Population dynamics of an intertidal 0-group flounder *Platichthys flesus* population in the western Dutch Wadden Sea

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ABSTRACT: Larval immigration and subsequent settlement, abundance fluctuations, growth, and mortality of a 0-group flounder population were studied in a tidal flat area, the Balgzand, in the western Wadden Sea. Larvae entered the area from early April to early May. The first settled flounder were found about 1 mo after larval immigration started. Settled flounder were restricted to the siltier areas of the tidal flats. Growth did not seem to be food-limited within the density range observed over the years and depended only on prevailing water temperatures. The life history pattern of flounder was similar to that of plaice in the same area: year-class strength was generated in the open sea and after settlement a period of density-dependent mortality followed, most probably due to predation by crustaceans. The instantaneous mortality rate Z during summer seemed to be higher (0 08 d^{-1}) than in plaice (0.03 d^{-1}), probably due to a combination of higher water temperature and higher abundance of predators in summer than during the settlement of plaice in spring. No relationship between the year-class strengths of plaice and flounder was found.

INTRODUCTION

Over the last decades plaice *Pleuronectes platessa* L. has been studied in detail in the western Dutch Wadden Sea. This research concentrated especially on the recruitment mechanisms of plaice during its juvenile stage in the coastal nursery areas, where the larvae settle and spend their first years of life (Zijlstra 1972, Kuipers 1973, 1977, Creutzberg et al. 1978, Rauck & Zijlstra 1978, Zijlstra et al. 1982, Rijnsdorp et al. 1985, van der Veer 1985, 1986, Zijlstra & Witte 1985, van der Veer & Bergman 1986, 1987, Bergman et al. 1988, 1989, van der Veer et al. 1990). The main conclusions of this research were: (1) The year-class strength of plaice is generated during the pelagic egg or larval stages (van der Veer 1986). (2) In spite of the high concentrations of juveniles in relatively small nursery areas and the fluctuations in density between years, food conditions are always optimal for the major part of the population (Zijlstra et al. 1982, van der Veer 1986, Bergman et al. 1987, 1988, van der Veer et al. 1990). (3) Mortality rates during the juvenile stages are low compared to other fish species due to the absence of most potential predators in the sheltered nursery areas (van der Veer et al. 1990). Variability in recruitment to the parent stock is low (van der Veer 1986, van der Veer & Bergman 1987), as a result of a period of density-dependent mortality caused by the brown shrimp *Crangon crangon* in at least the main nursery of plaice, the Wadden Sea.

It is feasible to test whether the above conclusions apply also to the flounder *Platichthys flesus* L., another common flatfish species in the western Wadden Sea (de Vlas 1979). Its life cycle resembles that of plaice. Spawning areas are also located in the open North Sea, and they overlap with those of plaice (Harding et al. 1978). As in plaice, large quantities of small larvae from the North Sea immigrate into the Wadden Sea every year (van der Veer 1985). After immigration, settling in the area occurs (de Vlas 1979). Due to a strong rheotaxis behaviour (Berghahn 1984), settling of larvae has only been observed in the siltier parts of the Wadden Sea (de Vlas 1979), especially near freshwater inlets (Berghahn 1984). Large parts of the settling flounder population are thought to migrate to fresh water (Berghahn 1984), and only part of the population remains in the estuary. Flounder apparently remain in the Wadden Sea for much longer than 3 yr (de Vlas 1979); then they emigrate to deeper waters. While plaice larvae immigrate in March and April, flounder larvae are only found in April (van der Veer 1985). As a

consequence, settlement and growth of flounder start later in the season.

This paper summarizes information on immigration and settlement of pelagic larvae and abundance of 0-group flounder in an intertidal flat area in the western Dutch Wadden Sea, the Balgzand. Distribution, growth, mortality rates and mortality factors of settled flounder are examined and compared with those found for 0-group plaice in the area.

MATERIAL AND METHODS

Study area. The intertidal Balgzand has an area of about 52 km^2 (Fig. 1); it is surrounded by dikes to the south and west and otherwise by 5 to 20 m deep tidal channels. Most of the area consists of barren tidal flats with only a few mussel beds in the northwestern part. Sediment composition of the flats varies from coarse sand in the exposed northern part to fine sands and mud in the sheltered southern areas (Dapper & van der Veer 1981). Median grain size is about 150 μm and mean silt content is about 5 %. For 8 to 10 h of the tidal cycle the flats are submerged and for 2 to 4 h they are exposed. At high water the water depth varies between

Fig 1 Location of the Balgzand tidal flat area in the western Wadden Sea (●) Pelagic sampling station in the Marsdiep inlet, (•) demersal sampling stations

0.8 and 1.5 m, the actual depth depending on prevailing weather conditions. The flats are intersected by numerous small gullies through which the water recedes to the deeper tidal channels during the later phase of the ebb tide.

Plankton sampling. Plankton sampling was carried out from 1979 to 1986 in the deep Marsdiep tidal inlet. Each year 4 to 6 surveys of 1 wk were conducted. Only the midwater stratum (depth 7 to 10 m) was sampled with a net of 14 m length, an opening of 3.1 m^2, a mesh size of 1.4 mm and a filtration area of 51 m^2 (definitions according to Smith et al. 1968). Haul duration was 45 min. For more details see Creutzberg et al. (1978) and Rijnsdorp et al. (1985).

All material was preserved in a 4 % formaldehyde seawater solution and sorted out in the laboratory. Flounder larvae were measured to the nearest mm total length within 3 mo. No correction was made for net efficiency, since a comparison of day and night catches did not suggest an increase in net avoidance with length (van der Veer 1985). For each haul, numbers caught were converted into densities per 1000 m^3 (n 1000m^{-3}) and the arithmetic mean was estimated per sampling date.

The variance consistently surpassed the arithmetic mean, indicating a contagious distribution of the larvae. Confidence limits for such distributions can be computed by using the factors from a logarithmic $(x+1)$ transformation and applying them to the arithmetic mean of the samples (Elliot 1971). For the 95 % confidence limits these factors of the Student's t-distribution range between 2.09 and 2.02, depending on the numbers of hauls made (20 to 40). Therefore, the 95 % confidence limits would lie between 47 and 209 % of the mean.

Demersal sampling. Demersal sampling was originally designed for 0-group plaice (Zijlstra et al. 1982, van der Veer 1986) and consisted of a grid of 36 stations distributed over the Balgzand area (Fig. 1). Sampling was carried out at fixed time intervals between February and October in 1976 to 1982. The fishing gear used was a 1.9 m beam-trawl (mesh size 5 × 5 mm) towed by a rubber dinghy with a 25 hp outboard motor at a speed of ca 35 m min^{-1}, according to Riley & Corlett (1966). Sampling was restricted to a period of 3 h around high water during the day, when the distribution of flatfish appeared to be random on the tidal flats (Kuipers 1977). The length of a haul was assessed with a meter wheel fitted outside the trawl. Each haul sampled a surface area of at least 200 m^2 All material was preserved in 4 % formalin seawater solution and sorted out within a few days From 1979 onwards, flounder were measured to the nearest mm total length class. All numbers caught were corrected for net efficiency, using the plaice data after Kuipers (1975) and Dapper (1978).
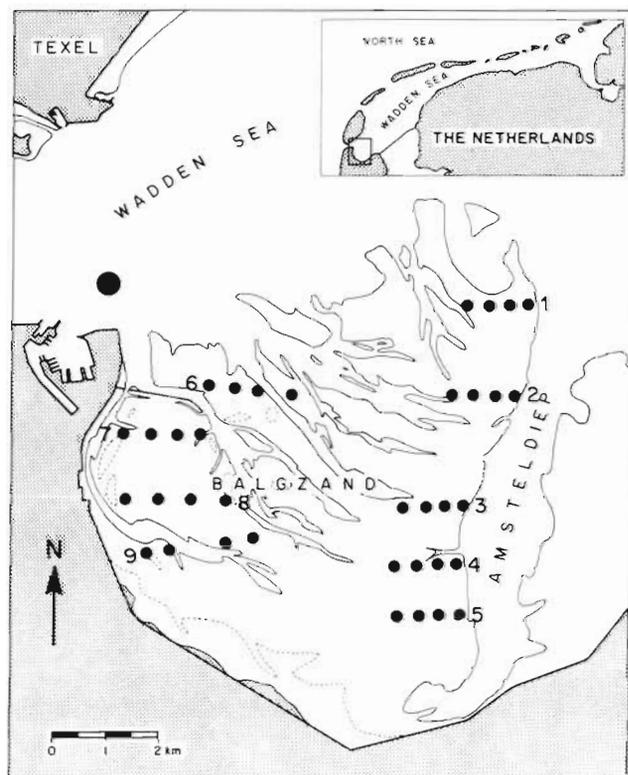
The corrected numbers were converted into densities per 1000 m² (n 1000m⁻²) and the arithmetic mean was calculated for each survey as an index of abundance for the population on the tidal flats at high water. To assess confidence limits of the mean, a number of surveys should be carried out simultaneously, but such data are lacking. Instead, the method developed by Zijlstra et al. (1982) for 0-group plaice was applied. Estimated confidence limits were based on the variation in mean abundance from July onwards, when the population had stabilized. The 95 % confidence limits obtained by this method were estimated at about 45 % of the mean. Statistical treatment of the data sets was restricted to Spearman rank correlation test. Since the various sampling programmes were not always carried out simultaneously, the different tests are based on varying numbers of observations (year).

Predation experiment. Predation experiments with brown shrimps *Crangon crangon* as predators and small 0-group flounder as prey were carried out similarly to the experimental set-up designed by van der Veer & Bergman (1987) for 0-group plaice. In the field the importance of shrimp predation on settled flounder was traced by examining fin damage among the 0-group flounder, indicating unsuccessful predation attempts by *Crangon crangon* (van der Veer & Bergman 1987).

RESULTS

Plankton data

Table 1 shows the mean flood abundance of flounder larvae during the period of immigration for the different years. This period of larval immigration is defined

Table 1. *Platichthys flesus.* Mean flood abundance of flounder larvae in the deep Marsdiep tidal inlet during the period of larval immigration (see text and Fig. 1)

Year	Abundance (n 1000m⁻³)
1974	0.2
1975	11.9
1977	6.9
1980	8
1981	13
1982	7
1983	2.8
1985	37.4
1986	6.0

as the time span between the first and last week when flounder larvae were caught in the plankton during flood tide. The mean weekly catches during that period were averaged and used as mean abundance over the whole period of immigration. Large differences in year-class strength between years were observed at the end of the larval stage: from 0.2 1000m⁻³ in 1974 to 37.4 1000m⁻³ in 1985. The first larvae appeared in the plankton in early April and they remained present until the beginning of May.

Demersal surveys

0-group flounder were absent at the northernmost sampling stations, both in the eastern and western parts of the area (Fig. 1; Transects 1, 2, 3 and 6). They were found in areas with a medium-sized sediment composition or in muddy areas (for sediment composition see Dapper & van der Veer 1981). Fig. 2 shows the
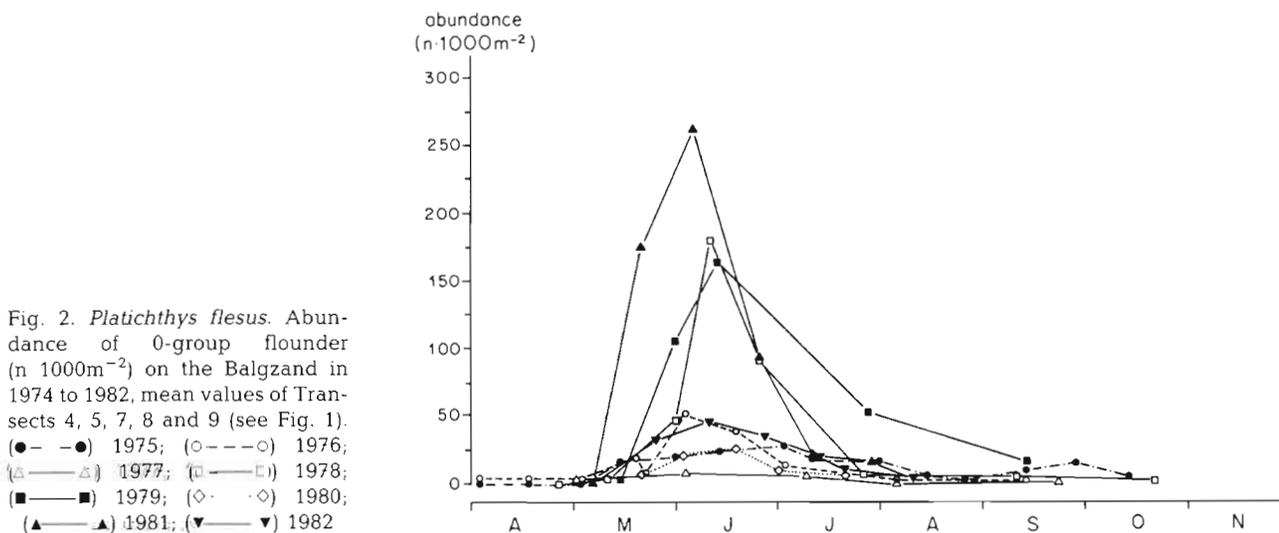
Fig. 2. *Platichthys flesus.* Abundance of 0-group flounder (n 1000m⁻²) on the Balgzand in 1974 to 1982, mean values of Transects 4, 5, 7, 8 and 9 (see Fig. 1). (●– –●) 1975; (○– – –○) 1976; (△———△) 1977; (□———□) 1978; (■———■) 1979; (◇·   ·◇) 1980; (▲———▲) 1981; (▼——— ▼) 1982
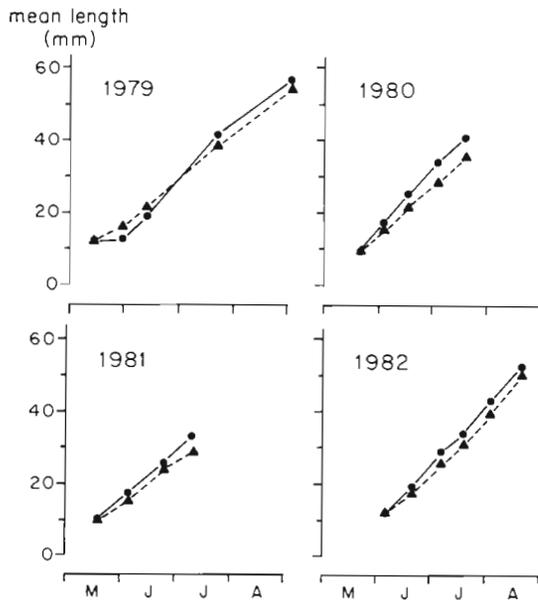
mean length
(mm)

Fig. 3. *Platichthys flesus.* Observed increase (●——●) in mean length of 0-group (mm) flounder in the Balgzand compared with predicted maximum growth (▲———▲) according to a growth model established under optimal food conditions in the laboratory (after Glazenburg 1983) for the years 1979 to 1982

mean abundance of 0-group flounder in the Balgzand area. Only those sampling stations were taken into account where flounder were found, omitting the northernmost sandy stations. In all years considered, the first flounder were not observed until the middle of May, 1 mo after the arrival of the first planktonic larvae. Then, the population increased rapidly, reaching maximum densities in June. These peak values varied considerably, from 10 $1000m^{-2}$ in 1978 to 267 $1000m^{-2}$ in 1981. From June onwards numbers declined, with only low densities after July.

In all years the size-frequency distribution was close to normal and therefore mean length has been estimated for the surveys of 1979 to 1982 (Fig. 3). The mean length in May when the first flounder were found varied from 9.6 mm in 1980 to 12.5 mm in 1981 In all years mean length showed a rapid increase from May onwards. The observed increase in mean length has been compared with a growth model obtained under excess feeding conditions in the laboratory, according to Glazenburg (1983):

$$\Delta L = 1.2T - 7.2 \ (\text{mm mo}^{-1})$$

in which ΔL = length increase in mm mo^{-1}; and T = mean water temperature in °C. Water temperatures were measured simultaneously with fishing (van der Veer 1986, van der Veer & Groenewold 1987). From early May onwards there was a high similarity between

observed and simulated lengths (Fig. 3), suggesting that growth of 0-group flounder was not food-limited in the Balgzand area.

Mortality

The abundance of 0-group flounder will be controlled by settlement, migration and mortality. As in 0-group plaice (Zijlstra et al. 1982), exchange with surrounding deep channels is negligible, because of the isolated location of the area. Due to the time lag between larval immigration and settlement at the Balgzand and the migration of settling larvae to the freshwater environment, the method used by van der Veer (1986) to estimate mortality between 2 successive surveys could not be applied to 0-group flounder.

Instead of a mortality estimate for every 2 wk period, the decrease between peak abundance in June and September was estimated for the different years according to:

$$Z = 1/t \ln (N_0/N_t) \qquad (\text{d}^{-1})$$

in which Z = instantaneous mortality rate (d^{-1}); t = time interval in days between June and September; and N_0 and N_t are the abundance estimates at respectively t_0 (June) and t_t (September). Relating the instantaneous mortality rate with the initial abundance resulted in a significant positive correlation between the two (Fig. 4) (r_s = 0.60; $p < 0.05$). Since abundance and mortality are not independent variables, it cannot be excluded that part of the correlation originates from statistical effects. However, for 0-group plaice in the same area, an independent estimate of the relation between mortality and density showed that statistical effects were negligible (van der Veer 1986, van der Veer & Bergman 1987).
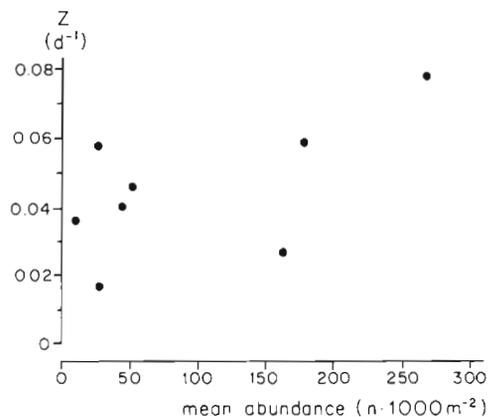

Fig. 4. *Platichthys flesus.* Daily instantaneous mortality rate Z (d^{-1}) between peak abundance and 1 September in relation to density at peak abundance (n $1000m^{-2}$)

Table 2. Predation rate (n 12h⁻¹) of 10 shrimps *Crangon crangon* on 10 0-group flounder *Platichthys flesus* under experimental conditions in darkness at 18°C. For more details see van der Veer & Bergman (1987). Mean values of at least 3 replicates

Shrimp size	0-group flounder	
	16–20 mm	31–35 mm
21–25 mm	0	0
41–45 mm	5	0
61–65 mm	7	0

The results of the predation experiments with *Crangon crangon* as predators are shown in Table 2. As in plaice, *C. crangon* was able to prey upon small 0-group flounder. The minimum size for shrimps to feed on 0-group flounder was between 25 and 41 mm. Flounder larger than about 30 mm were no longer vulnerable to this type of predation. Fig. 5 shows the mean percentage of the 0-group flounder population with fin damage at high water at the Balgzand. In early June 65 % of the population showed one or more points of fin damage. In June, this fraction decreased and from early July onwards no fin damage was found.

DISCUSSION

Larval abundance, immigration and settlement

The spawning grounds of flounder that supply the western Wadden Sea with larvae are located in the Southern Bight of the North Sea, as is the case for plaice
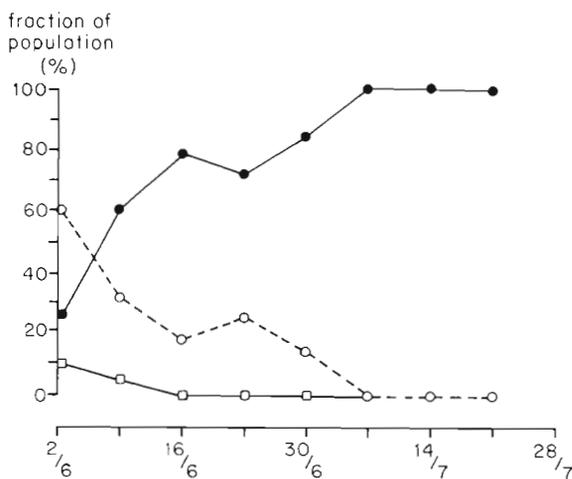

Fig. 5. *Platichthys flesus*. Mean percentage of 0-group flounder population at the Balgzand at high water in 1982 with respectively 0 (●——●), 1 (○－－－○) and 2 cases (□——□) of fin damage (n ≥ 100)

(see Houghton & Harding 1976). No information is available on larval transport from the spawning grounds towards the coastal zone, but a similar process as in plaice is assumed: passive transport in the plankton by the residual currents in a northeasterly direction (Cushing 1990), followed by selective transport by tidal currents into the Wadden Sea, as found for plaice by Rijnsdorp et al. (1985) and Bergman et al. (1989). Inside the area they maintain their position by positive rheotaxis (Berghahn 1983). The immigration of flounder does not start until early April, i.e. 1 mo later than plaice (van der Veer 1985). In early May, the immigration of both plaice and flounder larvae is abruptly terminated by the outburst of predatory coelenterates such as the ctenophore *Pleurobrachia pileus* and the scyphomedusa *Aurelia aurita* (van der Veer 1985). This means that the process of larval immigration is restricted to about 1 mo in flounder, compared with about 2 mo in plaice. Nevertheless, every year the western Wadden Sea is supplied with more flounder than plaice larvae, because the shorter period of immigration is amply compensated for by a much higher abundance (van der Veer 1985).

Little is known about the process of larval settling. There are some laboratory observations suggesting that as in plaice the search for food by the hungry larvae is the key factor (Creutzberg et al. 1978). There is a time-lag of about 1 mo between larval immigration and subsequent appearance in the demersal samples, which suggests that initial settling occurs in other areas. Before 1932, Lake IJssel, then known as the Zuiderzee, was still a major part of the western Wadden Sea where flounder could be found almost anywhere, even at very low salinities. Probably, initial settling of larval flounder still takes place in silty areas of low salinity close to the sluices where freshwater from Lake IJssel is discharged, as has been found by Berghahn (1984) in the German Wadden Sea and by Summers (1980) in a Scottish bay. After settlement an important part of the population is transported to Lake IJssel, as can be concluded from the high numbers found in fykes later in the year (Hortensius pers. comm.), and a part spreads out over the siltier tidal flats.

The relatively large size of the 0-group flounder that appear on the Balgzand, compared with the larval size, suggests that migration movements at relatively small sizes already occurred shortly after settlement. After their appearance on the tidal flats, part of the population migrate with ebb tide to the tidal gully (van der Veer & Groenewold 1987). The rest need about 4 to 6 wk to develop tidal migration movements, as do plaice (van der Veer & Bergman 1986). It is unknown to what extent juvenile flounder suffer from the unsuitable environmental conditions of high temperatures and low oxygen concentrations on the tidal flats at low water in July–August (van der Veer & Bergman 1987).

Demersal abundance

The seasonal pattern of abundance of 0-group floun-
der resembles that of 0-group plaice on the Balgzand
(Zijlstra et al. 1982, van der Veer 1986): increasing
densities up to a maximum, followed by a sharp
decrease to low numbers during the rest of the year.
The different timing of the larval immigration of floun-
der also results in a time-lag of about 1 mo between the
peak densities of flounder and plaice: June vs May
(van der Veer 1986), a period also observed in the
German Wadden Sea (Berghahn 1987).

Although larval abundance of flounder exceeds that
of plaice, densities of settled flounder are lower than
those of plaice. 0-group plaice are found throughout
the area, while 0-group flounder are restricted to the
siltier parts. In the areas sampled plaice are more
abundant, mainly because of the migration of a major
part of the larval flounder to fresh waters (Berghahn
1984).

If the general rule of decreasing mortality in fish with
increasing size applies (Cushing 1974), flounder will be
more vulnerable to predation than plaice during larval
immigration (flounder 8 mm; plaice 13 mm). There are
strong indications that flounder suffer heavy predation
by coelenterates in the plankton (van der Veer 1985).
As soon as the outburst of predatory coelenterates is
observed in early May, immigration of both plaice and
flounder ceases. After settlement, mortality among 0-
group plaice is rather low, except for a short period
directly after settlement, when a strong and density-
dependent predation by crustaceans, mainly the brown
shrimp *Crangon crangon*, is observed (van der Veer &
Bergman 1987). Plaice are preyed upon by shrimps
until they reach a size of about 30 mm (van der Veer &
Bergman 1987). Because shrimps occur throughout the
Balgzand area (Kuipers & Dapper 1984), flounder also

are believed to suffer this predation. Predation by
shrimps can be assessed either by stomach content
analysis of crustaceans, which is very time-consuming,
or by examining the fins of flounder In plaice preda-
tion by shrimps was not always successful and unsuc-
cessful predation attempts by shrimps resulted in
characteristic patterns of fin damage (van der Veer &
Bergman 1987), which were also observed in flounder.
Shrimps are able to prey upon flounder under labora-
tory conditions and presumably also in the field. There-
fore, shrimp predation will also be a major mortality
factor in 0-group flounder. Mortality due to food shor-
tage does not seem likely, because in all years of
observation length increases in the field were as large
as predicted by a maximum growth model established
under excess feeding conditions in the laboratory.

Mortality estimates among the 0-group flounder
might be biased by migration of juvenile flounder to
fresh water. However, the fact that in summer densities
stabilized when the flounder had reached a size of 3 cm
and were 'safe' from shrimp predation suggests that
mortality is the main factor causing the decrease in
numbers during summer. Mortality estimates among
the 0-group flounder could not be calculated over
biweekly periods as for 0-group plaice (van der Veer
1986), but only between the different years. In this way,
the summer mortality between years was density-
dependent, suggesting some regulation of the flounder
population. This supports the observed reduction in
between-year variation in abundance during summer.
Mortality among flounder is about 3 times as high as
among plaice. A comparison of mortality in various
nurseries around the North Sea showed a relation
between temperature and mortality in 0-group plaice
(van der Veer et al. 1990). This could suggest that 0-
group flounder also may suffer a higher mortality than
0-group plaice at Balgzand due to the higher water

Table 3. *Platichthys flesus*. Mean abundance during the larval (n 1000m^{-3}) and demersal stage (n 1000m^{-2}) together with the coefficient of variation (%). Wadden Sea data are from the international Demersal Young Fish Surveys (DYFS), put at our disposal by Rijnsdorp, RIVO IJmuiden

	Abundance	Coefficient of variation	No. of observations
Pelagic stage			
Larval abundance near Wadden Sea	50.0	172	9
Demersal stage			
Year-class index of 0-group at Balgzand at settling	95.6	99	8
Year-class index of 0-group at Balgzand in September	6.2	80	8
Year-class index of I-group in Wadden Sea in spring	1.14	80	12

temperatures and the higher shrimp abundance (van der Veer & Bergman 1987).

Year-class strength determination

Recruitment, defined as the number of juveniles joining the parent stock, can be studied by comparing estimates of abundance during various life stages over a number of years according to Beverton (1984) and van der Veer (1986). The trends in variability of these abundance estimates during the early life stages give an impression of periods of density-dependent and density-independent mortality processes and of the period in which year-class strength is determined. Periods of density-dependent processes are characterized by a decrease in between-year variability between successive life stages. The period in which year-class strength is determined is characterized by the fact that from that moment onwards, abundance estimates of that life stage are related to the ultimate recruitment (van der Veer 1986), and in plaice this period corresponds also with maximum variability between years (van der Veer 1986).
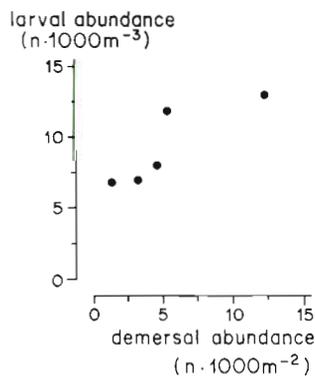
larval abundance
(n·1000m^{-3})

Fig. 6. *Platichthys flesus*. Relationship between abundance of settled 0-group flounder (n 1000m^{-2}) in August on the Balgzand and mean larval flood abundance (n 1000m^{-3})
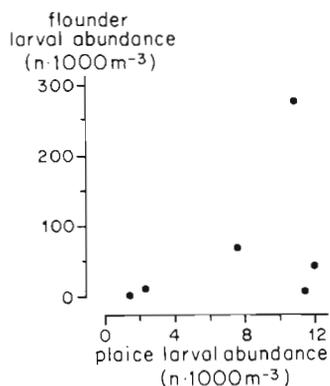
flounder
larval abundance
(n·1000m^{-3})

Fig. 7. Relation between mean larval flood abundance of plaice and flounder (n 1000m^{-3})

Table 3 shows estimates of mean abundance at various life stages of 0-group flounder together with an index of variability between years, the coefficient of variation, defined as standard deviation divided by the mean as percentage. This coefficient measures the relative dispersion, independent of the units. The pattern in the year-to-year variation during early life phases of 0-group flounder appears to be similar to that in 0-group plaice (van der Veer 1986): a decrease in variation from the pelagic egg and larval stages until autumn, suggesting some density-dependent regulation during this period. No information is available on the adult spawning stock. However, in plaice this variation remains the same after the first year of life (van der Veer 1986). Assuming the same for flounder, this would mean an annual variability in spawning stock biomass of about 80 %. In comparison with a coefficient of variation of 170 % during larval immigration, this suggests that the year-class strength of flounder is generated during the pelagic egg or larval stages, as in plaice (van der Veer 1986). This is further supported by the significant relationship ($r_s = 1.0$; $p < 0.05$) between mean larval flood tide abundance and density of 0-group flounder in August (Fig. 6). In plaice a much lower year-to-year variability in year-class strength during the pelagic stages has been generated, about 60 % (van der Veer 1986) compared with 170 % in flounder. There is no explanation for this difference.

In conclusion, 0-group flounder and plaice have a similar life history. In both species year-class strength is generated during the pelagic stages, but the year-class strength of plaice and flounder shows no relationship (Fig. 7) ($r_s = 0.37$; ns). After settlement of flounder some regulation of the population seems to occur, most probably caused by shrimp predation, as in plaice. Despite the concentration of high numbers in a relatively small area, growth conditions always were optimal. Differences between the 2 species might be attributed to a different timing in spawning and larval arrival in the nursery.

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