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REPORT OF THE STUDY GROUP ON THE FECUNDITY OF PLAICE AND SOLE IN SUBAREAS IV AND VIII AND DIVISIONS VIId,e

Lowestoft, 18 - 21 September 1990

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1. PARTICIPATION AND TERMS OF REFERENCE

At the 1989 Statutatory Meeting in the Hague (C.Res. 1989/2:10) it was decided that a "Study Group on the Fecundity of Plaice and Sole in Subareas IV and VIII and divisions VIId,e will be established and will meet in Lowestoft from 18 - 21 September 1990 to

a) evaluate available data on the fecundity of various stocks of sole and plaice;
b) resolve the question whether sole is a determinate or indeterminate spawner;
c) advice on future work in relation to the 1991 ICES sole egg survey.

The meeting was attended by the following persons:

F.A. van Beek	Netherlands
M. Giret	France
M. Greer Walker	England
R.S. Millner	England
A.D. Rijnsdorp (chairman)	Netherlands
J.D. Riley	England
A.P. Scott	England
P.R. Witthames	England

2. INTRODUCTION

At its annual meeting to provide management advice on flatfish stocks in the North Sea and Channel, the ICES North Sea Flatfish Working group has been confronted with deteriorating statistics on catch and effort data leading to uncertainties about the outcome of the stock assessment of plaice and sole. This situation increased the need for fishery independent information on the size of the stock. Various pre-recruit surveys have been started since 1970 covering the main nursery areas of plaice and sole in the North Sea, English Channel and Bay of Biscay (for review see Anon, 1990). Fishery independent data on adult stock size of North Sea plaice are available on a relative basis from UK Groundfish survey. For North Sea sole such data are available

from the Beam trawl survey carried out by the Netherlands and Belgium since 1985. In the eastern Channel and Bristol Channel, a beam trawl survey was started in 1988.

Egg surveys of sole have been carried out in the North Sea in 1984, 1988, 1989 and 1990 and have yielded estimates of the total egg production (Anon, 1986; van Beek, 1989). Plaice egg surveys have been carried out for the Southern Bight in a great number of years (Simpson, 1958; Harding *et al*, 1978). Surveys covering all the main spawning areas of North sea plaice have been carried out in 1987, 1988 and 1989 and have yielded estimates of the total production of stage 1 eggs and fertilized eggs (Heessen & Rijnsdorp, 1989; van der Land *et al*, 1990).

In order to convert estimates of total egg production into estimates of spawning stock biomass, data are needed on a) the length composition, b) maturity - length relationship and c) fecundity - length relationship or on a) the age composition, b) maturity - age relationship and c) the mean weight at age of mature females. This report presents a review of the fecundity studies carried out recently on sole and plaice and discusses aspects that are related to the conversion of egg production estimates from plankton surveys to estimates of spawning stock biomass.

3. METHODS.

3.1. Fecundity.

There are a number of methods currently used for estimating fish fecundity: gravimetry, volumetry and stereology.

Both gravimetric (Burd & Howlett, 1974) and volumetric (Simpson, 1951) methods rely upon counting eggs in a subsample and raising this value to the whole ovary. If eggs can be easily separated from ovarian tissue using Gilson's fluid and are > 200 µm in diameter they can be counted by an automated method (Witthames & Greer Walker, 1987) with no need for subsampling. However, all the above methods require histological screening to check whether the ovary is at the correct maturity stage. If post ovulatory follicles are present then spawning has commenced and potential fecundity is likely to be underestimated.

More recently, stereological methods (Emerson *et al.* 1990) have been introduced. These rely upon the fact that the fractional volume of a component in a tissue is proportional to its fractional cross sectional area. Tissue of a known volume is fixed in formalin, dehydrated in alcohol and embedded in resin. Sections of 4 μm are cut with a motorised microtome situated within a refrigerated cabinet at -12° C and stained with PAS Mallorys. Point and profile counts are made using a grid and a VIDS digital analysis system. This method of counting eggs has a number of distinct advantages over previous methods. Histological screening and egg counts can be made from the same sample, levels of atresia can be estimated and the vitellogenic threshold established. The latter method has been used in all sole fecundity estimates made at Lowestoft and presented herein.

The stereological method has the following advantages over volumetric, gravimetric and automated particle counter methods:

1. the toxicity and long digestion periods associated with Gilson's fluid is avoided;
2. atretic oocytes can be counted and subtracted from potential fecundity estimates;
3. post-ovulatory follicles, the presence of which are used to confirm spawning, can be identified and quantified;
4. the threshold for vitellogenesis can be established and borderline cases distinguished as either previtellogenic or vitellogenic oocytes;
5. the method can be used to quantify the smaller previtellogenic oocytes, which is not possible with any of the other methods;
6. there is potential for automation of some of the procedures.

3.2. Maturity

Developmental stage of the ovaries can be described histologically as well as by inspection with the naked eye. Table 1 and 2 illustrate the seasonal development of the ovaries as obtained from histological analysis of sole and plaice sampled on the west coast of Brittany (Deniel, 1981). This description is roughly similar for the various geographical areas although the timing may be slightly delayed in more northern areas. The maturity classification of sole and plaice as used by the Lowestoft laboratory and by RIVO is given in Tables 3 and 4. In Lowestoft the sole maturity scale is merely an interpretation of that of plaice.

4. SOLE

4.1.Determinate or indeterminate spawner

A controversy exists over whether sole is a determinate or indeterminate spawner. In a determinate spawner, the number of oocytes to be spawned in the following spawning period is already fixed before the start of spawning. In an indeterminate spawner, the recruitment of pre-vitellogenic to the vitellogenic oocytes occurs during the spawning period and counts of the number of vitellogenic oocytes just before spawning starts will give an underestimate of the potential fecundity. The question of the determinacy of fecundity is of direct relevance to the study of total spawning biomass using ichthyoplankton surveys to measure total egg production. Two different methods are available depending upon whether or not fecundity is determinate. For determinate spawners the total egg production method can be applied whereas for indeterminate spawners the batch fecundity method is available.

Hunter *et al* (1989) have summarized five criteria to distinguish determinate from indeterminate spawners, which are all based on histological analysis of the frequency distributions of developing oocytes:

1 - in mature ovaries a hiatus exists between the advanced stock of oocytes and smaller immature oocytes;
2 - the standing stock of advanced oocytes declines over the spawning season;
3 - the standing stock of advanced oocytes is lower in females having post-ovulatory follicles;
4 - the mean diameter of the oocytes in the standing stock increases over the spawning season;
5 - stock estimates of batch fecundity, total fecundity and spawning frequency and spawning duration should match.

In sole, the first study on the size frequencies of developing oocytes was carried out by Venema (1964, see also Anon, 1984) indicating that a hiatus occured at a size of about 200 micron suggesting that sole is a determinate spawner. This criterion was also used by Rosenboom (1985). Deniel (1981) and le Bec (1983), who studied size frequencies of oocytes in sole from the Bay de Douarnenez (Division VIIe) and the Bay of Biscay (Subarea VIII) sole and counted all oocytes > 240 µm, because in spent females only oocytes below this size were observed. All these studies thus assumed sole to be a determinate spawner.

This conclusion was criticized by Urban and Alheit (1985) who studied size frequency distributions of oocytes from sole sampled in the German Bight and could not find any evidence of a developing hiatus. They concluded that sole was an indeterminate spawner.

Recent work in the Fisheries Laboratory Lowestoft has provided evidence that sole is a determinate spawner in at least some of the areas studied. Horwood & Greer Walker (1990) showed from oocyte measurements of sole collected in the Bristol Channel prior to, or at the beginning of, spawning that there was a distinct break at about 170 micron. Greer Walker & Witthames (1990) showed that the proportion of oocytes in the size class of 170-194 micron decreased with an increase in the size of the vitellogenic oocytes, suggesting that the hiatus would develop more clearly towards the beginning of spawning (Fig.1). A study of the size frequency distribution of vitellogenic oocytes between November and March showed that the smallest vitellogenic oocytes were > 125 μm. Figure 2 shows as an example one fish from which the samples were taken during each month illustrating the growth of the developing oocytes between November and April. A study of the size-frequency distribution of vitellogenic oocytes between November and March showed that the smallest vitellogenic oocytes were above 125 μm in November but about 180 μm by March. Only in spawning fish, recognised by the presence of post ovulatory follicles, are these size groups of vitellogenic oocytes missing. Fecundity estimates from these months based on a count of the number of vitellogenic oocytes revealed no significant differences in slope or intercept of the fecundity - body length relationship. Also a study of the residuals of the observed fecundities and predicted values did not show a different value for November and March, indicating that no further recruitment of previtellogenic oocytes to the vitellogenic group occurred (Fig.3). Preliminary results of ovaries collected in the German Bight in 1990 indicate a similar pattern of size distributions of vitellogenic oocytes compared to other areas and this is at variance with the results of Urban & Alheit (1988). These results satisfy the first four criteria specified above.

In order to satisfy the fifth criterion and firmly establish that sole is a determinate spawner it would be necessary to derive an estimate of the number of hydrated eggs produced and spawned by a female over the course of the spawning season. If sole is a determinate spawner, this number should match the estimated 'standing stock' of vitellogenic eggs.

In order to derive such an estimate three pieces of information are required:
1) length of the spawning season of an individual female;
2) the average spawning frequency;
3) the average batch size.

The length of the spawning season can be derived from data held at RIVO (IJmuiden). New sampling programs will be needed to obtain figures for 2 and 3.

It is suggested that the average spawning frequency can be worked out if the proportion of fish (of those with hydrated eggs) which ovulate on any day can be reliably determined. This can be estimated by counting the number of fish with post-ovulatory follicles, however, the turnover rate of these follicles is unknown. There are plans to investigate this at Lowestoft. If it is shown that these post-ovulatory follicles do not resorb rapidly enough and are therefore not a good indicator that a fish has spawned that day, an alternative method should be adopted. One possibility is the sampling of fish in the hours before spawning start i.e just before nightfall, and carefully record the numbers of females with clearly recognisable batches of ovulated eggs (Lowestoft stage VI fish). The problem with this method is that unacceptable errors may be introduced due to some females having already spawned that day, some having not quite ovulated and others having had their eggs stripped out by undue pressure in the cod-end.

The average batch size is relatively easy to determine. A sample of ca. 50 females with hydrated eggs, but non-ovulated females will be required. The numbers of hydrated eggs can be measured using an automated egg counter or histometry.

In summary: the available data strongly suggest that sole is a determinate spawner in the Bristol Channel, English Channel and in the southern North Sea (Flamborough). No conclusive data have yet been provided for the German Bight (IVb) and the Irish Sea (VIIa). Additional work is needed to definitely establish determinacy in sole. Priority should be given to the German Bight, because of the conflicting evidence from that area. A programme to determine methods for the estimation of spawning frequency is being considered. An attempt to estimate batch size is quite feasible.

4.2. Variability in fecundity between areas and years.

Estimates of the fecundity of a modal sole (35 cm or 485 g) in the various areas and years are given in Table 5. Analysis of covariance has shown that differences are significant between years and areas. The results show large variations which might be partly due to inaccurate methodology. Studies that rely on collection of gonad samples during the spawning period may contain fish which have already started spawning. A histological check on postovulatory follicles is certainly needed. Comparisons using data from recent studies, in which the methodological problems might be fewer, indicate that the fecundity increases from the south to the north.

4.3. Geographical and annual variability in maturation

The proportion of mature North Sea female sole by age group has been investigated using Dutch market samples by De Veen (1970), Van Beek (1985) and Rijnsdorp *et al.* (1991). De Veen assumed that all soles with stage 4 and further developed gonads in spawning time would spawn in the current year, whereas van Beek and Rijnsdorp assumed that sole with stage 3 ovaries would also spawn.

The annual variability in percentage maturity is given in Figure 4. In 2-year old soles the percentage maturity in the period 1966-1988 varies between 0% and 15%, but in most years is 0%. In 3 year olds it varies between 41% and 85%, but without a clear trend. On average it is was about 60%. The factors responsible for the relatively large variations remain obscure. In 4 year olds it varies between 91% and 100% and in older fish it is 100%. Histological inspection of gonads of 3 year old females in 1988 from the English Channel (VIId) (Greer Walker & Witthames, 1990), indicate that about 60% of the sole would spawn at that age.

4.4. Egg production estimates and spawning stock biomass

Sole egg surveys in the North Sea were carried out in 1984, 1988, 1989 and 1990. Another international egg survey in the North Sea and English Channel is planned for 1991. Figure 5 shows the area covered by the surveys. Egg production in 1984 and 1988 has been calculated using techniques described in Anon. (1986) and van Beek (1989). The production of newly fertilized eggs was estimated by extrapolating the

production of stage I and II eggs using the egg mortality between these stages. As these estimates were unexpectedly low and even indicating negative mortality in some years, the egg production was recalculated for all years using egg mortality estimates from the linear regressions of production of all developmental stages against age. The estimate of the total egg production is given by the intercept of the regression line on the y-axis.

An attempt has been made to calculate egg production from VPA female spawning stock biomass and the recently derived English fecundity estimates. The VPA SSB was calculated at the beginning of spawning time (1st April) using a separate sex data base, fishing mortality for sexes combined from the Flatfish Working Group report (Anon. 1990), 1st quarter weight at age from the FWG data base and a maturity-ogive based on Dutch market samples (Rijnsdorp *et al.* 1991). Total egg production for the years 1984-1989 was calculated using the weight-fecundity relationships determined in 1987 and 1988 (Greer Walker & Witthames,1990).

The table below shows a comparison between the egg-production estimates from the surveys and from the VPA with the new fecundity data

YEAR	SURVEY $x10^{-12}$	VPA* $x10^{-12}$	VPA** $x10^{-12}$
1984	33.0	17.8	15.5
1985	-	17.3	15.0
1986	-	14.8	12.8
1987	-	10.4	9.0
1988	9.9	13.2	11.5
1989	13.4	10.6	9.2
1990	56.4***	-	-

* using 1987 fecundity data
** using 1988 fecundity data
*** preliminary

The survey estimate in 1984 is about twice the level of the VPA estimate. However, in 1988 and 1989 the estimates of both methods are close, although 1988 - 1989 show reverse changes. It is recognised that there are wide confidence limits around the survey estimates, which were estimated at +/-40% for the 1984 survey (Anon, 1986). Also the VPA estimates may be biased by the assumptions of fishing mortality and uncertainty in catch at age data in recent years.

5. PLAICE

5.1. Determinacy in fecundity

In plaice histological information and a study of the size distribution of developing oocytes has clearly shown that plaice is a determinate spawner. (Simpson, 1951; Bagenal, 1963; Witthames & Greer Walker, 1987).

5.2. Geographical and annual variability in fecundity

Fecundity in plaice was recently determined by Horwood *et al* (1986) and Rijnsdorp (in prep) and Witthames (unpublished). Coverage of areas and years are summarized in Table 6. Fecundity of a fish of 37 cm illustrates the variability between years and geographical areas. Analyses of covariance has shown significant differences between areas and years. Substantial changes in fecundity between the recent years and the historic records of Reibisch (1899), Franz (1910a, 1910b) and Simpson (1951) have been observed. These changes will not be dealt with in this report but are analysed in Rijnsdorp (in prep).

A study of the factors affecting the variability in fecundity suggested that somatic growth in length in the year preceding the spawning season, estimated from back-calculating of otoliths, was not, or only slightly, related to the level of fecundity. Fecundity showed a significant positive relationship with pre-spawning condition factor (Rijnsdorp, 1990). Further studies should focus on the time period during which the number of developing oocytes is determined. Once the time window is determined more detailed studies on the effects of growth rate prior to this on the number of eggs, and studies of growth between the window and spawning period on the size of the eggs can be carried out.

5.3. Geographical and annual variability in maturation

Annual variations in the percentage maturity in age groups recruiting to the spawning biomass occur also in plaice (Fig.5). Beside the variations between years a geographical trend in length and age at maturity is apparent in the North Sea (Rijnsdorp, 1989).

6. FUTURE WORK

In order to resolve the discrepancy between the results on sole in the German Bight from Urban & Alheit (1988) and those on sole in Division VIIf, VIId and the western part of IVb an additional study should be carried out in the German Bight in 1991.

In order to confirm that sole is a determinate spawner further work should be carried out to estimate the average spawning duration, the average batch size and the spawning frequency. This work which is described in section 4.1. can be carried out in a single substock.

A feature of previous studies on fecundity and maturity in sole has been the substantial annual and geographical variability. Therefore, it is important to determine these variables for the substocks covered in the 1991 ICES sole egg survey. As tagging data have shown differences between sole substocks within management divisions separate fecundity and maturity data should be collected for the substocks on the UK and French side of the eastern and western Channel separately, as well for the Flamborough and German Bight substock in IVb. This implies a large effort in sampling and processing. Priority should be given to three areas where previous surveys have shown high egg production or important nursery areas: German Bight (IVb), Southern Bight (IVc) and UK coast of VIId.

In order to understand the causal factors involved in governing the variability in fecundity between areas and years further studies should be carried out to determine the period during the annual cycle when the number of developing oocytes is fixed and to study the effect of growth before and after this on the number and size of the eggs. Future studies should include experimental work as well as descriptive studies.

7. RECOMMENDATIONS

1. A study on the determinancy of sole in the German Bight should be carried out.

2. Fecundity should be determined in the substocks covered in the 1991 ICES sole egg survey: VIIe north and south, VIId north and south, IVc west and east IVb west and east

(German Bight). Priority should be given to three substocks: IVb German Bight; IVc and VIId UK coast.

3. Proportion of maturing females in recruiting age groups should be determined.

4. A pilot study on the occurrence of atresia in sole should be carried out in the German Bight stock.

5. A study of the annual pattern in gonad development aimed at establishing the time when the number of oocytes is fixed and which factors affect their number and final size, should be encouraged. This study should preferably be carried out in plaice and could give us insights into the factors affecting variability in fecundity between areas and years.

8. PROTOCOL FOR SAMPLE COLLECTION.

This chapter summarizes the planned research for 1991 with regard to ovary sampling and data analysis, responsible scientist and the method for ovary preservation.

SAMPLE COLLECTION:

Fecundity samples: collect 2-3 prespawning fish per cm-group with a minimum of 60 from the following four priority areas: German Bight (Damm, Cuxhaven, Germany; van Beek/Rijnsdorp , IJmuiden, Netherlands), Southern Bight (van Beek/Rijnsdorp , IJmuiden, Netherlands) and VIId (Greer Walker/Witthames, Lowestoft, UK). Samples from the Flamborough area will be collected by the Lowestoft Laboratory as a aprt of an ongoing reasearch programme.
Determinacy: collect 10 pre-spawning, 10 spawning and 10 spent fish early and late in the season in the German Bight (total of 60 fish; Damm, Cuxhaven, Germany).
Atresia: collect the first 10 mature females/haul for 5 hauls. Collect this sample early and late in the spawning season (total 100 fish). Samples have to be collected in the morning (Damm, Cuxhaven, Germany).
Batch size and spawning fraction: collect 25 spawning fish (with hydrated eggs) early and late in the spawning period (total 50 fish). Length rage 30-45 cm at least 5 fish in each 5-cm group. Samples to be collected in the afternoon. (Damm, Cuxhaven, Germany).

Preservation of sole ovaries: dissect and preserve ovaries carefully in 10% buffered formaline 0.1 m phosphate which gives:
3.6 - 4.0 % w/w formaldehyde.
46.00 g - $NaH_2PO_4ZH_2O$
81.86 g - $Na_2HPO_4.2H_2O$ in 10 l of formalin.
The ratio of fixative to tissue should be not less than 3:1. If the ovaries are large the lobes can be preserved in separate jars, but care should be taken not to puncture the ovary skin. Place waterproof labels in the jars and record the length and weight of the carcass, guts and ovaries. The carcass and guts can be returned to the laboratory on ice for weighting and collecting of otoliths. If the ovaries can not be weighed fresh at sea, they can be weighed in the fixed state at Lowestoft. Transfer the gonads to 70% alcohol after 36 h.

DATA ANALYSIS:

Ovary samples: all ovary samples will be analysed in Lowestoft under the responsibility of Greer Walker and Witthames.
Maturity stage duration: the average spawning duration will be estimated from the market sampling data base held at RIVO IJmuiden (Rijnsdorp/van Beek).

The research programme is summarized below.

ICES area		Fecundity collection	Egg survey	Priority areas	Responsibility Fecundity samples	Egg samples
4b	west	U.K.	Neth		UK	Neth
	east	Germ/Neth	Neth/Germ	P	UK	Neth
4c		Neth	Neth	P	UK	Neth
7d	north	UK	UK	P	UK	UK
	south	France?	UK		UK	UK
7e	north	UK?	Belgium&		UK	Belgium&
	south	France?	France		UK	France

9. REFERENCES.

Anonymous, 1984. Report of the planning group on the 1984 sole egg survey. ICES CM 1985/G:78.

Anonymous, 1986. Report of the *ad hoc* working group on the 1984 and 1985 sole (*Solea solea* L.) egg surveys. ICES CM 1985/G:95, 93 pp.

Anonymous, 1990a. Report of the study group on beam trawl surveys in the North Sea and eastern Channel. ICES CM 1990/G:59, 58pp.

Anonymous, 1990b. Report of the North Sea flatfish working group, Copenhagen, 20-26 October 1989. ICES CM 1990/Assess:6.

Bagenal, T.B. 1963. Variations in plaice fecundity in the Clyde area. J. mar. biol. Ass. U.K. 43: 391-399.

Barr, W.A. 1963a. The endocrine control of the sexual cycle in the plaice (*Pleuronectes platessa* L.) I. Cyclical changes in the normal ovary. Gen. Comp. Endoc. 3: 197-204.

Barr, W.A. 1963b. The endocrine control of the sexual cycle in the plaice *Pleuronectes platessa* (L.) I. Cyclical changes in the normal ovary. Gen. Comp. Endoc. 3: 197-204.

le Bec, C. 1983. Fecondite de la sole *Solea vulgaris* (Quensel, 1806) du Golfe de Gascogne. ICES CM 1983/G:53, 16pp.

Beek, F.A. van. 1985. On the maturity of North Sea sole in Dutch market samples. ICES CM 1985/G:57.

Beek, F.A. van. 1989. Egg production of North Sea sole in 1988. ICES CM 1989/G:45.

Burd, A.C. & Howlett, G.J. 1974. Fecundity studies of North Sea herring. J. Cons. int. Explor. Mer, 35: 107-120.

Deniel, C. 1981. Les poissons plats en baie de Douarnenez: Reproduction, croissance et migrations. PHd thesis Univesite Brittany Ouest. 1981, 476 pp.

Emerson, L.S., Greer Walker, M. & Witthames, P.R. 1990. A stereological method for estimating fish fecundity. J. Fish Biol. 36: 721-730.

Franz, V. 1910a. Die Eiproduktion der Scholle (*Pleuronectes platessa* L.) Wissenschaftliche Meeresuntersuchungen. Neue Folge, Band IX: 58-142.

Franz, V. 1910b. Zur Eiproduktion der Scholle (*Pleuronectes platessa* L.) Wissenschaftliche Meeresuntersuchungen. Neue Folge, Band IX: 217-224.

Greer Walker, M. & Witthames, P.R. 1990. The fecundity of sole (Solea solea L.) from ICES areas IVb in 1987 and 1988 and VIId in 1988. ICES CM 1990/g:37.

Harding, D., Nichols, J.H. & Tungate, D.S. 1978. The spawning of the plaice (*Pleuronectes platessa* L.) in the southern North Sea and English channel. Rapp. P. -v. Reun. Cons. int. Explor. Mer, 172: 102-113.

Heessen, H.J.L. and Rijnsdorp, A.D. 1989. Investigations on egg production and mortality of cod (*Gadus morhua* L.) and plaice (*Pleuronectes platessa* L.) in the southern and eastern North Sea in 1987 and 1988. Rapp. P. -v. Réun. Cons. int. Explor. Mer 191: 15-20.

Horwood, J.W., 1990. Fecundity and maturity of plaice (*Pleuronectes platessa L.*) from Cardigan Bay. J. mar. biol. Ass.70: 515-529.

Horwood, J.W., Bannister, R.C.A. and Howlett, G.J., 1986. Comparative fecundity of North Sea plaice (*Pleuronectes platessa* L.). Proc. R. Soc. Lond. B 228, 401-431.

Horwood, J.W., Greer Walker, M and Witthames, P. 1989. The effect of feeding levels on the fecundity of plaice (*Pleuronectes platessa*).J. mar. biol. Ass. U.K. 69: 81-92.

Horwood, J.W. & Greer Walker, M. 1990. Determinacy of fecundity in sole (*Solea solea*) from the Bristol Channel. J. mar. Biol. Ass.70: 803-814.

Hunter, J.R., Macewicz, B.J. & Kimbrell 1989. Fecundity and other aspects of the reproduction of sablefish, *Anoplopoma*, in central California waters. CalCOFI Rep. 30:61-72.

Land, M.A. van der, Heessen, H.J.L. & Rijnsdorp, A.D. 1990. The results of the 1989 egg surveys for cod and plaice. ICES CM 1990/G:27.

Reibisch, J. 1899. Ueber die Eizahl bei *Pleuronectes platessa* und die Alterbestimmung dieser Form aus den Otolithen. Wissenschaftliche Meeresuntersuchungen. Kiel 4: 231-248.

Rijnsdorp, A.D. 1989. Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.). J. Cons. int. Explor. Mer. 46: 35-51.

Rijnsdorp, A.D. 1990. The mechanism of energy allocation over reproduction and somatic growth in North Sea plaice, *Pleuronectes platessa* L. Neth. J. Sea Res. 25: 279-290.

Rijnsdorp, A.D. & Leeuwen, P.I. van 1985. Variability in length and age at first maturity of North Sea plaice. ICES CM 1985/G:56.

Rijnsdorp, A.D, Daan, N., van Beek, F.A. and Heessen, H.J.L.. 1991. Reproductive variability in North Sea cod, plaice and sole. J. Cons. int. Explor. Mer. (in print).

Simpson, A.C. 1951. The fecundity of plaice. Fish. Invest. Ser II, 17(5): 1-27.

Simpson, A.C. 1959. The spawning of the plaice (*Pleuronectes platessa*) in the North Sea. Fish. Inv. Ser. 2, 22 (7), 111 pp.

Veen, J.F. de, 1970. On some aspects of maturation in the common sole Solea solea (L.). Ber. dt. wiss. Komm. Meeresforsch., 21: 78-91.

Veen, J.Fde . 1976. On changes in some biological parameters in the North Sea sole (*Solea solea* L.) J. Cons. int. Explor. Mer 37: 60-90.

Witthames, P.R. & Greer Walker, M. 1987. An automated method for counting and sizing fish eggs. J. Fish Biol. 30, 225-235.

Table 1. Description of the seasonal development of ovaries of sole in baie de Douarnenez (Division VIIe). From Deniel (1981).

MOIS	ETAPES DE LA MATURATION	Ø MAX. OVOCYTES
AVRIL	Accroissement lent	160 - 210 µ
MAI	Accroissement lent Hétérogénéité cytoplasmique	210 - 240 µ
JUIN	Accroissement lent Hétérogénéité cytoplasmique Premiers globules vitellins	148 - 240 µ
JUILLET	Accroissement lent Hétérogénéité cytoplasmique Début de vitellogenèse	130 - 240 µ
AOUT	Début de vitellogenèse Vitellogenèse assez avancée	160 - 315 µ
SEPTEMBRE	Début de vitellogenèse Vitellogenèse assez avancée	315 µ
OCTOBRE	Début de vitellogenèse Vitellogenèse assez avancée	130 - 410 µ
NOVEMBRE	Début de vitellogenèse Vitellogenèse avancée	260 - 470 µ
DECEMBRE	Début de vitellogenèse Vitellogenèse assez et très avancée Fin de vitellogenèse Début possible de pontes	180 - 650 µ
JANVIER	Ovocytes de taille très variable Vitellogenèse assez et très avancée Début de pontes	590 - 695 µ
FEVRIER	Ovocytes de taille très variable Vitellogenèse très avancée ou finie Pontes en cours	525 - 680 µ
MARS	Ovocytes de taille très variable Pontes en cours et finies	525 - 630 µ

Table 2. Description of the seasonal development of ovaries of plaice in baie de Douarnenez (Division VIIe). From Deniel (1981).

MOIS	ETAPES DE LA MATURATION	Ø MAX. OVOCYTES
MARS	Accroissement lent	135 - 157 µ
AVRIL	Accroissement lent	135 - 157 µ
MAI	Ovocytes de taille variable Début de vitellogenèse	315 - 367 µ
JUILLET	Début de vitellogenèse	367 µ
AOUT	Vitellogenèse assez avancée	367 - 420 µ
SEPTEMBRE	Vitellogenèse bien avancée	470 - 525 µ
OCTOBRE	Vitellogenèse avancée	680 µ
NOVEMBRE	Vitellogenèse très avancée	680 - 735 µ
DECEMBRE	Vitellogenèse très avancée Début de pontes	735 - 990 µ
JANVIER	Vitellogenèse très avancée Pontes en cours	840 - 990 µ
FEVRIER	Pontes en cours Stades de post-ponte	840 - 990 µ

Table 3. Description of the developmental stages of the female ovaries of sole and plaice as used by RIVO (IJmuiden, Netherlands).

SOLE.	
stage:	
1	juvenile; ovary transparent, sometimes reddish, eggs only visible with a microscope, small.
2	quiescence; ovary dull and transparent, red or grey-red, small, lumen filled with fluid, eggs visible with pocket lens.
3	ovary untransparent, grey-red to dark orange, rich in blood-vessels, some eggs (orange) visible with naked eye.
4	ovary untransparent, orange to reddish-white, size to about half of final size, ovary stiff and fragile, lumen still visible, orange to reddish-white eggs are polygonal compressed.
5	ovary untransparent, orange or reddish-white, lumen strongly compressed, eggs as in IV, only completely round, some ripe transparent eggs may be visible.
6	ripe, ovary transparent grey-red, some untransparent orange to white-grey parts, length as stage V, lumen filled with ripe transparent eggs.
7	half spent, ovary transparent grey to dark red, lumen very big and filled with some ripe eggs and fluid, no eggs of stage 5 are left.
8	spent, ovary dark-red, shrunken, lumen big with much fluid and only a small number of ripe transparent eggs, ovary walls slack, often folded, back to stage II.filled

Table 3. continued.

PLAICE	
stage	
1	immature; lumen transparent, colour grey
2	ripening; colour orange, oocytes visible,vitellogenesis in progress
3	spawning; as 2 but with few ripe hyaline eggs
4	spawning; ovary completely filled with hyaline eggs
5	spawning; egg partly shed
6	nearly spent; ovary contains only a small amount of hyaline eggs
7	spent; ovary small, flabby, and bloodshot, back to stage 2.

Table 4. Description of the developmental stages of the female ovaries as used by the Fisheries Laboratory Lowestoft (UK).

PLAICE & SOLE	
stage	
I	immature; ovary very small - not usually extending more than about 1.5" down side of body. Ovary wall thin and easily broken. Internally yellowish-orange in colour.
II	spent, recovering: all eggs resorbed. Little or no slime inside ovaries.
III	half full: ovaries half full with eggs.
IV	full: ovaries full and usually distending body. No sign of any hyaline eggs.
V	hyaline eggs: full. Hyaline eggs present. Maybe just a few or many hyaline eggs visible, but ovaries will not run even on heavy pressure.
VI	running: eggs can be extruded copiously under slight pressure.
VII	spent; few eggs in state of reabsorption (mainly opaque eggs) and much slime in ovaries.
I-III	maturing for the first time: ovaries half full but as in stage I the ovary wall is still thin.

Table 5. Summary of the fecundity studies on sole. Predicted fecundity (thousands) is given for a female sole of 35 cm or 485 g. Type of spawning is also indicated: D= determinate; I= indeterminate.

Area		Fecundity thousands	s.d. years	Number years	Type of spawning
Sub area VIII		204[3]	-	1	-
Div VIIf		202[2]	-	1	D[2]
Div VIIe	French coast	221	-	1	-
	UKcoast	-	-	-	-
Div VIId	French coast	-	-	-	-
	UKcoast	334[1+6]	37	3	D[1]
Div IVc		-	-	-	-
Div IVb	Flamborough	340[1]	-	1	-
	German Bight	433[5+6]	64	2	I[7] and D[8]

References: 1. Greer Walker & Witthames (1990); 2. Horwood & Greer Walker (1990); 3. le Bec (1983); 4. Deniel (1981); 5. Rosenboom (1985); 6. this report; 7. Urban & Alheit (1985); 8. Witthames &Greer Walker, unpublished.

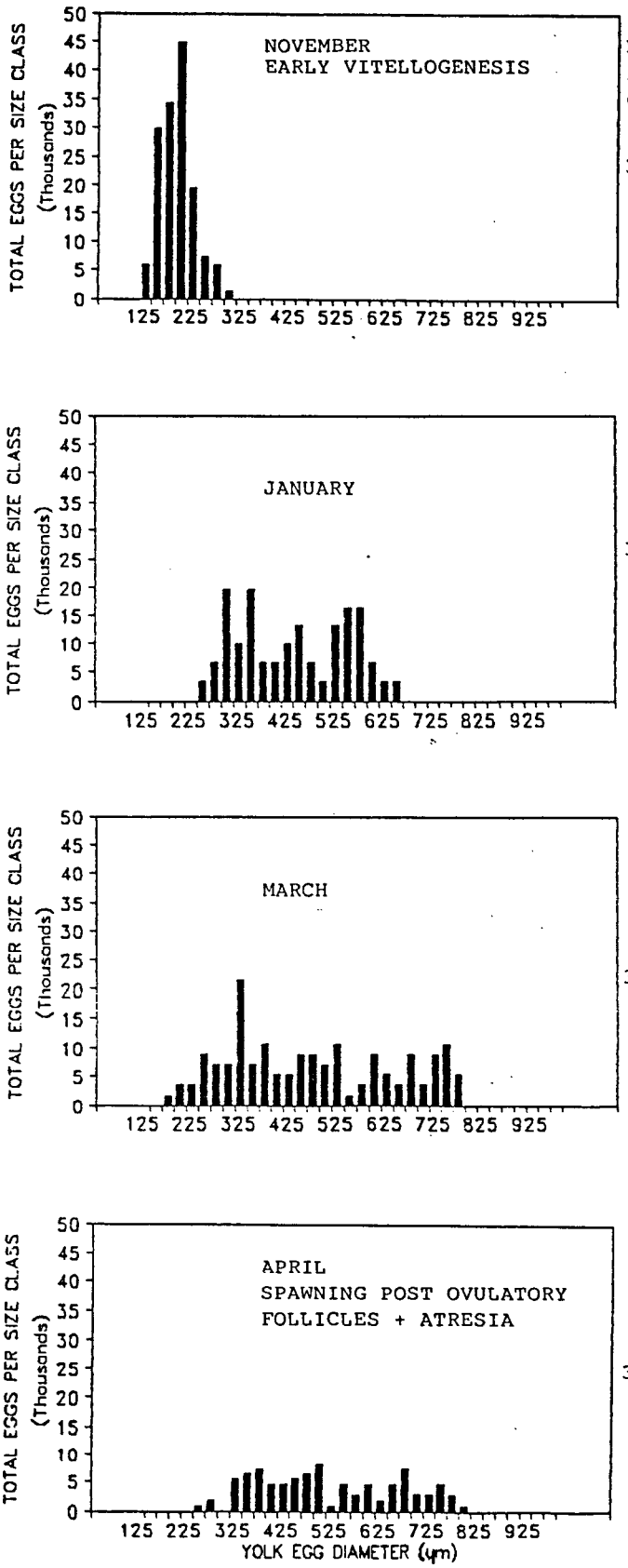
Table 6. Summary of the fecundity studies on plaice carried out in the past decade. Predicted fecundity (thousands) is given for a 5 year old female plaice of 37 cm. References: [1] Horwood *et al* (1986), [2] Horwood (1990); [3] Rijnsdorp (in prep); [4] Witthames (unpublished).

Year	Eastern** Channel	Southern Bight	Transition Area	German Bight	Flam-borough	Irish Sea
1977	-	124[1]	125[1]	112[1]	-	-
1979	138[1]	117[1]	112[1]	87[1]	-	-
1980	-	137[1]	122[1]	131[1]	121[1]	-
1982	-	139[3]	129[3]	129[3]	122[3]	-
1983	-	118[3]	130[3]	113[3]	104[3]	-
		145[4]				
1984	-	122[3]	99[3]	97[3]	98[3]	-
		117[4]				
1985	-	120[3]	96[3]	106[3]	-	-
1987	-	124[4]	-	-	-	-
1988	-	-	-	-	-	154[2]
mean	138	125*	116	111	111	154
s.d.	-	9.0*	14.1	15.9	12.1	-
%c.v.	-	7.3*	12.3	14.3	10.8	-
n	1	7*	7	7	4	1

* calculated over annual mean values

** data for 1979 and 1980 combined

SIZE FREQUENCY OF VITELLOGENIC OOCYTES IN THE OVARY



	Fish length (cm)	Fecundity thousands	Ovary weight (g)	Mean oocyte size (µm)	Smallest yolk oocyt recorded (µm)
NOVEMBER EARLY VITELLOGENESIS	31	149	2.3	191	125
JANUARY	31	163	12.5	437	250
MARCH	32	179	30.0	475	175
APRIL SPAWNING POST OVULATORY FOLLICLES + ATRESIA	32	91	11.7	517	250

Figure 1. Sole ovary development from November to April in sub area VIId during 1989.

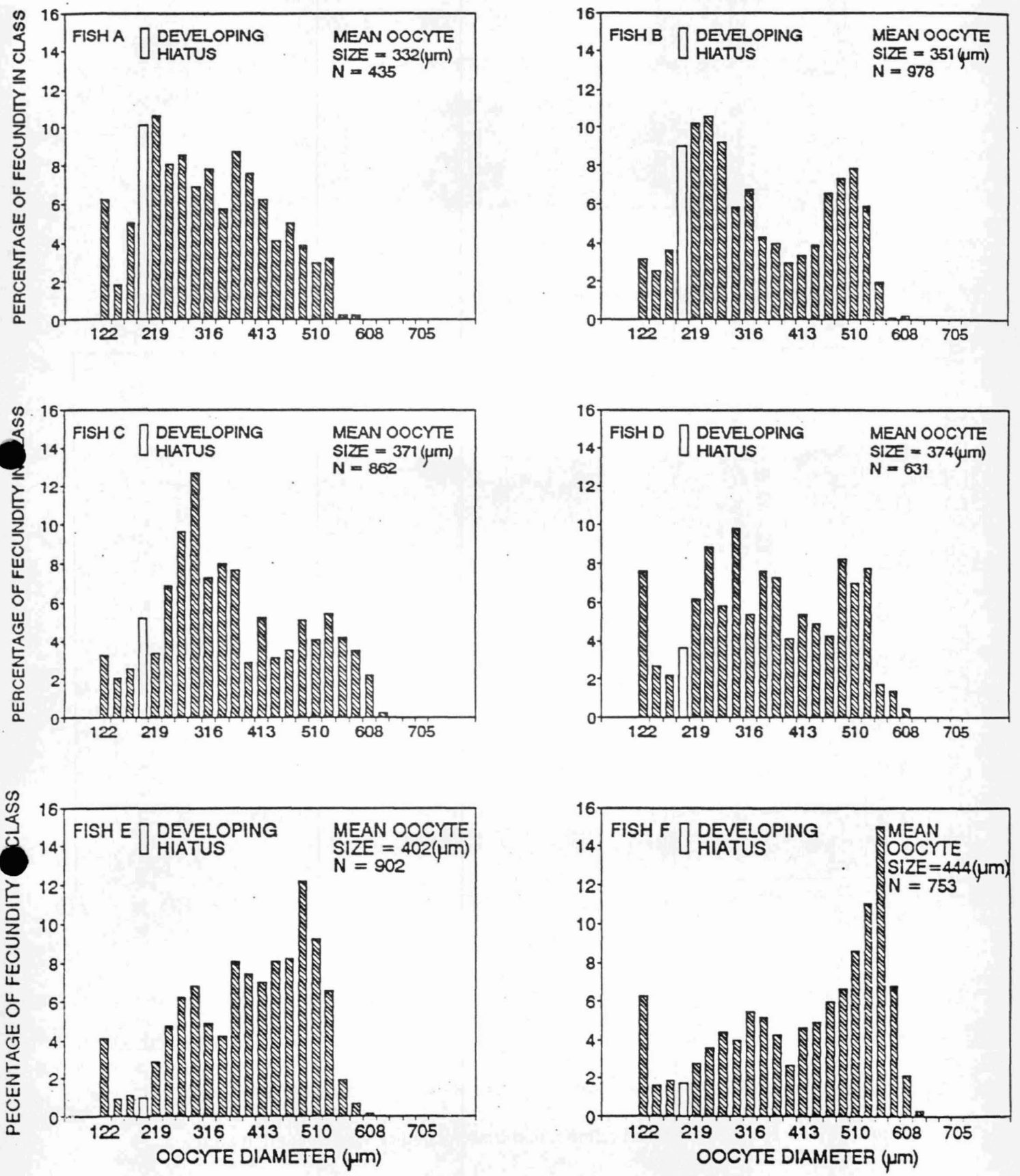


Figure 2. A-F. The oocyte size frequency distributions from six fish from area VIId showing the proportion of the total fecundity in each of the size classes.

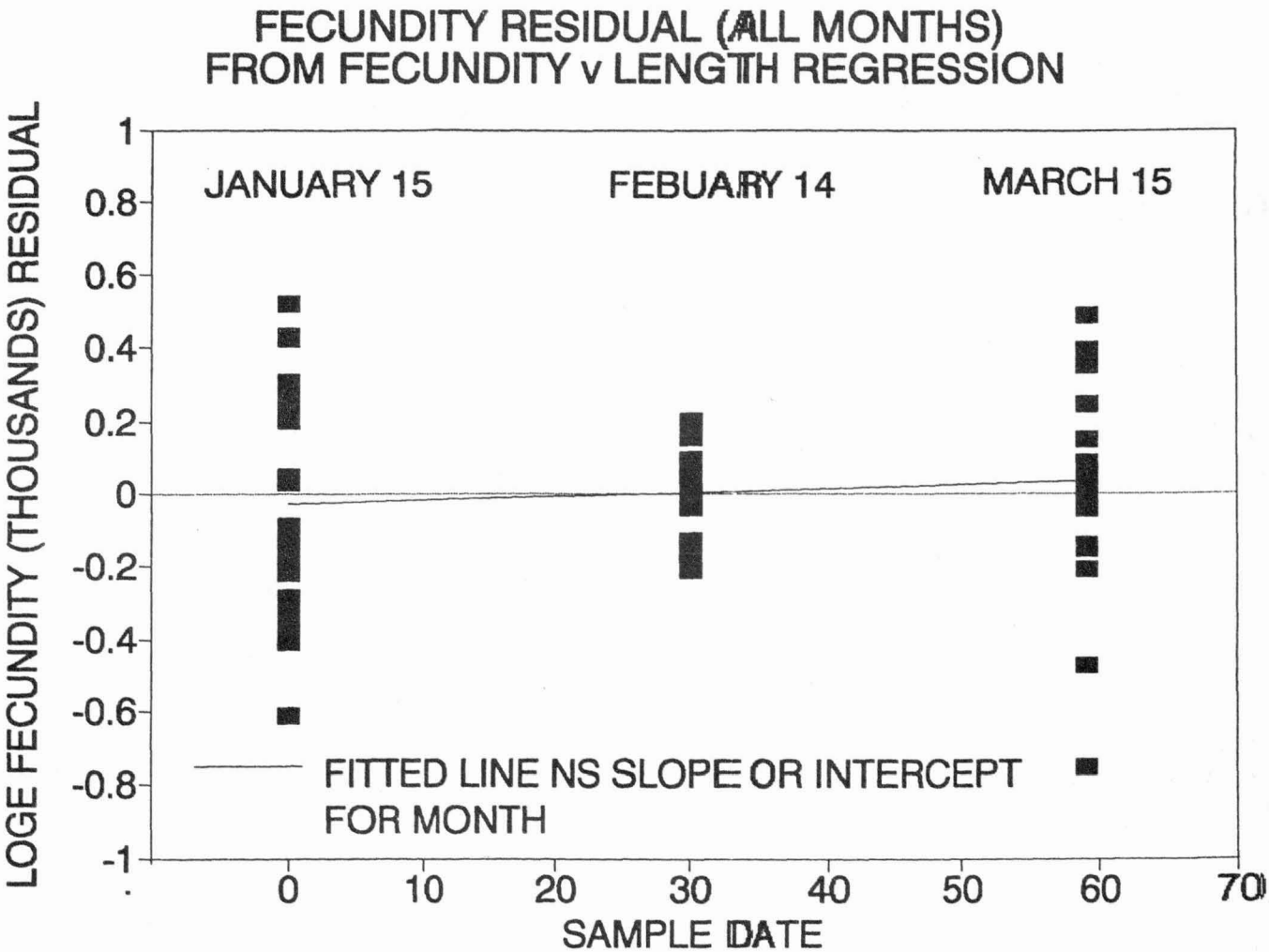


Figure 3. Sole fecundity residual (all months) from fecundity versus length regression.

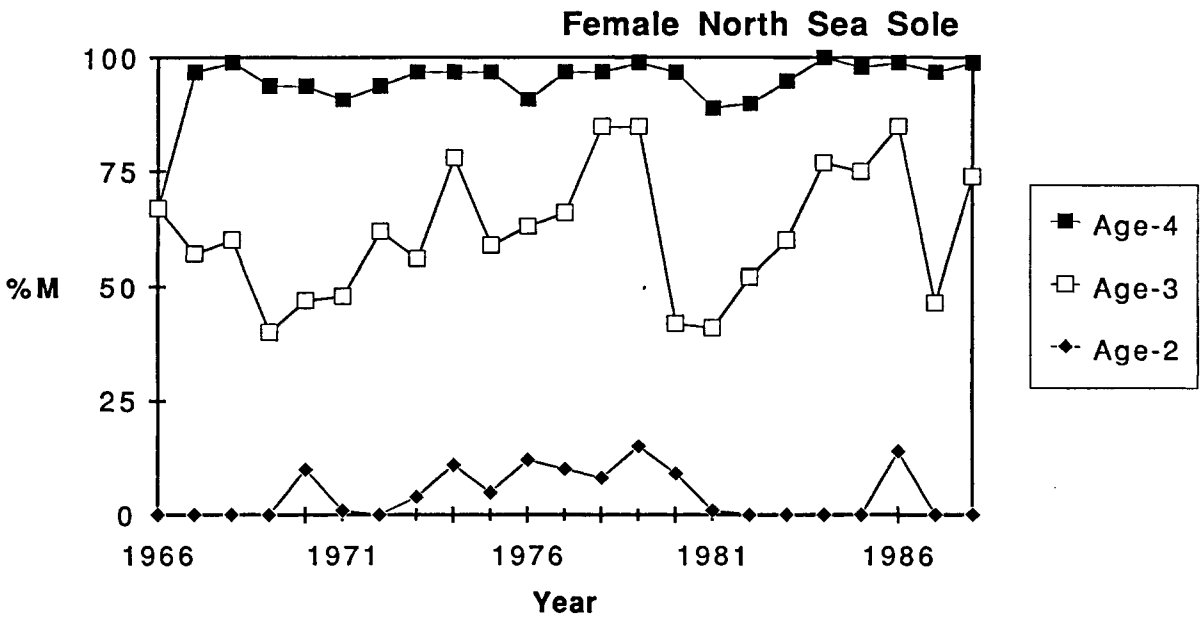


Figure 4. Sole in area IVb,c (North Sea): annual variability in the percentage mature fish in the spawning season (2nd quarter).

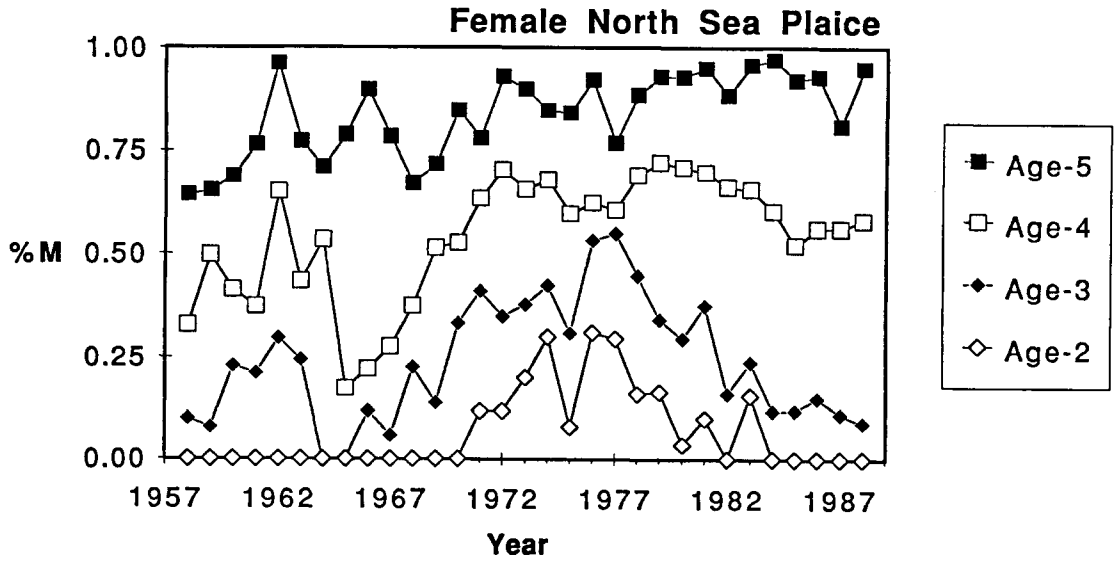


Figure 5. Plaice in area IVb,c (North Sea): annual variability in the percentage mature fish in the spawning season (1st quarter).