



Long-term trends in juvenile flatfish indicate a dramatic reduction in nursery function of the Balgzand intertidal, Dutch Wadden Sea

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ABSTRACT: Since 1975, juvenile flatfish (plaice and flounder) populations have been monitored at the Balgzand intertidal and, based on this data series (1975–2007), the interannual patterns in predation pressure were quantified. Temporal patterns in abundance have changed greatly, especially for plaice. Up to the early 1980s, 3 year classes (0-, I- and II-group) were present and growing up in the area, but from the late 1980s onwards, densities of the I- and II-group plaice dropped from a few hundred individuals per 1000 m² to levels close to zero. It appears that the Balgzand intertidal has lost its nursery function for I- and II-group plaice, although feeding conditions have remained the same or even slightly increased since the late 1970s. The absence of I- and II-group flatfish in the intertidal cannot be explained at present; however, processes operating offshore are most likely involved. As a consequence, the annual predation pressure by juvenile flatfish upon the intertidal macrozoobenthos dropped by 94 %, declining from an average of approximately 5 to 0.25 g ash free dry mass m⁻². Such a decline in top-down predation may not only have directly influenced the macrozoobenthic community, but may also have indirectly affected food availability and accessibility for other top predators (e.g. shorebirds).

KEY WORDS: Predation · Plaice · Flounder · *Pleuronectes platessa* · *Platichthys flesus* · Wadden Sea · Benthos–fish interaction · Top-down control · Nursery function

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INTRODUCTION

Intertidal benthic systems are often subject to strong fluctuations in abiotic conditions because of the combination of seasonal and daily variability in salinity and temperature between emersion and submersion. As a consequence, species richness of the macrobenthic infauna in these systems is relatively low; however, those species present often occur in high densities and biomasses (for overview, see Goodall 1983), attracting large numbers of predators. Predation in the intertidal occurs almost continuously, alternating between mobile

epibenthic species during immersion and wading birds during exposure of the flats. Predator–prey interactions in intertidal systems are complex (Freitas et al. 2008). Among the infauna, some polychaete worms are dominant opportunistic consumers, preying on other worms and crustaceans (Meire et al. 1994). Wading birds prey on a wide range of benthic organisms, especially bivalves and polychaetes, and thus their food supply is restricted by aspects such as accessibility (depth), digestibility (size) and profitability (energy content) (Zwarts et al. 1992). The most abundant mobile epibenthic species include opportunistic feed-

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ers such as crustaceans (the shore crab *Carcinus maenas* and the brown shrimp *Crangon crangon*) and various gobies and juvenile flatfish species.

The top-down effects of predation on the macrozoobenthic community are not clear. In general, macrozoobenthic biomass in temperate estuaries appears to be controlled bottom-up by primary production (Herman et al. 1999). However, top-down effects of predators can strongly influence species composition. For example, predation by *Carcinus maenas* can significantly reduce the numbers of the polychaete worm *Manayunkia aestuarina* on mudflats (McLusky 1989), and crustaceans can reduce the population of the amphipod *Corophium volutator* by over 50% (Pihl 1985). In terms of energy flow, gobies and crustaceans represent by far the highest predation pressure; apart from infauna, this also includes predation on other epibenthic species and substantial cannibalism on egg and juvenile stages. Predation by juvenile flatfish is linked more closely with macrozoobenthic prey items, with sole *Solea solea* feeding almost exclusively on polychaetes, and plaice *Pleuronectes platessa* and flounder *Platichthys flesus* feeding also on juvenile bivalve spat (Kuipers 1977, De Vlas 1979a, Summers 1980, Amara et al. 2001, Rijnsdorp & Vingerhoed 2001). Juvenile flatfish feed not only on whole prey items but also, to a large extent, on regenerating body parts such as the siphon tips of bivalves and the tail tips of lugworms (Kuipers 1977, Ansell et al. 1999). This may directly or indirectly influence the survival of their prey; predation on tail tips of lugworms affects and reduces longevity (Bergman et al. 1988) and predation on siphon tips forces bivalves to reduce burying depth, thereby increasing the risk of being eaten by probing predators such as shorebirds (De Goeij et al. 2001).

In the Balgzand area, a large intertidal ecosystem in the western Dutch Wadden Sea, juvenile plaice and flounder are the most abundant flatfish species, with dab *Limanda limanda* and sole occurring only incidentally (Bolle et al. 1994, van der Veer et al. 2001). Predation on macrozoobenthos by juvenile plaice and flounder was estimated to be approximately 6 g ash-free dry mass (AFDM) m⁻² (De Vlas 1979a), corresponding to one-third of the total predation pressure (Kuipers et al. 1981). Such predation might significantly affect macrozoobenthic species composition and abundance. These calculations were done a few decades ago in the late 1970s by Kuipers (1977) and De Vlas (1979a) but, since then, significant changes for the Wadden Sea area have been recorded. Regime shifts at multi-trophic levels have been described for 1979 and 1988 and perhaps also for 1998 (Weijerman et al. 2005). For plaice, an offshore shift in the distribution of juveniles to deeper waters in the 1990s (van Keecken et al. 2007) and a decrease of densities of II- and I-group plaice in

the deeper subtidal parts of the Dutch Wadden Sea (Tulp et al. 2008) has taken place. However, it is currently unknown to what extent this also applies to the intertidal area and how it affects predation pressure on the macrozoobenthos community.

The present study relies on 2 data sets in the western Dutch Wadden Sea: the NIOZ fyke net programme, during which daily catches of fish fauna were registered from 1960 onwards, and the NIOZ Balgzand high-water programme, carried out between 1975 and 2007, which quantitatively monitored the seasonal patterns in intertidal mobile epibenthic fauna. These long-term time series allow us to follow the temporal patterns in abundance and predation pressure by juvenile plaice and flounder on the Balgzand intertidal macrobenthos. In combination with information from stomach contents and prey abundance (intertidal macrozoobenthos), these data sets provide a basis for: (1) quantifying changes in the abundance and predation pressure of juvenile plaice and flounder over time; and (2) determining whether possible top-down effects of predation by juvenile plaice and flounder still affect the Balgzand macrozoobenthic community.

MATERIALS AND METHODS

Flatfish sampling. The temporal patterns in juvenile plaice and flounder abundance in the western Wadden Sea were analysed from the NIOZ fyke net programme. Trends in annual predation pressure on intertidal macrobenthos was determined for a large (50 km²) intertidal area in the western Wadden Sea from the NIOZ Balgzand high-water programme.

NIOZ fyke net programme: Passive fishing was set up near the southern part of Texel, de Hors, at the entrance of the Dutch Wadden Sea (Fig. 1). Fishing was done with a passive trap, known as a 'kom-fyke' (Nédélec 1982), which consists of a pound net and a fyke supported by wooden poles and with a leader of 200 m running from above the high water mark into the subtidal. At the end, 2 chambers catch and retain fish and other species (see Fig. 1 in van der Veer et al. 1992). The stretched mesh size of the leader and the 2 chambers is 20 mm. The semidiurnal lunar tide is the dominant component and tidal range varies between 1 and 2 m depending on conditions (neap versus spring tide, day versus night, wind stress and direction). Normally, tidal current velocity in the fishing area does not exceed 1 m s⁻¹, except for periods with strong wind stress. Fishing with the kom-fyke started in 1960 and has been run ever since in spring (April–June) and autumn (September–October). Usually, the kom-fyke is emptied every morning from Monday to Friday irrespective of tidal phase, except on occasions of bad



Fig. 1. The Balgzand intertidal in the western Dutch Wadden Sea. Location of NIOZ fyke net near the southern tip of Texel is indicated (■). Flatfish sampling was based on 9 transects, each consisting of 4 hauls (open circles). Thin lines indicate the low water mark, thick lines the high water mark

weather conditions. When catches are low, the net is emptied every other morning.

For the present study, catches from 1975–2009 were analysed. All catches were sorted immediately down to species level and individuals were measured to the nearest cm in total length. Age estimation of juvenile plaice and flounder was based on size. In case of doubt, individual age was verified by means of otolith reading. The mean number of individuals caught in autumn catches was taken as an index for the different age classes in the Wadden Sea and represents a mixture of the intertidal and subtidal flatfish populations present in the western Wadden Sea.

NIOZ Balgzand high-water programme: Over the period 1975 to 2007, the Balgzand intertidal was sampled at frequent intervals (2 to 4 wk) from February until (in most years) October during the daytime. During most surveys, all 36 fixed stations distributed over Balgzand (Fig. 1) were sampled within a 3 h period around high tide, during which the flatfish population is randomly distributed over the area (Kuipers 1977). Fishing was done from a rubber dinghy with a 25 HP outboard motor at a speed of approximately 35 m min^{-1} (Riley & Corlett 1966) using a 1.9 m beam trawl with 1 tickler chain and a net mesh size of $5 \times 5 \text{ mm}$. Water tempera-

ture was measured during each survey. The start positions of the hauls were indicated by wooden poles at the beginning of each transect, and determined by GPS in more recent years. The length of each haul was assessed with a meter wheel fitted to the trawl.

Catches were stored in 4% formaline (until 1990) or deep-frozen (from 1991 onwards) and all species were sorted within a few days. All juvenile plaice and flounder were measured and divided into 0.5 cm total length classes, except in 1979 and 1982 when only 0-group juveniles were analysed. The number of plaice caught was corrected for size-selective mesh (Dapper 1978) and catch efficiency (Kuipers 1975) and converted into individuals per 1000 m^2 (ind. $[10^3 \text{ m}^2]^{-1}$). For flounder, similar efficiencies as for plaice were assumed. Subsequently, catches were split into age classes according to length. In case of doubt, individual age was verified by means of otolith reading. The arithmetic mean of all stations sampled during a survey was calculated and considered to reflect the total mean density at Balgzand (cf. Zijlstra et al. 1982, van der Veer 1986, van der Veer & Witte 1999).

Estimation of predation pressure. Daily food intake was estimated for each survey for 0-, I- and II-group plaice and flounder separately, based on specific energy requirements following De Vlas (1979a) with some slight modifications. Energy requirements consisted of 2 components: (1) contribution for metabolism (daily maintenance) and (2) contribution for observed growth. Energy required for locomotion and other expenditures was considered to be negligible in juvenile plaice and flounder and was assumed to be included in the estimate of metabolism (cf. De Vlas 1979a).

Daily maintenance requirements (DMR): The DMR estimation was based on the relationships of daily maintenance with metabolic fish mass ($W^{0.8}$) and temperature (Fonds et al. 1992). Fish mass for both plaice and flounder was determined using known species-specific length–mass relationships (Fonds et al. 1992):

$$W = 0.010503L^3 \quad (1)$$

where L is total length in cm and W is wet mass in g. The wet mass (W_i) was estimated for each 0.5 cm length-based size class (L_i) taking the mean length of the size class. Next, W_i was converted into metabolic mass ($W_i^{0.8}$) and multiplied by the number of individuals of each size class (n_i) found per m^2 . Subsequently, the sum of $W_i^{0.8}$ for all size classes was calculated to obtain the total metabolic wet mass of the population per m^2 ($\sum n_i W_i^{0.8}$). Finally, the daily food intake per m^2 needed to meet daily maintenance requirements (DMR; $\text{g AFDW m}^{-2} \text{ d}^{-1}$) was calculated according to the same formula as applied by De Vlas (1979a):

$$\text{DMR} = 0.17 \times 2^{0.1T} \times 0.02 \sum_i (n_i W_i^{0.8}) \quad (2)$$

where T is temperature in °C, 2 is the Q_{10} (the increase in rate with a temperature increase of 10°C), 0.02 is the maintenance coefficient ($WW^{-0.8} \text{ d}^{-1}$) and 0.17 is the conversion factor from wet mass to ash-free dry mass (De Vlas 1979a). The maintenance requirements of the plaice and flounder populations were estimated for each sampling day separately. This procedure was identical to the method used by De Vlas (1979a).

Daily growth requirements (DGR): The daily food intake required to accommodate for the observed growth was estimated as follows. First, for the different age groups of both plaice and flounder, the survey-specific arithmetic mean length of all stations was estimated (see Zijlstra et al. 1982, van der Veer 1986). Next, Eq. (1) was applied to convert mean length per survey j into mean wet mass per cruise (W_j). The estimates of mean wet mass were used to determine the instantaneous growth rate (G ; d^{-1}) between 2 successive cruises as:

$$G_{j \rightarrow j+1} = \frac{\ln W_{j+1} - \ln W_j}{t} \quad (3)$$

where W_j and W_{j+1} are the mean wet mass at cruise j and the subsequent cruise $j+1$, respectively, and t is the time difference in days between the 2 cruises. G was considered to represent the growth rate at the midpoint between 2 successive cruises. The various estimates of G over time allowed fitting an exponential curve of G as a function of time for each age group of both species. For 0-group fish, this relationship was determined for each year separately; for I- and II-group fish, all years were pooled together because of a lack of reliable estimates in some years. Based on these relationships, an estimate of G at the various sampling dates was obtained for each age group of both species. The estimate of G on sampling date j 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 (ΔW_j). Daily population growth (DPG ; g wet mass d^{-1}) on sampling date j was calculated as the sum for all size classes i of the product of daily growth multiplied by the number of individuals per m^2 (n_i):

$$DPG_j = \sum_{\text{all } i} n_i \Delta W_j \quad (4)$$

The amount of food needed for growth was calculated as 2 times the increase in wet mass (De Vlas 1979a) and therefore total population growth was multiplied by this net efficiency factor ($\times 2$), and by 0.17 (conversion to AFDM, see De Vlas 1979a), resulting in an estimate of daily growth requirements per m^2 on sampling date j (DGR_j ; $\text{g AFDM m}^{-2} \text{ d}^{-1}$):

$$DGR_j = 0.17 \sum_{\text{all } i} 2n_i \Delta W_j \quad (5)$$

Total food intake: Daily food intake on sampling date j (DFI_j ; $\text{g AFDM m}^{-2} \text{ d}^{-1}$) of the 0-, I- and II-group plaice and flounder populations was calculated as the sum of daily maintenance requirements (DMR_j) and daily growth requirements (DGR_j) of each age group:

$$DFI_j = DMR_j + DGR_j \quad (6)$$

Next, for 0-, I- and II-groups, total annual food intake was determined by first fitting a polynomial through the DFI , and solving the function by integration over the growing season (March–October).

Macrozoobenthic prey items. Since 1975, the Balgzand macrozoobenthos community has been consistently monitored quantitatively at 12 fixed transects of 1 km each distributed over the area, twice a year in late winter (mostly March) and late summer (mostly August). Details of sampling sites and methods can be found in earlier publications (e.g. Beukema & Cadée 1997). In short, along each transect, cores to a depth of approximately 30 cm were taken at equal intervals (20 m), covering a total of 0.45 m^2 in summer or 0.9 m^2 in winter. All cores were sifted over a 1 mm sieve in the field and all macrozoobenthos retained were collected and sorted down to species level in the laboratory within a few days. For each species, numbers were counted, and the AFDM was determined by first drying for 2 to 3 d at 60°C in a ventilated stove, weighing and incinerating for 2 h at 520°C. The weight loss after incineration was considered to represent AFDM. Bivalve species were split up in age groups based on external rings before AFDM was determined. For each transect, mean densities and biomass were estimated and the mean of all 12 transects was calculated. Only data for late summer were used in this paper.

Identification of potential prey items for juvenile flatfish was based on stomach content analyses performed in 1976 and 1977 by De Vlas (1979a), combined with unpublished data from 2 other periods, 1986 and 2008 to 2010, to verify whether shifts in diet had occurred over time, in particular, related to increasing abundances of invasive macrobenthic species.

RESULTS

Flatfish abundance

The NIOZ fyke net catches showed that, from approximately 1980 onwards, I- and II-group plaice densities started to decrease, and within 10 yr they had reached zero. Young-of-the-year plaice (0-group) were present during the whole period, but numbers also decreased from the mid-1980s onwards, and stabilized at low numbers from 2000 onwards (Fig. 2a). For flounder, the differences between age classes were less

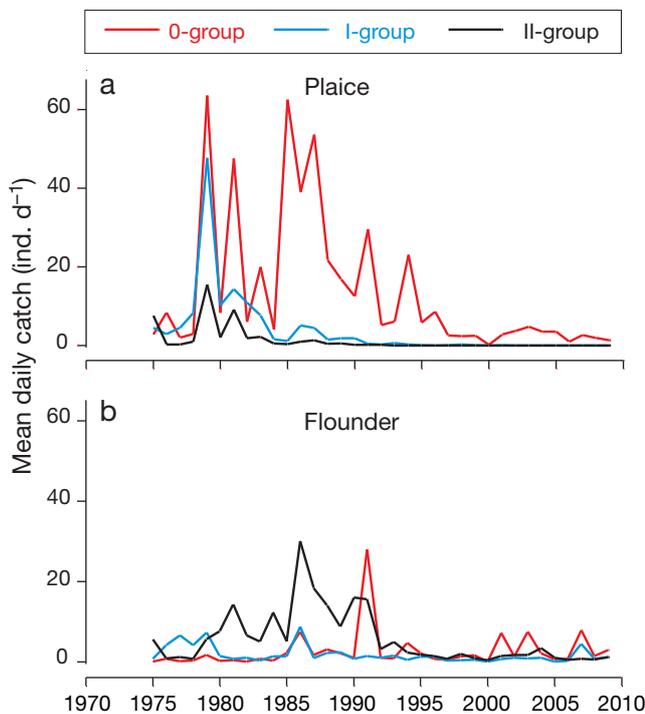


Fig. 2. *Pleuronectes platessa* and *Platichthys flesus*. Mean daily catch of the NIOZ fyke net in the western Dutch Wadden Sea in autumn for (a) juvenile plaice and (b) juvenile flounder

clear (Fig. 2b). Densities were on average lower than those of plaice and approached zero during a period in the late 1990s. In recent years, densities have increased, but they are still lower than in the past.

The abundance of juvenile plaice and flounder at the Balgzand intertidal during high water roughly showed a similar pattern over time as the fyke net catches (Fig. 3). 0-group plaice and flounder were present during all years of fishing; however, from the late 1980s onwards, no I- or II-group plaice were found in the area. I- and II-group flounder were still present, but in very low numbers. The seasonal pattern over time also changed, especially in plaice. In the 1970s, juvenile plaice were present from early spring until the end of October; however, from the mid-1980s, 0-group plaice (the only remaining age group) had already disappeared from the intertidal in July–August (data not shown). Overall, densities of flounder were approximately a factor of 10 lower than those of plaice.

Predation pressure

Total annual food intake was estimated in all years of sampling except for 1983, 1991, 1999 and 2002, when there were less than 3 cruises (1983 and 1991) or when cruises were only executed in the first part of the sea-

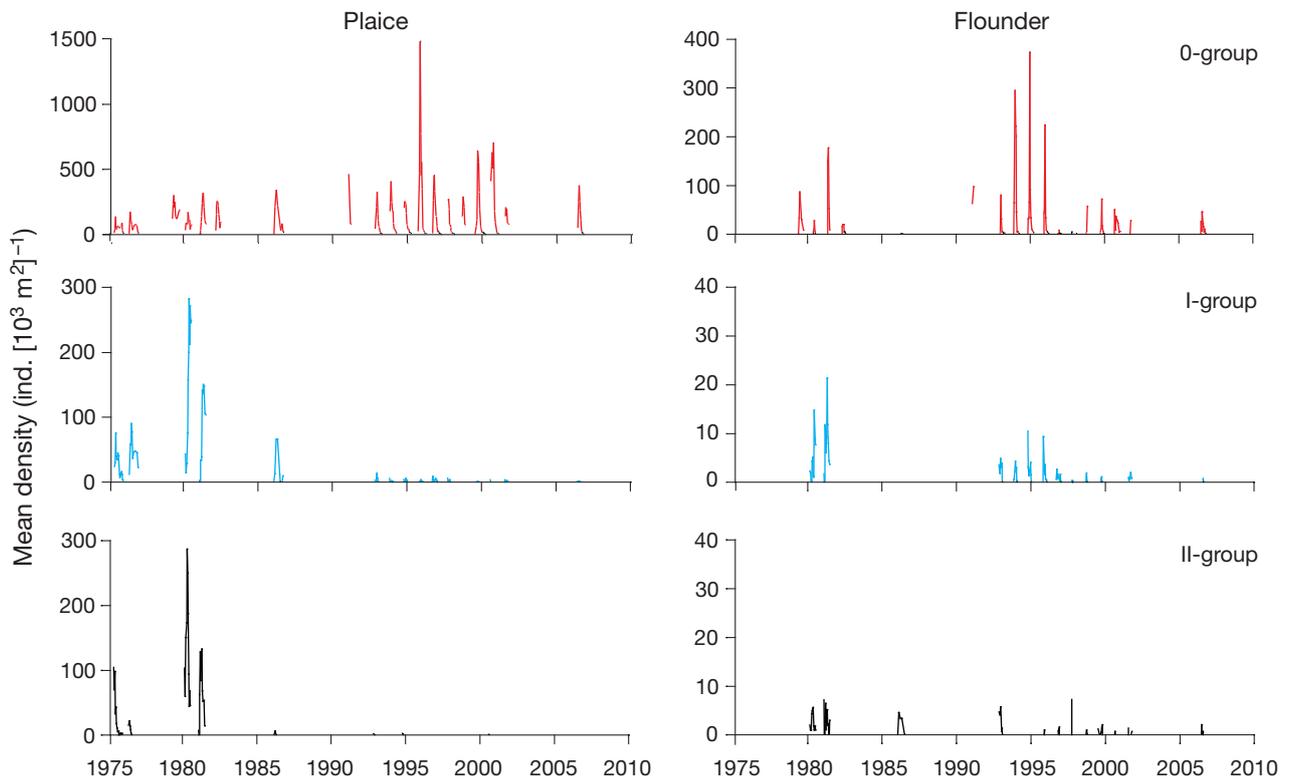


Fig. 3. *Pleuronectes platessa* and *Platichthys flesus*. Mean density of juvenile plaice and flounder at Balgzand intertidal during high water

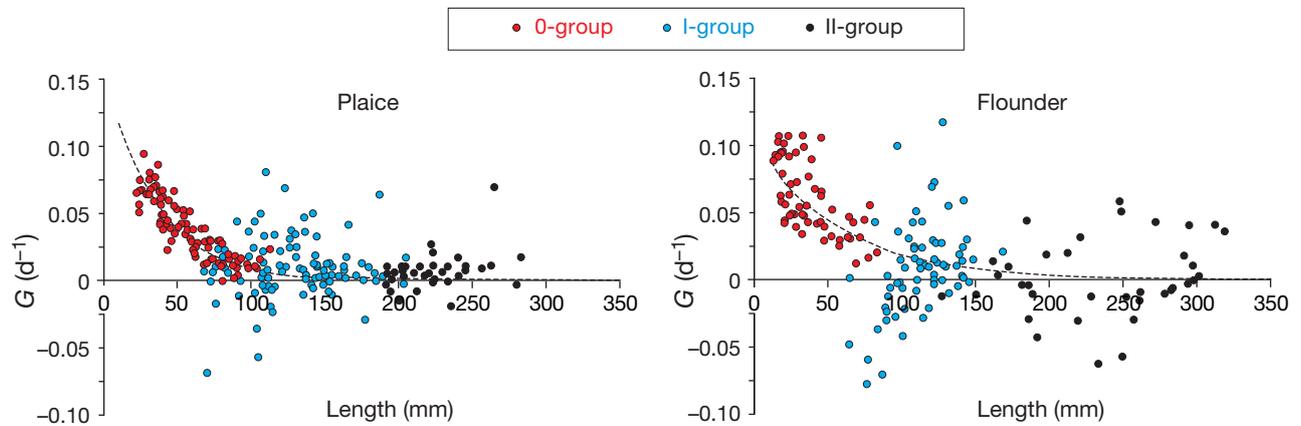


Fig. 4. *Pleuronectes platessa* and *Platichthys flesus*. Instantaneous growth rate of juvenile plaice and flounder after peak settlement at Balgzand intertidal in relation to fish size. All years combined

son (1999 and 2002). In the years 1979 and 1982, only 0-group plaice and flounder were sampled; therefore, food intake was not estimated for I- and II-group, although they were present.

For both plaice and flounder, the instantaneous growth rate decreased during the juvenile stage from approximately 0.10 d^{-1} in 0-group to almost zero in II-

group (Fig. 4). This was reflected in the energy flux into growth, which decreased from almost 80% in just-settled flatfish to zero in II-group fish at the end of their third growing season (Fig. 5). The increase in the energy flux into growth at the beginning of the growing season of I- and II- group fish compared with that of similar sized fish at the end of the previous sea-

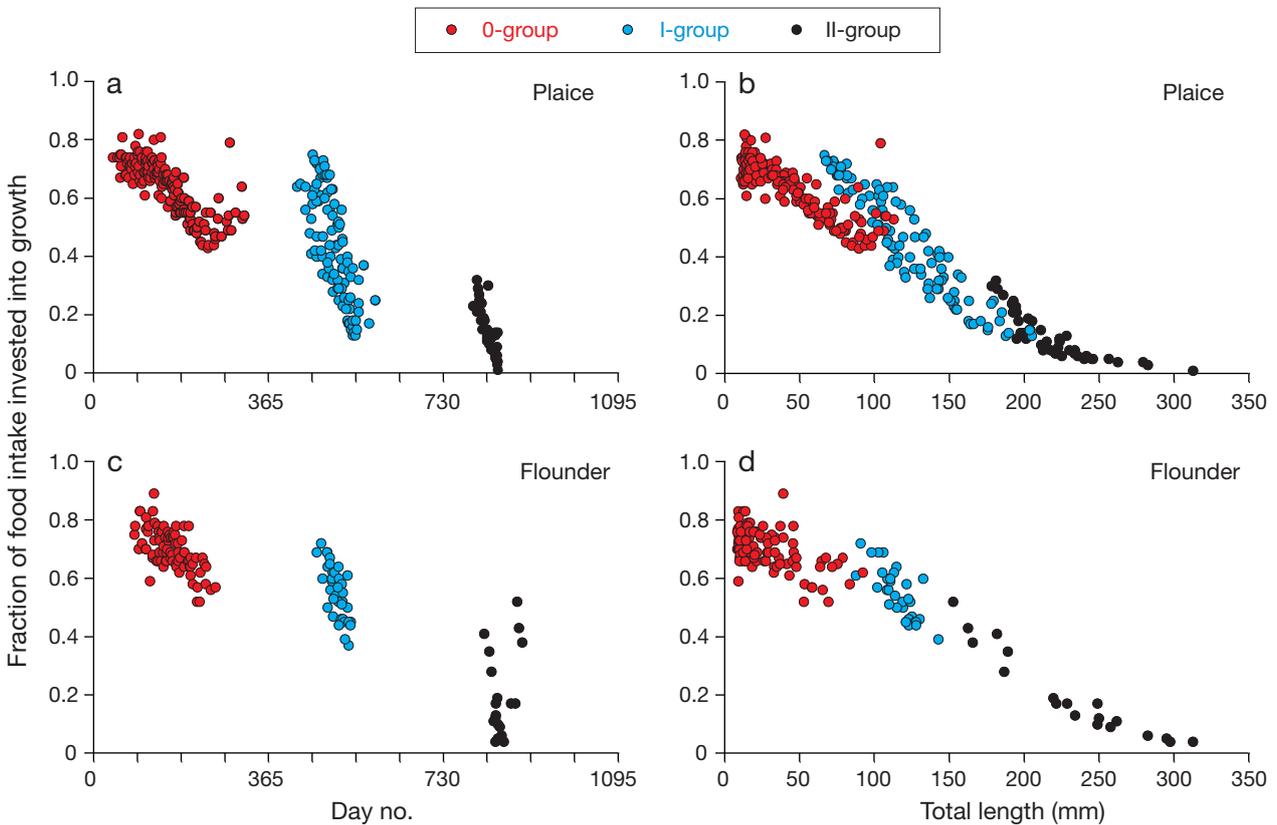
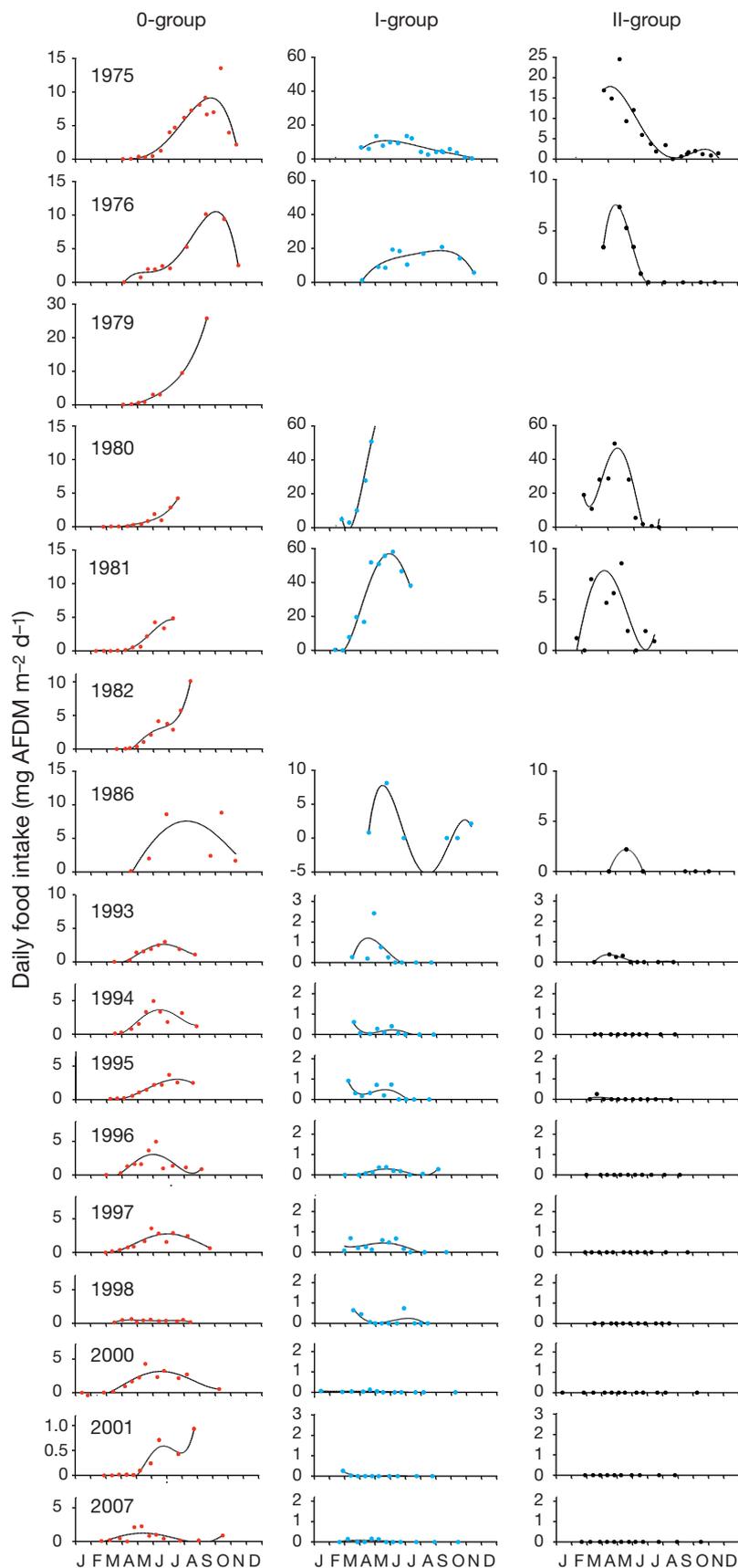


Fig. 5. *Pleuronectes platessa* and *Platichthys flesus*. Fraction of food intake invested into growth in juvenile plaice (a,b) and flounder (c,d) in relation to day number (a,c) and fish length (b,d) after peak settlement at Balgzand intertidal. All years combined



son reflected the lower temperature and, hence, lower maintenance requirements at the beginning of the season.

For each species, per year and age group, food intake was estimated by means of fourth-order polynomials (Figs. 6 & 7). In some cases, third- or second-order polynomials were sufficient. In some years, the growing season (March–October) was not sampled completely, resulting in a slight underestimation of annual predation pressure. Predation pressure by juvenile plaice far exceeded that of juvenile flounder. Over the period 1975 to 2007, annual predation pressure of both species decreased from around 4 to 6 g AFDM $\text{m}^{-2} \text{yr}^{-1}$ in the late 1970s to ~ 1.5 g AFDM $\text{m}^{-2} \text{yr}^{-1}$ in 1986 and to less than 0.25 g AFDM $\text{m}^{-2} \text{yr}^{-1}$ from 1993 onwards (Fig. 8). The decrease was mainly caused by the disappearance of II- and I-group plaice over time and, to a lesser extent, by the shorter growing season of 0-group plaice at Balgzand from the mid-1980s onwards (Table 1).

Macrozoobenthic prey items

Macrozoobenthic biomass in late summer at Balgzand showed a steady increase from ~ 20 in 1975 to 80 g AFDM m^{-2} in 2009 (Fig. 9a). Most of the biomass increase was due to the contribution of large bivalves such as *Mya arenaria* and *Crassostrea gigas* (data not shown).

Potential prey items for juvenile plaice and flounder consisted of intact specimens and parts of individuals (Table 1 in De Vlas 1979a). Body parts were found to consist mainly of siphon tips in bivalves, tail tips from the polychaetes *Arenicola marina* and *Heteromastus filiformis*, and heads and tentacles of *Pygospio elegans*. The group of whole individuals was formed by various juvenile bivalves except *Mytilus edulis* and a variety of polychaete species excluding *A. marina*. Differences in diet between juvenile plaice and flounder were small and mainly consisted of the relative contribution

Fig. 6. *Pleuronectes platessa*. Daily food intake of juvenile plaice at Balgzand intertidal during the various years of observations. Polynomial functions (maximum fourth-order) were fitted through the data points

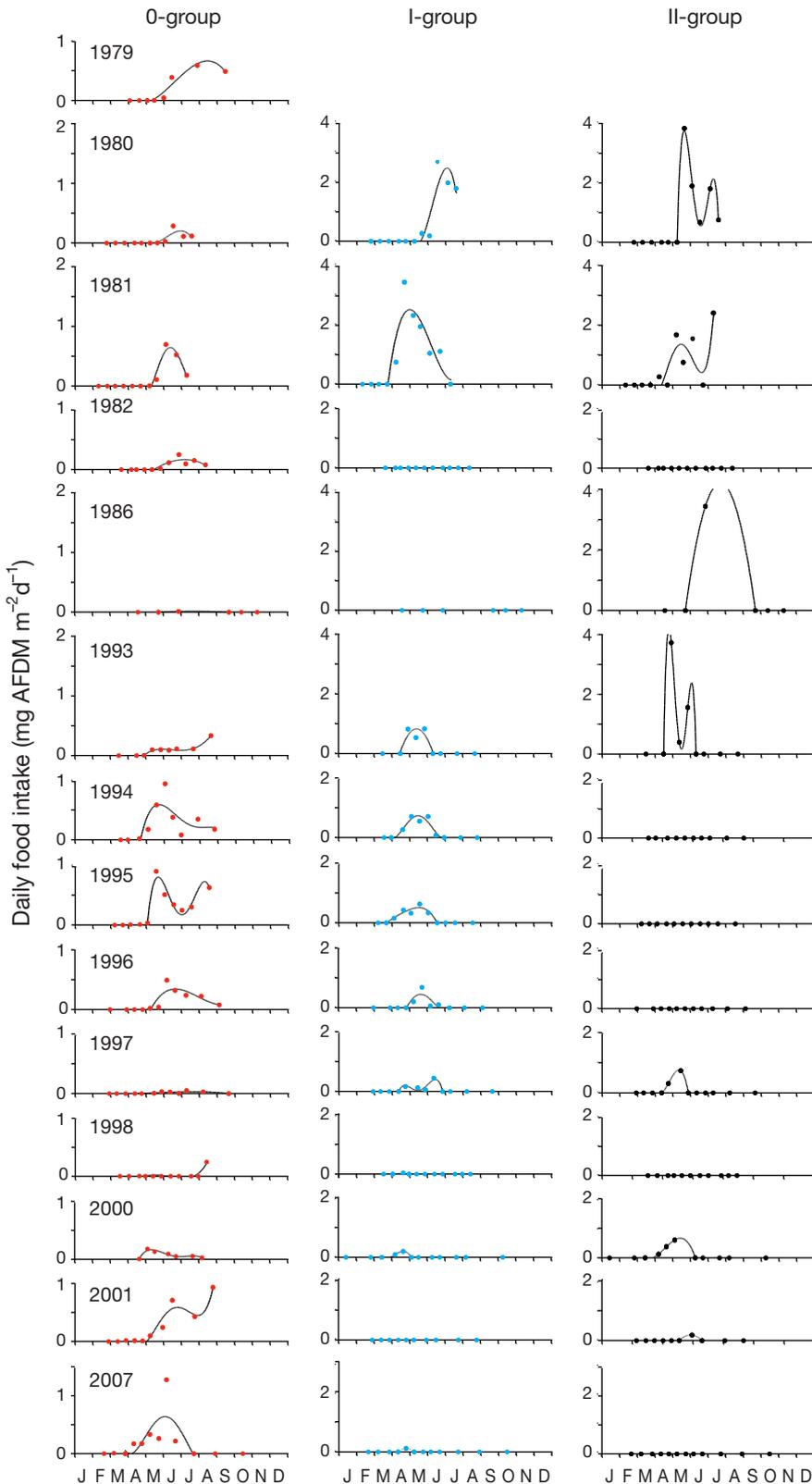


Fig. 7. *Platichthys flesus*. Daily food intake of juvenile flounder at Balgzand intertidal during the various years of observations. Polynomial functions (maximum fourth-order) were fitted through the data points

of the various prey items. Compared with juvenile plaice, the diet of flounder contained fewer body parts. Diet composition in 1986 and in 2008 to 2010 showed a similar pattern as in 1976 (data not shown). In addition, juveniles of the American razor clam *Ensis directus* were part of the diet in 1986 and 2008 to 2010 while the spionid polychaete *Marenzelleria viridis* was prey in 2008 to 2010. Stomach content data from the NIOZ fyke net programme showed that *E. directus* appeared in the stomachs from the late 1970s onwards and *M. viridis* appeared from the late 1980s (J. IJ. Witte unpubl. data). A summary of the main potential prey items for juvenile plaice and flounder is presented in Table 2.

The biomass of potential prey items of juvenile flatfish showed an increase over time, from ~ 10 g AFDM m^{-2} in 1975 to a maximum of 30 g AFDM m^{-2} in 2005, mainly consisting of polychaetes. In recent years, biomasses dropped back to a level of ~ 10 g AFDM m^{-2} (Fig. 9b).

DISCUSSION

The accuracy of annual predation pressure by juvenile plaice and flounder estimates relies to a large extent on the abundance estimates. Despite species-specific corrections for trawl and mesh efficiency (Kuipers 1975, Dapper 1978), variability in abundance estimates is substantial, on the order of 35% as revealed for plaice (Zijlstra et al. 1982). This means that, in analysing trends over time, an inter-annual variability of more than 35% should be taken into account. However, the observed changes, with a complete loss of especially II- and I-group plaice, are much larger. For juvenile flounder with a more patchy distribution in the silty areas of the Balgzand (van der Veer et al. 1991), this variability might be even higher, but because the abundance of juvenile flounder at Balgzand is an order of magnitude lower than that of juvenile

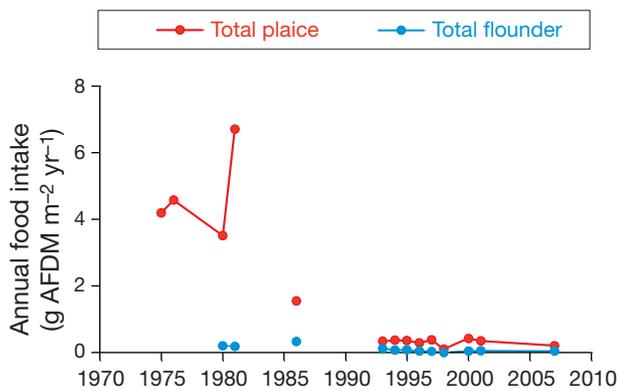


Fig. 8. *Pleuronectes platessa* and *Platichthys flesus*. Annual food intake of juvenile plaice and flounder at Balgzand intertidal at high water during the period 1975 – 2007

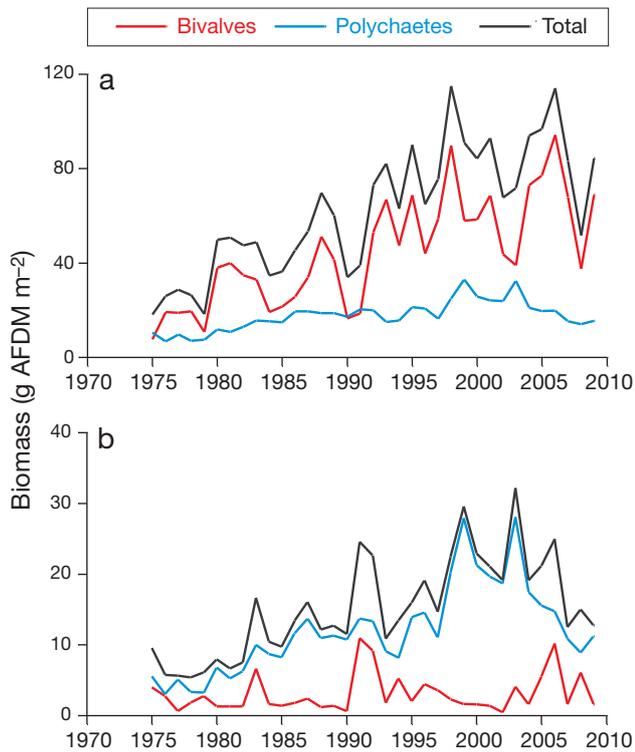


Fig. 9. Biomass of total macrozoobenthos (a) and potential food items for juvenile flatfish (b) at the Balgzand intertidal between 1975 and 2009

plaice, it will hardly affect the overall estimate of predation pressure of juvenile flatfish at Balgzand.

To allow for a direct comparison over time, the methods applied by De Vlas (1979a) were also followed in this study. The estimation of maintenance requirements was taken directly from De Vlas (1979a). For the contribution of growth, a slightly modified approach was followed: shifts in size-frequency distributions were used to derive a relationship between instantaneous population growth rate G (d^{-1}) over time and,

Table 1. *Pleuronectes platessa* and *Platichthys flesus*. Annual predation pressure ($g\ AFDM\ m^{-2}\ yr^{-1}$) by juvenile plaice and flounder at the Balgzand intertidal in various years over the period 1975–2007, based on ingestion estimates

Year	Predation by juvenile plaice	Predation by juvenile flounder	Total predation pressure
1975	4.2		>4.2
1976	4.6		>4.6
1980	3.5	0.2	3.7
1981	6.7	0.2	6.9
1986	1.5	0.3	1.9
1993	0.3	0.2	0.5
1994	0.4	0.1	0.5
1995	0.4	0.1	0.5
1996	0.3	0.04	0.3
1997	0.4	0.04	0.4
1998	0.1	0.01	0.1
2000	0.4	0.04	0.4
2001	0.3	0.05	0.4
2007	0.2	0.04	0.3

Table 2. *Pleuronectes platessa* and *Platichthys flesus*. Potential macrozoobenthic food items of juvenile plaice and flounder at the Balgzand intertidal over the period 1975–2010, based on stomach content analysis

Prey species	Items eaten	Biomass
Bivalves		
Juvenile spat	Whole individuals except <i>Mytilus edulis</i>	Total biomass except <i>M. edulis</i>
Adults	Only siphon tips except <i>M. edulis</i>	3% of total biomass except <i>M. edulis</i> (De Vlas 1985)
Polychaetes		
<i>Arenicola marina</i>	Only tail tips	15% of total biomass (De Vlas 1979b)
All other polychaetes	Parts and whole individuals	Total biomass

subsequently, this relationship was used to estimate G at each day of sampling. This method is more elegant and will hardly affect the resulting patterns: the estimate for plaice in 1975 in the present study for the whole Balgzand was in the same order of magnitude as the estimate by De Vlas (1979a) for the eastern part. The implicit assumption in the estimates by De Vlas (1979a) is that there are no losses associated with ingestion and thus ingestion is equal to the estimate of required energy for maintenance and growth (assimilation). For comparison purposes, the same approach has been followed in this paper, although in general, losses owing to ingestion are considered to be on the order of 20% (Brett & Groves 1979, van der Veer et al. 2009). Consequently, the estimates by De Vlas (1979a) and those in this paper might be underestimates.

Trends in juvenile flatfish abundance

Since the first reports of worldwide depletion of fish communities (Pauly et al. 1998, Myers & Worm 2003), it has become clear that these phenomena also occur on a smaller scale, such as in the highly productive North Sea; long-term trawl surveys show, for instance, that the absolute abundance of large fish has decreased and that of small fish has steadily and significantly increased during the last decades (Daan et al. 2005). Also, in the coastal zone of the North Sea, in the Dutch Wadden Sea, demersal fish biomass and abundance have shown a decreasing trend after the 1980s (Tulp et al. 2008).

The Wadden Sea is considered to be an important nursery area for various fish species, including plaice and sole (Zijlstra 1972), especially in the intertidal and the shallow subtidal (<5 m at low water) (Zijlstra et al. 1982). The present study shows that in a large intertidal area, the Balgzand, the abundance of juvenile plaice and flounder has changed substantially over time: 3 year classes (0-, I- and II-group) were present until the 1980s, after which densities of I- and II-group plaice and flounder dropped to levels close to zero. The decrease in the abundance of I- and II-group plaice and flounder in the western Wadden Sea is in line with the observations of a shift of larger plaice (20–39 cm) towards deeper water in the coastal zone of the North Sea before the 1990s (van Keeken et al. 2007). Since the 1990s, the abundance of 0-group flatfish, especially plaice, also decreased in the Wadden Sea in autumn, which might reflect an earlier emigration of 0-group flatfish to offshore. Based on long-term trends from a demersal fish survey, this pattern appears to apply for at least the whole Dutch Wadden Sea (Tulp et al. 2008). For the Balgzand intertidal, this suggests that the nursery function of the area has changed dramatically: from a system functioning as a suitable area for 0-, I- and II-group flatfish, it has become a nursery area for just-settling 0-group flatfish only.

The underlying mechanism for these shifts is unclear. The lack of I- and II-group flatfish suggests that juvenile I- and II-group plaice no longer re-immigrate from offshore into the intertidal in spring. The fact that here does not seem to be a consistent decreasing trend in plaice recruitment (Anonymous 2006) suggests that overall mortality during the juvenile stage has not changed. A shift towards deeper water caused by increased inshore predation by cormorants and seals (Leopold et al. 1998) therefore seems unlikely. In addition, the possibility that increased water temperatures might have exceeded the maximum tolerance range (cf. van Keeken et al. 2007) is questionable. In that case, all I- and II-group flounder

with a temperature tolerance similar to plaice (Freitas et al. 2010) would have also disappeared. However, larger flounder are still present in the area, although in low numbers. Furthermore, densities of II- and I-group plaice had already decreased before warming of the area began around 1985 (van Aken 2008), and so far, higher temperatures observed since 1989 have even had a slightly positive effect on growth of 0-group plaice (Teal et al. 2008). The analysis of growth versus maintenance requirements in this study indicates that, in both plaice and flounder, the energy available for growth decreases over time, reaching zero at the end of the third year of life. It might explain why, in the past, II-group plaice did not return in the following spring as III-group in the Wadden Sea (Kuipers 1977).

A recent analysis for 0-group plaice has shown that, during the growing season, food conditions decrease from optimal to suboptimal (van der Veer et al. 2010), thereby directly affecting and reducing the amount of energy available for growth. No information is available about the food conditions for flounder and I- and II-group plaice. If, for these groups, food conditions are also suboptimal in summer, it reduces the growth window for juvenile flatfish in the area. However, the analysis in the present study shows that this pattern has not changed since the 1970s, which is also supported by the fact that the biomass of potential prey items has not decreased. Another possibility, reduced immigration of I- and II-group flatfish because of a decrease in competition with larger plaice offshore (van Keeken et al. 2007), cannot be excluded. Regime shifts have been observed in the area in 1979 and 1988 (Weijerman et al. 2005). These have affected the system via shifts in a number of environmental factors, but it seems unlikely that there is any bottom-up control or a relationship with the abundance patterns observed in juvenile flatfish in the area.

Overall, the absence of I- and II-group flatfish in the intertidal cannot be explained at present; however, processes operating offshore are most likely involved.

Top-down effects of flatfish predation

The fact that macrobenthic biomass in temperate estuaries can be predicted from primary production data (Herman et al. 1999) suggests a bottom-up (resource-driven) control in these systems. Top-down effects of predation on whole individuals in such a bottom-up controlled system would be restricted to species composition and abundance. The stomach content analyses illustrate the wide prey field of both species. In addition, new invasive species such as the American

razor clam *Ensis directus* and the spionid polychaete *Marenzelleria viridis* appear in the diet of both flatfish species after some time. In the 1970s, predation pressure was around 4 to 6 g AFDM m⁻², which would be substantial enough to induce a top-down effect. However, this was not described at that time. In recent years, predation pressure seems to be too low to be exerting direct top-down effect.

Indirect top-down effects by predation are more likely, especially those related to the consumption of regenerating body parts. The cropping of tail tips of the lugworm *Arenicola marina* results in a loss of posterior segments and hence a reduction of the overall life span (De Vlas 1979b). At a frequency of amputation of once a week, growth and reproductive output also decreased (Bergman et al. 1988). Flatfish also heavily prey upon siphon tips of various bivalves (De Vlas 1979a). In some species, such as the Baltic clam *Macoma balthica*, siphon nipping by juvenile flatfish forces the bivalves to burry shallower in the sediment, thereby becoming within the reach of probing waders (De Vlas 1985, Zwarts 1996, De Goeij et al. 2001). In this way, siphon nipping by juvenile flatfishes facilitates predation by other top predators. In the 1970s, predation by juvenile flatfish at Balgzand might have been high enough to result in top-down effects in the form of facilitation for waders via siphon nipping. In recent time, this predation pressure has dropped to a level of approximately 0.25 g AFDM m⁻². At the same time, potential food abundance for juvenile plaice and flounder at Balgzand has not changed and total benthic biomass has increased substantially. To what extent this increase reflects the effect of a predation pressure release is unclear.

Although the sampling data do not cover the whole time period 1975 to 2009, results indicate that top-down predation by juvenile flatfish has decreased more or less gradually over time. In parallel, the nursery function of the Balgzand intertidal has degraded and it seems likely that this will also hold true for other intertidal areas. Besides the intertidal, the coastal zone and the subtidal are important flatfish nursery areas (Zijlstra 1972, van der Veer & Witte 1993). The trends in flatfish abundance in the Wadden Sea area (Tulp et al. 2008) suggest that the nursery function of subtidal areas has degraded as well. Data on different intertidal and subtidal nursery areas over time would offer the opportunity to apply McCall's theoretical basin model (McCall 1990) to test whether the degradation occurred in all areas simultaneously or whether marginal nurseries were vacated first.

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