Jung, A.S.; Dekker, R.; Germain, R.; Philippart, C.J.M.; Witte, J.IJ. & van der Veer, H.W. (2017). Long-term shifts in intertidal predator and prey communities in the Wadden Sea and consequences for food requirements and supply. *Marine Ecology Progress Series*, 579, 37-53

Published version: https://dx.doi.org/10.3354/meps12263

Link NIOZ Repository: www.vliz.be/imis?module=ref&refid=289698

Long-term shifts in intertidal predator and prey communities in the Wadden Sea and consequences for food requirements and supply

Running page head: Long-term shifts in intertidal predator-prey relationships

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Key words: long term dynamics, predation, epibenthic predators, intertidal, Wadden Sea, fish, crustaceans

ABSTRACT

Fluctuations in species composition can considerably change the functionality of an ecosystem, but studying such impacts is often complicated as the result of the occurrence of coinciding changes in other parts of the ecosystem during their appearance. In this study, we explored long-term (1975-2014) changes in predator-prey interactions following concurring changes in predatory epibenthic fish and crustaceans and macrozoobenthic bivalves and polychaetes in the western Wadden Sea. Historical and recent invasions resulted in an increase of relatively large and long-lived bivalves (*Mya arenaria, Ensis directus, Crassostrea gigas*) that reach a size refuge from epibenthic predators. The invasive polychaete *Marenzelleria viridis* probably became an important food source during the early 2000s. Whilst bivalves dominated the macrozoobenthic biomass, polychaetes were the main food source of epibenthic predators. Food requirements by epibenthic crustaceans, mainly *Crangon crangon*, almost doubled from 5 to 10 gAFDM m^{-2} y^{-1} and by epibenthic fish decreased by more than 80%, mainly due to the local disappearance of *Pleuronectes platessa*. Whilst 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 gAFDM m^{-2} until the 2000s and decreased to 10 gAFDM m^{-2} hereafter. This was the result of changes in native (*Nereis diversicolor* and *Heteromastus filiformis*) and invasive (*Marenzelleria 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 impacts on food web structure and functioning of coastal systems.

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 over the past, such as the bivalves *Mya arenaria* (400-700 years ago, Strasser 1998), *Ensis leei* (formerly known as *Ensis directus*, around 1982, Beukema & Dekker 2011), *Crassostera gigas* (around 2001, Beukema & Dekker 2011) and the polychaete *Marenzelleria viridis* (formally 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, Essink & Dekker 2002, Troost 2010, Beukema & Dekker 2011). 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. Whilst wading birds are feeding 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), whilst plaice 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 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 and mussels; Leonard et al. 1999, Smith & Jennings 2000) and clumping behaviour (e.g. mussels; Côté & Jelnikar 1999).

This means that for a new invasive species, its 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 (López et al. 2010, Stokesbury & Himmelman 1996). 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 theses invaders can be considered prey items for fish, crustaceans and birds. The relatively small invasive polychaete *M. viridis* that 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 as several of the invasions in the macrozoobenthic community in the Wadden Sea took place, for example, also changes in epibenthic predators were observed. Juvenile flatfish, mainly plaice (*Pleuronectes platessa*), declined in the western Wadden Sea between the 1970s and late 1980s (van der Veer et al. 2011, Freitas et al. 2016), possibly as the result of climate-induced temperature changes (Rijnsdorp et al. 2009, Teal et al. 2012). Large brown shrimp (*Crangon crangon*) appear to have increased since the 1990s (Temming & Hufnagl 2015, Tulp et al. 2012). This is most likely due to a decline in numbers and a shift in the distributional range of the shrimp's key predators (Temming & Hufnagl 2015) and also small brown shrimp have increased 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. Hereto, we compare the food requirements of fish and crustaceans with the availability of macrozoobenthos as a food source. This analysis is based upon data from long-term sampling programs on macrozoobenthos (since 1970) and epibenthos (since 1975) performed at the Balgzand tidal flats. From the 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 has changed over time.

MATERIAL AND METHODS

Sampling

Study area

All sampling took place at Balgzand, a tidal flat system of 50 km^2 bordering the Marsdiep tidal inlet in the western part of the Wadden Sea (Fig. 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 northerly, 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 years over the period 1975 to 2014 (1975-1983, 1986, 1991, 1993-2002, 2007, 2009 and 2014, Table A2). Over the years sampling methods have remained the same, however 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 (in principle 2 to 4 weeks) till autumn at a period of 3 h around high tide, because during this time the flatfish population is randomly distributed over the area (Kuipers 1977). Hauls of about 100 m were made during daytime using a 1.9 m beam trawl with one tickler chain, towed at a speed of about 35 m min^{-1} following Riley and Corlett (1966). Location of the hauls was established at the start of the series by wooden poles and later on by GPS. The length of the trawls was assessed with a meter-wheel fitted outside the trawl. Water temperature and, in later years, salinity was measured during each cruise. All samples were stored in plastic bags, transported to the laboratory and preserved at the same day in a 4 % formaline-seawater solution until 1990 and deep-frozen after 1990.

Samples were sorted to species level and the length of the individuals was measured to the nearest 1 mm total length (0-group flatfish) or nearest 5 mm (all others) within a few weeks after sampling. For the most abundant species, except for the shore crab *Carcinus maenas*, information about catch efficiency was available (plaice: Kuipers 1975; flounder: van der Veer et al. 1991; sole: van der Veer et al. 2001; shrimps: van Lissa 1977; gobies: van Beek 1976, Figure A1). For these species, the number of individuals caught was corrected and converted into age-specific densities. For all other species, being present in low numbers only, catches were converted into densities without correcting for net efficiency. Subsequently, total densities were split into densities per age class based upon species-specific length classes. In case of doubt with regard to age-length relationships in fish, individual age was verified by means of otolith reading. Following previous methodology (Zijlstra et al. 1982, van der Veer 1986, van der Veer et al. 1998, van der Veer et al. 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, in total less than 50 stations were sampled during various cruises over the whole year, 150 were sampled in 1998, 1999 and 2002, whereas the other years, between 260 and 400 stations were sampled.

Macrozoobenthic surveys

The macrozoobenthic community has been monitored since the 1970s, consistently and quantitatively for all groups from around 1988 onwards. Sampling was done at 15 stations scattered over Balgzand, twice a year in late winter (February-March) and late summer (August-September). For the present analyses, only data for late summer were used. However from 1975 up to and inclusive 1987, in summer polychaetes were not, or inadequately, sampled and quantified. For this reason, polychaete data for this period were calculated from the winter data of the following year (~ 0.5 y after the summer sampling), which were always sampled and quantified completely. A correction factor of 1.87 * the winter biomass values was applied, a factor derived from the period 1988-2009 (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 a total of 0.45 m^2 in summer. At the 3 permanent quadrats, a total of 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 square mesh screens. All macrozoobenthic organisms retained were collected and sorted alive in the laboratory down to species and, if possible, year-class level (bivalves, by means of the number of year marks on the shell) within 1 or 2 days after sampling. For each species (and year-class), the number per sample was counted. Each group of a particular species of a particular age class was put into one cup, which was dried for 3 days in a ventilated stove at 60 °C, weighted, incinerated for 3 h at 560 °C and weighted again. Weight loss after incineration, defined as Ash-Free Dry Mass (AFDM), was considered to be a measure for biomass. After conversion to total biomass (all age classes combined) per surface area per station for each species *i*, the species-specific total mean biomass (B_i; g AFDM m^{-2}) at Balgzand was calculated as the arithmetic mean of the 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}; gWM m^{-2}; 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}; gWM) was determined from average length per size-class of 0.5 cm (L_{ijk}; cm) using species-specific length-mass relationships:

$$W_{ijk} = (a\ L_{ijk})^{b} \qquad \text{Equation 1}$$

where *a* (shape coefficient; $gWM^{1/3}$ cm^{-1}) and *b* (-) are species-specific parameters (Table A1). Second, the species-, age- and size-specific wet mass W_{ijk} (gWM) was converted into species-, age- and size-specific metabolic mass (M_{ijk}; $gWM^{0.8}$) as $M_{ijk} = W_{ijk}^{0.8}$. For each species from each age-class, the corresponding metabolic mass was multiplied by the density of that size-class (n_{ijk}; m^{-2}). Subsequently, the sum for all size classes was calculated to obtain the total metabolic wet mass of the age class of each species per m^2, so:

$$M_{ij} = \sum k \, (n_{ijk} \, M_{ijk}) \qquad \text{Equation 2}$$

The species-specific daily food requirement needed to meet daily maintenance requirements (DMR_{ij}; g AFDM m^{-2} d^{-1}) as part of the total food requirement equals:

$$DMR_{ij} = c_i \, Q_{10i}^{0.1T} \, m_i \, M_{ij} \qquad \text{Equation 3}$$

where c_i (g AFDM gWM^{-1}) is the species-specific conversion factor from wet mass to ash-free dry mass (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} (gWM m^{-2}) the species' metabolic mass per age class. Daily maintenance requirements (DMR_{ij}; g AFDM m^{-2} d^{-1}) were calculated for each species for each age class for each sampling event.

The estimation of daily growth requirements (DGR_{ij}; g AFDM m^{-2} d^{-1}) was based on observed increase in length (L_{ijt}; cm) 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 survey t. Subsequently, these mean lengths (L_{ijt}; cm) were converted to mean wet mass (W_{ijt}; gWM) using species-specific length-mass relationships (see Equation 1). Hereafter, instantaneous growth rate (g_{ijt}; d^{-1}) between two sampling events (from t to $t+1$) was determined from the change in mean wet masss (W_{ijt}; gWM) in the period t to t+1 between the two surveys (Δt; days) according to:

$$g_{ijt*} = (\ln W_{ijt+1} - \ln W_{ijt}) \, / \, \Delta t \qquad \text{Equation 4}$$

Here, g_{ijt*} (d^{-1}) was considered to represent the instantaneous growth rate at the midpoint in time (t*; day number) between the two successive sampling events. To get estimates for growth rates (for each species and each age class) at the time of the sampling events (g_{ijt}; d^{-1}), an exponential curve was fitted through the growth rates at the midpoints in time (g_{ijt*}; d^{-1}) for each year. From this relationship of *g* over time (day number), estimates of *g* at exactly the various sampling dates could be determined. This estimate of *g* on a sampling date was taken to represent growth of all size classes of an age group, and applied to determine daily growth in mass for each size class. For those species for which this approach was not possible (e.g. crustaceans which show a continuous immigration of small individuals and emigration of large individuals), the average growth rates (g_{ijt}; d^{-1}) 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.

Daily growth rate per species *i* per age class *j* per size class (DGR_{ijt}; gWM d^{-1} m^{-2}) was calculated during each sampling event *t* as the sum of the products of the growth rate (g_{ijt}; d^{-1}) and the wet mass per size-class *k* (W_{ijkt}; gWM m^{-2}), so:

$$DGR_{ijt} = \sum k\ (g_{ijt}\ W_{ijkt}) \qquad \text{Equation 5}$$

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

$$DFRG_{ijt} = c_i\ DGR_{ijt}/E_i \qquad \text{Equation 6}$$

where c_i (g AFDM gWM^{-1}) is the species-specific conversion factor from wet mass to ash-free dry mass (de Vlas 1979).

For each sampling date *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 the sum of daily maintenance requirements (DMR_{ijt}; g AFDM m^{-2} d^{-1}) and daily food requirements for growth ($DFGR_{ijt}$; g AFDM m^{-2} d^{-1}):

$$DFI_{ijt} = DMR_{ijt} + DFGR_{ijt} \qquad \text{Equation 7}$$

To estimate the total food requirement per year (DFI_{ij}, g AFDM m^{-2} y^{-1}), a polynomial was fitted through the total daily food requirement (DFI_{ijt}, g AFDM m^{-2} d^{-1}) of each species *i* and each age class *j* during time *t* for each year separately. Maximum a fourth-order polynomial was fitted through the individual data points and the surface area during the growing season (1 March – 31 October) was calculated by integration of the polynomial function from day 60 to day 300. In some cases, a third-order or second-order polynomial was sufficient. The growing season (1 March- 31 October) was not sampled completely in all years, probably resulting then in an underestimation of 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 in 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 (i) juvenile bivalve spat (newly settled), (ii) 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 (iv) total biomass off all other polychaetes. The species- and age-specific contribution of potential prey items (as weight fraction of total stomach contents) to total food requirement was based upon published information from various sources, i.e. Baeta et al. (2006) for shore crabs (*Carcinus 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; -) ranged between 0.15 for gobies (*Pomatoschistus microps*, *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* ($DFIm_{ij}$, g AFDM m^{-2} y^{-1}) was subsequently calculated as this weight fraction multiplied with the total food requirement per year (DFI_{ij}, g AFDM m^{-2} y^{-1}).

Available macrozoobenthic prey for epibenthos

For each of the individuals of each species that was encountered during the macrozoobenthic surveys, its potential as food item for epibenthos was defined in line with the above (Table 2). So, for each survey, the average biomass (g AFDM m^{-2}) was calculated for (i) juvenile bivalve spat, (ii) siphons of adult bivalves (except *M. edulis*), (iii) tail tips of the polychaete *A. marina*, and (iv) total biomass off all other polychaetes. All data were stored in a Microsoft Access 2010 database, which was directly accessed with the open source Program R (R Core Team 2016) that was used to do all calculations and estimations.

RESULTS

Sampling

In principle, the 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 and 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 numbers of stations, their location and also the month changed per year and therefore the accuracy of the estimation of density, biomass and annual food requirement by the epibenthic community might be affected. Also, subsampling could have an influence on the abundance estimations and was relatively high in some cases (e.g. up to a factor of 512 in brown shrimps (*Crangon crangon*)). Furthermore, some species or size classes are not distributed randomly over the area: flounder only occurred in the siltier areas and just settled shrimps mainly occurred in the most sheltered part (closer to the shore) of the Blagzand tidal flats. The accuracy of the results largely depended on the abundance estimates of species in the system. For plaice, Zijlstra et al. (1982) estimated a sampling error of up to 35%.

Food requirements

During the study period (1975-2014), the total biomass (gWM m^{-2}) of epibenthic predators at the Balgzand tidal flats was, on average, dominated by brown shrimp (*C. crangon*) and juvenile plaice (*Pleuronectes platessa*). Whilst 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 hereafter (Fig. 3). Other relatively dominant fish with regard to biomass were the European flounder (*Platichthys flesus*, in particular the II-group) and two gobies 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 (*Gasterosteus aculeatus),* shorthorn sculpin (*Myoxocephalus scorpius*), European smelt (*Osmerus eperlanus*) and eelpout (*Zoarces viviparous*) (Fig. 2). Because of their generally low numbers, it was not possible to estimate their growth in time and annual food requirement could, therefore, not be calculated for these fish species.

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

Within this period, the sum of the total annual food requirement by these seven epibenthic species ranged from less than 13 g AFDM m^{-2} y^{-1} in 2001 to more than 40 g AFDM m^{-2} y^{-1} in 1980 and 2007 (Table 3). On average, shrimp (*C. crangon*) contributed most with their total food requirement ranging from less than 5 g AFDM m^{-2} y^{-1} in 1999 to almost 40 g AFDM m^{-2} y^{-1} in 2007 (Table 3, 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} y^{-1} in 2009 and 2014 (Table 3, 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 1974-1986, to gobies (*P. microps* and *P.minutus*, in particular the 0-groups) during the rest of the study period (Table 3, Fig. 4).

Overall, the summed total annual food requirement of crustaceans appeared to have increased whilst 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} $month^{-1}$) 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-April to I-group plaice in May-July (Fig. 5). After 1990, the seasonal pattern in total food requirement showed an increase (June-Sept) 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 hereafter (Fig. 6, all panels). This trend was apparent in the biomass of both bivalves and polychaetes (Fig. 6), as well as *Peringia* and other groups. On average, the biomass consisted for more than 70% of bivalves, whilst the potential macrozoobenthic prey items consisted for more than 80% of polychaetes (Fig. 6) only in the most recent years *Peringia* showed biomass values that were comparable with the ones found for polychaetes.

With respect to the bivalves, only a minor part (approximately 10%) of the total biomass was spat that could be considered as prey for epibenthic fish and crustaceans (Fig. 6). Within the study period, the biomass of spat varied from year to year between 0.1 (in 1977) and more than 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 the 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 (in Fig. 6 the *Arenicola* tails and other polychaetes) generally increased from less than 5 g AFDM m^{-2} in the 1970s to more than 20 g AFDM m^{-2} in the early 2000s and less than 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

In spite of 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 over these last decades mainly refer to changes in seasonal presence and abundance: a decline in juvenile plaice and absence from July onwards and an increase in the abundance of the brown shrimp. The observed decline in juvenile plaice 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 predation pressure from them on other epibenthic predators such as juvenile shrimp. Average landings of large shrimp (> 50 mm) originating from the NE North Sea (including the Wadden Sea) are indeed ~40% higher since 2000 than in the 1980s and 1990s, which is attributed to a reduced predation by juvenile whiting and cod (Temming and Hufnagl, 2015). The decline of fish as a competitor may allow other species to take over. From our data, we cannot determine if the increase in food requirement by shrimp is due to a release of predation or competition, 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 with exception of the autumn of the year 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 exception of the first year (1974) of the study period. Thereafter, the biomass of polychaetes as potential prey increased till the early 2000s and started to decrease again after that to levels that are similar to what had been 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 from 1989 onwards (Essink & Dekker 2002). Its relatively high P:B ratio (ca. 6 g g^{-1} y^{-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; 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 prey-predator relationships

For the epibenthic fish species, the potential predation on macrozoobenthos more or less covers their total food requirements, in particular for the juvenile plaice. During the study period, however, the overall abundance and the average size of this flatfish strongly declined.

This implies that siphon nipping by flatfish was reduced over time. Such a release may affect anti-predatory behaviour of former prey items, e.g. burrowing depth of bivalves, possibly resulting in enhancement of their growth (Persson & 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 in order to gather enough energy to survive and grow. The diet of *C. crangon* is highly variable in time and space, including 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 for 100% on meiofauna; del Norte-Campos & Temming 1994). Changes in the abundance and size-structure of shrimp may, therefore, not only change food requirement of macrozoobenthos but also of other potential prey items within the ecosystem.

The analysis of the food web structure of the Balgzand intertidal flats in the western Dutch Wadden Sea in the 1970s by Kuipers et al. (1981) indicated a total food requirement by epibenthic carnivores of 15.6 g Ash Free Dry Mass [AFDM] m^{-2} y^{-1} (Table 4). The two groups of these predators took more or less an equal share: the summed predation by the various fish species was 7.4 g AFDM m^{-2} y^{-1} whilst that by the crustacean species accounted for 8.2 g AFDM m^{-2} y^{-1} (Table 4). 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 g AFDM m^{-2} y^{-1}) is approximately 45% higher than the previous estimate for this period (Table 4). 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, being 26 g AFDW m^{-2} y^{-1} (Pihl 1985). As for the Balgzand tidal flats, brown shrimp accounted for most (46%) of the total food requirement in that area in that year (Pihl & Rosenberg 1984).

In spite of the shifts in relative dominance of species and in the size-structure of the epibenthic predators, their summed food requirement of macrozoobenthic prey remained more or less constant, around 10 g AFDM m^{-2} y^{-1}, during the study period. Total biomass of the potential food items for epibenthos was less than 5 g AFDM m^{-2} in the 1970s, more than 20 g AFDM m^{-2} in the 2000s and less than 10 g AFDM m^{-2} hereafter. This implies that the P:B ratio must have been at least between 0.5 g g^{-1} y^{-1} in the 2000s and 2 g g^{-1} y^{-1} in the 1970s in order to sustain these food requirements, which is within the order of magnitude as 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 (*Marenzelleria 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 impacts of shifts in species composition (invasions or disappearance) on trophic transfer within coastal intertidal systems should take into account species-specific changes and interactions of both prey and predators. Adult bivalves have generally outgrown their epibenthic predators. At the Balgzand tidal flats, bivalve spat was only an important food source for epibenthic predators during years of low polychaete biomass (as in the 1970s) or high bivalve recruitment success (as in 1991). If the adult bivalves such as *Mya arenaria* and *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 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 macrozoobenthos was still considerable (ca. 5 g AFDM m^{-2} y^{-1}, representing approximately 50% of the total epibenthic food requirement) to a system where these fish almost disappeared and shrimp became more abundant with an increase of their food requirement from 5 to 10 g AFDM m^{-2} y^{-1}. Increase in brown shrimp appears not to be restricted to the Balgzand tidal flats. A fourfold increase in summer densities from the 1970s to the 2000s of relatively small shrimp (20-53 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 (*C. crangon*) 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* (Kuipers 1977, de Vlas 1979) to other prey items, i.e. bivalve spat and small polychaetes (van der Veer et al. 1978, Pihl & Rosenberg 1984). This might have released adult bivalves and lugworms from flatfish predation. The observation, that the bivalve *Limecola balthica* (formerly known as *Macoma balthica*) now lives deeper and has a higher body condition (Compton et al. 2016) might be an indication of the release of their siphons from flatfish predation. On the other hand, the increased shrimp predation on bivalve spat might have increased their role in regulating bivalve recruitment success (van der Veer et al. 1978). This suggests at least the possibilities that some top-down effects on the species- and size-structure of the macrozoobenthic community are likely in the intertidal Balgzand food web.

Whether also bottom-up regulation occurs cannot be determined with 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 less prey items. It was hypothesised that behavioural components were acting, a less active macrozoobenthos after the spring/summer phytoplankton bloom, reducing prey availability and hence causing a reduction in food requirement.

Long-term changes: the shifting baseline syndrome

The ecological times series used in this study all started around the 1970s. However, it is clear that the Wadden Sea has a much longer history and has changed already considerably centuries before the 1960s (Wolff 1983, Lotze et al. 2005, Wolff 2013). However, still in the twentieth century, the Wadden Sea suffered from the cumulative effects of habitat loss, overexploitation, pollution, eutrophication and species invasions (see Lotze et al. 2005).

For the western Wadden Sea and the Balgzand intertidal, also severe pollution and eutrophication has 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 Wadden Sea food web structure and ecosystem functioning is not possible, but Lotze et al. (2005) speculate 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, which 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 found in the early 1970s. Because our study area used to be covered by seagrass beds and roamed by top predators before that time, the Balgzand food web structure was most likely already partly degraded and simplified by then.

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TABLES

Table 1: Adjusted coefficients for different species for calculating the food requirement. Q_{10} values were taken from Freitas et al. (2010b), the wet weight- ash-free dry mass conversion factors (c_i) and maintenance coefficients (M_i) from de Vlas (1979), van Beek (1976), Brey et al. (2010), van der Veer et al. (2001) and van Lissa (1977).

Species	Q10	c_i	M_i
Solea solea	2.79	0.2	0.02
Pleuronectes platessa	2.33	0.17	0.02
Pomatoschistus microps	1.53	0.19	0.01
Pomatoschistus minutus	1.53	0.19	0.01
Platichthys flesus	2.33	0.17	0.02
Carcinus maenas	2.16	0.14	0.01
Crangon crangon	2.90	0.19	0.02

Table 2: Food selection of the different species according to various studies in proportions.

Age	Prey	*Pleuronectes platessa*	*Platichthys flesus*	*Solea solea*	*Pomatoschistus minutus*	*Pomatoschistus microps*	*Carcinus maenas*	*Crangon crangon*
0-group/all-groups for crustaceans	Macrozoobenthos	0.95	0.95	1	0.15	0.15	0.4	0.3
	Crangon crangon				0.6	0.2		
	small crustaceans				0.26	0.64		0.35
	Other	0.05	0.05				0.5	0.3
	Cannibalism						0.1	0.05
I group	Macrozoobenthos	0.95	0.95	1	0.35	0.28		
	Crangon crangon				0.57	0.32		
	small crustaceans				0.06	0.16		
	Other	0.05	0.05		0.02	0.06		
II group	Macrozoobenthos	0.95	0.95					
	Other	0.05	0.05					
	Literature	Kühl & Kuipers 1978	Kühl & Kuipers 1978	Kühl & Kuipers 1978	Kühl & Kuipers 1978	Kühl & Kuipers 1978	Baeta et al. 2006	del Norte-Campos & Temming 1994

Table 3: Annual food requirement [g AFDM m^{-2} y^{-1}] by epibenthos at the Balgzand intertidal over the period 1975-2014. Empty cells indicate that the species was not counted in these years, in bold years all analysed species have been sampled over a sufficient period.

Year	*Pleuronectes platessa*			*Platichthys flesus*			*Solea solea*		*Pomatoschistus microps*		*Pomatoschistus minutus*		*Carcinus maenas*	*Crangon crangon*	Total
	0-group	I-group	II-group	0-group	I-group	II-group	0-group	I-group	0-group	I-group	0-group	I-group	All ages	All ages	
1975	0.907	1.498	2.655				0.071	0.000	0.321	0.066	0.377	0.012			
1976	**0.924**	**2.907**	**0.580**	**0.094**	**0.874**	**1.445**	**0.027**	**0.000**	**0.345**	**0.057**	**0.519**	**0.017**	**0.311**	**12.921**	**21.02**
1977	1.129	4.182	1.226										0.311	7.611	
1978	1.848	2.777	1.804										0.868	18.174	
1979	2.259			0.096			0.047	0.000					0.548	22.662	
1980	**0.464**	**9.177**	**8.493**	**0.015**	**0.171**	**0.524**	**0.023**	**0.154**	**0.111**	**0.070**	**0.089**	**0.007**	**0.475**	**21.521**	**41.29**
1981	**0.631**	**5.249**	**3.721**	**0.043**	**0.076**	**0.931**	**0.007**	**0.000**	**0.072**	**0.039**	**0.008**	**0.001**	**0.316**	**20.345**	**31.44**
1982	1.091	0.000	0.000	0.016	0.004	0.000	0.014	0.055							
1986	**1.035**	**1.109**	**0.163**	**0.001**	**0.099**	**0.590**	**0.006**	**0.000**	**0.087**	**0.050**	**0.000**	**0.000**	**0.133**	**16.554**	**19.83**
1993	**0.283**	**0.100**	**0.027**	**0.030**	**0.090**	**0.975**	**0.009**	**0.000**	**0.895**	**0.023**	**0.214**	**0.023**	**0.633**	**33.798**	**37.10**
1994	0.411	0.034	0.000	0.065	0.053	0.001	0.026	0.000							
1995	0.347	0.042	0.017	0.082	0.112	0.010	0.041	0.000							
1996	**0.374**	**0.042**	**0.000**	**0.031**	**0.197**	**0.062**	**0.009**	**0.000**	**0.733**	**0.038**	**0.224**	**0.008**	**0.584**	**26.711**	**29.01**
1997	**0.302**	**0.047**	**0.000**	**0.003**	**0.030**	**0.021**	**0.002**	**0.003**	**0.297**	**0.043**	**0.925**	**0.009**	**0.886**	**20.511**	**23.08**
1998	0.178	0.037	0.002	0.011	0.010	0.100	0.001	0.000							
1999	0.220	0.002	0.000	0.020	0.012	0.003			0.000	0.013	0.000	0.014	0.274	4.324	
2000	**0.402**	**0.004**	**0.001**	**0.010**	**0.042**	**0.126**	**0.010**	**0.000**	**0.569**	**0.031**	**0.669**	**0.035**	**0.683**	**25.003**	**27.59**
2001	**0.477**	**0.004**	**0.000**	**0.108**	**0.014**	**0.012**	**0.002**	**0.000**	**0.000**	**0.027**	**0.001**	**0.020**	**1.096**	**11.473**	**13.23**
2002	0.284	0.038	0.000	0.009	0.027	0.016	0.007	0.015	0.000	0.020	0.000	0.015	0.325	11.474	
2007	**0.149**	**0.008**	**0.000**	**0.039**	**0.003**	**0.028**	**0.049**	**0.035**	**0.470**	**0.008**	**0.116**	**0.052**	**0.912**	**39.463**	**41.33**
2009	**0.149**	**0.006**	**0.000**	**0.048**	**0.042**	**0.062**	**0.006**	**0.001**	**0.974**	**0.017**	**0.624**	**0.031**	**2.250**	**32.270**	**36.48**
2014	**0.324**	**0.000**	**0.000**	**0.039**	**0.014**	**0.001**	**0.007**	**0.000**	**0.970**	**0.047**	**1.338**	**0.102**	**2.282**	**34.380**	**39.50**
Average	0.64	1.30	0.89	0.04	0.10	0.27	0.02	0.01	0.39	0.04	0.34	0.02	0.76	21.13	30.08
sd	0.54	2.33	1.97	0.03	0.19	0.42	0.02	0.04	0.35	0.02	0.39	0.02	0.61	9.69	8.95

Table 4: Total food requirement (g AFDM m^{-2} y^{-1}) around the 1970s as derived from previous findings (Kuipers & Dapper 1981; original references in Kuipers et al. 1981) and in this paper of main epibenthic predators on the Balgzand tidal flats.

	Previous	Years	Sources	This study	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
Sum	15.6			23.1	

FIGURES

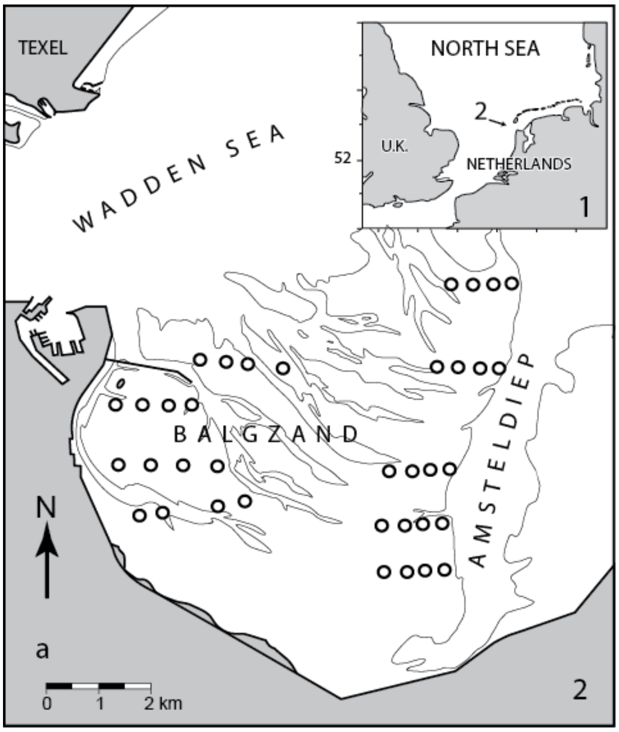


Figure 1: The Balgzand intertidal in the western Dutch Wadden Sea. Sampling of epibenthic species was based on 9 transects, each consisting of 4 hauls (open circles). Thin lines indicate the low-tide mark, thick lines the high-tide mark.

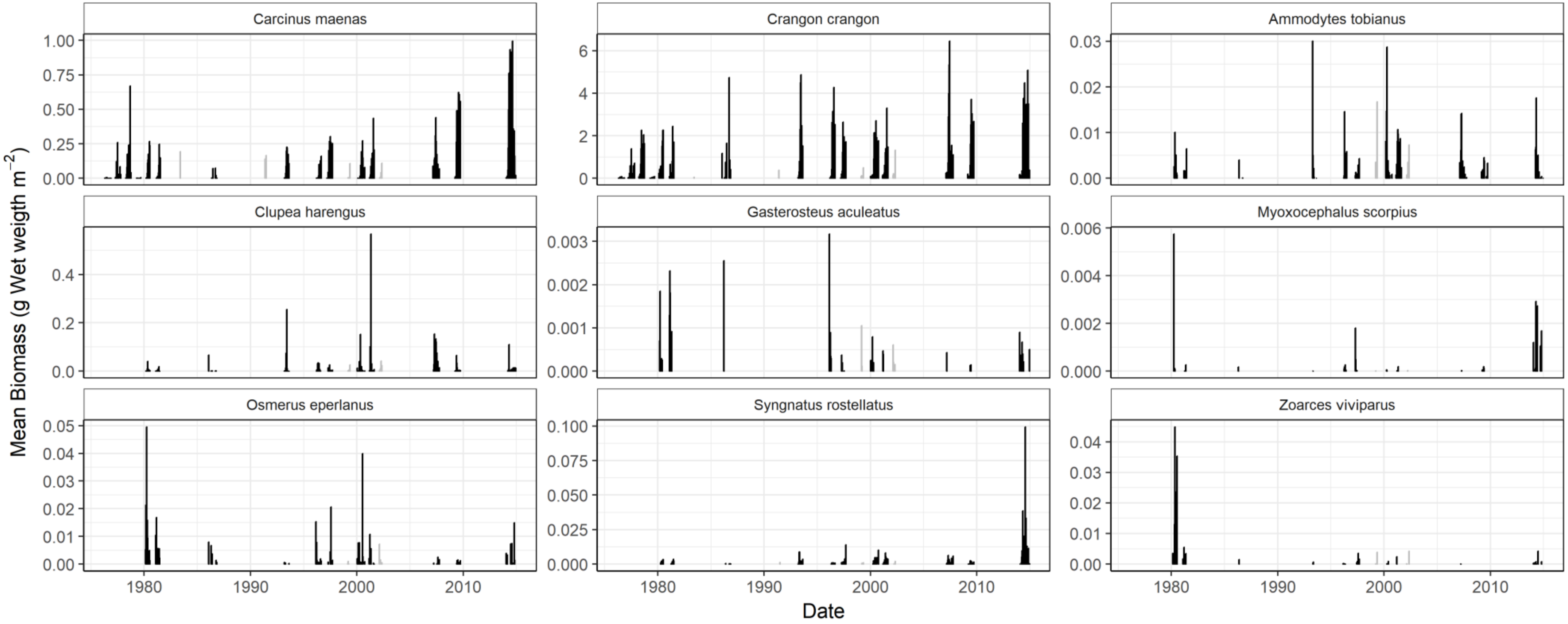
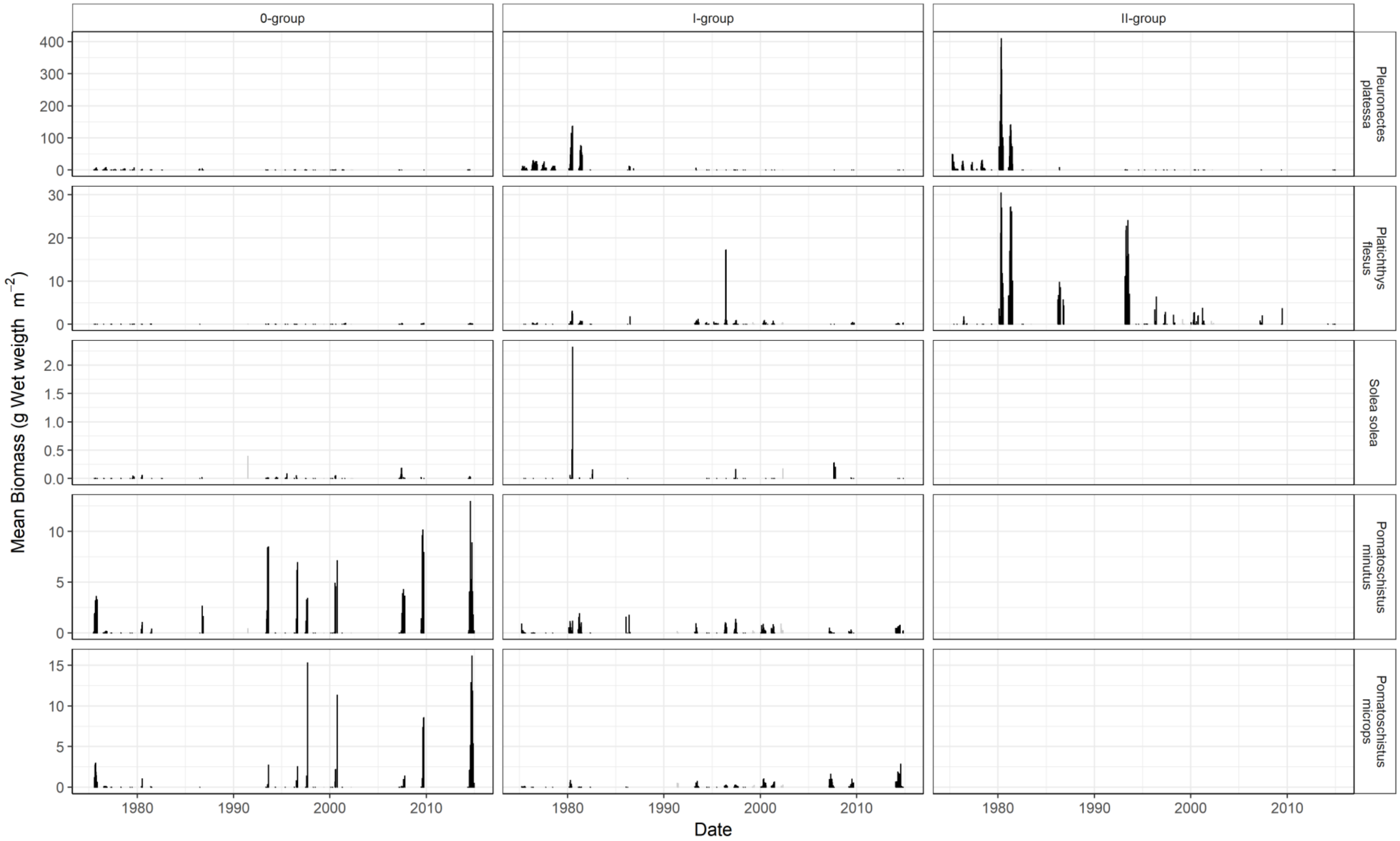


Figure 2: Biomass (gWW m^{-2}) of crustaceans and fish species caught for which no age distinction was present as caught during the epibenthic surveys at the Balgzand intertidal flats between 1975 and 2014. Grey lines indicate years with less than 4 sample events.



Figu

Figure 3: Biomass (gWW m^{-2}) of age classes of various flatfish and gobies species as caught during the epibenthic surveys at the Balgzand intertidal flats between 1975 and 2014. Grey lines indicate years with less than 4 sample events.

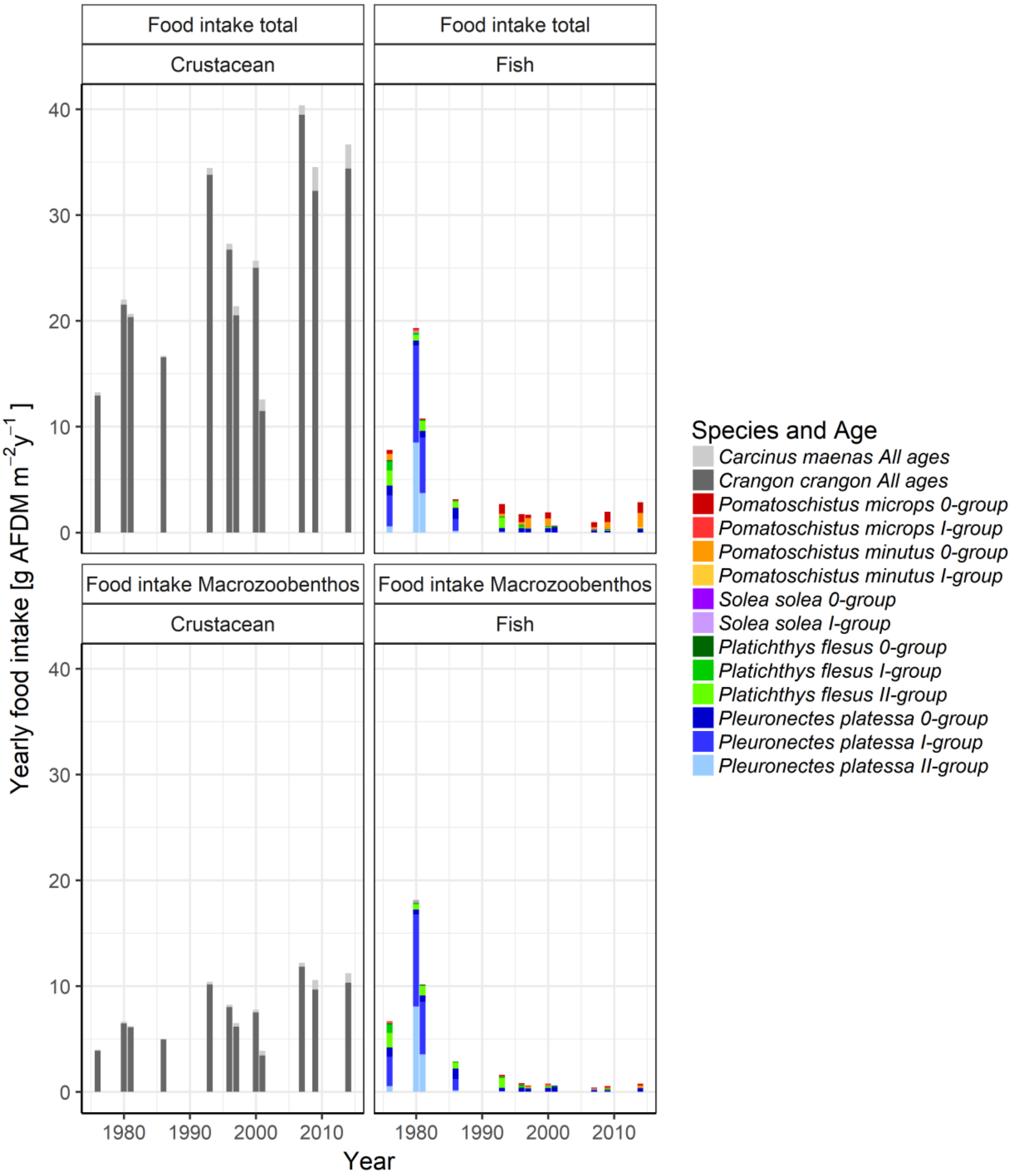


Figure 4: Annual food requirement (g AFDM m^{-2} y^{-1}) of all prey (top panels) and macrozoobenthic prey only (bottom panels) by crustaceans (left panels) and fish (right panels) at the Balgzand intertidal flats during the growing season (March-October) between 1975 and 2014 for those years when sufficient data were available.

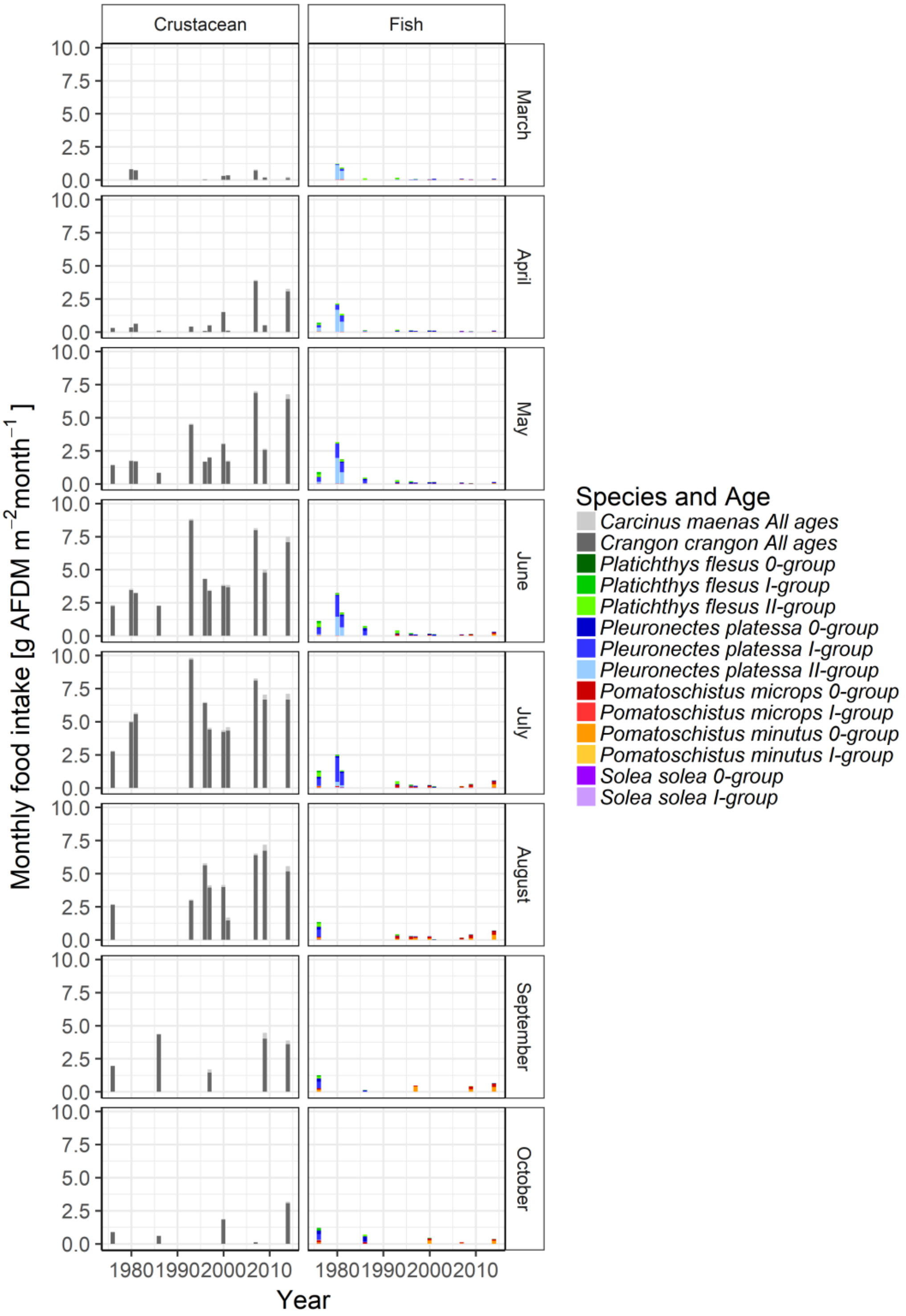


Figure 5: Monthly food requirement (g AFDM m^{-2} y^{-1}) of all prey by crustaceans (left panels) and fish (right panels) at the Balgzand intertidal flats during each month of the growing season (March-October) between 1975 and 2014 for those years when sufficient data were available.

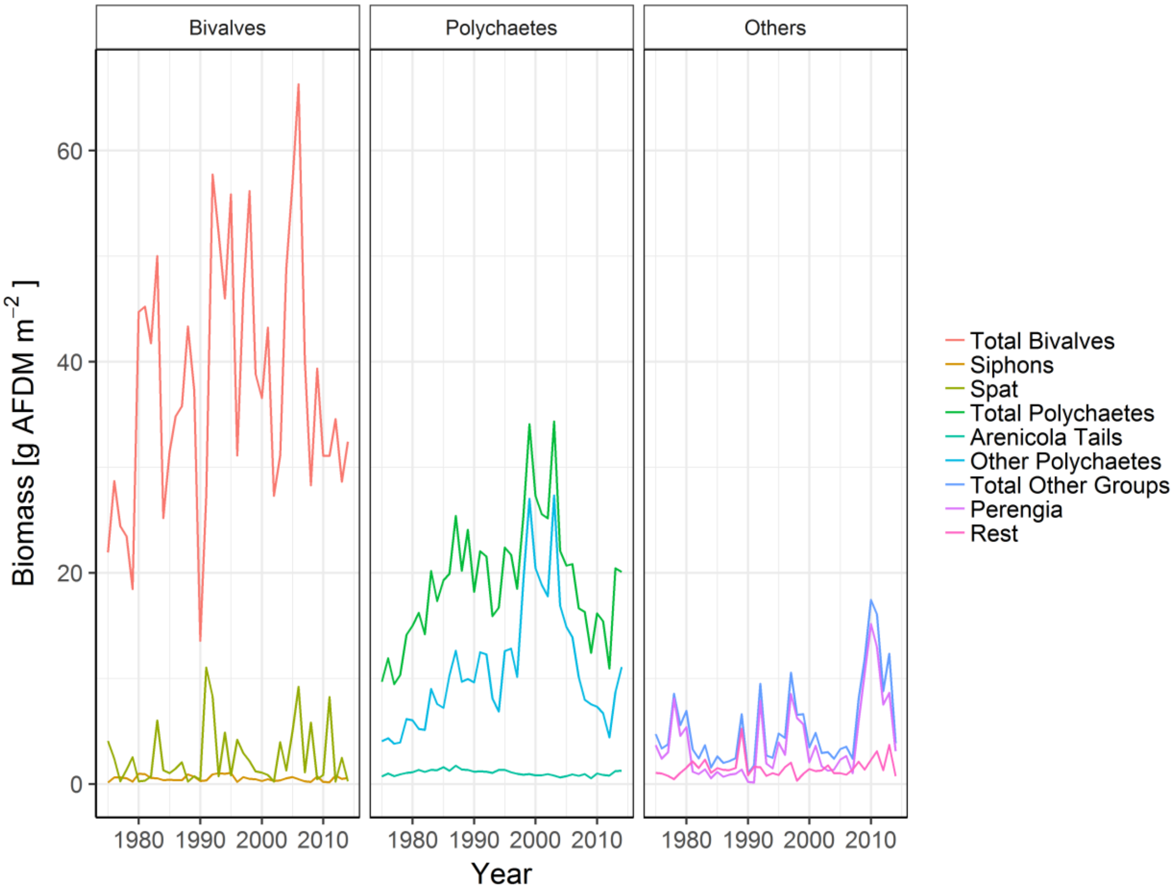


Figure 6: Biomass (g AFDM m^{-2}) of macrozoobenthos divided into bivalves (left) and polychaetes (mid) and other groups (right) at the Balgzand between 1975 and 2014, red and turquois and blue represent total biomass in bivalves, polychaetes, and others, respectively. The other colours represent biomass of potential food items as part of the total biomass.

APPENDIX

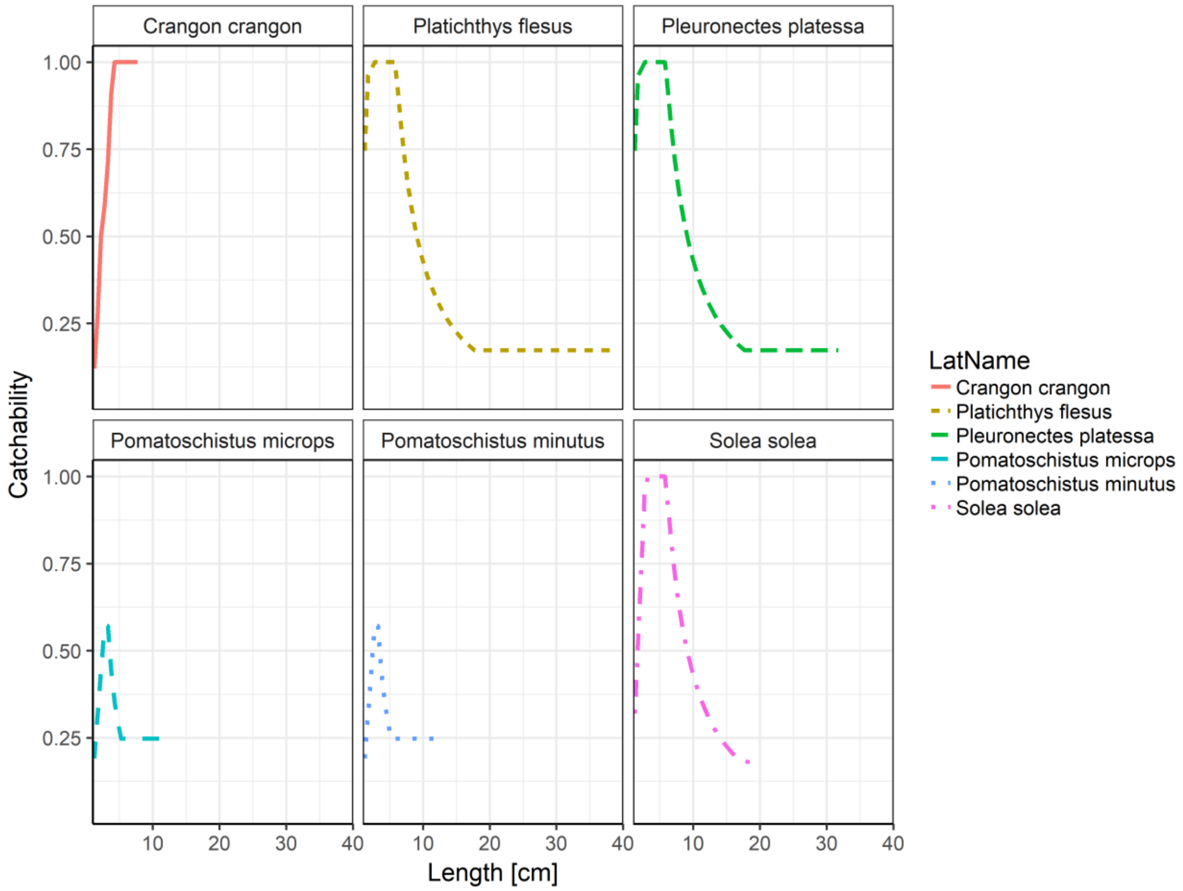


Figure A1: Net efficiency for different species and animal length taken from several references (*Pleuronectes platessa* Kuipers, 1975; *Platichthys flesus*: van der Veer et al., 1991; *Solea solea*: van der Veer et al. 2001; *Crangon crangon*: van Lissa 1977; *Pomatoschistus microps* and *P. minutus*: van Beek, 1976)

Table A1: Specific species coefficients a and b of the length (L; cm) wet mass (W; g) relationships W = $(a*L)^b$ afterLeopold et al. (2001)

Species	a	b
Clupea harengus	0.18	3.11
Osmerus eperlanus	0.17	3.40
Syngnatus rostellatus	0.07	3.99
Ammodytes tobianus	0.13	3.46
Zoarces viviparus	0.16	3.34
Pomatoschistus minutus	0.21	2.83
Myoxocephalus scorpius	0.23	3.19
Gasterosteus aculeatus	0.20	3.21
Pleuronectes platessa	0.22	3.02
Platichthys flesus	0.22	3.00
Solea solea	0.20	3.05
Pomatoschistus microps	0.22	3.27
Carcinus maenas	0.38	2.81
Crangon crangon	0.17	3.18

Table A2: List of all sampling dates, years separated by thick border.

Cruiseid	Date
197501	02.04.1975
197502	17.04.1975
197503	02.05.1975
197504	15.05.1975
197505	29.05.1975
197506	14.06.1975
197507	01.07.1975
197508	11.07.1975
197509	29.07.1975
197510	12.08.1975
197511	28.08.1975
197512	08.09.1975
197513	11.09.1975
197514	24.09.1975
197515	08.10.1975
197516	24.10.1975
197517	07.11.1975
197601	03.04.1976
197602	05.05.1976
197603	19.05.1976
197604	02.06.1976
197605	16.06.1976
197606	01.07.1976
197607	02.08.1976
197608	08.09.1976
197609	13.10.1976
197610	10.11.1976
197701	29.03.1977
197702	05.05.1977
197703	02.06.1977
197704	04.07.1977
197705	01.08.1977
197706	20.09.1977
197707	20.10.1977
197801	30.03.1978
197802	13.04.1978
197803	25.04.1978
197804	10.05.1978
197805	29.05.1978
197806	07.06.1978
197807	27.06.1978
197808	26.07.1978
197809	04.09.1978
197810	02.10.1978
197901	02.04.1979
197902	18.04.1979
197903	01.05.1979
197904	14.05.1979
197905	29.05.1979
197906	12.06.1979
197907	25.07.1979
197908	10.09.1979
198001	19.02.1980
198002	06.03.1980
198003	24.03.1980
198004	10.04.1980
198005	21.04.1980
198006	06.05.1980
198007	19.05.1980
198008	01.06.1980
198009	13.06.1980
198010	02.07.1980
198011	14.07.1980
198101	09.02.1981
198102	24.02.1981
198103	09.03.1981
198104	23.03.1981
198105	07.04.1981
198106	21.04.1981
198107	06.05.1981
198108	18.05.1981
198109	03.06.1981
198110	19.06.1981
198111	08.07.1981
198201	20.03.1982
198202	06.04.1982
198203	14.04.1982
198204	28.04.1982
198205	10.05.1982
198206	24.05.1982
198207	08.06.1982
198208	21.06.1982
198209	06.07.1982
198210	21.07.1982
198211	09.08.1982
198301	31.05.1983
198601	21.01.1986
198602	19.03.1986
198603	17.04.1986
198604	22.05.1986
198605	25.06.1986
198606	18.09.1986
198607	09.10.1986
198608	05.11.1986
199101	21.05.1991
199102	25.06.1991
199301	15.03.1993
199302	14.04.1993
199303	27.04.1993
199304	10.05.1993
199305	25.05.1993
199306	08.06.1993
199307	21.06.1993
199308	19.07.1993
199309	18.08.1993
199401	15.03.1994
199402	30.04.1994
199403	18.04.1994
199404	02.05.1994
199405	17.05.1994
199406	31.05.1994
199407	13.06.1994
199408	27.06.1994
199409	25.07.1994
199410	22.08.1994
199501	07.03.1995
199502	21.03.1995
199503	03.04.1995
199504	19.04.1995
199505	02.05.1995
199506	16.05.1995
199507	31.05.1995
199508	15.06.1995
199509	29.06.1995
199510	13.07.1995
199511	14.08.1995
199601	28.02.1996
199602	27.03.1996
199603	09.04.1996

Cruiseid	Date
199604	22.04.1996
199605	06.05.1996
199606	20.05.1996
199607	03.06.1996
199608	17.06.1996
199609	04.07.1996
199610	31.07.1996
199611	28.08.1996
199701	27.02.1997
199702	10.03.1997
199703	26.03.1997
199704	08.04.1997
199705	22.04.1997
199706	13.05.1997
199707	26.05.1997
199708	09.06.1997
199709	24.06.1997
199710	07.07.1997
199711	04.08.1997
199712	11.09.1997
199801	17.03.1998
199802	01.04.1998
199803	17.04.1998
199804	29.04.1998
199805	12.05.1998
199806	26.05.1998
199807	11.06.1998
199808	25.06.1998
199809	16.07.1998
199810	28.07.1998
199811	11.08.1998
199901	25.02.1999
199902	08.03.1999
199903	24.03.1999
199904	19.04.1999
199905	03.05.1999
199906	10.05.1999
200001	13.01.2000
200002	14.02.2000
200003	24.02.2000
200004	13.03.2000
200005	04.04.2000
200006	18.04.2000
200007	02.05.2000
200008	14.05.2000
200009	06.06.2000
200010	19.06.2000
200011	17.07.2000
200012	02.08.2000
200013	03.10.2000
200101	26.02.2001
200102	12.03.2001
200103	26.03.2001
200104	10.04.2001
200105	24.04.2001
200106	07.05.2001
200107	28.05.2001
200108	13.06.2001
200109	20.07.2001
200110	21.08.2001
200201	18.02.2002
200202	04.03.2002
200203	20.03.2002
200204	02.04.2002
200205	17.04.2002
200206	09.05.2002
200701	19.02.2007
200702	07.03.2007
200703	26.03.2007
200704	10.04.2007
200705	23.04.2007
200706	07.05.2007
200707	22.05.2007
200708	04.06.2007
200709	19.06.2007
200710	19.07.2007
200711	23.08.2007
200712	11.10.2007
200901	03.03.2009
200902	31.03.2009
200903	15.04.2009
200904	19.05.2009
200905	02.06.2009
200906	15.06.2009
200907	29.06.2009
200908	27.07.2009
200909	25.08.2009
200910	23.09.2009
201401	21.01.2014
201402	24.02.2014
201403	21.03.2014
201404	03.04.2014
201405	14.04.2014
201406	01.05.2014
201407	02.06.2014
201408	30.06.2014
201409	28.07.2014
201410	25.08.2014
201411	23.09.2014
201412	21.10.2014
201413	10.11.2014
201414	15.12.2014