Interannual patterns in predation pressure by juvenile plaice *Pleuronectes platessa L.* on intertidal macrobenthos in the Dutch Wadden Sea

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Inhoudsopgave

ABSTRACT

The Wadden Sea is an important nursery area for juvenile plaice and due to their high abundance their predation might have a significant top-down effect on the macrobenthic communities, affecting species composition and size distribution. Since 1975 juvenile plaice has been monitored at the Balgzand intertidal and from this data series (1975 – 2007) the interannual patterns in predation pressure were quantified. The seasonal abundance of juvenile plaice has changed significantly over the last three decades (1975-2007). Three year classes (O-, I- and II-group) were present in the first decade (1975 -1988) of the monitoring series after which the density of I- and II-group dropped to levels close to zero. Parallel, the annual predation pressure on the intertidal macrobenthos has dropped by 94 % from an average of 5.01 (1975-1988) to 0.32 grammes AFDW m^{-2} (1989-2007).
The top-down effect by plaice predation on the macrobenthic community is thought to be decimated and it might have directly or indirectly influenced food availability for other predators (eg. birds).

KEYWORDS: predation, plaice, *Pleuronectes platessa* L., Wadden Sea, benthos-fish interactions

1. INTRODUCTION

Intertidal areas such as the Wadden Sea are important as resting and refueling areas for migratory wading birds and as nursery areas for various fish and crustacean species, because of the large abundance of macrozoobenthic food items (Wolff 1983). In temperate areas such as the Wadden Sea, the biomass and productivity of the macrobenthic biomass is thought to be driven by bottom-up processes as is reflected in the relationship between primary production and macrozoobenthos biomass (Herman et al., 1999). Nevertheless, top-down processes such as predation are thought to be crucial in structuring the species composition and size distribution of benthic communities (Kuipers 1977).

At a large intertidal area in the western Wadden Sea, the Balgzand area, with a macrozoobenthic biomass and production of about 25 g ash free dry mass (AFDM) per m^2, predation pressure in the 1970-ties equaled about two thirds of the production whereby the main predators were: birds (5 g AFDM m^{-2}), crustaceans (3.5 g AFDM m^{-2}) and various fish species (8.5 g AFDM m^{-2}) (Kuipers et al. 1981). Among all predators, juvenile plaice *Pleuronectes platessa* L. was the most important predator accounting for a predation pressure of 4.0 g AFDM m^{-2}).

Plaice spawns at in the southern North Sea or offshore in spring and after hatching the developing eggs and larvae drift from the spawning grounds towards the coastal zone. At the end of their pelagic stage, the larvae metamorphose into demersal juveniles and settle in shallow coastal areas such as the Wadden Sea (Rijnsdorp et al. 1995). Inside the Wadden Sea, settlement occurs mainly at the intertidal and the sublittoral zone (Zijlstra et al. 1982, Van der Veer & Witte 1993). During the first month after settlement, O-group plaice can be found on the tidal flats during the entire tidal cycle: at low water they remain in small pools a few centimeters deep (Van der Veer & Bergman 1986). Thereafter, they develop a tidal movement: during ebb tide they migrate from the tidal flats, at first to the tidal creeks and gullies and later to the deeper tidal channels (Gibson 1973, Kuipers 1973, Van der Veer & Bergman 1986). In autumn the O-group plaice disappears to deeper waters offshore to return next spring as I-group. This I-group plaice again leave the area in autumn to return one year later as II-group before they become mature and join the adult population. Summarizing, the juvenile plaice stay up to three years in the Wadden Sea (O-, I- and II-group) before joining the adult population in the North Sea where they spend the rest of their life.

The top-down effect of predation depends on the predator's preference for the prey species (Kuipers 1977) which can be depending on food abundance and predator size . Extensive studies in the late 1970s showed that the diet of juvenile plaice mainly consisted of regenerative parts of prey items such as the tail ends of the lugworm Arenicola marina and siphons of bivalves; Cerastoderma edule and Macoma balthica (De Vlas 1979). Predation on the tail tips of Arenicola was considered to impact and reduce the survival of these lugworms (Bergman et al. 1988). Also the 'grazing' on the siphons reduced siphon length and forced these bivalves to reduce their burying depth causing them to come into reach of probing predators like red knots (Calidris canutus) (De Goeij et al. 2001). Predation by juvenile plaice therefore seemed to be an example of the top-down effect of predation on the benthic community and structure, both directly and also indirectly by facilitating shore bird predation.

However, since the late 1970s, significant changes for the Wadden Sea area have been recorded. Regime shifts have been described for 1979 and 1988 and perhaps also for 1998 (Weijerman et al. 2005) in combination with an offshore shift in the distribution of young juvenile plaice to deeper waters in the 1990s (Van Keeken et al. 2007). It is questionable to what extend the top down effect of plaice predation in the 1970s still holds for the present situation.

The Royal Netherlands Institute for Sea Research (NIOZ) has collected data on the epibenthic predators at the Balgzand intertidal starting in 1975. This monitoring series has been continued regularly ever since and consists at present of 20 years of observation over a 33 years (1975 – 2007) time period. This monitoring series allows analyses of interannual patterns in predation pressure by juvenile plaice on the Balgzand intertidal macrobenthos. The aim of this paper is:

[1] to quantify the predation pressure of juvenile plaice over time;

[2] to determine whether top down effect of plaice predation described for the 1970s still occurs.

2. MATERIALS AND METHODS

2.1. Sampling

Sampling at the Balgzand area took place in 20 years out of the 33 years from 1975 to 2007. Fishing was done in principle from February onwards at frequent intervals (2 to 4 wk). Each survey consisted of sampling on a grid of 36 stations distributed over Balgzand (Fig. 1), within a 3 h period around high tide, during which the flatfish population is randomly distributed over the area (Kuipers 1977). Hauls were taken during day-time with a 1.9 m beam trawl with 1 tickler chain and a net mesh size of 5 x 5 mm, towed by a rubber dinghy with a 25 HP outboard motor at a speed of approximately 35 m min^{-1} (Riley & Corlett 1966). Location of the hauls was initially established by wooden poles and later by the global positioning system (GPS).The exact length of the hauls was assessed with a meter wheel fitted to the trawl. During all cruises, except for the years 1975 and 1976, water temperature measurements were taken to the nearest °C. For 1975 and 1976, water temperature was estimated from the linear regression model on mean Marsdiep temperature per month and Balgzand temperature data for 1975 – 2002 [T_Marsdiep = 1.02*T_Balgzand + 0.36 (R^2=0.95, n=228)]. Data on the nearby long-term observation point at Marsdiep, Texel were taken from Van Aken (2003).
Catches were stored in 4% formaline (until 1987) or deep-frozen (from 1987 onwards) and all species were sorted out within a few days. All juvenile plaice were measured to the nearest mm total length, except in 1979 when only O-group juveniles were measured. Numbers caught were corrected for mesh size-selective (Dapper 1978) and catch (Kuipers 1975) efficiency and hereafter converted into numbers per 1000 m^2 (ind. $[10^3\ m^2]^{-1}$). Subsequently, catches were split up into age classes according to size. In case of doubt, individual age was verified by means of otolith reading.

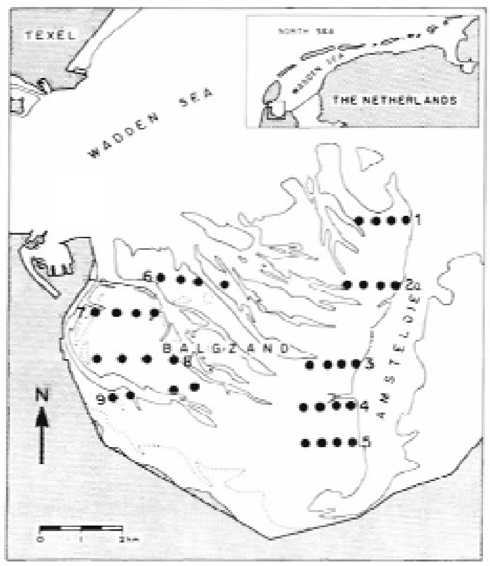

Figure 1. Sampling stations at Balgzand

2.2 Estimation of density

Not all stations were sampled during each cruise, because of eg. occasional bad weather. To prevent a bias in the density estimates, missing stations were accounted for. Cruises with all 36 stations sampled were used to estimate the relative contribution (fraction P) of each individual haul(s) to the overall sum of all 36 hauls. This fraction was used to estimate missing values in cruises whereby differences in seasonal distributions at Balgzand were incorporated by taken into account day number of the cruise).
Hereafter, the arithmetic mean of all stations sampled during a survey was calculated per 0.5 cm size class and considered to reflect the total mean density at Balgzand (Zijlstra et al 1982; Van der Veer 1986). This approach deviates slightly from the method used by De Vlas (1979), which included only the sampled, stations to calculate mean density.
In the years 1979 and 1982 only O-group was sampled, therefore density was not estimated for I- and II-group in these years although they might have been present. Additional catch data was collected from 1983 to 1993 during the annual Marine Biology student course at the NIOZ . During this course, samples on the Balgzand tidal flats in June-July were taken and measured. Similarly to the seasonal monitoring, the catches were split up into age classes according to size. In case of doubt, individual age was verified by means of otolith reading.

2.3. Estimation of food intake

Daily food intake in terms of grammes AFDM was estimated for O-, I- and II-group separately following the methods of de Vlas (1979) and consisted of two components: [1] contribution for metabolism and [2] contribution representing observed growth. The energy expenditure above maintenance and growth for example energy needed for swimming is considered to be negligible in juvenile plaice (De Vlas 1979) and therefore omitted from the calculations.

2.3.1. Daily maintenance requirements (DMR)

The estimation of maintenance of plaice was based on the fact that maintenance requirements are related to temperature and the metabolic weight ($W^{0.8}$), irrespectively of fish size or weight (Fonds et al. 1992). The estimation procedure for each cruise included the following steps: [1] The shape-weight relationship from Van der Veer et al. (2001) was converted into a length-weight relationship:

$$W = 0.010503\ L^3 \qquad [I]$$

were L is total length in cm and W is wet mass in g, and applied to convert mean length per size class i into mean weight (Wi); [2] This weight per size class was converted into metabolic weight per size class (Wi0.8); [3] Next, the metabolic weight per size class (Wi0.8) was multiplied by the numbers found per 1000 m2 (ni) in that size class and summed up over all classes to get the total metabolic mass per 1000 m2 (∑niWi0.8); [4] The total metabolic mass was used to estimate the daily food intake per 1000 m2 needed to meet the daily maintenance requirements (DMR; g AFDW 1000m-2 d-1) according to De Vlas (1979):

$$DMR= 0.17 * 2^{0.1*T} * 0.02*(\sum n_i W_i^{0.8}) \qquad [II]$$

were 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 (W $W^{-0.8}$ d^{-1}) and 0.17 is the conversion factor from wet mass to grammes ash free dry weight (De Vlas 1979).
In this way for each cruise the maintenance requirements of the population (O-, I, and II- group separately) at the day of sampling was determined. This procedure was identical to the method used by De Vlas (1979).

2.3.2. Growth

The estimation of the daily food intake of an individual fish necessary to accommodate the observed growth was based on laboratory experiments. Daily growth in mass was estimated according to the following steps: [1] For each cruise, the mean length of the population was estimated according to the procedure described in (Zijlstra et al. 1982) and (Van der Veer 1986) eg. the arithmetic mean of all stations; [2] Next the length – wet mass relationship (W = 0.010503 L^3) was applied to convert mean length per cruise i into mean weight per cruise (W_i); [3] The estimates of mean weight were used to determine the instantaneous growth rate (G; d^{-1}) between two successive cruises as:

$$G = \frac{\ln W_{i+1} - \ln W_i}{t} \qquad [III]$$

where W_i and W_{i+1} are the mean weights at respectively cruise i and the subsequent cruise i+1 and t is the time differences in days between the two cruises. G was considered to represent the growth rate at the midpoint between two successive cruises; [4] To smooth out some of the uncertainty in the G-estimates and to allow for the estimation of G when no sampling took place, an exponential curve was fitted to those individual G estimates, to describe the relationship of G over time for each year separately (Van der Veer et al. 2009). [5] Subsequently, the relationship of G over time was applied to estimate G of the O-group population at the various dates of sampling, whereby the growth rate directly after settlement was assumed to represent also the growth rate during settlement since during settlement G does not resemble the actual growth. The estimate of the population growth rate G was assumed to be similar for all size classes of an age group on a sampling date. To estimate G for I- and II-group the relationship of G with O-group size was extrapolated to I- and II-group lengths. [6] Next, growth per size class was determined by applying the length – weight relationship (W = 0.010503 L^3) to convert mean length per size class i into mean weight (W_i); [7] and estimating ΔW for each size class with the estimate of G. [8] The total amount of food needed for growth is 2.8 times the increase in weight (De Vlas 1979) therefore the weight change for each size class was multiplied by the net efficiency factor (2.8), by the number per 1000 m^2, and by the number of days between two cruises. Summing up these values for all size classes and multiplying by 0.17 (conversion to AFDW (De Vlas 1979)) resulted in an estimate of total food intake for growth per 1000 m^2 in grammes AFDW ($0.17 * \sum 2.8 * n_i \Delta W_i$):

$$DGR = 0.17 \sum_{\text{all } i} 2.8 n_i \Delta W \Delta t \qquad [IV]$$

Whereby DGR (g AFDW 1000 m^{-2} d^{-1}) are the daily growth requirements.

2.3.3 Total annual food intake

The total annual food intake for growth and maintenance can be estimated by integrating the food intake over time, using as starting date March 1st and as ending date November 1st (see Results). This requires a complete estimate of food intake through time, which was achieved by fitting a polynomial through the available food intake estimates. Food intake was estimated in all years of sampling in the period 1975-2007 except for 1983, 1991, 1999 and 2002 when there were less than 3 cruises (1983 and 1991) or when all cruises were executed only within the first part of the season (1999 and 2002).

3. RESULTS

3.1 Density

Density estimates (Fig. 2a-c) show that the seasonal abundance of juvenile plaice had changed significantly in the last three decades (1975-2007). Three year classes (O-, I- and II-group) were present in the first decade of the monitoring series (1975 -1986) after which the density of I- and II-group dropped to levels close to zero. Based on the age groups present, the series could be split up into two periods: [A] all three year classes (O, I, II) present and [B] only O-group present. The peak densities of the O-group (Fig.2a and Table 1) were variable between years, ranging from 112 individuals per 1000 m2 in 1975 to 1183 in 1996 and with an average of 355 (SD = 241) over the period 1975 - 2007. When fitting a linear regression model to the annual peak densities over the years there was no significant change (P=0.100) over time in peak density. Visually comparing peak densities in phase A with B suggested an increase of O-group peak abundance, but this was not a significant change (Two-sampled t-test, df=18, P=0.065).

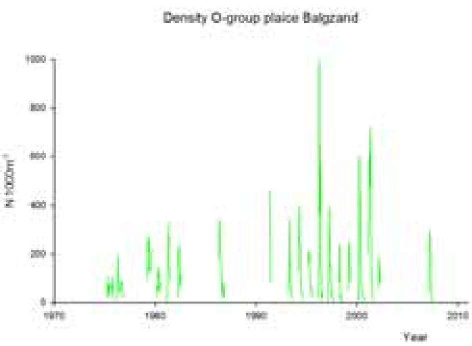

Fig.2a

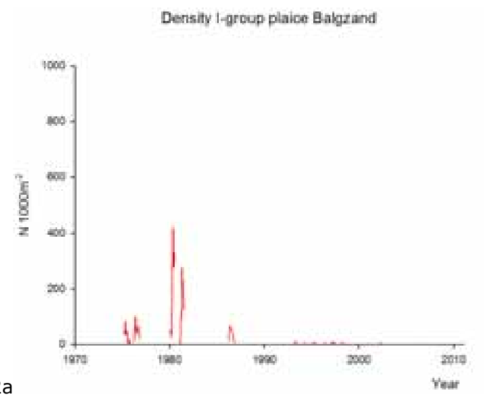

Fig.2b

Fig.2c

Figure 2. Fish density at Balgzand of O-group (a), I-group (b), and II-group (c) plaice

Table 1. Peak density of O-group plaice (ind. $[10^3\ m^2]^{-1}$) at Balgzand in 1975 – 2007

Year	Individuals $[10^3\ m^2]^{-1}$
1975	112
1976	191
1979	273
1980	141
1981	324
1982	236
1986	340
1993	350
1994	397
1995	218
1996	1182
1997	391
1998	230
2000	567
2001	698
2007	299

Table 2. Density of O-, I-, and II-group plaice (ind. $[10^3\ m^2]^{-1}$) in June at Balgzand (1975 – 2007). (*) No data available.

Year	Individuals $[10^3\ m^2]^{-1}$		
	O-group	I-group	II-group
1975	46	39	13
1976	90	90	5
1977			
1978			
1979	144	*	*
1980	83	295	7
1981	170	193	4
1982	138	*	*
1983	140	25	4
1984	374	20	3
1985			
1986	450	26	2
1987			
1988	201	6	1
1989			
1990			
1991	208	0	0
1992	133	2	0
1993	66	0	0
1994	79	0	0
1995	57	0	0
1996	202	1	0
1997	51	2	0
1998	9	0	0
1999			
2000	66	0	0
2001	46	39	13
2002	90	90	5
2003			
2004			
2005	144	0	0
2006	83	295	7
2007	170	193	4

The estimations for I-group (Fig.2b) and II-group (Fig.2c) showed a different pattern. Both year classes were present on Balgzand in significant numbers in 1975-1981, and I-group even up to 1986. Also sampling during the NIOZ marine biology course in the period 1983-1993 shows that I- and II-group plaice were present in significant numbers until 1988 (Fig.3 and Table 2). The two phase in the data series were therefore defined as: [A] 1975-1988 and [B] 1989-2007.

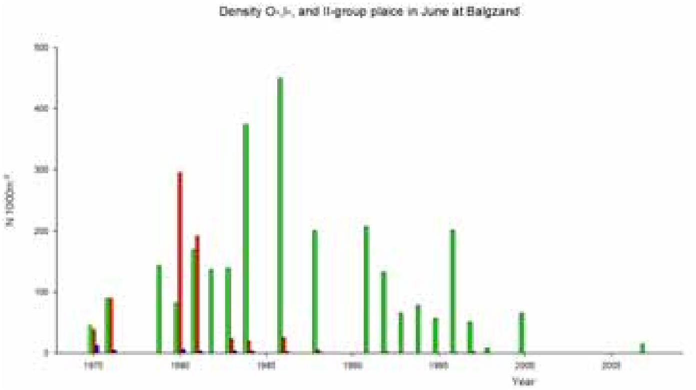

Figure 3. Average fish density at Balgzand in June of O-group (green), I-group(red), and II-group (blue) plaice

In the period 1975-1988, I-group had peak density of on average 186 individuals (SD=153) and II-group of 83 individuals (SD=64) per 1000m^2 (1975-1988). After 1988 the population of I- and II-group collapsed with both age classes no longer present at Balgzand.

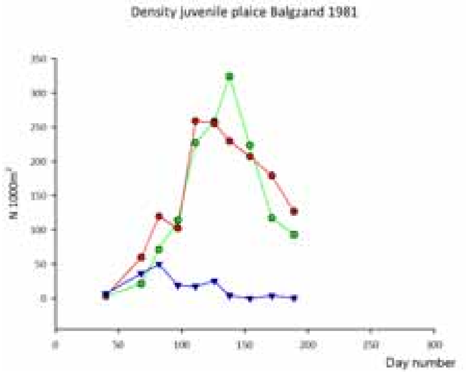

Figure 4. Seasonal density pattern of O-group (green), I-group (red), and II-group (blue) plaice at Balgzand in 1981

The general seasonal pattern is illustrated for 1981, a year with all year classes present and a representative seasonal sampling (Fig. 4). At the start of the season (February) all year classes were almost absent. The youngest juveniles (O-group) rapidly increased in numbers reaching their peak density at 324 ind. [10^3 m^2]$^{-1}$ at the start of May (day 138). After the peak in density the population declined towards the end of the summer. In 1981 the last day of sampling was half of July (day 189) but the population trend in the period of 1975-1988 showed that the abundance declined continuously until November and the estimated density of O-group at the end of the season approximately equalled the density of the I-group at the start of the subsequent season. The I-group patterns in density resembled the O-group with slightly lower densities on each cruise date. Peak density in 1981 was reached in half of April (day 111) and the numbers in the second half of the season declined slightly slower. The II-group reached their peak density earlier in the season (half of March). After the beginning of May the numbers decreased.

The analysis of the seasonal pattern for O-group plaice over the 32 years of sampling showed a change in the time of peak density (Fig.5). The peak density of O-group plaice in the seventies and eighties occurred on average in the second week of May whereas nowadays it is one month earlier, in the second week of April. So the day number of peak density in phase B was nearly 30 days earlier in the season than in phase A (Two-sampled t-test, mean difference=28.6; df=17.9; P=0.001).

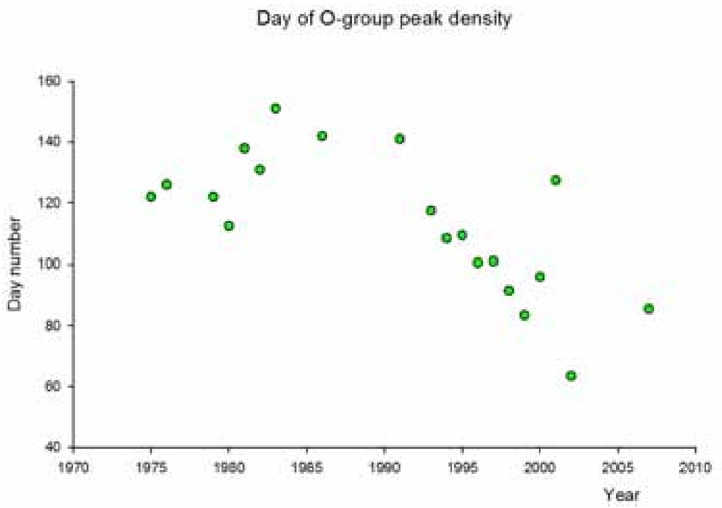

Figure 5: Day number of O-group plaice peak density at Balgzand

3.2 Growth

Estimations of the instantaneous growth rates (G; d^{-1}) of O-group plaice before and after peak density are shown in Fig. 6a. The maximum growth rate was just below 0.1 d^{-1} at a mean length of approximately 30 mm. After peak density the instantaneous growth rates decreased exponentially with length up to a maximum length of 110 mm for O-group. In the I- and II-group data this decreasing curve continued to a length of over 300 mm but with a higher variability (Fig. 6b). These two older year classes even showed negative G values. The negative G values were all after 1988 when the I- and II-group were caught only incidentally and estimates of the instantaneous growth rate were highly uncertain due to the low sample size and the high variability in length of these individuals.

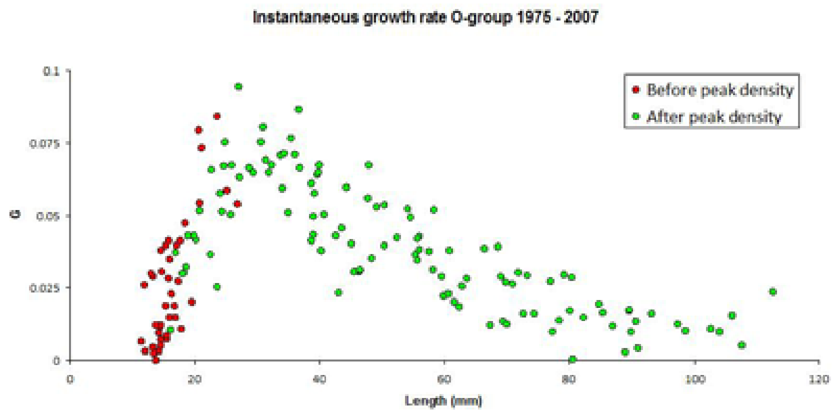

Figure 6a. Instantaneous growth rate (G; d-1) of O-group plaice at Balgzand. Red: during larval immigration; green: from peak densities onwards (1975 – 2007).

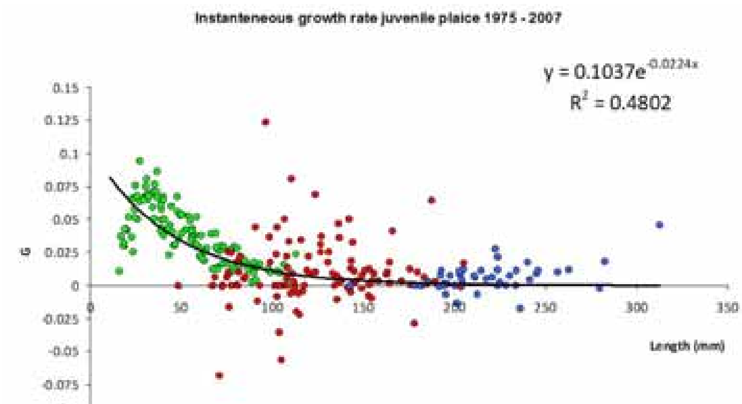

Figure 6b. Instantaneous growth rate per length in mm for O-group (green), I-group (red), and II-group (blue) plaice at Balgzand. Exponential regression model; G= 0.1037e-0.0244L, R2=0.4802

The annual G patterns over time for O-group used for estimating G at the sampling data were plotted in Fig. 7 and the relationships for the different years are presented in Table 3. No significant differences in G between years were found by fitting a linear regression model on the slope (R^2=0.007, P=0.761).

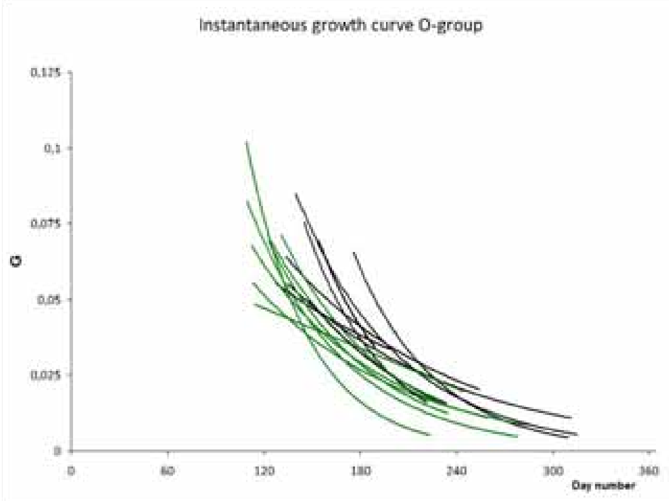

Figure 7. Annual instantaneous growth pattern of O-group plaice after peak settlement at Balgzand 1975-1988 (black), 1989-2007 (green).

Table 3. Parameters of instantaneous growth curve O-group plaice 1975- 2007. $G=A*e^{Bt}$ (t is day number).

Year	A	B	R^2
1975	0.19	-0.01	0.74
1976	0.75	-0.02	0.96
1979	0.23	-0.01	0.60
1980	0.14	-0.01	0.07
1981	1.51	-0.02	0.85
1982	1.39	-0.02	0.57
1986	2.18	-0.02	0.72
1993	0.51	-0.02	0.72
1994	0.46	-0.02	0.66
1995	0.37	-0.01	0.59
1996	0.13	-0.01	0.40
1997	0.27	-0.01	0.50
1998	1.70	-0.03	0.42
2000	0.51	-0.02	0.69
2001	0.37	-0.01	0.84
2007	0.19	-0.01	0.72

3.3 Predation pressure

3.3.1 Daily Maintenance Requirements (DMR)

The total amount of food taken up by the juvenile plaice for maintenance was determined by temperature, metabolic weight and density. Although abundant in high numbers, O-group plaice had the lowest metabolic weight per fish and therefore their food intake for maintenance (DMR) (Fig.8a) was only a fraction of that of the I- and II-group (Fig.8b and c).
Maximum DMR for O-group per year was on average 5.5 g AFDW $1000m^{-2}$ d^{-1} (SD=4.0) in 1975-1988 with a peak value of 13 g AFDW $1000m^{-2}$ d^{-1} in 1979. While in the last two decades (1989-2007) the maximum DMR dropped and had an average of 1.3 g AFDW $1000m^{-2}$ d^{-1} (SD=0.5). The maintenance requirements for I- and II-group were much higher but also more variable. The year 1980 was for both age classes the season with a high peak value and in 1981 for I-group again DMR following observed high densities.
On average DMR for I-group was 28.3 g 1000m-2 d-1 (SD=26.1) in phase A with a peak in 1980 and 1981 of respectively 66.2 and 43.9 g. II-group averaged at 23.1 g (SD=23.2) and peaked in 1980 at 56.7 g. In phase B DMR dropped to low values caused by the disappearance of the two age classes.

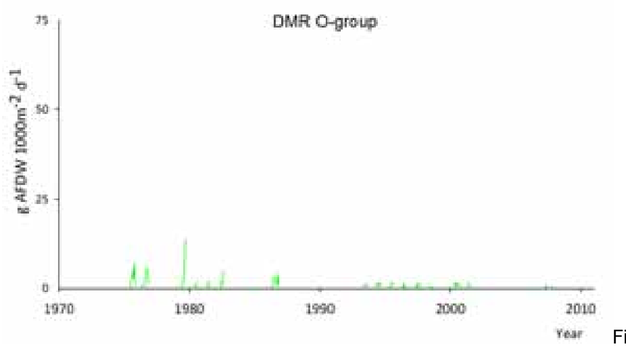

Fig.8a

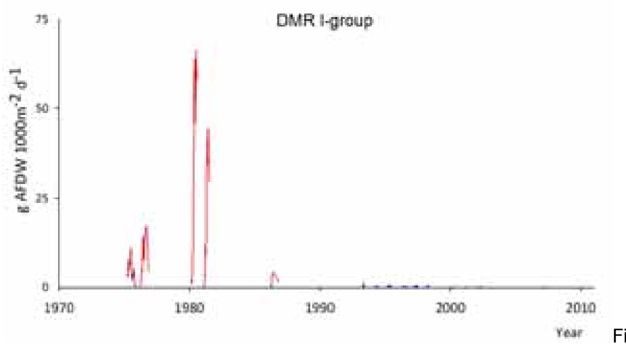

Fig.8b

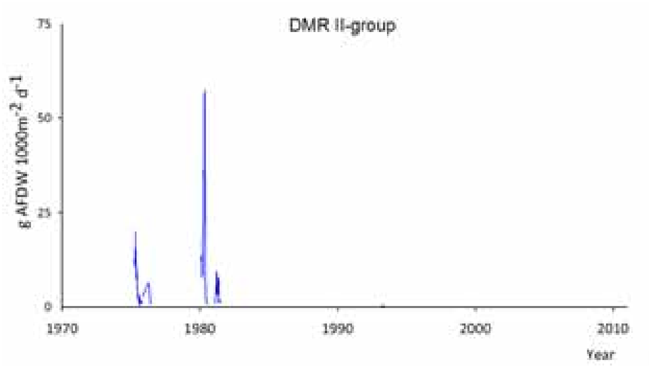

Fig.8c

Figure 8. Daily maintenance requirements for O-group (a), I-group (b), and II-group (c) plaice at Balgzand 1975-2007 in g AFDW per 1000m2 per day

3.3.2 Daily Growth Requirements (DGR)

The energy spent on growth was smaller for I- and II-group compared to the energy spent on maintenance but the annual patterns in DGR (Fig.9a-c) were the same as for DMR. I-group DGR peaked in 1980 and 1981 with 31.9 and 17.8 g AFDW 1000m^{-2} d^{-1} with an average maximum value of 13.2 g (SD=11.7). The highest II-group DGR was in 1980 at 7.3 g and on average 3.1 g (SD=2.8).
O-group spent always more energy on growth then on maintenance. In phase A the average DGR was 5.7 g AFDW 1000m^{-2} d^{-1} (SD=3.2) with again a high peak in 1979 at 12.2 g. In phase B DGR slightly decreased to 2.25 g AFDW 1000m^{-2} d^{-1} (SD=0.91).
All values for DMR and DGR are summarized by time phase in Table 4.

Table 4. Mean daily energy required for maintenance (DMR) and growth (DGR) from March 1st to November 1st in [g AFDW 1000m^{-2} d^{-1}] in different time phases. Average and standard deviation between brackets

	Age	Phase A	Phase B
DMR	O-group	5.49 (4.03)	1.29 (0.49)
	I-group	28.29 (26.05)	0.35 (0.41)
	II-group	23.08 (23.18)	0.26 (0.04)
DGR	O-group	5.67 (3.20)	2.25 (0.91)
	I-group	13.23 (11.74)	0.32 (0.28)
	II-group	3.14 (2.8)	0.07 (0.05)

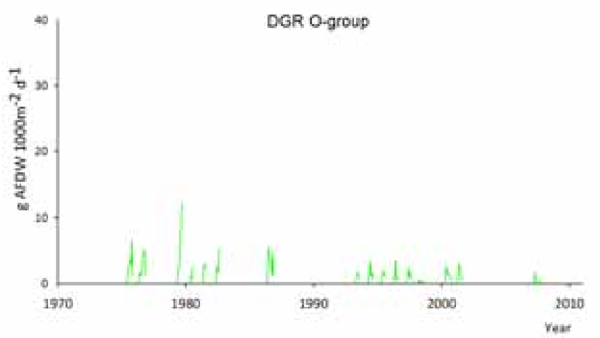

Fig.9a

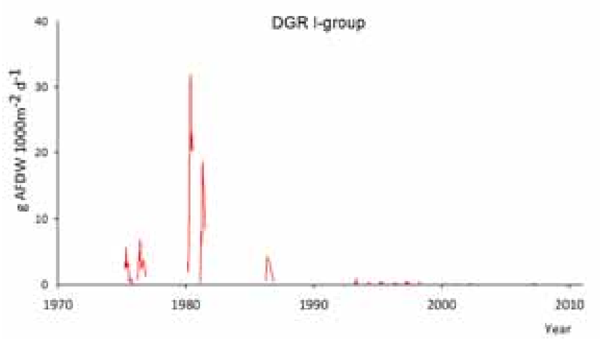

Fig.9b

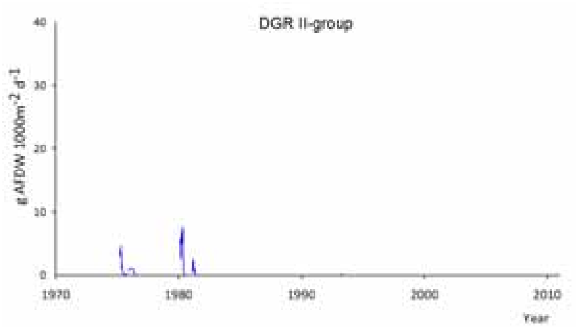

Fig.9c

Figure 9. Daily food requirement for growth O-group (a), I-group (b), and II-group (c) plaice at Balgzand 1975-2007 in g AFDW per 1000m2 per day

3.3.3 Annual Food Intake

DMR and DGR were plotted for each year and annual food intake for maintenance (Fig. 10a-c) and for growth (Fig. 11a-c) was estimated by fitting a 4th degree polynomial through the data and calculating the surface area within the season starting at March 1st till November 1st (Fig.11a-b).

Due to declining numbers of age I and II plaice, the total annual food intake on Balgzand had dropped dramatically for both the food intake (FI) for maintenance as well as for growth. The average FI for growth in phase A for all ages was 1.49 g AFDW m^{-2} (SD=0.85) and that value dropped to an average of 0.18 gr AFDW m^{-2} (SD=0.06) which is a decrease of 88 %. For O-group alone it went from 0.59 (SD=0.24) to 0.17 gr AFDW m^{-2} (SD=0.06) (-72 %).

The average FI for maintenance was higher compared to FI for growth in phase A with a average of 3.52 g AFDW m^{-2} (SD=2.53) for all ages but it dropped with 96 % to an average of 0.13 g AFDW m^{-2} (SD=0.05). The average over phase B resembles the FI for growth. The FI for maintenance for O-group alone decreased 78 % from 0.52 (SD=0.28) to 0.12 g AFDW m^{-2} (SD=0.05). The O-group food intake dropped significantly (Student t-test, P<0.000) but the disappearance of the I-group was the most important cause of the changes in total predation pressure. The I-group consumption for growth in phase A was 76 % of the total consumption of all ages. The I-group consumption for maintenance was 55 % of the total.

Combining the food intake for maintenance and growth shows a reduction of 94 % of the annual predation pressure from an average in phase A of 5.01 g AFDW m^{-2} (SD=3.36) to only 0.32 g AFDW m^{-2} (SD=0.10) in phase B.

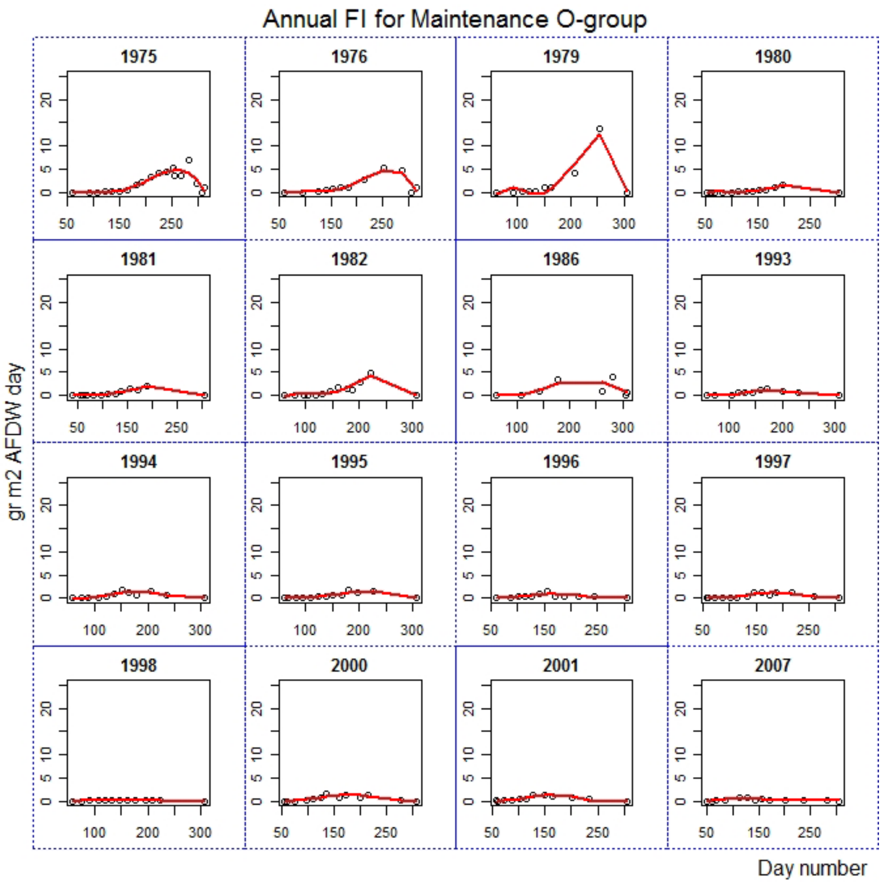

Fig.10a

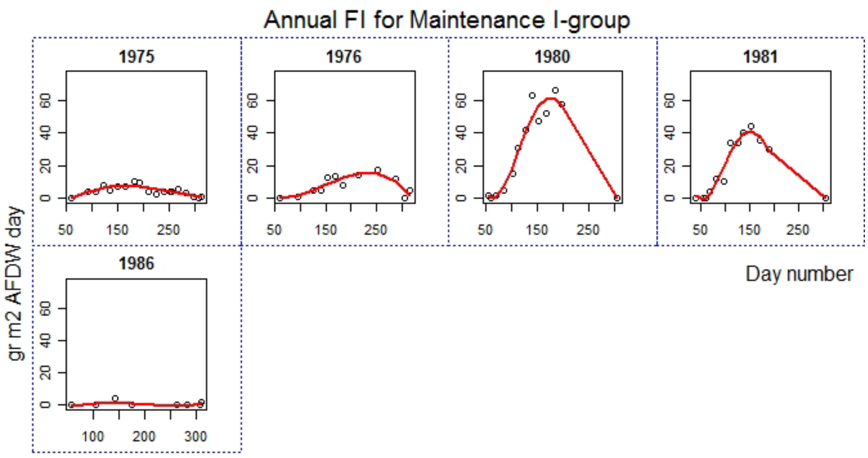

Fig.10b

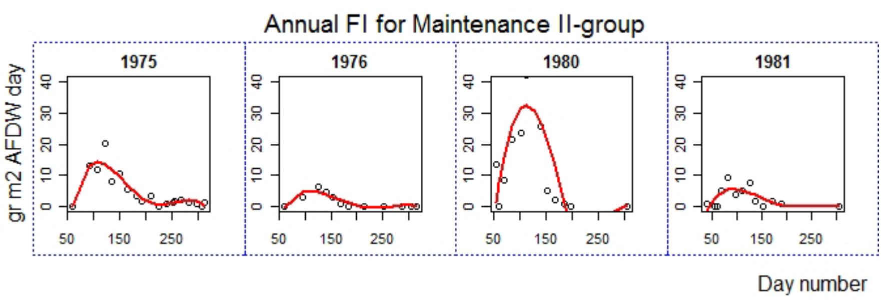

Fig.10c

Figure 10. Annual Food Intake for maintenance of O-group (a), I-group (b), and II-group (c) plaice at Balgzand (1975-2007) in g AFDW per m2.

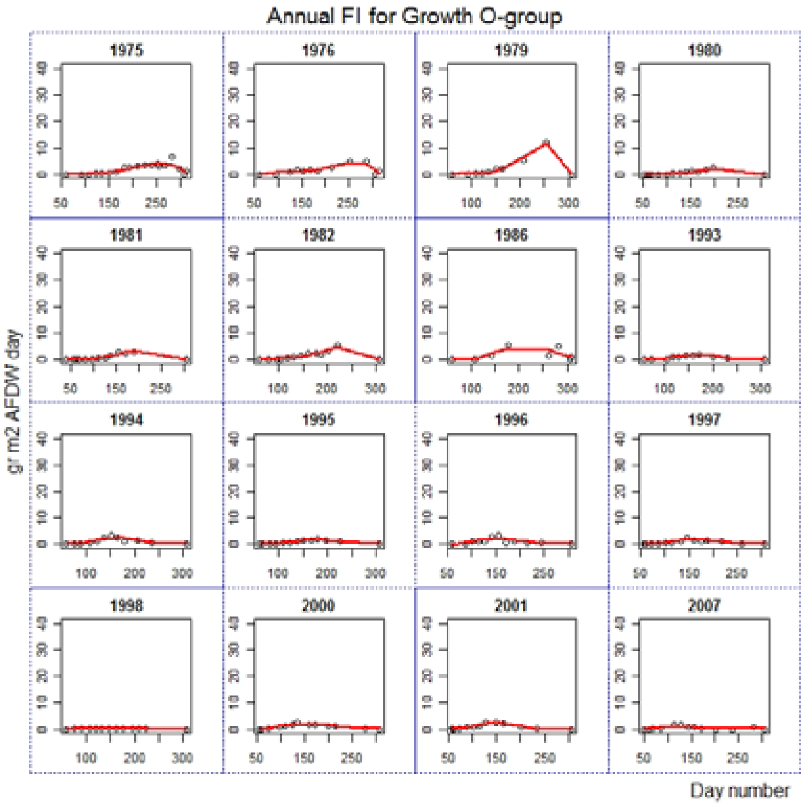

Fig.11a

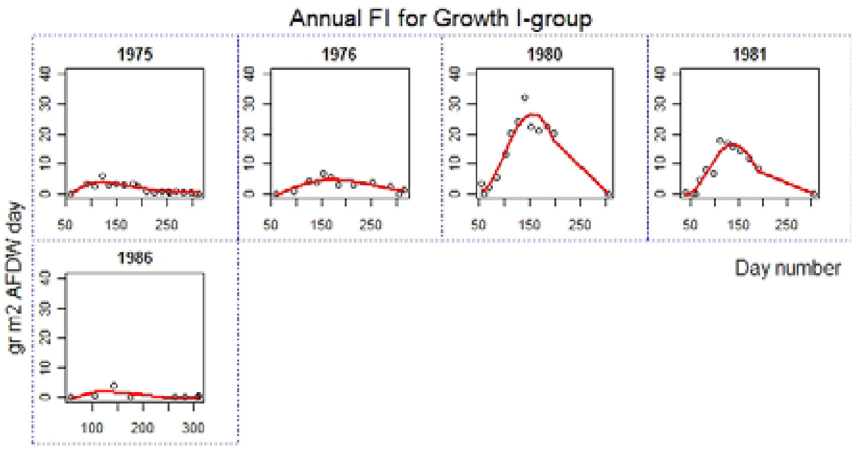

Fig.11b

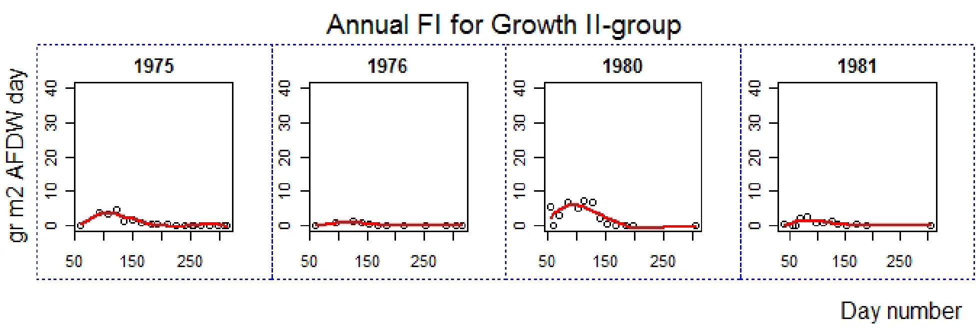

Fig.11c

Figure 11. Annual Food Intake for growth of O-group (a), I-group (b), and II-group (c) plaice at Balgzand (1975-2007) in g AFDW per m2.

4. DISCUSSION

4.1 Density

The seasonal abundance of juvenile plaice has changed dramatically since 1975. The two time phases used earlier are based on the age classes present: [A] All three year classes (O, I, II) present, [B] only O-group present. Unfortunately in the period 1983-1992, sampling was carried out only in the season of 1986 during the seasonal monitoring program. The annual marine biology student course in June at the NIOZ (1983-1993) was used to pinpoint the approximate moment of transition from one phase to the next. From this data series the transition from A to B was dated 1988-1989 with the last significant densities for I- and II group in 1988. Although I-group densities decreased partly after 1981. The reason why I- and II-group are no longer present on the tidal flats of Balgzand is not clear. There could be a change in the food availability of this nursery area. The Wadden Sea is a dynamic region and it is know to have a natural variability as well as anthropogenic influences that cause the system to change. Beukema (1991) showed that the composition and production of the benthic community had changed. The increased production does not *directly suggest decrease of food availability. Other causes could be changes in sea surface temperature in the North Sea creating a shift in spawning period or speeding up larval development, increased predation e.g. by harbour seals and seabirds or increased food competition with shrimps and shore crabs.*
Another interesting observation is the forward shift in time of peak density (Fig.5) from phase A to B. Juvenile plaice lacks competition for food in the period from March till May but it is known that during the summer they compete with the common shrimp (*Crangon crangon*) for food (Fonds, pers. comm.) Being present earlier in the season may avoid this inter-specific competition for food.

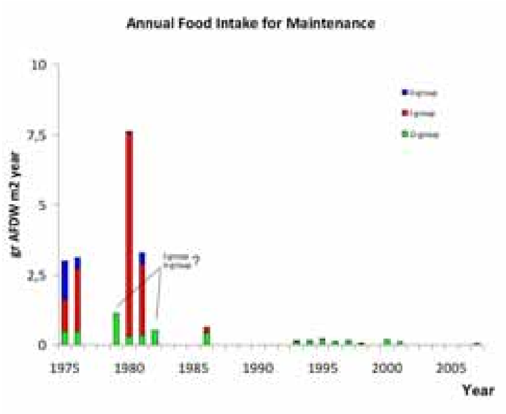

Fig.12a

Figure 12a. Annual Food Intake for Maintenance of O-group (green), I-group(red), and II-group(blue) plaice (1975-2007) in g AFDW per m2.

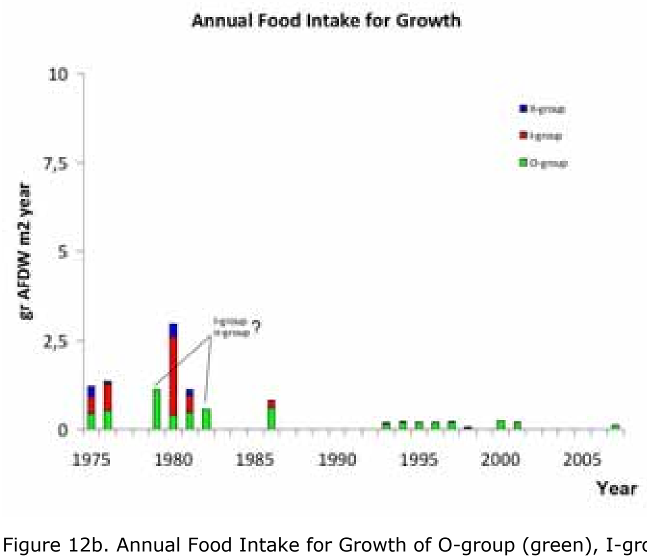

Fig.12b

Figure 12b. Annual Food Intake for Growth of O-group (green), I-group(red), and II-group(blue) plaice (1975-2007) in g AFDW per m2.

4.2 Growth

The observed length increase of plaice caught at Balgzand was assumed to represent average growth of the population and was used to estimate individual growth (G). But by this assumption the effect of plaice immigrating in and emigrating out of Balgzand and fish mortality could bias the outcome. There is little known about the level of isolation of this population. In the course of the growing season, large plaice leave the area earlier than small ones parallel to the earlier emigration of II- and I-group in summer. This obviously counteracts the length-growth in these groups. For example while mean lengths of O-group plaice on Balgzand followed a normal growth curve, the I- and II-group hardly showed any increase in length from May onwards (Kuipers 1977). The normal growth in O-group supports the suggestion that these fish form a temporary closed population without significant migrations. This is supported by Edwards & Steele (1968). They reported that O-group plaice tend to stay within the 4-m depth line until September-October. Lockwood (1973), in Filey Bay, observed the first offshore movement of O-group in late August. After settlement on Balgzand in April and May, O-group density stays high during the summer (at least till 1986). Although the population shows during the season a shift in the northern direction, it seems unlikely that the fish leave the area, which in the north is surrounded by a 10 to 20 metres deep water channel, the Malzwin (Kuipers 1977).
The variance of individuals per length class gets larger during the season, at least for O-group. Fast and slow growing individuals cause the growth rate to have an increasing range towards the summer. This could indicate that maximum growth is not reach by all individuals but another suggestion has been made that female and male plaice have a different maximum growth capacity with females growing slightly faster than males (Van der Veer et al. 2009). Unfortunately all sampled data consist of unknown mixtures of males and females and separating the data into sex classes seems difficult.
The conversion used to calculate weight from length ($W = 0.010503\ L^3$) is a simplistic conversion but it is based on large amounts of length, weight and fish condition data collected (De Vlas 1979, Van der Veer et al. 2001). Nevertheless it is a generalization of this data therefore it is advisable for continuing this series to weigh each sample.

4.3 Predation pressure

The estimated total annual food intake in 1975 and 1976 of respectively 4.2 and 4.5 gr AFDW m^2, closely resembled the estimations done by de Vlas (1979) of 5.9 respectively 5.6 gr AFDW m^2. The deviation can be attributed to the different methodology used.
Juvenile plaice density changed significantly in the sampled period. Correspondingly with enormous decreases in (seasonal) juvenile plaice abundance, the daily (DMR and DGR) and seasonal predation pressure (FI) on the intertidal macrobenthos collapsed. The level of predation pressure is divided into the two different phases [A] and [B] with the transition period from [A] to [B] dated in 1988. With seasonal predation pressure decreasing dramatically in the transition period. The transition coincides with the described regime shifts in 1988 (Weijerman et al. 2005) while the regime shift in 1979 is not seen in this data series. The predominant factors in the 1979 regime shift are thought to be salinity and weather conditions which do not influence the young plaice that much while in 1988 when the situation for plaice changed dramatically it is thought that also temperature played an important role.
Predation pressure was also affected by the shift in time of peak density of the O-group. Although the day number of O-group peak density is one month earlier in the year, the growth rate and maximum length at the end of the season did not change hence the O-group predation pressure peak is at an earlier day in the growth season. The cumulative metabolic biomass ($\sum n_i W_i^{0.8}$) (CMB) used for estimating DMR and reflecting the number of individuals present and their cumulated weight was plotted in Figure 13. The seasonal pattern has changed from phase A to phase B. In A CMB increases over the season peaking towards the end with an average of 110.7 g AFDW $1000m^{-2}$ (SD=88.4). While in phase B CMB is more constant over the season with an increase limited to the first 2 months of the season and an average peak of 26.1 g AFDW $1000m^{-2}$ (SD=11.4). The average temperature of the sea surface during the growth period of O-group is lower in phase B because they settle one month earlier and with their maintenance requirement decreasing with lower temperatures, they need less energy for their metabolism. Hence the annual predation pressure decreases. Interestingly this project shows that the amount of food taken up by the juvenile plaice is declining with time of arrival. Therefore the variability in population food intake is only partially dependent on the density of the individual. The predation pressure is depending not only on density, growth rate and temperature but also spatial variability should also be taken into account. Several factors such as plaice abundance, prey composition and abundance, sediment type and distance to the gully can be quantified and qualified to get a more accurate estimation of predation pressure in this area.

The offshore shift of juvenile plaice (I- and II-group) to deeper waters and the temporal shift of O-group peak density has decimated the role of this important secondary consumer (Kuipers et al. 1981) in the food web at Balgzand. The top down effect of structuring the macrobenthic community and the facilitation of bird predation (De Goeij et al. 2001) cannot be as significant as it was in the 1970s with the reduction of annual predation pressure by 94 %. This conclusion and the results presented in this paper clarifies the importance of long term monitoring series in linking ecosystem changes and pointing out regime shifts which otherwise could have been mistaken for annual variability.

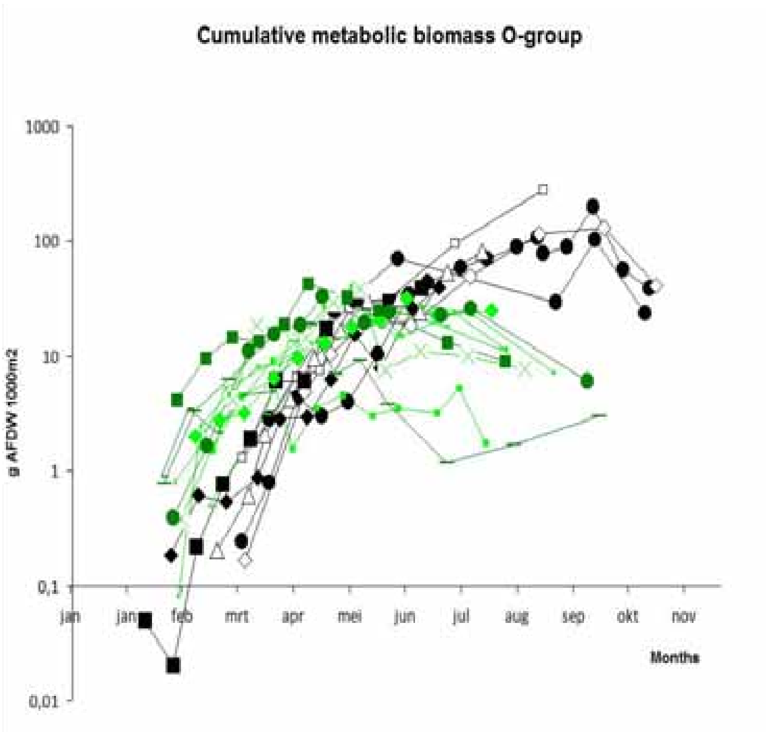

Figure 13. Cumulative metabolic biomass ($\sum n_i W_i^{0.8}$) of O-group plaice at Balgzand in g AFDW per 1000m2 1975-1988 (black), 1989-2007 (green).

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