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**SIZE SELECTIVE MORTALITY IN PLAICE AND COD EGGS:  
A NEW APPROACH TO THE STUDY OF EGG-MORTALITY?**

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### Abstract

In this paper a new approach to the study of egg-mortality in pelagic fish eggs is proposed, which is based on the observed difference in egg-mortality between eggs of different sizes. The difference in mortality is suggested to be related to size-selective predation. This hypothesis is explored by studying changes in size of plaice and cod eggs in plankton samples collected over the total spawning season in 1987 in the Southern Bight of the North Sea. Egg-size increased during incubation in both plaice and cod. The size-selective mortality estimated from the change in egg-size of plaice and cod separately, appeared to be close to the size selective mortality estimated from the difference in mortality between species. This suggests that one common process is operating. Implications of size-selective mortality in fish eggs are discussed for the study of the causes of egg-mortality and the estimation of spawning stock biomass from egg surveys.

### Introduction.

Egg size in teleost is species characteristic, although a substantial variability in egg-size is observed within species. In marine species egg-size decreases between January and August and increases again from September to December. Coinciding with the decrease in egg-size in spring also the range of egg size decreases. This seasonal pattern is observed within as well as among species (Bagenal, 1971; Ware, 1975). The seasonal change in egg-size was already known from the earliest studies of fish eggs (Ehrenbaum, 1911). The ecological implications of egg-size received little attention until the work of Blaxter and Hempel (1963), who showed that herring larvae hatching from large eggs were better able to survive periods of food shortages than larvae hatching from small eggs. In line with the concept of the critical period in the early life history (Hort, 1914; May, 1974) most research focussed on the relation between egg-size and subsequent larval survival. Cushing (1967, 1975) suggested that the seasonal pattern in egg-size was related to the seasonal cycle of larval food production. Bagenal (1971), following Cushing's approach, showed that also in plaice and in some freshwater species a similar correlation was apparent. Lambert and Ware (1988) suggested that egg-size was related to abundance and distribution of particle sizes of larval food.

Studies that specifically address the problem of egg-mortality and its causes are scarce. Data given in Dahlberg (1979) show that mortality of pelagic eggs is generally high and

may show large differences between years and geographical areas. Small variations in mortality rate of eggs may result in large variations in subsequent year-class strength. Therefore, the study of the causes of egg-mortality is crucial to the understanding of the reproductive variability in fish stocks. In North Sea plaice yearclass strength is already determined at the moment when 2 - 3 month old larvae enter the estuarine nursery areas (Rijnsdorp et al., 1985; van der Veer, 1986). Brander and Houghton (1982) even suggested that yearclass strength might already be determined in the egg-stage as the abundance of hatching eggs was significantly correlated with subsequent yearclass strength.

The causes of egg-mortality are not well known. Although factors such as fertilization rate, aberrant embryonic development and mortality through mechanical forces due to wave action may play a role in egg-mortality, it is generally believed that predation is the major cause (Rothschild, 1986; Houde et al., 1987). Predation of herring and sprat has been suggested as a possible cause in cod and plaice (Daan, 1976; Pommeranz, 1981), but a quantitative study showed that egg-predation by herring was negligible for cod and less than 1% for plaice (Daan et al, 1985). The study of egg-mortality appears to have moved into a dead-end street as it is not known which organisms could be potential egg-predators.

However, a new tool in the study of egg-mortality, that could lead us out of the dead-end street, might be deduced from the following observation. Egg-surveys, simultaneously carried out on plaice and cod, showed a correlation between egg-mortality and egg-size. The smaller cod eggs (1.4 mm) always had a higher mortality rate than plaice eggs (1.9 mm) (Heessen and Rijnsdorp, 1989). If egg-mortality is due to predation, the correlation implies that predation mortality is size selective and operates on the entire range of egg-sizes encompassing several fish species. Size-selective mortality also implies that egg-size will change during incubation. Jones (1958) showed that size-selective mortality can be estimated from the change in mean size and the variance in size. Thus by studying the changes in egg-sizes during incubation estimates can be made of the size-selective component of egg-mortality. In order to explore this hypothesis the change in egg-size of the different developmental stages of plaice and cod were estimated from plankton samples collected in the Southern Bight of the North Sea in 1987.

## Material and Methods.

Plankton samples were collected in oblique vertical hauls with a modified Gulf III Sampler (Zijlstra, 1970) at 5 miles per hour. Mesh-size was 280  $\mu\text{m}$ . The volume of water was measured with a current meter mounted in the net opening. Water depth and surface temperature were recorded at each station. In each ICES rectangle six stations were fished and for our particular purpose plankton samples were selected from the Southern Bight area (Fig.1). On board the plankton samples were washed in sea-water and stored in 4% formaldehyde solution buffered with borax to pH 7-8. Egg stage was determined and development time calculated, using the recorded surface temperatures, according to the formulae given by Thompson & Riley (1981) for cod and Ryland & Nichols (1975) for plaice. The eggs were well preserved and no deformities were noticed. In spring 1989 egg-size was measured under a microscope to the nearest eye piece unit of 0.05 mm.

Egg-production was calculated for each stage by integrating the estimates of daily egg production over the time interval between the midpoints of the surveys. Daily egg-production was estimated by correcting the abundance per  $\text{m}^2$  for the stage duration at the recorded temperature. The daily mortality rate was estimated from the regression of egg-production estimates against the mean age of each stage.

Size selective mortality was estimated following Jones (1958), see also Ricker (1969), assuming that mortality rate is linearly related to size and that the size distribution is normal. The difference in mortality rate ( $b$ ) of eggs differing one size-unit equals:

$$b = d / s^2$$

where  $d$  is the decrease in egg-size per unit of time and  $s^2$  is the variance of egg-size. In the present paper the unit of size and time are respectively 1 mm and 1 day.

Changes in egg-size during incubation were estimated following two approaches. The first approach (A) is to calculate the mean egg-size at each stage weighting over the daily stage production values and the time intervals between the midpoints of the surveys. The second approach (B) is to follow cohorts of eggs from one survey to the next.

## Results.

The size-distribution of stage 1 and stage 5 eggs is shown in Fig.2 and 3 and show that egg-sizes are about normally distributed. Mean egg-size and its variance and the estimates of daily egg-production are given in Table 1 for each survey. Standard deviations do not show a trend during the spawning season nor during the incubation period. Egg-size generally decreases during the spawning season and is most pronounced at the end of the season.

Following approach A, the size of an average egg was found to increase during incubation. (Fig.4) with respectively  $d = 0.0031 \text{ mm.d}^{-1}$  in plaice and  $d = 0.0022 \text{ mm.d}^{-1}$  in cod (Table 2). Also in approach B, when various cohorts of eggs between successive surveys are followed, an increase in egg-size is apparent (Fig.5). Table 3 gives the change in egg-size for each cohort. Because the expected change in egg size between stage 1 and stage 2 is small and the time interval is short the mean  $d$  was calculated over stage 3 - stage 5 only. Comparison of the change in egg-size in early and late cohorts indicated that the change was slightly bigger in the early cohorts of plaice eggs, although the difference is not significant (t test). In plaice the estimated  $d$  following approach A ( $d = 0.0031$ ) showed a close correspondence with the estimates following approach B ( $d = 0.0030 - 0.0038$ ). However, in cod approach B gave a lower mean  $d = 0.0015$  compared to approach A ( $d = 0.0022$ ).

The component of size-selective mortality can now be estimated from the daily change in egg-size ( $d$ ) and the variance in egg-size ( $s^2$ ). The variance in stage-1 eggs was used in the calculations. The results are given in Table 4. The difference in egg-mortality between cod and plaice corresponds to the estimates of size selective mortality obtained for the species separately (Fig.6). The slope of the size-selective component, indicated by the difference in mortality of the smallest and largest plaice or cod egg (mean  $\pm 2.58 \times$  standard deviation), is slightly more steep than the difference between the average plaice and cod egg. The size-selective mortality component  $b$ , estimated from the between species difference in egg-mortality ( $0.234 - 0.116 = 0.118$ ) and egg-size ( $1.867 - 1.417 = 0.447 \text{ mm}$ ), gives an estimate of  $b = 0.118 / 0.447 = 0.26$ , which is lower than  $b \sim 0.40$  as estimated from the change in egg size (Table 4).

## Discussion.

This pilot study showed the daily mortality rate of eggs was correlated with egg-size both between and within species, which suggests that one common process affects the mortality of both plaice and cod eggs. Predation is a likely candidate because it can easily generate size-selective mortality as predators have their own prey-size preferences, which is strongly related to body-size. Studies on the size distributions of organisms in the marine ecosystems show an exponential decline in abundance with increasing size (Peters, 1983). Hence the average number of potential predators will be higher for smaller egg-sizes. In a specific area or year deviations from the average size-distribution of the predator community may occur, that will result in differences in the size-selective mortality. A hypothetical example is shown in Fig.7. In Fig.7a the typical decline in abundance of pelagic organisms with body-size is shown. If all organisms are equal predators of fish eggs, with a prey-size preference of 0.01 times their own body size, the resulting relation of egg-mortality and egg-size is shown in Fig.7b. As we are interested in the mortality differences over a relatively small range of prey-sizes the actual abundance curve of egg-predators might be more erratic as illustrated in Fig.7b. A study of the change in egg-size of several fish species, preferably over the entire range of egg-sizes, may reveal the actual pattern of size-selective mortality. In combination with a study of the size-distribution of potential egg-predators and their prey-size preference, such an approach could allow the discrimination of the likely candidates of egg-predators in a multiple comparison of these data for different areas or years. That the egg-mortality curve may differ between areas or years is indicated by the annual variations in the differences in egg-mortality of plaice and cod (Table 6).

Another important implication of size-selective mortality in eggs is that the egg-mortality decreases during incubation as egg-size increases. Studies that use the number of fertilized eggs to estimate spawning stock biomass, generally assume a constant mortality rate during incubation and thus will underestimate the spawning stock biomass if size-selective mortality occurs. Taking account of the estimated daily change in egg-size in plaice from Table 2, the number of fertilized eggs is 14% higher in comparison with the assumption of constant egg-mortality. In cod the difference is 8%. Thus size-selective mortality can explain part of the observed discrepancy between estimates of spawning stock biomass from egg-surveys and from virtual population analysis (Bannister, 1974; Heessen and Rijnsdorp, 1989).

In this study, changes in egg-size during incubation were estimated from samples that were preserved in 4% formaldehyde, buffered with Borax to constant pH of 6-7. Whether the observed changes reflect real changes in egg-size depends on two conditions: 1) the size of an individual egg does not change during incubation; 2) change in egg-size due to preservation is equal between the different developmental stages. With regard to the first condition it should be realized that the biochemistry of eggs shows complex changes during development, which could in theory affect egg-size (Alderdice, 1988; Blaxter, 1988). However, Davenport et al. (1981) were unable to measure changes in egg-size in cod during development, but the structure of the chorion indicated that a small increase in egg-size might have occurred. With regard to the second condition, it is well known that egg-size decreases due to fixation (Hislop and Bell, 1987), but it is not known whether the decrease is equal for the different developmental stages. Because no information exists on the validity of the two conditions, it had to be assumed that the observed changes in egg-size quantitatively reflect the changes in egg-size in the sea. Therefore, it should be emphasized that the interpretations and conclusions given in this paper are preliminary and final conclusions or further application of the proposed method has to await future tests of the validity of the two conditions.

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Table 1. Mean size and standard deviation of plaice and cod eggs by stage in each survey. The mean egg-size and standard deviation over the total spawning period was estimated as the average in each survey weighted over the daily production. Survey midpoint is given as the day after 1 January.

Stage	Survey		Production per day (10 <sup>6</sup> )	Number measured	Mean egg-size (mm)	sdev	Total spawning period			
	number	mid- point					Mean egg-size (mm)	sdev	Stage duration (days)	Mean age
plaice 1	I	28	41640	740	1.877	0.0858	1.871	0.089	4.99	2.50
	II	56	35063	583	1.878	0.0939				
	III	83	7252	125	1.812	0.0841				
plaice 2	I	28	18647	294	1.898	0.0765	1.885	0.087	3.58	6.78
	II	56	32682	355	1.879	0.0926				
	III	83	2091	84	1.861	0.0724				
plaice 3	I	28	8502	128	1.905	0.0759	1.913	0.090	4.87	11.01
	II	56	13047	239	1.919	0.0989				
	III	83	653	53	1.889	0.0841				
plaice 4	I	28	3835	68	1.901	0.0758	1.913	0.083	4.38	15.63
	II	56	13838	209	1.922	0.0840				
	III	83	1203	83	1.851	0.0939				
plaice 5	I	28	899	18	1.919	0.0572	1.927	0.079	7.98	21.81
	II	56	5670	131	1.935	0.0836				
	III	83	604	43	1.866	0.0595				
cod 1	I	28	84883	540	1.449	0.0628	1.424	0.068	4.47	2.23
	II	56	120326	676	1.414	0.0704				
	III	83	18481	112	1.376	0.0800				
cod 2	I	28	35691	190	1.451	0.0595	1.434	0.066	1.56	5.24
	II	56	55727	290	1.427	0.0687				
	III	83	3081	48	1.365	0.0792				
cod 3	I	28	5258	68	1.454	0.0679	1.445	0.070	6.16	9.10
	II	56	5721	126	1.439	0.0710				
	III	83	321	46	1.390	0.0929				
cod 4	I	28	3750	33	1.452	0.0552	1.440	0.060	3.77	14.06
	II	56	4189	54	1.431	0.0625				
	III	83	132	10	1.430	0.0949				
cod 5	I	28	1760	30	1.462	0.0611	1.459	0.071	5.00	18.45
	II	56	2984	45	1.469	0.0624				
	III	83	730	9	1.411	0.1112				

Table 2. Change in egg-size ( $b$ ) in  $\text{mm.d}^{-1}$  over the total spawning period (approach A) as indicated by the regression of  $Y_i = a + b X_i$ , with  $Y_i$  is egg-size (mm) and  $X_i$  is mean age of egg stage 1 - 5.

	Plaice		Cod	
	mean	SE	mean	SE
$a$	1.864		1.417	
$b$	0.0031		0.0022	
$r^2$	0.93		0.91	
$n$	5		5	

Table 3 Change in egg-size ( $d$ ) in  $\text{mm.d}^{-1}$  estimated for different cohorts of eggs (approach B). The observed egg-size and the time between stage 1 and stage 2 - 5 for different cohorts of eggs in the February and March survey are given with the interpolated mean size at stage 1 of each cohort and the estimated change ( $d$ ) in  $\text{mm.d}^{-1}$ .

	observed size	interpolated size at stage 1	time interval since stage 1	$d$
Plaice				
February				
stage 2	1.879	1.877	4.28	.0005
stage 3	1.919	1.877	8.51	.0049
stage 4	1.922	1.877	13.13	.0034
stage 5	1.935	1.877	19.31	.0030
mean 3-5				.0038
March				
stage 2	1.861	1.859	4.28	.0005
stage 3	1.889	1.844	8.51	.0053
stage 4	1.850	1.833	13.13	.0013
stage 5	1.866	1.822	19.31	.0023
mean 3-5				.0030
Cod				
February				
stage 2	1.427	1.418	3.01	.0030
stage 3	1.439	1.423	6.87	.0023
stage 4	1.431	1.429	11.83	.0002
stage 5	1.469	1.435	16.22	.0023
mean 3-5				.0015
March				
stage 2	1.365	1.381	3.01	-.0053
stage 3	1.390	1.386	6.87	.0006
stage 4	1.430	1.393	11.83	.0031
stage 5	1.411	1.399	16.23	.0007
mean 3-5				.0015

Table 4. Size-selective mortality in cod and plaice eggs as estimated from the change in egg-size and variance in egg-size following approach A and B.

Approach		Daily increase in egg-size $d$ (mm)	Standard Deviation $s$	Change in mortality $b = d / s^2$
Plaice	A	0.0031	0.089	0.391
	B	0.0034		0.429
Cod	A	0.0022	0.068	0.476
	B	0.0015		0.324

Table 5. Difference in mortality rate between the biggest and smallest egg due to size selective mortality as estimated over the total spawning season (approach A) and from separate egg cohorts (approach B).

	Mean egg-size at fertilization (mm)	Size range of eggs (mean $\pm$ 2.58s)	Difference in mortality rate	
			A	B
Plaice	1.864	1.634 - 2.094	0.180	0.197
Cod	1.417	1.242 - 1.592	0.167	0.113

Table 6. Comparison of daily mortality rates in North Sea plaice and cod eggs estimated in the same area and time period. Sources: 1) Harding et al, 1978a; 2) Harding et al. 1978b; 3) Daan, 1979; 4) Heessen and Rijnsdorp, 1989.

Year	Area	Plaice	Cod	Source
1971	Southern Bight	0.12	0.41	1, 3
1976	Flamborough	0.04	0.14	2
1987	Southern Bight	0.12	0.23	this study
1988	South-eastern North Sea	0.17	0.22	4

Table 7. Procedure to calculate the number of fertilized eggs corrected for size-selective mortality during incubation.

Mortality ( $Z$ ) is assumed to be linearly related with egg-size.

$$Z_t = Z_0 - b \Delta D_t \quad [1]$$

with  $Z_0$  is the mortality at time 0,  $b$  is the change in mortality corresponding to a change in egg-size ( $D$ ) of 1 mm.

The change in egg-size at time  $t$  since time 0 ( $\Delta D_t$ ) is

$$\Delta D_t = d \ t \quad [2]$$

Following Jones (1958)

$$b = d / s^2 \quad [3]$$

with  $s^2$  is the variance in egg-size.

From [1], [2] and [3] it follows that

$$Z_t = Z_0 - t (b^2 / s^2) \quad [4]$$

The decrease in egg-numbers at time is given by

$$N_t = N_0 e^{-t Z} \quad [5]$$

substituting [4] in [5] and taking logarithms gives

$$\log_e N_t = \log_e N_0 - t (Z_0 - t b^2 / s^2) \quad [6]$$

$$\log_e N_t = \log_e N_0 - t Z_0 + t^2 b^2 / s^2 \quad [7]$$

When the daily change in egg-size  $b$  and the variance  $s^2$  is known and a number of observations of  $N_t$  at  $t$  are available the number of fertilized eggs ( $N_0$ ) can be determined by regression analysis of

$$\log_e N_t - t^2 b^2 / s^2 = \log_e N_0 - t Z_0 \quad [8]$$

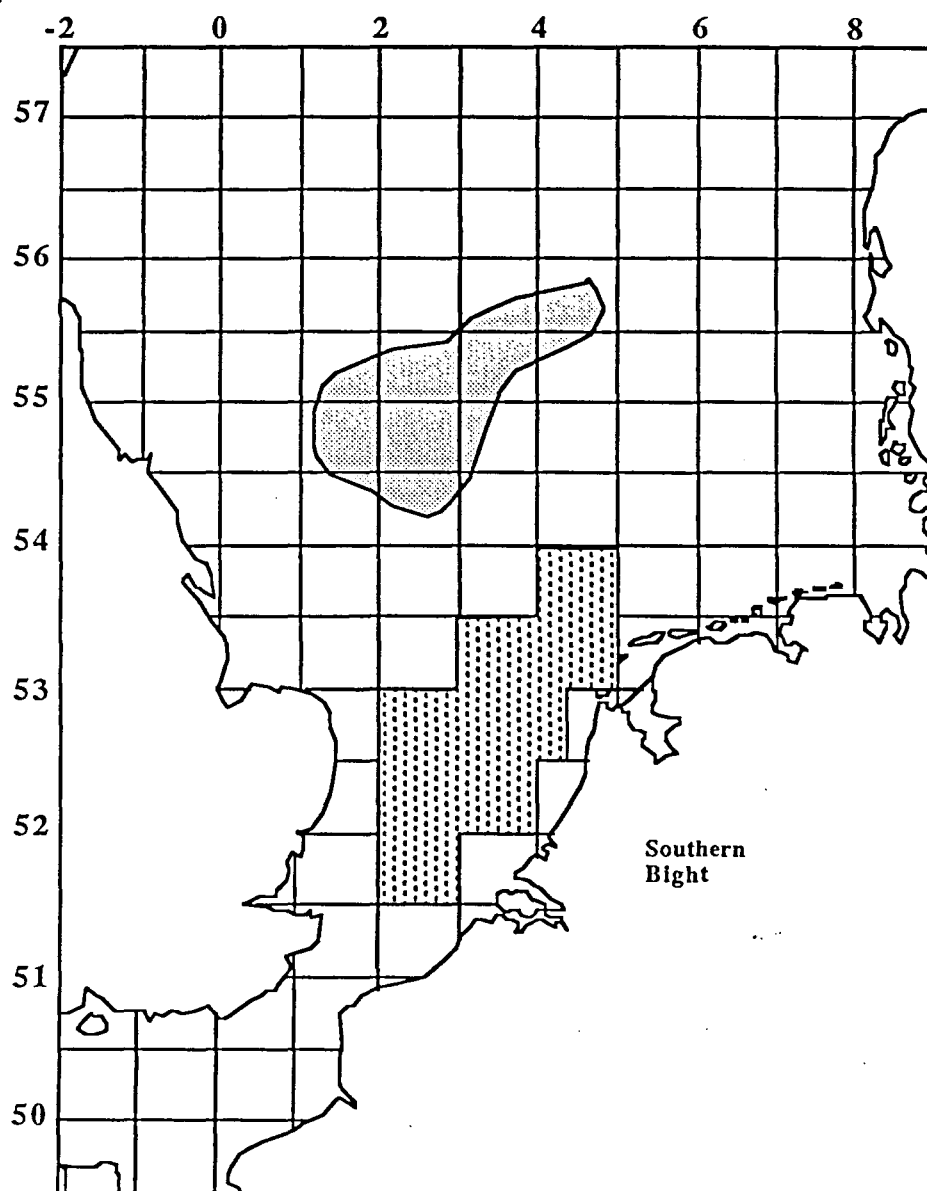


Figure 1. Sampling area in the Southern Bight of the North Sea for egg-sizes of plaice and cod in the surveys of January, February and March 1987

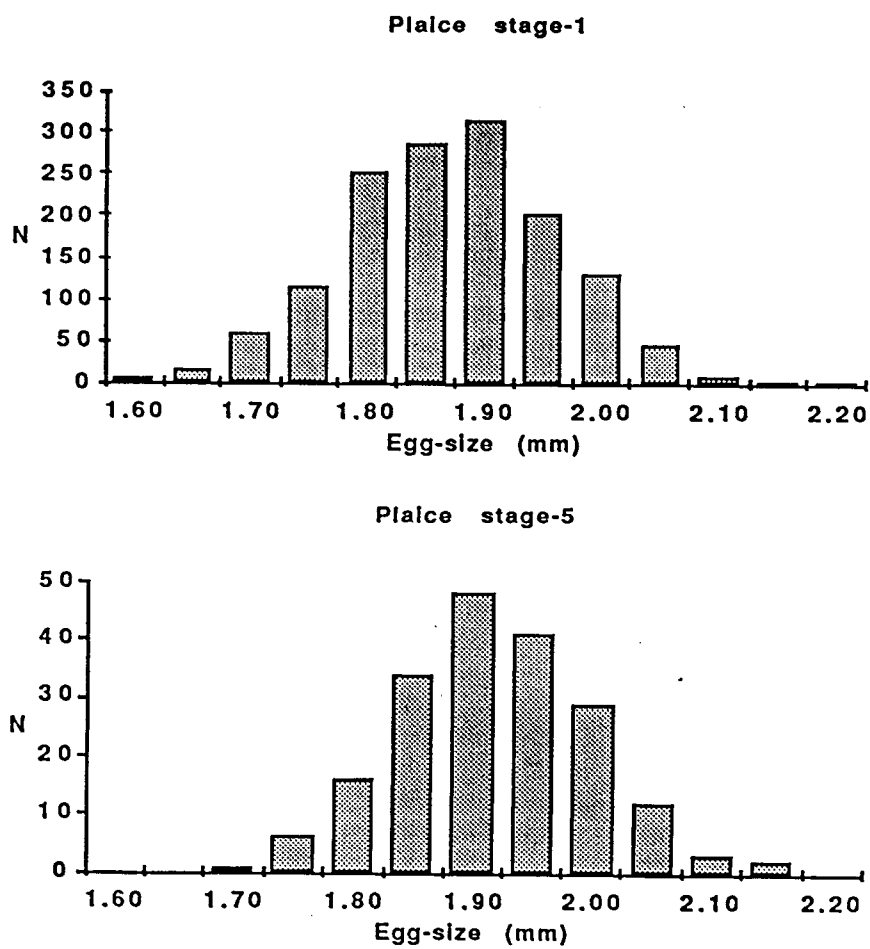


Figure 2. Size distribution of stage 1 and stage 5 eggs of plaice collected in January, February and March surveys.

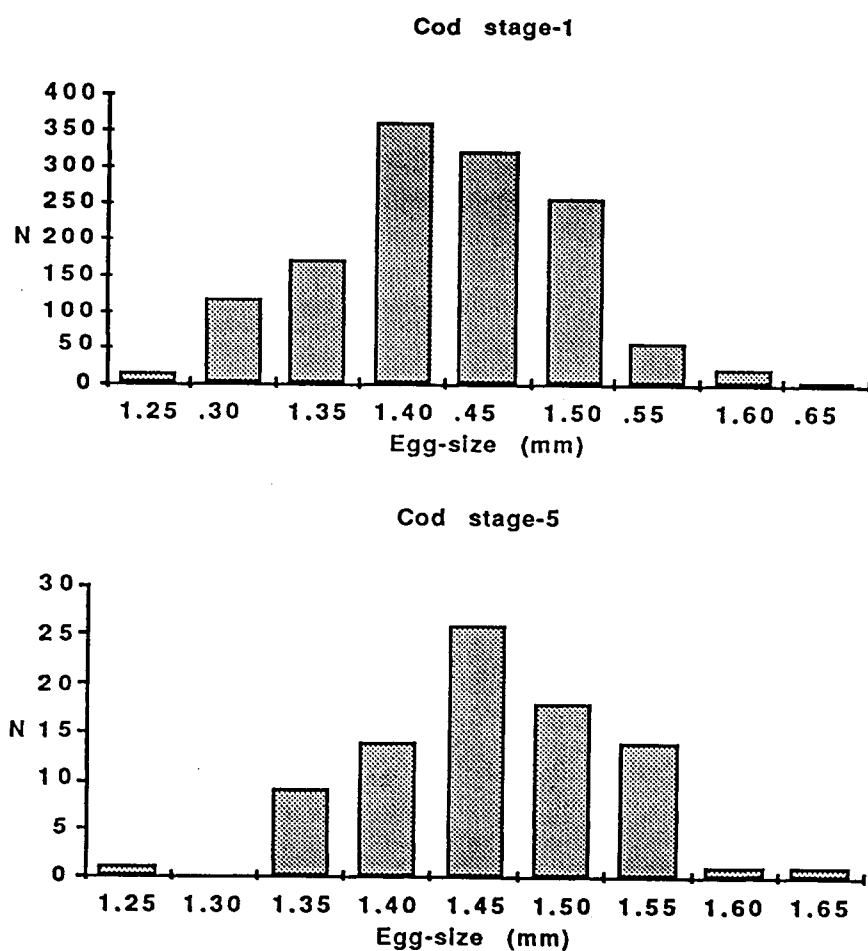


Figure 3. Size distribution of stage 1 and stage 5 eggs of cod collected in January, February and March surveys.



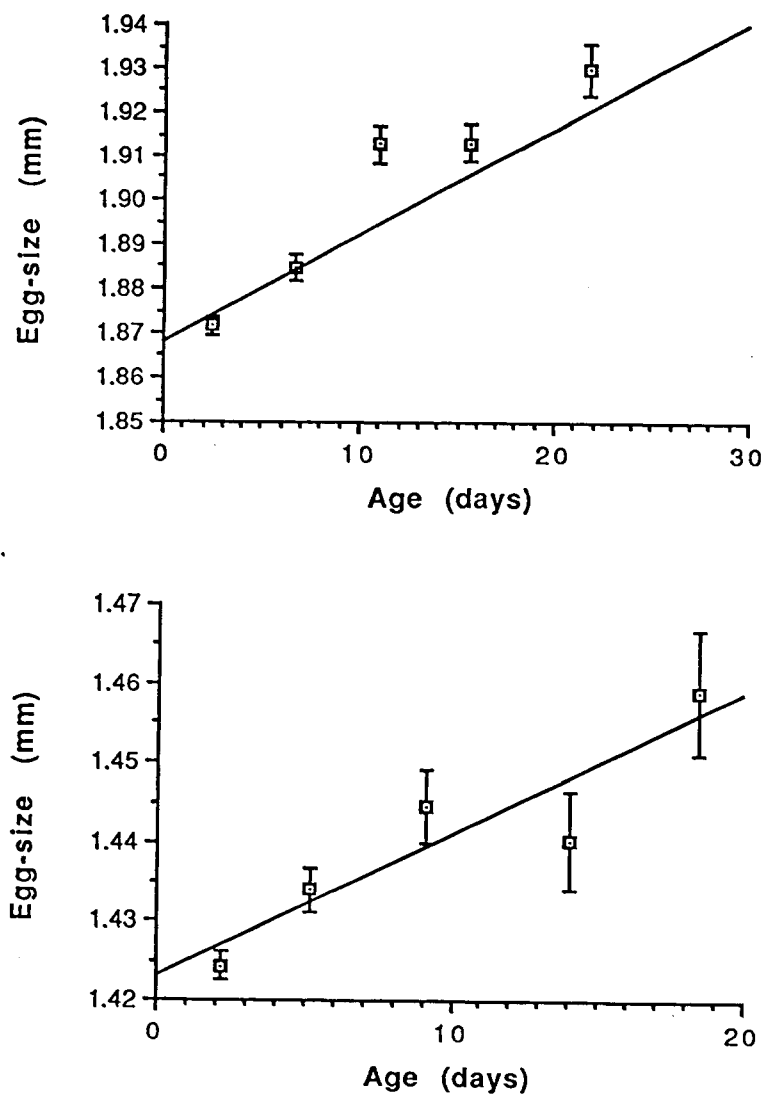


Figure 4. Change in egg-size during incubation as indicated by the mean egg size of stage 1 - stage 5 against the mean age in days. Error bars indicate  $\pm 1$  S.E. around the mean.

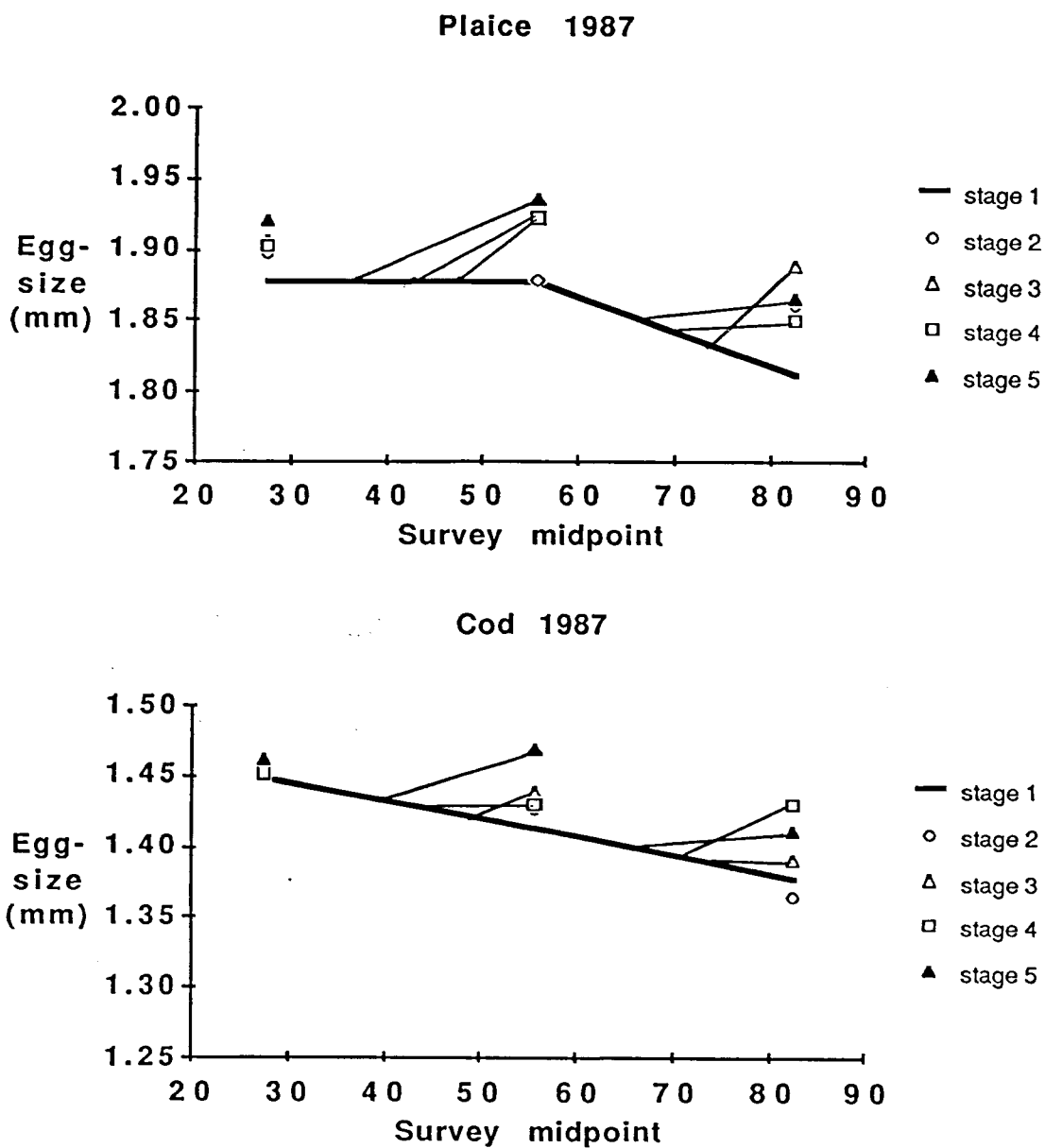


Figure 5. Change in egg-size of early and late cohorts of eggs. The thick line connects the egg-size of stage 1 eggs.

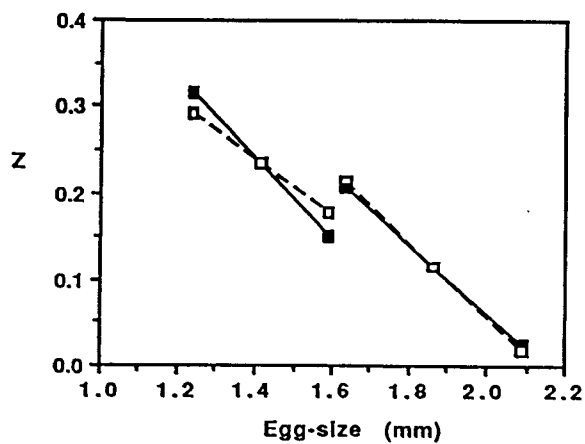


Figure 6. Relation between egg-mortality and egg-size in plaice and cod eggs as estimated following approach A (full line) and B (broken line). The lines for each species connect the mortality of egg sizes that differ  $2.58 \times s$  from the mean. Egg-size ranges between 1.2 - 1.6 mm in cod and between 1.6 - 2.1 mm in plaice.

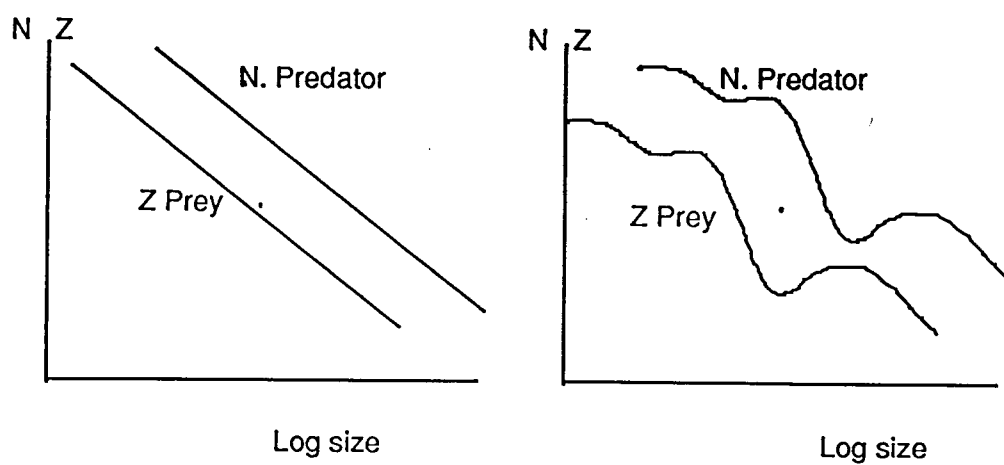


Figure.7 Some hypothetical relations between the abundance (N) of organisms against body size and the resulting relation between predation mortality (Z) and prey size.