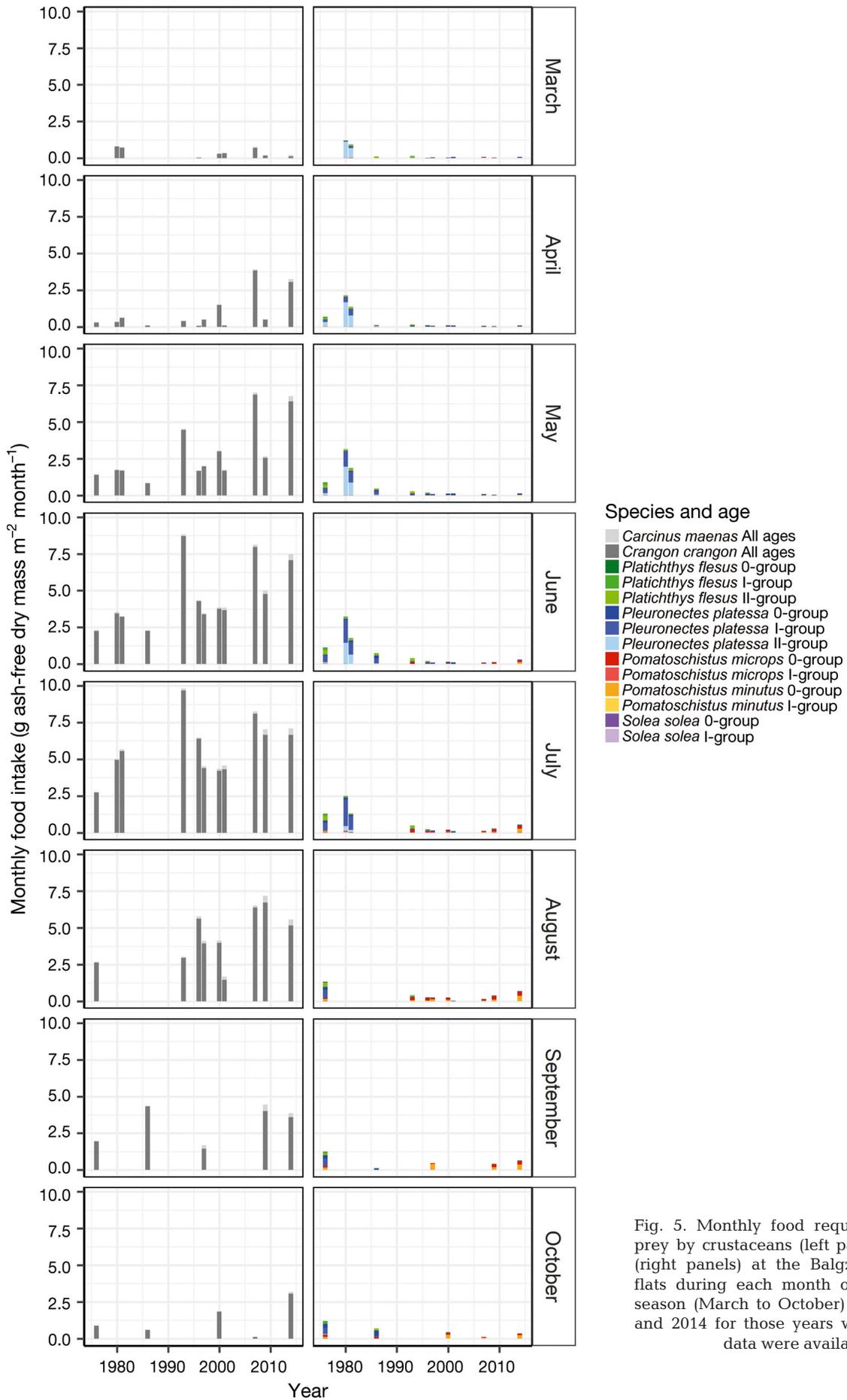


Fig. 5. Monthly food requirement of all prey by crustaceans (left panels) and fish (right panels) at the Balgzand intertidal flats during each month of the growing season (March to October) between 1975 and 2014 for those years when sufficient data were available

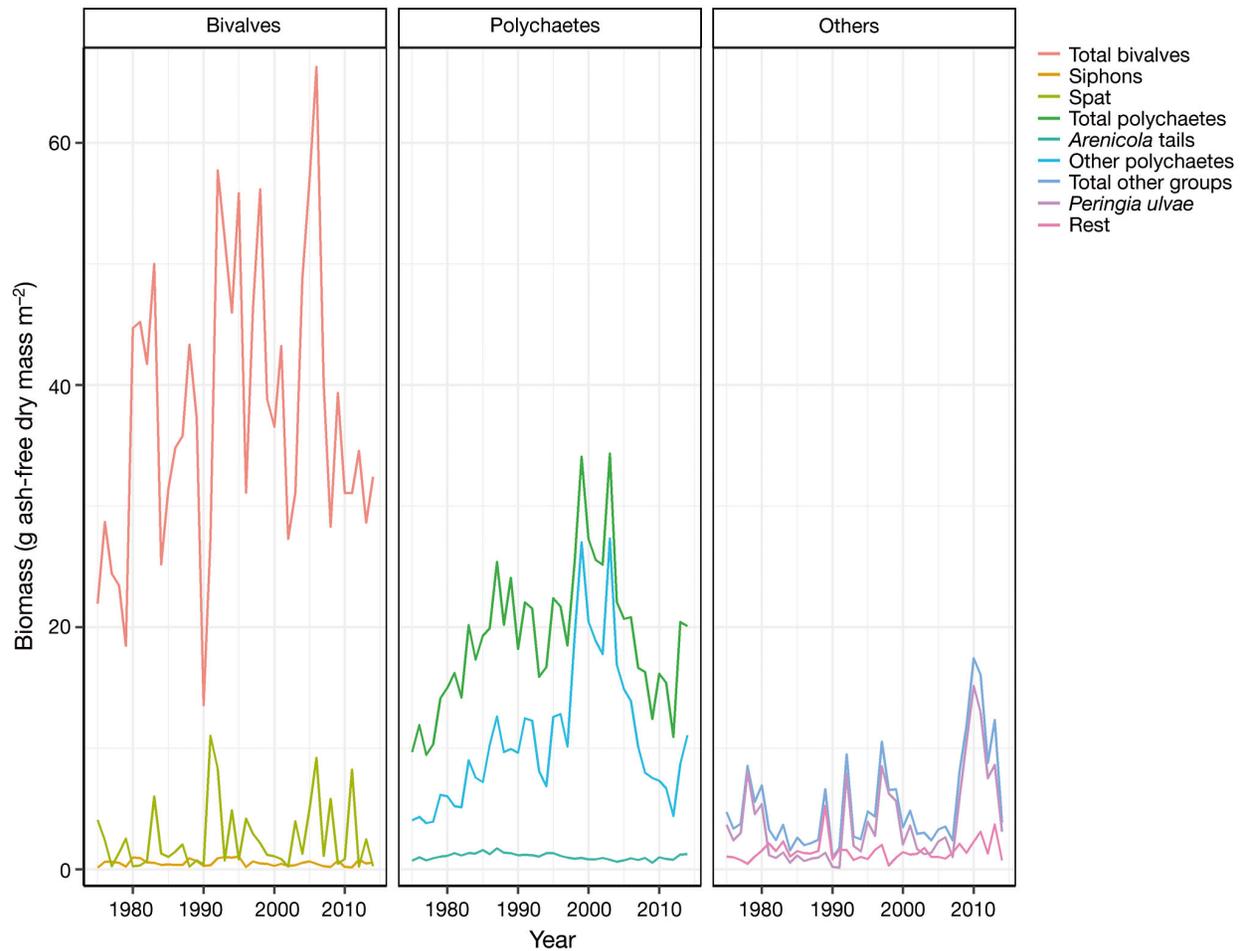


Fig. 6. Biomass of macrozoobenthos divided into bivalves, polychaetes and other groups at the Balgzand between 1975 and 2014. Red, turquoise and blue represent total biomass in bivalves, polychaetes and others, respectively; other colours represent biomass of potential food items as part of total biomass

deed ~40% higher since 2000 than in the 1980s and 1990s, which is attributed to reduced predation by juvenile whiting *Merlangius merlangus* and cod *Gadus morhua* (Temming & 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 requirements 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).

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 & Zuidema 1995, Beukema & 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 & 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 of the Wadden Sea from 1989 onwards (Essink & Dekker 2002). Its relatively high productivity:biomass (P:B) ratio (ca. $6 \text{ g g}^{-1} \text{ yr}^{-1}$) compared to native polychaete species (Sarda et al. 1995) in combination with its high standing stock (ca. 10 g AFDM m^{-2} , Essink & Dekker 2002, R. 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.

Long-term changes in predator–prey relationships

For 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. This implies that siphon nipping by flatfish was reduced over time. Such a release from predation may affect anti-predatory behaviour of former prey items, e.g. burrowing depth of bivalves, possibly resulting in enhancement of their growth (Persson & Svensson 2006, Fässler & Kaiser 2008, Flynn & 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 & Rosenberg 1984, van der Veer & Bergman 1987, del Norte-Campos & 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 & 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 $15.6 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$ (Table 3). The 2 groups of these predators took more or less an equal share: the summed predation by the various fish species was $7.4 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$, whereas that by the crustacean species

accounted for $8.2 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$ (Table 3). A comparison between the study from the 1970s (Kuipers & 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 ($23.1 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$) is approximately 45% higher than the previous estimate for this period (Table 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, 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: $26 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$ (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 & 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 $10 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$, during the study period. Total biomass of the potential food items for epibenthos was $<5 \text{ g AFDM m}^{-2}$ in the 1970s, $>20 \text{ g AFDM m}^{-2}$ in the 2000s and, again, $<10 \text{ g AFDM m}^{-2}$ thereafter. This implies that the P:B ratio must have been between at least $0.5 \text{ g g}^{-1} \text{ yr}^{-1}$ in the 2000s and $2 \text{ g g}^{-1} \text{ yr}^{-1}$ 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 et al. 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 adult bivalves such as *Mya arenaria* and *Crassostrea gigas* get too large to be predated by birds (Zwarts & Wanink 1989, Scheiffarth et al. 2007, Markert et al. 2013), then this will lead to shorter cycles of energy transfer (dead-end

Table 3. Total food requirement around the 1970s as derived from previous studies (Kuipers & Dapper 1981 and original references in Kuipers et al. 1981; for original references see sources in this table) and in this paper of main epibenthic predators on the Balgzand tidal flats. AFDM: ash-free dry mass

Species	Previous studies			This study	
	Food req. (g AFDM m ⁻² yr ⁻¹)	Years	Source	Food req. (g AFDM m ⁻² yr ⁻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	1.0	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 & Dapper (1981)	15.3	1976–1979
Total	15.6			23.1	

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*.

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 the macrozoobenthic community was still considerable (ca. 5 g AFDM m⁻² yr⁻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 g AFDM m⁻² yr⁻¹. The increase in brown shrimp appears not to be restricted to the Balgzand tidal flats. A 4-fold 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 & 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 (Pihl & Rosenberg 1984, van der Veer et al. 1998). This might have reduced the predation of flatfish on adult bivalves and lugworms. 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 & 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, van der Veer et al. 2016). The observed growth reduction coincided with a decrease in stomach content, suggesting the availability of fewer prey items. It was hypothesised that behavioural components, such as a less active macrozoobenthos after the spring/summer phytoplankton bloom, were causing a reduction in prey availability, and were therefore responsible for the reduced growth.

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, 2013, Lotze et al.

2005), and after the 1960s the Wadden Sea suffered from the cumulative effects of habitat loss, overexploitation, pollution, eutrophication and species invasions (see Lotze 2005). For the western Wadden Sea and the Balgzand intertidal, severe pollution and eutrophication have occurred (Duinker et al. 1979, van Beusekom 2005) in combination with serious habitat loss. Until the closure of the former Zuiderzee in 1932, extensive subtidal and intertidal seagrass beds were present (Philippart & 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 (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 readjusts 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.

Data archive. Original data and R script for calculation can be found under <http://doi.org/10.4121/uuid:5afaef7a-aeed-7402-9f54-52bad31af9fd>

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