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# Recruitment variability in dab (*Limanda limanda*) in the southeastern North Sea

Loes J. Bolle[a,b,*], Adriaan D. Rijnsdorp[a], Henk W. van der Veer[b]

[a]*Netherlands Institute of Fisheries Research (RIVO–DLO), PO Box 68, 1970 AB IJmuiden, The Netherlands*
[b]*Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands*

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**Abstract**

Data from three annual surveys, covering inshore and offshore waters of the southeastern North Sea, were analysed to study recruitment variability in dab (*Limanda limanda*) over the period 1978–1997. Geometric mean abundance of 0- to 5-group dab was estimated using general linear models. Juvenile dab (0- and 1-group) were found over the entire area, from inside the estuaries to 50 m depth offshore. Environmental conditions (water temperature, wind stress, turbidity) affected the catch rates. The potential errors in the estimates of year-class strength, caused by differences in catchability, are discussed. The inter-annual pattern of year-class strength appeared to be established between ages 1 and 2, suggesting that factors determining recruitment are not restricted to the pelagic early life phase only, but also operate during the demersal juvenile phase. Recruitment variability at age 2 was in the order of 50–60% and appears to be equal to, or lower than, recruitment variability in plaice and sole. These results contradict expectations based on the concentration hypothesis, which states that the degree of variation in recruitment is inversely related to the degree of concentration during early life phases. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords*: Recruitment; Year-class strength; Dab; *Limanda limanda*; North Sea

## 1. Introduction

The classical stock-recruitment models assume that at higher stock levels, recruitment in marine fish stocks is independent of the parent stock size (Beverton and Holt, 1957), or even inversely related with the parent stock (Ricker, 1954). This implies that density-dependent regulation occurs between spawning and recruitment. However, recruitment variability (synonymous with variability in year-class strength at a specified age) is a pervasive feature of the population dynamics of many marine fish species and largely caused by density-independent factors. Year-class strength in marine fish species seems to be established during the pelagic egg and larval stages (Leggett and DeBlois, 1994).

The study of recruitment level and variability in flatfish in the North Sea has mainly focussed on plaice *Pleuronectes platessa* (Zijlstra et al., 1982; Van der Veer, 1986; Van der Veer and Witte, 1999; Van der Veer et al., 2000) and sole *Solea solea* (Rijnsdorp et al., 1992). For plaice, year-class strength seems to be determined at the time when metamorphosing larvae enter the coastal nurseries such as the Wadden Sea (Bannister et al., 1974; Rijnsdorp et al., 1985; Van der Veer, 1986) or shortly thereafter (Nash and Geffen, 2000). Density-dependent processes only

* Corresponding author.
*E-mail address:* loes@rivo.wag-ur.nl (L.J. Bolle).


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fine-tune year-class strength during the first weeks after settlement (Van der Veer, 1986). However, when recruitment data from all nursery areas, including both sheltered estuarine areas and open coastal nurseries, were pooled, density-dependent mortality was observed to be present throughout the time spent in the nurseries (Beverton and Iles, 1992). For sole, recruitment also appears to be determined in the pelagic and the early demersal phase, although additional mortality in older fish during cold winters may further adjust recruitment (Rijnsdorp et al., 1992).

Plaice and sole exhibit a clear spatial segregation of juveniles and adults. The demersal 0-group stages are found exclusively in shallow water (Zijlstra, 1972; Van Beek et al., 1989). In this respect these species differ from dab (*Limanda limanda*) and solenette (*Buglossideum luteum*), the two most abundant flatfish species in the southern North Sea (Daan et al., 1990). Solenette does not have distinct nurseries, and the distribution of juveniles and adults is broadly the same (Baltus and Van der Veer, 1995). Although densities of 0-group dab are highest in shallow coastal waters, settlement is not restricted to these areas. Both coastal and offshore areas contribute to the overall recruitment of dab (Bolle et al., 1994). These two species with offshore recruitment meet different environmental factors during their early life phases, and therefore the processes responsible for recruitment variations and the life phase in which year-class strength is determined might differ from species with distinctly segregated coastal nurseries. Beverton (1995) suggested that the degree of variation in recruitment might be inversely related to the degree of concentration during early life phases. If true, one would expect a higher variability in recruitment in dab compared to plaice and sole.

We examine the recruitment pattern of dab in the southeastern North Sea. The major goals are to determine the age at which year-class strength is established, and to estimate the level and the variability of recruitment. The results are discussed in relation to the patterns reported for plaice and sole.

## 2. Material and methods

### 2.1. Surveys

Data from three ongoing annual beam-trawl surveys were used to obtain abundance estimates for dab. The Demersal Young Fish Survey (DFS) and the Sole Net Survey (SNS) started in 1970, the Beam Trawl Survey (BTS) in 1985. The three surveys covered different geographical areas, with a considerable overlap in the coastal zone. Together they comprise the entire southeastern North Sea and the adjacent estuaries (Fig. 1). Although these surveys were originally designed to estimate the abundance of (juvenile) plaice and sole, they also provide valuable information on other fish species. Catch rates and size frequency distributions have been recorded for all fish species since the onset of the surveys, and otolith samples have been taken for many species, including dab, since 1978.

The DFS is carried out in September–October and covers the shallow coastal and estuarine waters from the Dutch–Belgian border to Esbjerg in Denmark (Fig. 1). Most hauls are within the 20-m depth contour and the few observations in deeper waters have been eliminated from this analysis. The minimum fishing depth is approximately 2 m because of the draught of the three research vessels used. Thus, only the tidal channels in the Scheldt estuary and the Wadden Sea are sampled. The sampling stations are stratified by depth and area, and these areas have been combined to eight regions (Fig. 1) for the analysis. The vessel sampling the coastal waters has changed several times, but the gear (6 m beam trawl with a bobbin rope and one tickler chain; cod-end stretched mesh size: 20 mm) has not been altered and the gear-efficiency is presumed to be unchanged. The estuarine vessels use a 3-m version of the same trawl. Standard haul duration is 15 min at a towing speed of approximately 1.5 m s$^{-1}$. Data from 1978 to 1997 have been analysed, resulting in a total of 5204 hauls (Table 1).

The SNS is also carried out in September–October. This survey consists of more or less fixed stations on transects which run parallel or perpendicular to the coast in Dutch and Danish waters (Fig. 1). The Danish coast north of Esbjerg was surveyed in the years before 1991 using slightly different gear, but these data are not included in the analysis. The SNS covers a depth range from 10 to 40 m. The survey area has been divided into four regions, which correspond with the DFS regions (Fig. 1). The gear used is a 6-m beam trawl with a standard ground rope and four tickler

Table 1
The number of hauls per year and survey, together with the number of otoliths examined each year for age determinations

| Year | Hauls | | | Otoliths |
|---|---|---|---|---|
| | DFS | SNS | BTS | |
| 1978 | 247 | 62 | | 421 |
| 1979 | 231 | 61 | | 200 |
| 1980 | 255 | 57 | | 166 |
| 1981 | 235 | 56 | | 164 |
| 1982 | 270 | 61 | | 169 |
| 1983 | 250 | 56 | | 194 |
| 1984 | 265 | 64 | | 271 |
| 1985 | 263 | 60 | 60 | 570 |
| 1986 | 266 | 63 | 59 | 517 |
| 1987 | 265 | 61 | 64 | 300 |
| 1988 | 254 | 57 | 82 | 503 |
| 1989 | 266 | 56 | 82 | 544 |
| 1990 | 261 | 51 | 94 | 664 |
| 1991 | 267 | 46 | 98 | 625 |
| 1992 | 262 | 55 | 97 | 626 |
| 1993 | 266 | 50 | 100 | 1196 |
| 1994 | 259 | 61 | 91 | 479 |
| 1995 | 271 | 56 | 87 | 460 |
| 1996 | 294 | 57 | 87 | 436 |
| 1997 | 257 | 55 | 83 | 469 |
| Total | 5204 | 1145 | 1084 | 8974 |

chains and a cod-end stretched mesh size of 40 mm. Standard haul duration is 15 min at a towing speed of approximately 2.0 m s$^{-1}$. A total of 1145 hauls were carried out during 1978–1997 (Table 1).

The BTS has been conducted annually in August–September since 1985 and covers the southeastern North Sea and a depth range of 11–53 m (Fig. 1). The sampling stations are stratified by ICES rectangles, which have been combined to three regions (Fig. 1) for the analysis. The BTS uses an 8-m beam trawl with a standard ground rope and eight tickler chains; the cod-end stretched mesh size is 40 mm. Standard haul duration is 30 min at a towing speed of approximately 2.0 m s$^{-1}$. The data for 1985–1997 represent a total of 1084 hauls (Table 1).

In all three surveys, the entire catch or a sub-sample is sorted by haul and a representative sample of each species is measured (total length) to the cm below. Otolith samples are collected by area and cm class

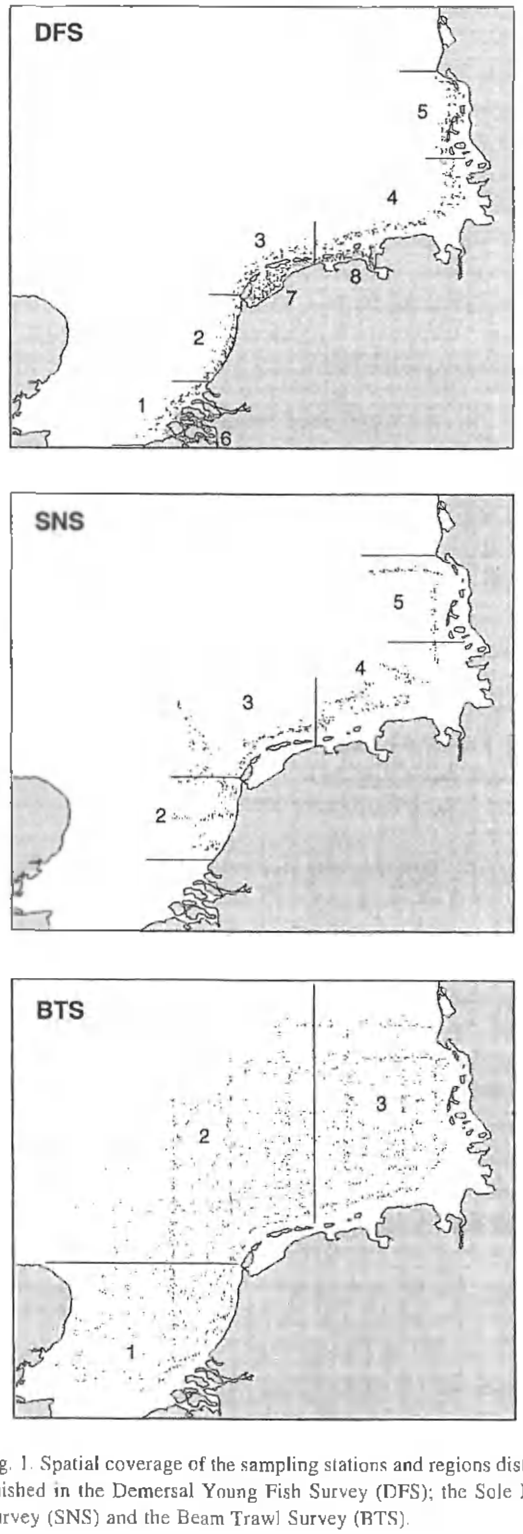



Fig. 1. Spatial coverage of the sampling stations and regions distinguished in the Demersal Young Fish Survey (DFS); the Sole Net Survey (SNS) and the Beam Trawl Survey (BTS).

(with a minimum of 10 cm). The total number dab otoliths examined per year are listed in Table 1.

Wind force, wind direction and surface water temperature are measured during all surveys. Turbidity is measured with a Secchi disc in the Wadden Sea and the Scheldt estuary. In principle, these variables should be recorded for each haul, but unfortunately data are missing for a large number of hauls.

### 2.2. Data analysis

Age was determined from otoliths by counting the opaque bands using two different preparation techniques: the break and burn method (Blacker, 1974) and the thin transversal section method (Bedford, 1983). The size frequency distribution of dab < 10 cm was split into 0- and I-group by eye because of the more or less discrete size range of 0-group. Area-specific age-length keys were established for each year, and used to convert the size frequency distributions into age compositions. The reliability of the age-length keys decreases with age because of lower catch rates and larger size ranges of the older age groups. Therefore, older age groups have been combined into a 5+ group (DFS and SNS) or a 6+ group (BTS).

For the DFS, the numbers caught per haul were converted into numbers per square km, thus implicitly assuming that the 6-m beam trawl catches twice as many fish as the 3-m beam trawl. The BTS and SNS catches per haul were converted to numbers per fishing hour. Since the relative gear efficiencies are unknown, the catch rates of the different surveys cannot be converted into one standard.

A general linear model of log-transformed catch rates is used for the statistical analysis of the variation in catch rates and for the calculation of geometric means. Log-transformation was necessary because the data have a lognormal distribution and the independent factors have a multiplicative rather than an additive effect on abundance. The geometric mean catch rate per year, region and depth class is estimated, for each age group and survey separately, using the following model:

$$^{e}\log(C_{S,A} + 1) = Y + R + D + Y^{*}R + Y^{*}D + R^{*}D, \quad (1)$$

in which $C$ = catch rate, $S$ = survey, $A$ = age group, $Y$ = year, $R$ = region and $D$ = depth class. The regions (Fig. 1) are aggregations of smaller geographical sampling strata. The depth classes correspond with 5 m (DFS) or 10 m, (SNS and BTS) depth intervals.

The environmental factors wind, temperature and turbidity have not been recorded for all hauls and therefore only a subset can be used to test the significance of these factors in affecting catch rates. Because extreme weather conditions do not occur each year, the effects may be aliased by the factor year. Therefore, the significance of the environmental factors is tested in a model without the factor year:

$$^{e}\log(C_S + 1) = A + R + D + A^{*}R + A^{*}D + Te + Tu + Wi + A^{*}Te + A^{*}Tu + A^{*}Wi \quad (2)$$

in which $C$ = catch rate, $S$ = survey, $A$ = age group, $R$ = region, $D$ = depth class, $Te$ = temperature, $Tu$ = turbidity (Secchi disc), $Wi$ = wind stress = wind force * wind direction. Preliminary analysis showed that wind force or wind direction alone hardly affect the catch rates; therefore only the interaction term between these two variables has been included in the model. Because the effect of environmental factors on catch rates may differ between estuarine and coastal areas, the DFS results were analysed separately for the estuaries (regions 6–8) and for the coastal zone (regions 1–5).

The major objective of the analysis is to obtain estimates of the relative year-class strength at different ages, which in principle are provided by the geometric means calculated in model 1. However, estimates of year-class strength may be confounded by differences in catchability between years. Catchability may be affected by the environmental factors included in model 2. Correcting for their effect by inclusion in model 1 is not possible, because of lacking data and potential aliasing. The statistical significance of year of capture versus year of birth was assessed by stepwise including either year or year-class and both year and year-class in the following model:

$$^{e}\log(C_S + 1) = A + R + D + A^{*}R + A^{*}D + YC + YR, \quad (3)$$

in which $C$ = catch rate, $S$ = survey, $A$ = age group,

$R$ = region, $D$ = depth class, $YC$ = year-class and $YR$ = year.

## 3. Results

### 3.1. Distribution patterns

The abundance of all age groups varies significantly between regions and depth classes (Table 2). Region has a stronger effect than depth for all age groups, with the exception of 0-group in the SNS and BTS. Distribution patterns vary inter-annually and depth distributions vary between regions. The overall depth and geographic distributions (Fig. 2) indicate that the BTS and SNS underestimate the abundance of 0-group fish in comparison to the older age groups. 0-group dab occurs over the whole depth range sampled by the surveys, but the highest densities are observed in shallow waters <20 m. Peak abundance of 1-group dab occurs in the 10–20 m depth bands according to the DFS and the BTS, but the SNS does not show a clear peak in abundance. In the BTS, the 2-group and older are most abundant in the 20–30 m depth band, whereas in the SNS the abundance of these age groups increases with depth.

Relatively high densities of 0- and 1-group dab are observed in all coastal regions (regions 1–5) during the DFS. All age groups are less abundant in the estuaries (regions 6–8) than in the coastal regions. In shallow waters (DFS) 1-group dab is equally abundant in the different parts of the coastal zone, whereas in deeper waters (BTS and SNS) the abundance seems to increase from south to north. The abundance of the 2-group and older in coastal waters also clearly increases from south to north.

### 3.2. Environmental conditions

Wind stress and temperature significantly affect the catch rates in all surveys (Table 3). Turbidity has only been measured in the estuaries, and also has a significant effect on the DFS catches. These environmental conditions only explain a small proportion of the total variance (2–7%). However, compared to the variance explained by the other factors in the model, wind stress and temperature have a stronger influence on the catch rates in the estuarine areas of the DFS (16%) than in the SNS, the BTS and the coastal regions of the DFS (5–6%).

The relationship between environmental factors and catch rates has been examined separately for various surveys, regions and age groups. A selection of these relationships is presented in Fig. 3. The top panels show the relationship between catch rates (all age groups combined) and wind stress (for four wind directions separately) for the SNS and the Wadden Sea region of the DFS. East to northeasterly winds negatively affect the abundance estimates in the Wadden Sea, while strong west to southwesterly winds have a positive effect. The SNS catch rates slightly decline with increasing wind force, and with strong winds catch rates are slightly lower if the wind comes from north to northwest.

The catch rates in the Wadden Sea are strongly negatively correlated with temperature (left middle panel). Such an inverse relationship between catch rates and temperature was also very clear in the Scheldt estuary, but less so in the coastal regions of the DFS. In the BTS, the catch rates of 0- and 1-group dab increase, whereas the catch rates of older dab decrease with increasing temperature (right middle panel), which is similar to the pattern observed in the SNS.

Turbidity has only been measured in the Wadden Sea (lower panel) and the Scheldt estuary. Maximum catch rates were reached in waters with a visibility of 1–1.5 m) and the effect was similar in both regions. Turbidity and wind force are significantly correlated ($R^2 = 0.46$; $P = 0.004$), stronger winds causing more turbid waters.

### 3.3. Inter-annual variability

The inter-annual variations in catch rate (model 1) were significant for all age groups in all three surveys (Table 2). To test if these differences are related to year of capture or year of birth, all age groups are combined in one model (model 3). Table 4 shows the proportion of variance (sequential sums of squares) explained by these two factors. Both year of capture and year of birth significantly affected the abundance estimates of dab, year class having a stronger effect in the SNS and BTS and year of capture in the DFS. The colinearity, which quantifies the proportion of the variance that can be explained by

Table 3
Statistical evaluation of the influence of age (*A*), region (*R*), depth class (*D*), water temperature (*Te*), turbidity (*Tu*) and wind stress (*Wi*) on the catch rates of dab in the various surveys (ANOVA table of model 2, for more information see text). (**$P < 0.01$; *$P < 0.05$; ns $P \geq 0.05$)

| Source | DFS-estuaries | | | | DFS-coast | | | | SNS | | | | BTS | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DF | seq. SS | F | $R^2$ | DF | seq. SS | F | $R^2$ | DF | seq. SS | F | $R^2$ | DF | seq. SS | F | $R^2$ |
| Model | 124 | 56798 | 63 | 45% | 99 | 54170 | 61 | 46% | 89 | 11646 | 49 | 50% | 119 | 20988 | 74 | 59% |
| Error | 9330 | 68350 | | | 7075 | 63761 | | | 4430 | 11788 | | | 6048 | 14479 | | |
| Total | 9454 | 125149 | | | 7174 | 117931 | | | 4519 | 23434 | | | 6167 | 35467 | | |
| *A* | 4 | 44664 | 1524 | ** | 4 | 41425 | 1149 | ** | 4 | 8154 | 766 | ** | 5 | 13700 | 1145 | ** |
| *R* | 2 | 520 | 36 | ** | 4 | 2394 | 66 | ** | 3 | 1168 | 146 | ** | 2 | 3360 | 702 | ** |
| *D* | 3 | 1483 | 67 | ** | 3 | 2169 | 80 | ** | 2 | 64 | 12 | ** | 3 | 139 | 19 | ** |
| *A* **R* | 8 | 737 | 13 | ** | 16 | 4354 | 30 | ** | 12 | 1072 | 34 | ** | 10 | 1559 | 65 | ** |
| *A* **D* | 12 | 496 | 6 | ** | 12 | 1350 | 12 | ** | 8 | 518 | 24 | ** | 15 | 982 | 27 | ** |
| Te | 5 | 3409 | 93 | ** | 4 | 1165 | 32 | ** | 4 | 60 | 6 | ** | 6 | 236 | 16 | ** |
| Tu | 6 | 880 | 20 | ** | – | – | – | – | – | – | – | – | – | – | – | – |
| Wi | 8 | 1592 | 27 | ** | 8 | 760 | 11 | ** | 8 | 159 | 7 | ** | 8 | 126 | 7 | ** |
| *A* *Te | 20 | 1946 | 13 | ** | 16 | 231 | 2 | ns | 16 | 251 | 6 | ** | 30 | 574 | 8 | ** |
| *A* *Tu | 24 | 340 | 2 | ** | – | – | – | – | – | – | – | – | – | – | – | – |
| *A* *Wi | 32 | 732 | 3 | ** | 32 | 321 | 1 | ns | 32 | 199 | 2 | ** | 40 | 312 | 3 | ** |

both factors, is higher in the DFS than in the SNS and BTS.

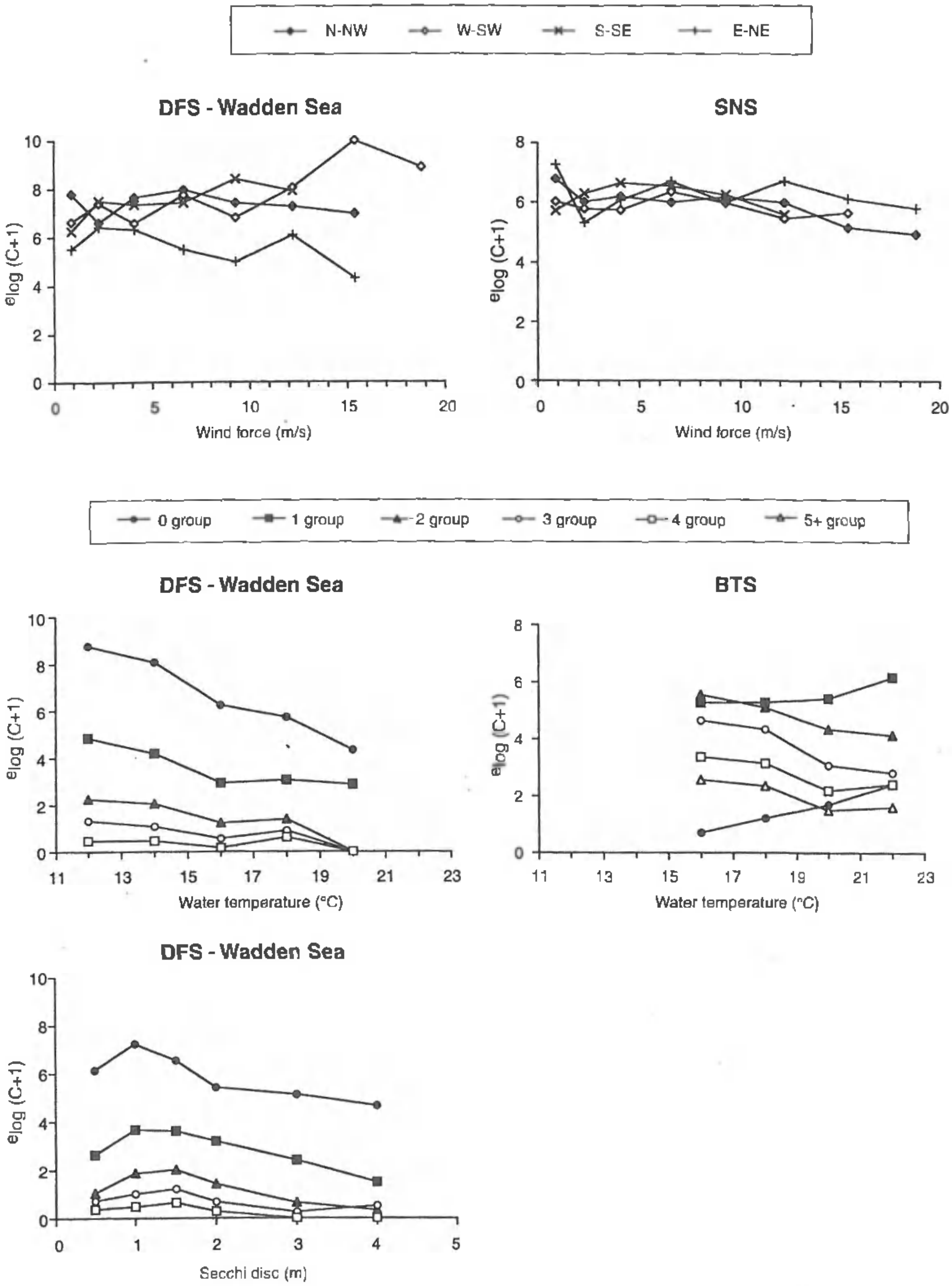
The geometric mean catch rate per year and age group (least square mean estimates of model 1) is plotted as a function of year-class in Fig. 4. 0-group estimates have been omitted for the SNS and BTS, because they were highly underestimated. The general pattern observed in 2-group and older fish is very similar in all surveys. Abundance estimates increase until year-class 1985, remain high up to 1988, followed by a decrease. The abundance of 1-group dab largely follows these trends in parts of the time series, but the 0-group abundance fluctuates without a clear trend.

In some cases, shifts in peaks and valleys indicate clear effects of year of capture: the sudden increase at the end of the SNS curves and relatively high catch rates of several age groups in the DFS in sampling years 1980, 1983, 1988, 1990 and 1997. The effect of sampling year is examined more closely in Fig. 5 by plotting the abundance estimates of 0- and 2-group (DFS) against year of capture. Apparently, the high catch rates in 1988 occurred in the coastal regions, the Scheldt estuary and the Wadden Sea. These were surveyed by three different vessels and thus do not reflect a ship effect. Peaks in catch rates in other years are usually observed in at least two of the three vessels. High surface temperatures tend to correspond with dips in the abundance estimates (Fig. 5). The combined abundance estimates are averages of the eight regions and therefore dominated by the coastal zone catch rates (5 regions). The inter-annual variability in abundance is higher in estuarine regions than in the coastal zone. The abundance of 0-group dab in the estuaries appears to decline from 1979 to 1997.

Table 5 presents the correlations between the relative abundance of a year class at age $= a$ and age $= a + 1$. There is no significant correlation between the abundance at age 0 and at age 1. The abundance at age 2 is significantly correlated with the abundance at age 1 in the DFS, less so in the SNS ($P = 0.047$), and not significantly correlated in the BTS. The abundance estimates at ages 3–5 are significantly correlated to estimates at ages 2–4.

For each survey the geometric mean (least square

Fig. 3. Relationship between geometric mean abundance and environmental conditions (left panels: DFS Wadden Sea; right panels: SNS or BTS): top panels: all age groups combined in relation to mean wind force (m s$^{-1}$) for different wind directions; middle panels: individual age groups in relation to temperature (°C); bottom panel: individual age groups in relation to turbidity (Secchi disc depth in m).


N-NW
W-SW
S-SE
E-NE
DFS - Wadden Sea
SNS
ᵉlog (C+1)
Wind force (m/s)
0 group
1 group
2 group
3 group
4 group
5+ group
DFS - Wadden Sea
BTS
Water temperature (°C)
DFS - Wadden Sea
Secchi disc (m)

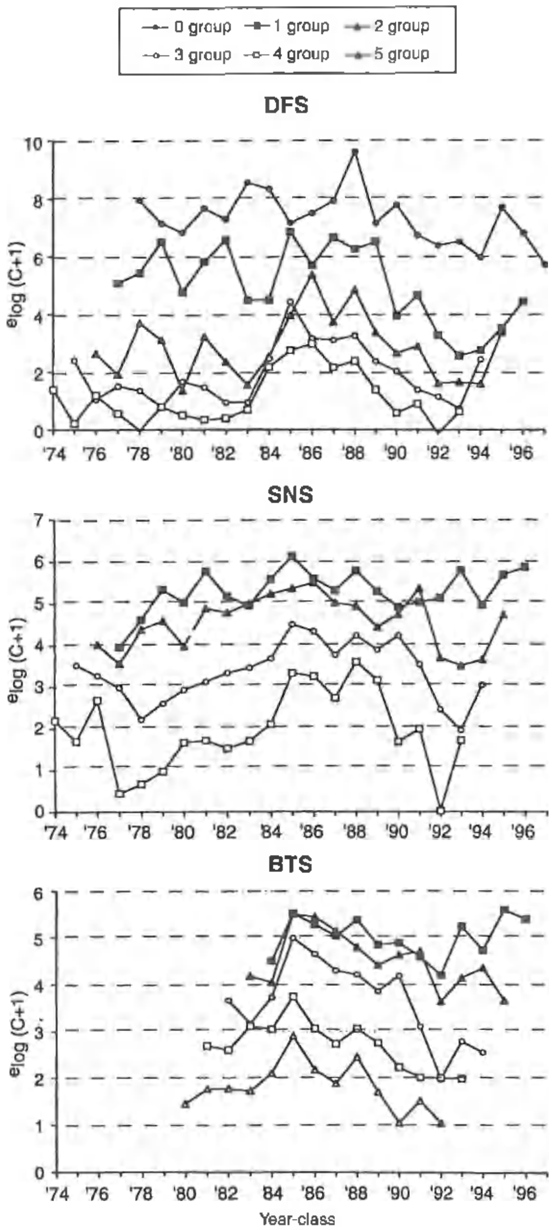



Fig. 4. Geometric mean abundance by age group and year-class for the DFS (top), the SNS (middle) and the BTS (bottom).

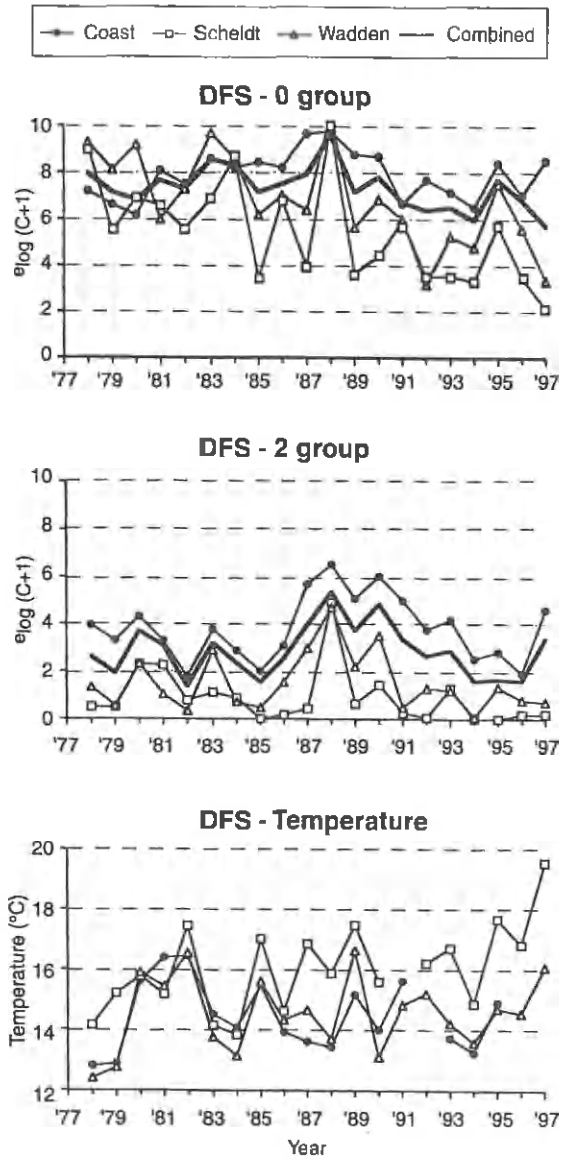



Fig. 5. Geometric mean abundance by year of capture and area for 0-group (top) and 2-group dab (middle) and the mean temperature by area as observed during the DFS (bottom). The areas are the coastal zone: regions 1–5, the Scheldt estuary: region 6 and the Wadden Sea: regions 7–8.

means of model 1) and the arithmetic mean abundance per age group and year class have been averaged to obtain the mean abundance per age group. These means are based on a similar set of year classes for all age groups (DFS and SNS: 1978–1993, $N = 16$ for age groups 0–4; BTS: 1984–1992, $N = 9$ for age groups 1–5). The standard deviation (SD) of the geometric mean, and the coefficient of variation (CV) of the arithmetic mean both quantify the inter-annual variability in year-class strength (Table 6). In each survey, variability in year-class strength is lowest in the youngest age group

Table 4
Statistical evaluation of the influence of sampling year (YR) versus year-class (YC) on the catch rates of dab in the various surveys (summary of ANOVA table of model 3, for more information see text). (**$P < 0.01$; *$P < 0.05$; ns $P \geq 0.05$)

| Source | DFS | | | | SNS | | | | BTS | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DF | seq. SS | F | $R^2$ | DF | seq. SS | F | $R^2$ | DF | seq. SS | F | $R^2$ |
| Total | 26019 | 396084 | | | 5724 | 29412 | | | 6503 | 37164 | | |
| Model | 77 | 199441 | 342 | 50% | 52 | 15423 | 120 | 52% | 52 | 21485 | 170 | 58% |
| YC | 23 | 19430 | 111 | ** | 23 | 1444 | 26 | ** | 17 | 957 | 23 | ** |
| Model | 73 | 201378 | 368 | 51% | 48 | 14853 | 121 | 51% | 47 | 21199 | 182 | 57% |
| YR | 19 | 21367 | 150 | ** | 19 | 874 | 18 | ** | 12 | 671 | 23 | ** |
| Model | 95 | 211476 | 313 | 53% | 70 | 16208 | 99 | 55% | 63 | 22004 | 148 | 59% |
| YC | 23 | 19430 | 119 | ** | 23 | 1444 | 27 | ** | 17 | 957 | 24 | ** |
| YR | 18 | 12035 | 94 | ** | 18 | 785 | 19 | ** | 11 | 519 | 20 | ** |
| Colinearity | | 30% | | | | 4% | | | | 10% | | |

of the survey and tends to increase with age. The overall level of inter-annual variability is higher in the DFS than in the SNS and BTS.

The decline of the geometric mean abundance with age provides an estimate of the total mortality rate. The slopes of the lines fitted through all data points vary from −0.85 in the BTS to −1.71 in the DFS. However, a breakpoint at age 2 is observed in all surveys (Fig. 6). The decrease in abundance until age 2 is above average in the DFS and below average in the SNS and BTS. The slopes after the breakpoint are almost equal in the DFS and BTS (−1.05 and −1.03) and is slightly steeper in the SNS (−1.32).

## 4. Discussion

### *4.1. Nursery grounds*

The survey design of the DFS and BTS (pseudo-random sampling stratified by area and depth) is more suitable to describe the geographic and depth-related distribution of fish than the survey design of the SNS based on transects running parallel or perpendicular to the coast. The latter causes unbalanced sampling for a region and depth class matrix. This is especially a problem for the 30–40 m depth class, in which the geographical coverage is poor. Therefore, more weight should be given to the DFS and BTS results in this respect.

Table 5
For each of the surveys: the correlations between the relative abundance of a year-class at age = *a* and age = *a* + 1. (**$P < 0.01$; *$P < 0.05$; ns $P \geq 0.05$)

| *X* | *Y* | DFS | | SNS | | BTS | |
|---|---|---|---|---|---|---|---|
| | | $R^2$ | *P* | $R^2$ | *P* | $R^2$ | *P* |
| 0 gr | 1 gr | 0.17 | ns | – | – | – | – |
| 1 gr | 2 gr | 0.37 | ** | 0.21 | * | 0.16 | ns |
| 2 gr | 3 gr | 0.39 | ** | 0.52 | ** | 0.72 | ** |
| 3 gr | 4 gr | 0.64 | ** | 0.58 | ** | 0.53 | ** |
| 4 gr | 5 gr | – | – | – | – | 0.81 | ** |

In autumn, juvenile dab (0 and 1-group) occur in the entire survey area, from inside the estuaries to 50 m depth offshore. However, this distribution pattern only partly reflects the distribution at the time of settlement. Inshore movement in autumn is responsible for the occurrence of 0-group dab in the Wadden Sea and increased densities in shallow coastal waters (Bolle et al., 1994; Henderson 1998). The nursery grounds of dab, defined as the areas in which recently settled dab occur, range from shallow coastal waters to offshore waters (Bolle et al., 1994). In this respect, the life history pattern of dab clearly differs from that of plaice and sole, which exclusively use shallow coastal and estuarine areas as nursery grounds (Zijlstra, 1972; Van Beek et al., 1989). Of the different flatfish species, dab seems to have the most extended nursery grounds, which overlap the shallow nursery grounds of plaice and sole and also cover the offshore nursery grounds of solenette and scaldfish (Baltus and Van der Veer, 1995).

Rijnsdorp et al. (1992) drew attention to the relationship between size of the nursery area and level of

Table 6
For each of the surveys and age groups: the inter-annual variability in abundance as measured by the coefficient of variation (CV) of the arithmetric mean and the standard deviation (SD) of the geometric mean

| Age | DFS (1978–1993) | | SNS (1978–1993) | | BTS (1984–1992) | |
|---|---|---|---|---|---|---|
| | CV | SD | CV | SD | CV | SD |
| 0 gr | 0.77 | 0.83 | – | – | – | – |
| 1 gr | 1.31 | 1.30 | 0.39 | 0.40 | 0.49 | 0.43 |
| 2 gr | 1.04 | 1.17 | 0.56 | 0.59 | 0.56 | 0.62 |
| 3 gr | 1.21 | 1.08 | 0.68 | 0.78 | 0.74 | 0.90 |
| 4 gr | 1.51 | 1.00 | 1.01 | 1.01 | 0.74 | 0.57 |
| 5 gr | – | – | – | – | 0.82 | 0.62 |

recruitment in northeast Atlantic sole stocks. They introduced the 'nursery size' hypothesis stating that the recruitment level is related to the size of the nursery grounds. This hypothesis has later been confirmed for plaice (Van der Veer et al., 2000) and further indirect support was provided by Gibson (1994), who found a significant positive correlation between the habitat requirements of juvenile North Sea flatfish species, including dab, in terms of depth range and their abundance. Indeed, the extensive distribution of juvenile dab, in combination with their being by far the most abundant flatfish species in the North Sea (Sparholt, 1990), supports the nursery size hypothesis.

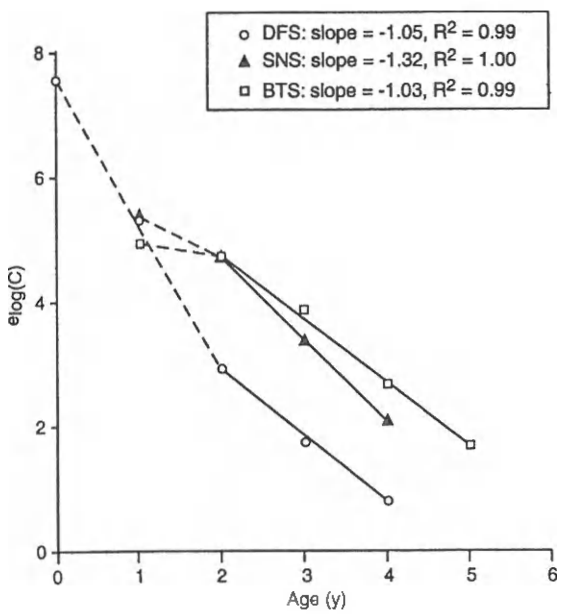



Fig. 6. Plot of geometric mean abundance against age for the DFS, the SNS and the BTS.

### 4.2. Variability in catchability

Annual catch rates can be used as indices of year-class strength if catchability does not vary between years. Variations in environmental conditions may cause variations in catchability because of changes in the gear efficiency or changes in the distribution of fish relative to the survey area. Our results showed that wind stress, temperature and turbidity indeed influence the catch rates of dab, but that these factors only explain a small proportion (2–7%) of the variance.

High temperatures may reduce the gear efficiency because of higher escape rates induced by increased activity, as observed in plaice and flounder (Doornbos and Twisk, 1984). The decline in catch rates with temperature in the DFS (all age groups) and BTS (age group 2 and older) also suggests a reduction in gear efficiency at higher temperatures. However, the increase in catch rates of 0- and 1-group in the BTS suggests that the strong decline of these age groups in the DFS is largely due to dab moving towards deeper water and out of the DFS survey area when temperatures increase.

The relationship between catch rates and turbidity showed reduced catch rates in clear water, possibly owing to enhanced escape possibilities. The peak in DFS catch rates in 1988 coincided with a relatively low water temperature and high turbidity (second highest in the time series).

Wind stress, especially strong winds from the north, is known to affect gear efficiency (Harden Jones and

Scholes, 1980). We observed a significant wind effect in all surveys. In exposed (offshore) areas this may result from its effect on ship motion. Fishermen report a reduced catch rate with strong north to northwesterly winds, but such an effect is only vaguely visible in the SNS. In the sheltered estuarine areas, wind stress is less likely to affect ship motion, but may influence gear efficiency through its effects on turbidity.

The conclusion of the analysis of the effect of environmental factors is that these factors can influence catch rates, especially in the coastal and estuarine areas. Short-term variations may just add to the variance without a major effect on the annual means, but persistent features such as temperature may cause inter-annual variability in catchability that confounds the year-class signal. Although year of capture, as well as year of birth, has a significant effect on the catch rates of dab in all three surveys, the analysis of variance clearly shows that the inter-annual variations in offshore waters (SNS and BTS) are mainly determined by variability in year-class strength. However, in coastal and estuarine waters (DFS), a great deal of the inter-annual variability can be explained by both factors (colinearity = 30%). Therefore, it remains unclear if the long-term trends are due to year or year-class effects. Taking into account the patterns observed in the other surveys it is concluded that the trends are due to year-class rather than sampling year. The peaks and dips super-imposed on the trends in the DFS show a stronger correlation with year than with year-class. The inverse patterns observed in the time series of temperature and catch rate strongly suggest that inter-annual variations in temperature cause the year effect observed in the DFS.

### *4.3. Recruitment variability*

The plots of year-class strength and the correlations between consecutive age groups suggest that the pattern of relative year-class strength is largely fixed at age 2. However, it is unclear whether or not this pattern is already established at age 1, because the three surveys provide inconsistent results. This could be caused by varying degrees of redistribution of 1-group fish among the different areas surveyed.

The coefficient of variation of year-class strength is lowest in the youngest age group of each survey (0-group in the DFS, 1-group in the SNS and BTS). In previous studies, a decline in inter-annual variability as measured by the coefficient of variation has been used as an indication of the age at which year-class strength is set. However, this only works if random year-to-year variation exceeds any variation due to trends. The latter is obviously not the case in these data sets, where the youngest age groups, although variable on a year-to-year basis, do not reveal the trend-induced degree of variation that is observed in the older age groups.

The general picture of the processes determining year-class strength includes a period with variability-generating processes during the egg and larval stages in which year-class strength seems to be established (Leggett and DeBlois, 1994), and a subsequent demersal stage with density-dependent regulating processes in which the inter-annual variability is reduced (Beverton and Iles, 1992). It has been suggested that the relative duration of the two periods is of influence on ultimate recruitment variability (Van der Veer et al., 2000). There is hardly any quantitative information available about the processes operating in the early life of dab. Limited information on the 0-group demersal stage suggests that density-dependent processes similar to those observed in plaice also apply to dab (Iles and Beverton, 1991). Henderson (1998) argues that events during the pelagic egg stage, possibly pathogens affecting egg mortality, are critical for determining recruitment success in dab. However, our results provide evidence that the factors determining year-class strength of dab are not restricted to the pelagic early life phase only, but also occur during in the demersal juvenile phase.

Recruitment variability refers to the variability in year-class strength at a specified age (for example, the age at which fish recruit to the adult population or to the fisheries). In the present study recruitment variability is defined as the coefficient of variation in year-class strength at age 2, firstly because dab mature at 2–3 years of age (Bohl, 1957), secondly because year-class strength is fixed at age 2. Thus, recruitment variability is estimated at 104% in the DFS and 56% in the SNS and BTS. Because the higher variability in the DFS data is probably related to annual variations in catchability, the BTS and SNS estimates are considered to be more reliable than the DFS estimate. Therefore recruitment variability in the southeastern

North Sea is estimated at 56%. This estimate is similar to the values estimated for dab in the UK coastal waters, which range from 45 to 69% (Henderson, 1998). Most of the estimates of recruitment variability in dab presented by Philippart et al. (1998) range between 50 and 100%, but two estimates are much higher. They emphasise that additional sources of variation, such as varying age compositions and survey areas, can have biased their estimates. Indeed our results confirm that inter-annual variability in year-class strength is age dependent, and therefore recruitment variability should be estimated at a specified age. Furthermore, our results show that inter-annual variations in the distribution of fish, relative to the survey area, can cause an overestimation of the variability in year-class strength.

The estimated recruitment variability in dab is close to the values estimated for plaice (Van der Veer, 1986; Rijnsdorp et al., 1991) and probably lower than the 100% estimated for sole (Rijnsdorp et al., 1991; 1992). This is the opposite of predictions based on the concentration hypothesis of Beverton (1995), which states that the degree of variation in recruitment will be inversely related to the degree of concentration during early life phases. Iles and Beverton (2000) provided statistical evidence that the observed patterns in recruitment in various species are in line with this hypothesis. Because a spatial concentration into nursery areas is lacking for dab, the concentration hypothesis predicts a higher variability than in plaice and sole. Recently, Van der Veer et al. (2000) expressed some doubt about whether the degree of concentration during early life is responsible for low recruitment variability. They argued that regulating (variability-reducing) processes are only observed after settlement in the demersal stage when flatfish transfer from a three-dimensional pelagic habitat into a two-dimensional demersal habitat. They illustrate their view by pointing to lemon sole (*Microstomus kitt*), which is also characterised by low recruitment variability without spatial concentration in nursery areas (Rae, 1970). This alternative hypothesis stating that low recruitment variability is a reflection of a demersal way of life has also been suggested by Leggett and Frank (1997). They compared recruitment variability is in four flatfishes species (plaice, sole, American plaice *Hippoglossoides platessoides* and yellowtail flounder *Limanda ferruginae*), two gadoids (cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*) and herring (*Clupea harengus*), and concluded that variability is lowest in flatfishes, intermediate in gadoids and highest in herring. This hypothesis is supported by our results, but it does not explain the relatively high recruitment variability in sole. Here, the species range hypothesis by Miller et al. (1991) might apply. These authors provide arguments that recruitment variability is a function of the position of a stock relative to the distribution range of the species. Rijnsdorp et al. (1992) show that recruitment variability in the central areas of the distribution range of sole is in the same order of magnitude as that of dab, but in the North Sea increases to more than 100% due to additional mortality in severe winters. The low recruitment variability of sole in the Bay of Biscay supports this interpretation, but the low variability in the in the Skagerrak does not (Leggett and Frank, 1997). After examining the relationship between recruitment variability and latitude in sole, American plaice and yellowtail flounder, Leggett and Frank (1997) rejected the species range hypothesis for flatfishes.

The observed trends in recruitment must be related to variations in mortality of 0- and 1-group dab. The data used are not suitable for estimating mortality rates in the juvenile life phase. Mortality rates of 0- and 1-group are overestimated in the DFS owing to emigration: juvenile dab move to deeper water further offshore with increasing age. Consequently, mortality rates of 1-group dab in the SNS and BTS are probably underestimated. Such a bias does not occur in the older age groups because the depth-related distribution pattern does not change greatly with age in adult fish. The estimates of total annual mortality (Z), based on the decrease in abundance from age 2 to age 4 or 5, ranged from 1.0 to 1.3. These estimates are very similar to the mortality rate of 1.15 reported by Lee (1972) for 4 group and older dab. A substantial part of this mortality will be due to fishing as high numbers of dab are being discarded in the beam-trawl fisheries for brown shrimp and flatfish (Van Beek, 1998). In 1989, a major part of the coastal zone was closed to fishing by larger vessels to protect juvenile plaice. The establishment of this 'plaice box' has led to a local reduction in beam trawl effort for flatfish by 60% during the period 1989–1994, and by 85% since

1995 (ICES, 1999; Pastoors et al., 2000). This reduction might have contributed to the improved survival of dab, but the increase in abundance started well before 1989 and must be related to other factors.

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