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THE ECOLOGICAL SIGNIFICANCE OF GEOGRAPHICAL AND SEASONAL DIFFERENCES IN EGG SIZE IN SOLE *SOLEA SOLEA* (L.)

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ABSTRACT

Egg size of the common sole *Solea solea* (L.) was studied from ichthyoplankton surveys conducted between 1987 and 1991 in seven different areas ranging from the Bristol Channel and western English Channel to the German Bight of the North Sea, encompassing central as well as peripheral parts of the distribution range of the species. Egg size showed a seasonal decline of 0.00179 $\text{mm}\cdot\text{d}^{-1}$. Egg size at peak spawning decreased from 1.37 mm in central areas in the south-west to 1.13 mm in peripheral areas in the northeast, corresponding to a decrease in egg volume of 44%. The difference in egg size between areas coincided with differences in the timing of spawning, but a significant small geographical difference in egg size remained after removing the seasonal effect. Egg size was largest in the southwestern areas and decreased to the northeast. The close relationship between spawning time, egg size and egg number (fecundity) suggest that these are three aspects of a common process of ovarian development which is influenced by the photoperiod and temperature. Egg size increased between fertilization and hatching, suggesting that the mortality process is size-selective with a higher mortality rate for smaller eggs. A negative relationship between egg mortality and egg size was observed among the seven sole stocks studied and also in a study of literature data on egg mortality rate of various species spawning in the North Sea and adjacent areas. The ecological implications of these results are discussed.

1. INTRODUCTION

Seasonal patterns in egg size in marine fish are well documented (Ehrenbaum, 1905, 1909; Bagenal, 1971). Egg size declines from winter to spring and increases again during autumn. This seasonal pattern is apparent within, as well as among, species.

Geographical patterns in egg size are less well documented. In their classical study, Blaxter & Hempel (1963) showed that the mean size of herring eggs differed widely between various areas in the North Sea: small eggs being produced in northern spawning populations, large eggs in southern. Fleming & Gross (1990) showed that egg size in Pacific salmon decreased with latitude, but Miller *et al.* (1991) found that egg size increased with the northern limit of the latitudinal range in North American flatfish. In northwestern Pacific flatfish, Minami & Tanaka (1992) showed that egg size decreased from offshore to inshore spawning species. In the above studies the geographical differences were only related to differences in spawning time and therefore did not allow us to test whether differences in egg size occur between geographical areas which are not related to the differences in the timing of spawning.

Egg size is viewed as having evolved in response to the probability for larvae to find suitable food and to the mortality risk due to predation (Svärdson, 1949; Rothschild, 1986). The seasonal decline in egg size is seen as an adaptation to the change in the size structure of the plankton to smaller particles (Hempel & Blaxter, 1967; Jones & Hall, 1974; Ware, 1977; McEvoy & McEvoy, 1991). However, others have interpreted the seasonal decline as an eco-phenotypic response to increasing water temperatures without an adaptive significance (Bromley *et al.*, 1986; Devauchelle *et al.*, 1987; Daouglas & Economu, 1986).

Variations in egg size may have important ecological implications because it may affect the survival of eggs and larvae (Knutsen & Tilseth, 1985; Rothschild, 1986; Hinckley, 1990; Pepin, 1991; Heath, 1992; Minami & Tanaka, 1992). Although the causes of egg and larval mortality are not well known, it is generally believed that predation is a major cause (McGurk, 1986; Houde, 1987; Bailey & Houde, 1989). Support for the predation hypothesis was given by Rijnsdorp & Jaworski (1990), who showed that egg mortality in plaice and cod eggs was size-selective. The size-selective mortality led to a higher mortality of the smaller cod eggs as compared to plaice eggs, and to an increase in the mean egg size between fertilization and hatching. The size-selective mortality estimated from the difference in mortality between the species,

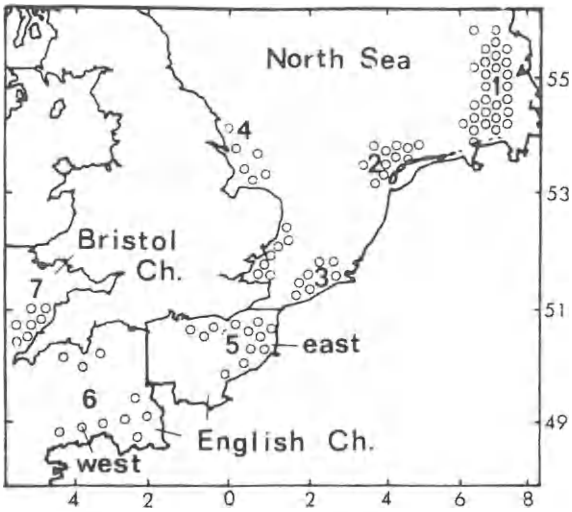

Fig. 1. Map of the study area with the geographic names, and sampling areas for egg size. The major concentrations of sole eggs are indicated according to ICES (1992a).

appeared to be close to the size-selective mortality estimated from the change in egg size from fertilization to hatching in both plaice and cod eggs.

In this paper we study the seasonal and geographical patterns in egg size in sole by measuring the diameter of eggs sampled during a series of ichthyoplankton surveys conducted in the spawning season of seven stocks of sole encompassing both the centre of the distribution range and peripheral areas. These areas are inhabited by distinct sole stocks, characterized by different levels and patterns of variability in recruitment (Rijnsdorp *et al.*, 1992) and fecundity (Greer Walker & Witthames, 1990; Horwood, 1993; Witthames *et al.*, ms.). Special attention is given to the relation between egg size and mortality, by studying changes in egg size between fertilization and hatching in separate areas, and by reviewing the relationship between egg mortality and egg size from several fish species that spawn pelagic eggs in the North Sea and adjacent areas.

2. MATERIAL AND METHODS

2.1. PLANKTON SAMPLING

Sole eggs were collected during routine ichthyoplankton surveys carried out principally in 1991. In two areas some sampling was conducted in 1989 and 1990. The surveys were aimed at estimating the total egg production of sole in various management areas for assessment purposes (Van Beek, 1989; ICES 1991, 1992a). In the present study, sub-areas were defined through known differences in the fecundity-size relationship. The sub-areas distinguished are shown in Fig. 1 and include: 1. German Bight, 2. Texel, 3. Belgian coast, 4. Flamborough. 5. eastern English Channel, 6. western English Channel and 7. Bristol Channel.

Plankton samples were collected with a high speed torpedo which is fished in oblique hauls from the sea surface to about 5 m above the sea bed (ICES, 1986). Mesh size was 540 µm. Egg samples were fixed in buffered 4% formaldehyde. Egg diameter was measured with an ocular micrometer to the nearest 0.033 or 0.05 mm. Measurements were carried out on fixed material at least 6 months after fixation. The reported egg sizes will be smaller than the actual egg size due to shrinkage (Hislop & Bell, 1987). Throughout the paper, egg size will refer to the diameter of the eggs.

2.2. SIZE-SELECTIVE MORTALITY

All estimated egg morality rates are expressed as instantaneous mortality rates (d^{-1}). If egg mortality is a linear function of egg size (Φ): $M = a + b\,\Phi$, and if egg size is normally distributed with mean μ and variance σ^2, the change in mean egg size per unit of time (d) can be described as (Jones, 1958; Rijnsdorp & Jaworski, 1990):

$$d = b\,\sigma^2 \qquad \text{(eq. 1)}$$

where b equals the difference in mortality rate of eggs differing by one size unit. In the present study the units of size and time are 1 mm and 1 day, respectively.

The change in egg size between fertilization and hatching was estimated from the regression of the seasonal mean egg size of the four developmental stages, defined according to Riley (1974), against their mean age. Seasonal mean egg size was calculated following the procedure of Rijnsdorp & Jaworski (1990) that averages the survey mean egg size by weighting over the stage-specific daily production over the complete spawning season. The mean age of each developmental stage was calculated according to the formulae given in ICES (1992a) based on Riley (1974), and using the temperatures recorded during the surveys at 5-m depth. Stage specific measurements were collected for the 1991 surveys in areas 1, 2, 3 and 5.

2.3. LITERATURE REVIEW

The review of egg mortality rates and egg size was restricted to the North Sea and adjacent continental shelf areas, excluding other ecosystems such as upwelling zones. The analysis was further restricted to data sets that covered the total spawning period. Studies that estimated mortality rate from a single survey were excluded. For those studies that did not report egg sizes, mean size was based on literature data: plaice 1.871 mm, cod 1.424 mm (Rijnsdorp &

TABLE 1

Mean egg diameter (Φ, mm), standard deviation (SD) and number (n) of sole eggs measured, the midpoint of the surveys (days after 1 January) and the ambient sea water temperature (°C) measured at 5 m and weighted over the daily production of stage 1 eggs. Data are for sole eggs that were fixed in 4% buffered formaldehyde.

year	*midpoint* *(days after 1 January)*	Φ *(mm)*	*S.D.*	*n*	*temperature* *(°C)*
1 - North Sea: German Bight (IVb east)					
1989	118	1.244	0.054	104	6.8
1989	192	1.083	0.058	263	16.7
1990	115	1.196	0.057	286	9.2
1990	171	1.045	0.052	117	14.4
1991	113	1.204	0.058	184	7.7
1991	150	1.107	0.048	358	11.0
1991	169	1.072	0.041	152	11.8
2 - North Sea: Texel (IVb, c)					
1991	79	1.275	0.039	8	6.5
1991	108	1.207	0.052	473	8.0
1991	140	1.089	0.064	368	10.3
1991	168	1.077	0.049	55	12.4
1991	192	1.150	0.024	2	15.6
3 - North Sea: Belgian coast (IVc)					
1989	110	1.227	0.054	562	8.7
1990	86	1.243	0.054	408	8.7
1990	142	1.143	0.050	282	13.7
1991	106	1.223	0.050	354	9.0
1991	134	1.218	0.055	343	9.8
1991	162	1.136	0.066	59	12.3
4 - North Sea: Flamborough (IVb west)					
1991	106	1.311	0.019	3	6.6
1991	135	1.287	0.040	26	9.1
1991	164	1.235	0.058	31	11.4
5 - eastern English Channel (VIId)					
1991	83	1.292	0.060	335	7.8
1991	105	1.271	0.068	634	8.8
1991	139	1.242	0.064	185	10.1
1991	154	1.219	0.077	152	11.3
6 - western English Channel (VIIe)					
1991	60	1.441	0.062	142	8.8
1991	79	1.421	0.076	48	8.6
1991	111	1.324	0.068	391	9.6
7 - Bristol Channel (VIIf)					
1990	70	1.404	0.050	640	9.2
1990	93	1.334	0.056	794	9.2
1990	120	1.301	0.048	142	9.7

Jaworski, 1990) and sprat 1.05 mm (Russell, 1976). For sole the egg size at peak spawning time was taken as predicted from our results (Table 5).

Temperature has been included in the analysis because egg mortality may be affected by it (Harding *et al.*, 1978a; Van der Land, 1991; Pepin, 1991). Temperature data used are the ambient temperature experienced by stage-1 eggs. If temperature data

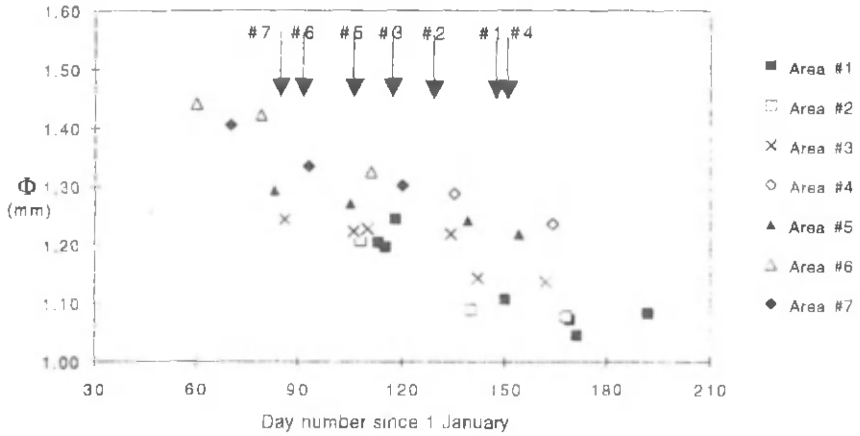

Fig. 2. Relationship between the mean egg size (mm) and the midpoint of the sampling period.

were not available from the original paper, they were estimated from the reported age at hatching and the relationship between developmental rate and temperature available in the literature: plaice - Ryland & Nichols (1975); cod - Thompson & Riley (1981); sprat - Milligan (1986).

In the analysis of egg mortality (*M*) the following model was used:

$$\ln M = \Phi + T + S + S \cdot T, \qquad \text{(eq. 2)}$$

where Φ is egg size, *T* is temperature, *S* is species and $S \cdot T$ is the interaction of temperature and species. The rationale for choosing the natural logarithm of mortality is that with this transformation the model becomes multiplicative.

2.4. STATISTICAL METHODS

Analysis of (co)variance technique was applied to study the effect of various variables on egg size using the NAG statistical package GLIM (Baker & Nelder, 1978). The contribution of each covariable was estimated by backward elimination. Variance that could not be ascribed to a single covariable was included as multicollinearity.

3. RESULTS

3.1. EGG SIZE

Data on mean egg size are presented in Table 1 and encompass the total spawning period for areas 1 - 6 in 1991 and for area 7 in 1990. For area 1 and area 3, additional data are given from samples taken in 1989 and 1990. Egg size gradually declined from maximum values around 1.45 mm in late February to around 1.05 mm in June (Fig. 2).

The seasonal decline in egg size coincided with a shift in the spawning period between the areas indicated by the arrows in Fig. 2. The time of peak spawning was determined by fitting a parabolic

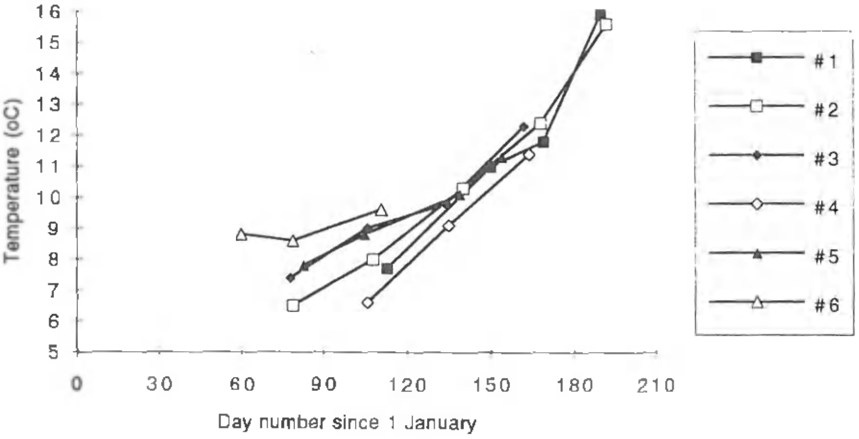

Fig. 3. Seasonal changes in water temperature (°C) at 5 m depth observed during the ichthyoplankton surveys.

TABLE 2

Results of the ANOVA of mean egg diameter (Φ) as function of the day number (D), area (A) and temperature (T) according to the GLM model: $\Phi = \alpha + \beta D + A + \gamma T + \beta' A.D$, weighted over the number of eggs measured in each sample. The multicollinearity term shows the part of the explained variance that can not be ascribed to either A or D.

covariable	*sum of squares*	*degrees of freedom*	*mean square*	*F*	*P*
D	12.235	1	12.235	76.66	<0.01
A	15.207	6	2.535	15.88	<0.01
multicollinearity	41.765				
error	3.671	23	0.160		
T	0.301	1	0.301	2.35	NS
A.D	1.483	6	0.247	1.93	NS
error	2.046	16	0.128		
total	72.879	30			

regression through log-transformed daily production values of stage 1 eggs as given in ICES (1992a) and Horwood (1993). Peak spawning shifted by two mo from southwest to northeast, respectively, from late March in areas 6 and 7 to late May in areas 1 and 4. The other areas were intermediate. The earlier spawning in the southwestern areas coincided with higher winter temperatures (Fig. 3).

To disentangle the seasonal, geographical and temperature effects on egg size, an analysis of covariance was carried out that employed a generalized linear model (GLM) of mean egg size (Φ) as a function of day number (D), area (A) and temperature (T). Area was entered as a categorial variable with seven levels coding for the areas distinguished in the present study. Because not all mean egg size measurements were equally precise, the number of eggs measured was used as a weighting factor. Analysis of the GLM model:

$$\Phi = \alpha + \beta D + A + \gamma T + \beta' A \cdot D$$

showed that day number (D) and area (A) were significant, but temperature and the interaction of area and day were not (Table 2). The model, including only significant variables, explained 95% of the variance in mean egg size, of which 17% and 21% could be ascribed to D and A, respectively. A substantial part of the variance (57%) could not be ascribed to a single covariate due to the multicollinearity of A and D. The non-significant interaction term A.D indicated that the seasonal decline in egg size did not differ significantly between areas. The common slope showed that egg size declined by 0.00179 mm·d^{-1} (SE=0.00020; Table 3). The significant contribution of area implied that mean egg size, corrected for the decline through the season, differed among areas. Among area differences in egg size corrected for the seasonal decline indicated a maximal differences of 0.135 mm between area 1 and area 6. The corrected egg size declined from the southwest (areas 6 and 7) to the northeast (area 1). A striking difference in egg size of 0.13 mm existed between area 1 in the eastern North Sea and area 4 in the western North Sea, although the SE for area 4 is rather wide compared to the SE of other areas due to the small sample sizes (Table 3).

TABLE 3

Parameter estimates of the GLM model of mean egg size (Φ) as function of the day number (D) and area (A) according to the GLM model: $\Phi = a + b\ D + A$.

	Φ (mm)	*SE*
a	1.460	0.0255
b	-0.00179	0.00020
areas:		
1	-0.0637	0.0136
2	zero aliased	
3	-0.0423	0.0113
4	0.0661	0.0448
5	0.0020	0.0127
6	0.0715	0.0170
7	0.0528	0.0137

TABLE 4

Results of the ANOVA of mean egg diameter (Φ) as function of the day number (D), area (A) and sampling year (YR) according to the GLM model: $\Phi = a + b\ D + A + \mathrm{YR}$, weighted over the number of eggs measured in each sample. Data for area 1 and 3 for the years 1989, 1990 and 1991.

covariable	*sum of squares*	*degree of freedom*	*mean square*	*F*	*P*
D	6.572	1	6.572	39.3	<0.01
YR	0.615	2	0.312	1.87	NS
A	0.251	1	0.251	1.50	NS
multicollinearity	4.628				
error	1.338	8	0.167		
total	13.404	12			

For areas 1 and 3, egg size measurements were available for three years allowing the analysis of dif-

TABLE 5

Estimated time of peak spawning (days after 1 January) and the associated mean egg diameter (Φ) in mm calculated from the parameter estimates of Table 3.

area	*time of peak spawning*	*egg diameter (Φ)*	
	mean	*mean*	*SE*
1	148	1.132	0.012
2	131	1.226	0.013
3	118	1.207	0.009
4	151	1.257	0.052
5	111	1.264	0.011
6	91	1.369	0.017
7	86	1.360	0.012

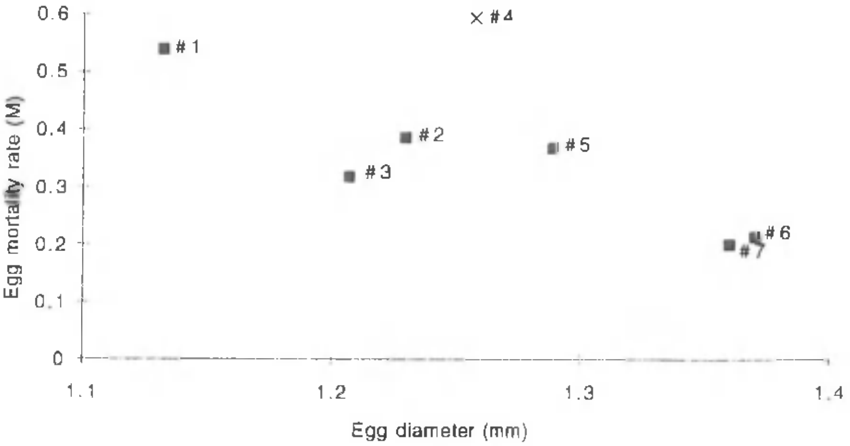

Fig. 4. Relationship between instantaneous egg mortality rate (M; d^{-1}) and egg diameter (mm) estimated from the ichtyoplankton surveys in 1991.

ferences in egg size between years. The available data for 1989 and 1990 did not comprise the full spawning period. ANOVA of these data did not indicate a significant difference in mean egg size among the three years, nor between the two areas (Table 4).

Egg size at the time of peak spawning was calculated from the regression parameters of Table 3 and is given in Table 5. This egg size reflected the size of the average egg produced by the particular sole stock.

TABLE 6

Seasonal mean diameter (Φ, in mm) of sole eggs in 1991 for each developmental stage 1-4, standard deviation (SD), number of eggs measured (n) and the mean age (in days) at the ambient water temperature. The seasonal mean egg diameter was weighted over the stage-specific daily production values for each survey.

stage	*Φ (mm)*	*SD (mm)*	*n*	*age (days)*
1 - North Sea: German Bight				
1	1.102	0.0478	332	1.0
2	1.103	0.0443	171	2.4
3	1.106	0.0447	142	4.0
4	1.112	0.0395	49	6.1
2 - North Sea: Texel				
1	1.136	0.0583	394	1.2
2	1.133	0.0632	230	2.8
3	1.151	0.0488	212	4.8
4	1.172	0.0490	60	7.3
3 - North Sea: Belgian				
1	1.209	0.0566	273	1.2
2	1.207	0.0509	226	2.9
3	1.219	0.0500	200	4.9
4	1.234	0.0495	57	7.5
5 - eastern English Channel				
1	1.267	0.0669	826	1.2
2	1.261	0.0637	247	2.9
3	1.259	0.0665	187	4.9
4	1.280	0.0685	46	7.4

3.2. SIZE-SELECTIVE MORTALITY

The relationships between egg size and daily mortality rate (*M*, d^{-1}) was explored by regressing *M* against egg size at peak spawning (Fig. 4). *M* was estimated from the regression of the estimated daily egg production by developmental stage against the midpoint of each developmental stage and was obtained from ICES (1992a). The linear regression in Fig. 4 was not significant at the 5% level (r^2=0.51, n=7, $p<0.10$). The main outlier from the suggested linear relationship was the high mortality rate estimated for area 4. For this area both the mean egg size and mortality estimate were rather imprecise due to a relatively small sample size and the incomplete coverage of the shallow inshore areas where the highest production of eggs was expected (Riley, 1974). Excluding the data for area 4 improved the correlation (r^2=0.82, n=6, $p<0.05$), and suggested that the daily instantaneous mortality rate (d^{-1}) declines by 1.2 per mm increase in egg size.

In Table 6 the seasonal mean egg size is presented for the four developmental stages. Because the egg size declined in time, the mean size was calculated as a weighted average over the stage specific daily production values for each survey. Table 6 suggested that between fertilization and hatching egg size increased in areas 1, 2 and 3, but not in area 5. Regression analysis of mean egg sizes against age for each separate area indicated that the change in egg size during incubation differed significantly from zero in only one area (1). However, the analysis of the total data set showed that the increase in egg size between fertilization and hatching was significant and

TABLE 7

Results of the ANOVA of mean egg diameter (Φ) as function of the age and area according to the GLM model: $\Phi = a + b\,Age + Area + Area{\cdot}Age$, weighted over the number of eggs measured in each sample. Data for area 1, 2, 3 and 5 for the year 1991.

covariable	sum of squares	degrees of freedom	mean square	F	P
Age	0.060	1	0.060	5.80	<0.05
Area	15.045	3	5.015	484.9	<0.01
Age·Area	0.0532	3	0.0177	2.35	NS
error	0.0605	8	0.0076		
total	15.167	15			

TABLE 8

Size selective mortality component estimated according to two approaches: A: from the mean change in egg diameter per day (d) between fertilization and hatching and the variance (σ^2) in egg diameter according to $d = b\,\sigma^2$ for areas 1, 2 and 3, and 5. B: from the regression of M against mean egg diameter in the 6 areas studied in 1991 from Fig. 4.

	d ($mm{\cdot}d^{-1}$)	σ^2 (mm^2)	b ($mm^{-1}{\cdot}d^{-1}$)
appraoch A:			
area 1	0.00233	0.00228	1.02
area 2	0.00233	0.00340	0.69
area 3	0.00233	0.00320	0.73
area 5	0.00233	0.00440	0.53
approach B			1.2

that the slope of the regressions did not differ significantly among areas (Table 7: non-significant interaction term *Area·Age*). The common regression slope for these areas was estimated at 0.00233 mm·d^{-1} (SE = 0.00096). The significant *Area* effect indicated that the instantaneous mortality rate differed significantly among the areas.

From the observed change (*d*) and the variance (σ^2) in egg size, the size-selective mortality (*b*) could be estimated according to eq. (1). The variance in egg size was calculated for each area as the average variance weighted over the number measured. Estimates of the size-selective mortality (*b*) ranged between 0.53 and 1.02 per mm increase in egg size (Table 8) and are plotted in Fig. 5. These estimates of size-selective mortality are slightly lower than the value of 1.2 per mm increase in egg size obtained from the analysis of population mortality and population egg size in the seven sole stocks (Fig. 4).

3.3. LITERATURE REVIEW

Analysis of literature data on the relationship of ^{e}log egg mortality (ln*M*) *vs* egg size (Φ) and temperature (T) comprised data sets of sole, plaice, cod and sprat (Table 9). Ln*M* showed a positive relationship with temperature (Fig. 6a), but a negative relationship with egg size (Fig. 6b). These relationships, however, did not suggest which of the factors are actually involved, because both egg size and temperature are related to the time of year. A study of the residual ln*M*, calculated as the observed minus the predicted ln*M* from the regression of ln*M* against egg size, showed that egg mortality was lower than expected at temperatures below 6°C (Fig. 6c). The residual ln*M*, calculated from the regression of ln*M* against temperature, plotted against egg size (Fig. 6d) showed a relatively lower mortality rate for the larger eggs of plaice. In this figure the mortality rates of cod appeared to be relatively high for their size. Analysis of covariance of the GLM model:

$$\ln M = a + b\Phi + cT + S + (S \cdot T)$$

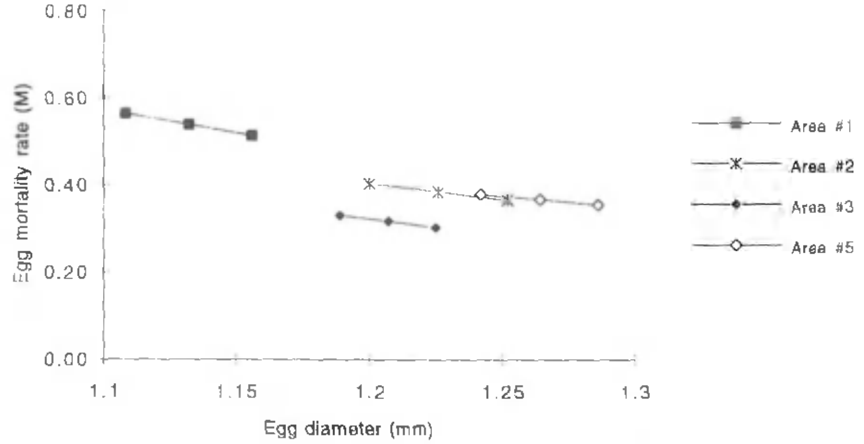

Fig. 5. Relationship between instantaneous egg mortality rate (M; d^{-1}) and egg diameter (mm) in four sub-stocks of sole. The lines show the size selective mortality component estimated from the increase in egg size during incubation from Table 8.

TABLE 9

Summary of data on egg diameter (Φ), daily egg mortality rates (M) and temperature (T) for fish species with pelagic eggs spawning in the North Sea, English Channel and Bristol Channel.

	egg diameter (mm)	*M* (*d*$^{-1}$)	*T* (°*C*)	*area*	*source*
Solea solea (L.)					
	1.132	0.724	10.4	1 - German Bight	ICES, 1992a
	1.132	0.745	11.3		
	1.132	0.500	8.7		
	1.132	0.601	9.4		
	1.132	0.539	11.1		
	1.226	0.337	8.8	2 - Texel	
	1.226	0.560	9.4		
	1.226	0.295	8.5		
	1.226	0.328	9.2		
	1.226	0.385	9.6		
	1.207	0.547	10.5	3 - Belgian coast	
	1.207	0.607	10.6		
	1.207	0.304	9.5		
	1.207	0.375	9.9		
	1.207	0.317	9.4		
	1.257	0.592	9.7	4 - Flamborough	
	1.264	0.367	9.4	5 - VIId	
	1.369	0.213	9.4	6 - VIIe	
	1.360	0.203	9.2	7 - Bristol Channel	Horwood, 1993
Pleuronectes platessa L.					
	1.871	0.068	4.6	SE North Sea	Heessen & Rijnsdorp, 1989
	1.871	0.165	7.9		
	1.871	0.096	7.1	SE North Sea	Van der Land *et al.*, 1990
	1.871	0.039	5.0	Southern Bight	Harding *et al.*, 1978a
	1.871	0.135	7.6		
	1.871	0.084	8.9		
	1.871	0.063	6.6		
	1.871	0.055	8.3		
	1.871	0.090	8.3		
	1.871	0.074	7.4		
	1.871	0.017	3.8		
	1.871	0.071	7.3		
	1.871	0.074	7.7		
	1.871	0.119	8.6		
	1.871	0.128	10.6	English Channel	Harding *et al.*, 1978a
	1.871	0.040	5.9	Flamborough	Harding *et al.*, 1978b
Gadus morhua L.					
	1.424	0.027	5.2	Southern Bight	Daan, 1981
	1.424	0.411	5.9		
	1.424	0.277	6.1		
	1.424	0.245	7.0		
	1.424	0.297	7.4		
	1.424	0.141	4.0	Southern Bight	Heessen & Rijnsdorp, 1989
	1.424	0.215	6.5		
	1.424	0.205	7.1	Southern Bight	Van der Land *et al.*, 1990
	1.424	0.140	5.9	Flamborough	Harding *et al.*, 1978b
Sprattus sprattus L.					
	1.050	0.420	11.5	SE North Sea	Van der Land, 1990
	1.050	0.544	9.0	VIIe	Milligan, 1986

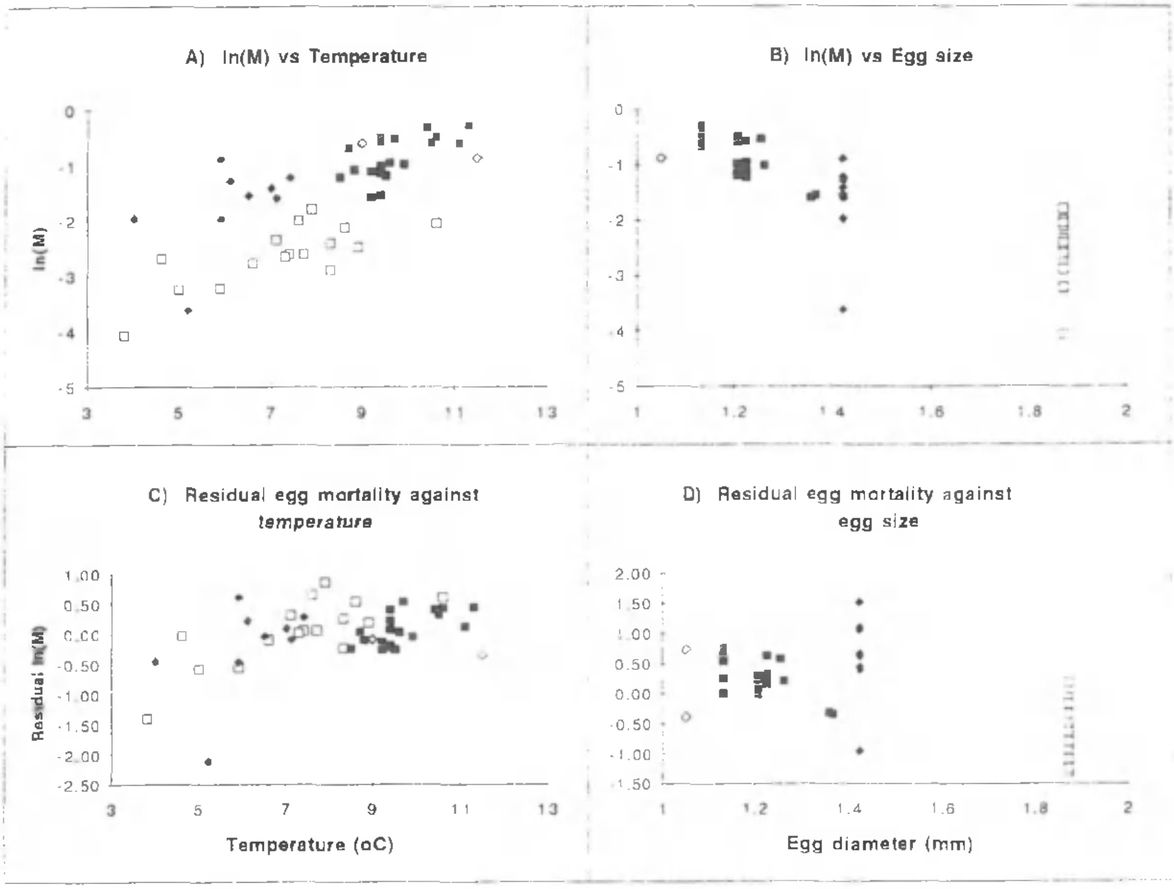

Fig. 6. Relationship between the ^{e}log instantaneous egg mortality rate and a. temperature and b. egg size, and the relationship between the residual egg mortality rate after correcting for c. temperature against egg size and d. egg size against temperature. Data from Table 9 refer to sole (■), plaice (□), cod (◆) and sprat (◊).

where S is a categorial variable coding for species and $S \cdot T$ is the interaction between temperature and species, showed that neither the interaction $S \cdot T$ nor S explained a significant part of the variance in ln$M$, but both Φ and T were highly significant (Table 10). The parameter estimates of the model indicated that egg mortality decreased with increasing Φ and increased with increasing T (Table 11).

4. DISCUSSION

4.1. SEASONAL AND GEOGRAPHICAL DIFFERENCES IN EGG SIZE

The seasonal decline in egg size observed within, as well as between, the geographical areas confirms the field data reported by Ehrenbaum (1905, 1909) and Hiemstra (1962), and experimental data of Houghton *et al.* (1985) and Devauchelle *et al.* (1987). Various factors have been suggested to contribute to the seasonal decline in egg size. A temperature effect on egg size was suggested for pilchard (Southward & Demir 1974), whiting (Hislop, 1975), turbot (Bromley *et al.* 1986) and sole (Devauchelle *et al.*, 1987). Devauchelle *et al.* (1987) compared changes in egg size in two experiments. In the first experiment sole were kept under the natural photoperiod and an increase in temperature. In the second experiment egg size was determined of sole spawning in late summer and autumn under an artificial photoperiod and a constant high temperature. In the second experiment egg size did not change during spawning, whereas in the first experiment egg size decreased during spawning. In contrast, McEvoy & McEvoy (1991) observed that egg size decreased during the spawning season in turbot that were kept at a constant temperature. These results suggest that an increase in temperature may enhance a decrease in egg size, but cannot fully explain the decrease observed in the field. Another contributing factor may

TABLE 10

Results of the ANOVA of the natural logarithm of egg mortality rate (ln *M*) as a function of egg diameter (Φ), temperature (*T*), fish species (*S*) according to the GLM model: $\ln M = a + b\,\Phi + T + S + S.T$ for four fish species. See text for sources of data.

covariable	*sum of squares*	*degrees of freedom*	*mean square*	*F*	*P*
Φ	12.244	1	12.244	64.68	P<0.01
T	3.646	1	3.646	19.26	P<0.01
multicollinearity	16.866				
error	8.140	43	0.189		
S	0.340	3	0.113	0.63	NS
S.T	0.527	3	0.176	0.97	NS
error	6.677	37	0.180		
total	40.896	45			

be the decrease in egg size over the successive batches of individual fish (Kjesbu, 1988; Kjesbu *et al.*, 1992; McEvoy & McEvoy, 1991). Although Kjesbu *et al.* (1992) showed that this decrease was related to the declining reserves for vitellogenesis as spawning progresses, it is not directly clear why a fish should not support a smaller number of oocytes to grow to the 'normal' size, because this is expected to enhance fitness. The decrease may be related to the shift in the age and size composition of spawning fish. In several species it has been shown that older females start spawning earlier in the season than younger females (Simpson, 1959; Eltink, 1987; Rijnsdorp, 1989), and that egg size increases with the age or size of the mother (Hislop *et al.*, 1978; Hislop, 1988; Kjesbu, 1988, 1989). Data presented by Hislop & Bell (1987) showed a negative relationship between percentage shrinkage and egg size. Egg size of species with the largest eggs showed a percentually larger decrease than in eggs of species with smaller eggs. Hence, if preservation equally affected the eggs of sole, the reported seasonal decline and geographical differences will have been underestimated. However, the shrinkage reported by Hislop & Bell (1987) referred to unfertilized eggs and may have overestimated the shrinkage of fertilized eggs suggested in the present study. Van der Wateren *et al.* (1990) showed a decrease in egg size after fixation of fertilized eggs of plaice of less than 0.5% compared to the 3% shrinkage after fixation of unfertilized eggs reported by Hislop & Bell (1987).

The observed geographical differences in egg size were largely due to the seasonal decline in egg size, although differences were still apparent after correction for the time of spawning. It is unlikely that the differences in temperature have contributed to differences in egg size between areas because the analysis of variance did not show a significant temperature effect. However, there is some evidence that the age composition of the spawning population differed between the areas. In 1991 the spawning population in the North Sea was dominated by the 4-year-old females of the 1987 year class which was 4-5 times average size (ICES, 1992b). In contrast to the English Channel, where the spawning population was composed of older age groups. This year class has recruited to the spawning population as 3-year-old in the Channel and southern North Sea, but as 4-year-old in the southeastern North Sea (unpubl. data RIVO). If first year spawners produce smaller eggs than repeat spawners, the differences in the age composition of the spawning population may have contributed to the relatively smaller egg size in north-eastern areas.

Also, systematic bias cannot be ruled out because measurements were carried out by various people at two laboratories, and because the differences in egg size (<0.13 mm) are small compared to the unit of measurement (0.033 mm - 0.05 mm).

The differences in egg size between geographic areas was small after correction for spawning time (<0.135 mm). However, because the spawning time differed by up to 60 d between the southwestern areas and the north(eastern) areas, the differences in egg size at peak spawning were much larger. Mean egg size at peak spawning decreased from 1.37 mm in the southwestern areas to 1.13 mm in the northeast, corresponding to a decrease in egg volume of 44%. This decrease in egg volume appears to be related to an increase in relative fecundity (Witthames *et al.*, in prep.). Relative fecundity estimates for various areas are summarized in Table 12. Given the observed mean egg size at peak spawning (Table 5) and assuming that egg weight shows a positive relation with egg size, the reproductive investment in terms of dry weight was estimated. Because no data on the size/weight relationship of sole eggs were available, a relationship for gadoids was used as a first approximation (eq. 14 of Hislop & Bell, 1987). The gadoid relationship refers to eggs without oil globules. Although this relationship may be inaccurate with regard to the elevation, it is thought to provide a reasonable estimate of the slope of the relationship for sole. Estimated as such, the reproductive investment expressed in g dry weight per g wet body weight appears to be much less different between the areas than the relative fecundity (Table

TABLE 11

Parameter estimates of the GLM model of the natural logarithm of egg mortality rate (ln *M*) as a function of egg diameter (Φ) and temperature (T): $\ln M = a + b\,\Phi + cT$. The analysis corresponds to the one in Table 10 including only the significant covariables.

	parameter estimate	*SE*
a	-0.075	0.611
b	-2.016	0.251
c	0.173	0.039

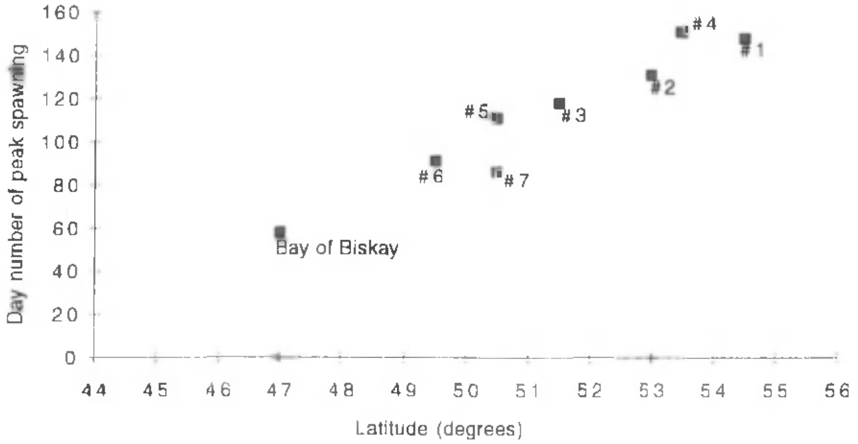

Fig. 7. Relationship between the time of peak egg production and latitude (data from ICES 1992a; Arbault *et al.*, 1986). For area code see text.

12). The calculations further suggest that the reproductive investment is slightly higher in the areas in the northeast (North Sea areas 1 to 4) than in the southwestern areas (6 and 7). A study of the differences in dry weight of eggs in sole is necessary to test the suggested geographic pattern in reproductive investment. Since Hislop & Bell (1987) showed that preservation affects the dry weight of eggs, this work should be carried out on fresh material.

The observed geographical pattern in egg size and fecundity are intimately related to the timing of spawning, which appears to be strongly correlated with latitude (Fig. 7). The timing of spawning, however, is not very rigid and substantial differences occur between years, especially in northeastern areas characterized by a large amplitude in the annual temperature cycle. Thus, in the North Sea, spawning was advanced after a mild winter and delayed after a cold winter (ICES, 1965, 1992a; Van der Land, 1991). In the western areas that are under direct influence of the Atlantic Ocean winter temperatures are more stable (Horwood, 1993).

An important question is whether the differences in spawning time, egg size and egg numbers are genetically determined or a phenotypic response to different environmental conditions. No information is available about the genetic relationships between the various spawning groups. However, tagging experiments suggest that there must be some mixing between neighbouring subgroups, which make the existence of genetically distinct subpopulations rather unlikely (ICES, 1965, 1989; Rijnsdorp *et al.*, 1992). This inference is supported by the weak genetic differentiation in turbot *Scophthalmus maximus* and brill *Scophthalmus rhombus*, two flatfish species with reproductive ecologies similar to that of sole, studied by allozyme variation over a wide distribution range including the Mediterranean and northwest Atlantic

TABLE 12

Relative fecundity (eggs·g^{-1}), egg volume (mm^3) and reproductive investment (g dry weight of eggs per g wet body weight) of mature females sole in various areas. Egg volume was calculated from the mean egg diameter at time of peak spawning from Table 5. Reproductive investment was estimated as the relative fecundity times the egg dry weight predicted from the relationship observed in gadoid egg (eq. 14 of Hislop & Bell, 1987). Data sources of relative fecundity are: 1. Greer Walker & Whitthames (1990); 2. Horwood & Greer Walker (1990); 3. Deniel (1981); 4. Roosenboom (1985); 5. ICES (1991); 6. ICES (1992a).

area code	*area description*	*relative fecundity (eggs·g^{-1})*	*egg volume (mm^3)*	*reproductive investment eggs g dry·g wet body^{-1}*	*data source*
1	North Sea: German Bight	893	0.760	0.0553	4+5
4	North Sea: Flamborough	701	1.040	0.0591	1
5	eastern English Channel	687	1.057	0.0588	1+6
6	western English Channel	456	1.343	0.0494	3
7	Bristol Channel	416	1.317	0.0442	2

coasts from Morocco to the North Sea and the Kattegat (Blanquer *et al.*, 1992).

If genetic differences among areas are unlikely, what environmental factors may have contributed to observed geographic and seasonal pattern in egg size? Comparison of the environmental conditions among the areas suggests that temperature conditions during winter and spring may be important. The areas in the west are under a strong influence of the Atlantic Ocean reducing the seasonal fluctuation in temperature as compared to the areas in the east. Hence, in the western Channel (area 6) and Bristol Channel (area 7) the winter temperature generally does not fall below 9°C, whereas in the German Bight (area 1) the winter temperature may drop to values of 3°C and may even decrease further. The other areas are intermediate (Lee & Ramster, 1981). These differences in temperature regimes may affect the rate of ovarian development and oocyte growth and so may affect final oocyte size.

The timing of ovarian development and of spawning seems to be under the control of the photoperiod (Devauchelle *et al.,* 1987). The close relationship between spawning time and latitude (Fig. 7) supports the importance of photoperiod, although temperature may advance or delay the spawning up to 4-5 weeks as observed in various areas in the North Sea in 1990 (ICES, 1992a).

The close relationship between spawning time, egg size and egg number (fecundity) suggests that these are three aspects of a common process of ovarian development, which is influenced by the photoperiod and temperature. If the observed patterns are a phenotypic response to photoperiod and temperature, the decrease in egg size from southwest to northeast is related to the later start of vitellogenesis at higher latitudes and to a reduced oocyte growth at lower winter temperatures in more northern and eastern waters. A comparative study of the histology of ovarian development could yield important information to test the above hypothesis.

4.2. ADAPTIVE SIGNIFICANCE OF EGG SIZE, EGG NUMBER AND TIMING OF SPAWNING

Spawning time in marine fish has been generally adapted to the availability of suitable food for larval stages (Cushing, 1967; Bagenal, 1971; Rothschild, 1986; Ware, 1975, 1977; Brander, 1994). The seasonal decrease in egg size appears to be related to the decline in the size spectrum of zooplankton, which forms the main food for pelagic fish larvae (Ware, 1977; McEvoy & McEvoy, 1991), although these hypotheses have not been subjected to a critical test.

In the English Channel and southern North Sea small sole larvae feed primarily on lamellibranch larvae and *Pseudocalanus* nauplii, whereas larger individuals feed on polychaete larvae (Last, 1978). If the above hypotheses are correct, a decrease in size of these food items during the season can be expected. Further we can infer from the observed significant differences in egg size after correction for the seasonal effect that sole larvae will show a difference in food choice between areas. In southwestern areas larvae may prefer the larger polychaete larvae, whereas in the northeastern areas they may prefer lamellibranch larvae and *Pseudocalanus* nauplii. These prediction may easily be tested from field observation in the various areas.

4.3. EGG SIZE AND DEVELOPMENTAL RATE

The observed differences in sole egg size raises the question whether the developmental rate of eggs is related to egg size. Such a relationship is clearly established among species (eq. 8 in Pepin, 1991). Although interspecific relationships do not necessarily apply within a species (Chambers, pers. comm.), it is relevant to explore its possible effect on the estimated mortality rates of eggs. Egg mortality is generally estimated by linear regression of the ^{e}log daily egg production values against the mean age or midpoint of each developmental stage (Gunderson, 1993). Developmental time affects both the estimation of stage-specific daily production and the mean age at each developmental stage. Assuming that the relationship described in Pepin (1991) does apply to sole, the hatching time of eggs for the geographic area with the largest eggs (area 6 - 1.37 mm) will be about 9% longer than that of eggs in the area with the smallest eggs (area 1 - 1.13 mm). Simulation of the effect of applying an incorrect developmental rate shows that an overestimation of developmental rate causes an equal underestimation of the mortality rate and *vice versa*. The bias in egg mortality rate due to application of an incorrect developmental rate, therefore, is opposite to the observed relationship between egg mortality and egg size. Hence, the observed negative relationships between egg mortality and egg size cannot be an artefact from a possible relationship between developmental rate and egg size.

4.4. ECOLOGICAL IMPLICATIONS OF DIFFERENCES IN EGG SIZE

Estimation of the size-selective mortality component from the increase in egg size between fertilization and hatching assumes that the size of individual eggs do not change during incubation although no evidence for this assumption is available for sole eggs. Van der Wateren *et al.* (1990) showed that egg size of preserved plaice eggs decreased slightly between fertilization and hatching, which is the opposite of the change observed in the sea. Hence, the observed increase in egg size is unlikely to be an artefact due to preservation.

The correspondence between the size-selective

TABLE 13

Stage duration (*D* in days) of sole eggs as a function of temperature (*T* in °C): $\ln D = a + b\,T$ (modified from Riley, 1974; Horwood, 1993). Time to hatching can be calculated from $D = D_{\text{stage 1}} + D_{\text{stage 2}} + D_{\text{stage 3}} + D_{\text{stage 4}}$.

	a	*b*
stage 1	2.0193	-0.1227
stage 2	1.4941	-0.1530
stage 3	2.5075	-0.1509
stage 4	1.4106	-0.0687

mortality estimated from the change in egg size and the regression of the population mortality and population egg size suggests that egg mortality in sole is governed by a common size-selective process that operates between February and July over an area ranging from the western English Channel (area 6) and Bristol Channel (area 7) in the southwest to the German Bight (area 1) in the northeast. It is not surprising that exceptions to this general pattern (area 5) will occur because variations in the size spectrum of predators may locally lead to differences in the size selective mortality.

The inference of a common size-selective process affecting egg mortality is further supported by the significant negative relationship between mortality and egg size as observed in the analysis of the 46 data sets of four species. The observation that egg mortality increases with temperature is in agreement with the analysis of Pepin (1991) and is in line with the general hypothesis that egg mortality is mainly governed by predation, because an increase in temperature will lead to an increase in the daily rate of food consumption of predators (Bailey & Houde, 1989; Pepin, 1991). The alternative egg mortality agent, *viz.* embryonic deformations (Rothschild, 1986; Bailey & Houde, 1989), is less likely to be a function of temperature.

In contrast to our study, Pepin (1991) was unable to find a significant relationship between mortality and egg size, possibly due to several factors. First, the data set he analysed encompassed various types of marine ecosystems for which different relationships may apply. Second, his analysis included various anchovy stocks that are characterized by oval-shaped eggs. Third, mortality estimates were included that were based on a single survey which may have enhanced the variance in the estimated mortality rates. Therefore, we conclude that in the North Sea and adjacent areas, egg mortality rate is negatively related to egg size.

The ecological implications of the observed relationship between egg mortality rate and egg size and temperature will depend on the temperature dependence of the developmental rate of eggs and on the trade-off between egg size and egg numbers. The cumulative effects of egg mortality as a function of egg size and temperature were explored in a simulation of the survival probability

$$(P)\cdot\ P = F\exp(-MD),$$

where *F* is the relative fecundity, *M* is the rate of egg mortality and *D* is the stage duration. M is a function of egg size (Φ) and temperature (*T*):

$$M = \exp(a + b\,\Phi + c\,T)$$

with parameter estimates given in Table 11. The stage duration of sole eggs is a function of temperature (*T*):

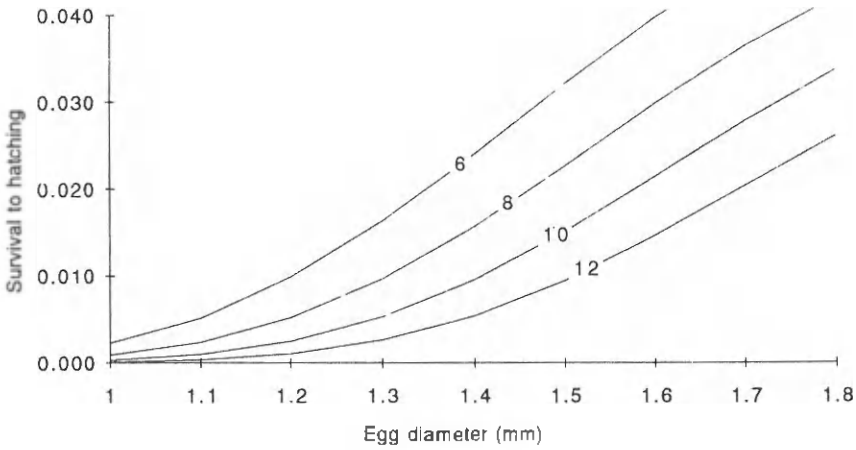

Fig. 8. Ecological consequences of a trade-off between egg size and egg number under different temperature regimes. The lines show the relative number of larvae that will hatch from eggs as a function of egg size and temperature assuming the relationships between egg mortality and egg size and temperature given in Table 11.

$$\ln D = a + b\,T$$

(Riley, 1974; Horwood, 1993; Table 13).

In our analysis we explicitly assumed a trade-off between egg numbers and egg size by including a term for relative fecundity which was defined as $F = \Phi^{-3}$. Survival probability increased with egg size, but decreased with temperature (Fig. 8). This simulation suggested that, based on the mortality during the egg phase, it would be advantageous for sole to produce larger eggs than they do. If egg size is adaptive, this implies that the disadvantage of smaller eggs should be compensated for during the larval phase by an increased survival. This deduction is just the opposite of the pattern found by Pepin (1991), who also showed that initial energy investment into each egg had very little influence on the stage-specific survival for pelagic early life history stages of marine fish. However, as Pepin (1991) based his analysis on differences between species, his conclusion may not be directly applicable to a comparison of substocks from different parts of their distribution range.

The above considerations are concerned with general species-specific patterns. If the combination of spawning time, egg size and egg number is adaptive, and, as argued above, the differences in spawning time, egg size and egg number between areas are phenotypic, we may wonder whether the combination is equally adaptive over the whole of the distribution range of the species. It can be expected that the combination of traits has evolved in response of the conditions in the centre of the distribution range of the species. Following this reasoning we might expect that in peripheral parts of the range, such as in area 1 and area 4, the survival of the pelagic phase might be lower than in more central areas such as area 6 and area 7. This would imply that per unit of reproductive investment the reproductive success would be lower in the peripheral areas. It is interesting that the reproductive efficiency in the North Sea (total of areas 1 - 4) was indeed lower than in areas 5, 6 and 7 (Rijnsdorp *et al*., 1992). However, because the estimates of reproductive efficiency were based on results of virtual population analysis and thus are sensitive to the assumption of natural mortality, this aspect remains uncertain. Nevertheless, the pattern is in agreement with the pattern in reproductive investment, estimated by the product of relative fecundity and egg dry weight, which suggested that the sole stocks in the peripheral parts of the range have a higher reproductive investment (Table 12). Along the same lines there may be a relationship between the better adapted larger eggs in the central parts of the range and the lower variability in recruitment. However, in a review of 86 stocks comprising of 21 species, Pepin & Myers (1991) were unable to find a relationship between recruitment variability and the size of eggs and larvae.

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