Egg Weight in Atlantic Herring
(*Clupea harengus* L.)

By

G. Hempel*

Universität Hamburg, Institut für Hydrobiologie
und Fischereiwissenschaft.

and

J. H. S. Blaxter**

Marine Laboratory, Aberdeen.

The dry weight of mature herring eggs, measured from samples taken from about 25 spawning grounds, is very variable from ground to ground, while there may also be age and year-to-year differences. The mean weight varies by at least a factor of three, from 1·2 mg per egg in Baltic spawners of the late spring, to 3·7 mg per egg for early winter spawners of the southern North Sea. In general egg weight is high for fish spawning in winter and early spring, and low in late spring, summer and autumn. As a characteristic it can be useful for defining "races" as well as having wide ecological implications. Usually fecundity and egg weight are inversely related. Thus spawners with fewer, heavier eggs will produce few, but large larvae with considerable yolk reserves at a time of poor food supply and a low predator population. Under warmer conditions a larger number of small eggs are produced which can be seen as an adaptation to adequate larval food, but high predation.

Introduction

The highly complex nature of the north-east Atlantic herring stocks and the apparent great adaptability of the species have recently been emphasized by Parrish and Saville (1965). In contrast to many other marine fish, herring seem to differ widely in their requirements for spawning with regard to season and hydrographical conditions. Spawning may take place in late winter or early spring prior to the feeding season, in late spring and summer during the feeding season or in autumn when the main feeding has just finished. The difference in spawning time affects the seasonal pattern of metabolism (Iles, 1964). Related to this are differences in the *number of eggs* (fecundity) produced by a single female of a given size; in general summer/autumn spawners produce more eggs

* Present address: Institut für Meereskunde der Universität Kiel, Hohenbergstrasse 2, Germany.

** Present address: Natural History Department, Marischal College, Aberdeen, Scotland.

J. Cons. perm. int. Explor. Mer	31	No. 2	170–95	Copenhague, Août 1967

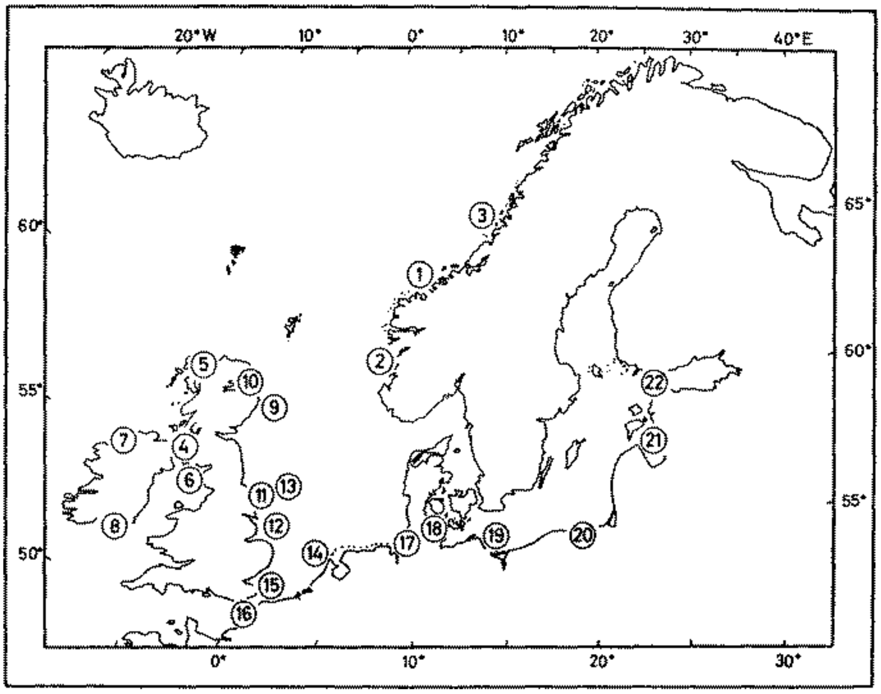


Figure 1. Location of spawning grounds from which samples have been obtained (see also Table 1).

than winter/spring spawners. This can be seen from the data of various authors, *e.g.* for Irish herring (FARRAN, 1938), Icelandic spring and summer spawners (FRIÐRIKSSON and TIMMERMANN, 1951; LIAMIN, 1959), White Sea (ANOKHINA, 1961), parts of the Baltic (KÄNDLER and DUTT, 1958; RANNAK, 1958; STRZYZEWSKA, 1960 and others) and North Sea (BAXTER, 1959, 1963). Published data on the *size or weight of ripe eggs* of these groups of herring are, however, rather scarce. Reference should be made to contributions by FARRAN (1938) and BAXTER (1959) on fecundity, where differences in egg size are mentioned as being inversely related to fecundity, winter/spring spawners having bigger eggs than summer/autumn spawners. For the eastern Baltic, however, ANOKHINA (1962) mentions similar egg size for spring and autumn spawners. Differences in number and yolk content of eggs have been considered as basic adaptations to the wide variety of environmental conditions met by young larvae of the various spawning groups (HEMPEL, 1965). Whereas high numbers of eggs are necessary to compensate for heavy predation, high yolk content facilitates survival as a result of the larger size of the larvae at hatching and by a longer lifespan on the yolk reserves, both factors placing the larvae in a more favourable position at the commencement of feeding (BLAXTER and HEMPEL, 1963; BLAXTER, 1965). Efficiency of the conversion of yolk into body tissue at low

Table

Origin of egg samples and mean

Spawning group	Spawning place	Date (day/month/year)	n
Norwegian spring	Off Møre	3.–17. March 1961	46
	Off Møre	7.–8. March 1962	92
	Store Sotra	17.–21. March 1962	82
	Sklinna-Bank	9. March 1963	72
Clyde spring	Ballantrae Bank	8. March 1961	20
	Ballantrae Bank	21. Feb.–2. March 1962	72
	Ballantrae Bank	13. March 1963	85
Irish spring	Donegal, Stags of Broadhaven	March 1963	23
Minch autumn	Ullapool	11. Sept. 1962	34
Manx autumn	Isle of Man	13.–21. Sept. 1962	35
Donegal autumn	Killybegs	17.–25. Oct. 1962	20
	Inver Bay		52
Dunmore winter	Bagibun Bay	18. Jan. 1962	56
	Dunmore East	29.–30. Nov. 1962	46
	Dunmore East	8.–15. Jan. 1963	97
Buchan summer	Turbot Bank	22.–24. Aug. 1961	14 }
	Moray Firth	28. Aug. 1961	34 }
	Clythness	24. Aug. 1962	27
Whitby-Dogger autumn	Whitby	Sept. 1962	15
	Dowsing + Haisborough	Sept. 1962	35
	Dogger various positions	14. Sept.–13. Oct. 1961	59
	Bolders Bank	21. Sept. 1962	20
	Outer Silver Pit	22. Sept. 1962	69
	West of Den Helder	21. Nov. 1961	24
	Dogger	23. Sept. 1964	67
Downs winter	Sandettié	3. Dec. 1961	25
	Sandettié	22. Nov. 1961	26
	Dieppe-Fécamp	24.–26. Nov. 1961	52
	Sandettié	29. Nov. 1962	100
Continental coastal spring	Elbe Estuary	18. May 1962	11 }
	Elbe Estuary	April 1963	12 }
Western Baltic spring	Kieler Förde	20. Apr.–12. May 1961	20
	Kieler Förde	9.–18. May 1962	40
	Nord-Ostsee Kanal (Rendsburg)	16. Apr. 1962	42
	Kieler Förde	13. Apr. 1964	64
Eastern Baltic spring-summer	Rügen	22. Apr. 1963	4
	Bay of Puck (Kuznice)	25. Apr. 1964	11
	Bay of Riga	18. May–20. June 1962	78
	Bay of Finland (Espoo)	16. June 1962	40

temperatures appears, however, somewhat higher in larvae from small eggs than in those from large eggs (BLAXTER and HEMPEL, 1966).

The biological importance of the size of eggs for survival of the offspring and the possible use of egg weight as a character for discriminating the various spawning groups of herring suggested a comparative study between the var-

1

length and age of the mother

Average length (cm)	Average age (years) where available	Source of material	Reference number on map (Fig. 1)
35·1	10·7	Havforskningsinstituttet,	1
36·2	11·6	Bergen, Norway and	1
29·7	4·0	Noregs Sildesalslag in	2
36·0	12·4	Aalesund and Kristiansund	3
26·9	3·9	Marine Laboratory,	4
27·6	3·9	Aberdeen, Scotland	
28·0	4·2	(R.V. "Clupea")	
36·0	9·1	Mr. J. Bracken, Dept. of Lands, Dublin, Eire	7
28·2	4·8	Marine Laboratory, Aberdeen, Scotland	5
27·0	4·9	Mr. A. Bowers, Port Erin, Isle of Man	6
30·4	4·2	Mr. J. Bracken, Dept. of Lands, Dublin, Eire	7
25·7			7
26·5	4·6		8
27·9	6·6		8
27·6	5·0		8
28·5	4·8	Marine Laboratory,	9
		Aberdeen, Scotland	10
29·2	5·7	(R.V. "Clupea")	10
28·5	5·3	Fisheries Laboratory,	11
27·6	4·3	Lowestoft, England	12
26·4	4·0		13
23·7	2·8	Inst. f. Seefisch., Hamburg and	13
28·1	4·8	Universität Hamburg	13
25·0	3·2	(R.V. "Anton Dohrn")	14
28·3	4·2		13
24·2	3·2	Fisheries Laboratory, Lowestoft, England	15
25·9	3·8	R.V. "Anton Dohrn"	15
26·2	4·1		16
26·4	4·0		15
21·0	2·4	Universität Hamburg	17
23·4	3·4	Universität Hamburg	18
23·5	2·2	with assistance from	
27·5	3·8	Institut f. Meereskunde	
25·3	3·5	d. Univ. Kiel	
26·8	5·5	Dr. K. Anwand, Berlin	19
27·5	5·4	Dr. J. Popiel, Gdynia, Poland	20
17·5	4·0	Dr. M. Lishev, Riga, U.S.S.R.	21
19·3	–	Dr. V. Sjöblom, Helsinki, Finland	22

rious groups of *Clupea harengus* L. in the north-eastern Atlantic and adjacent seas. Some preliminary results of this study have already been presented at the International Council's Herring Symposium in 1961 (Hempel and Blaxter, 1963).

Table 2

Variation of dry weight of single eggs. Five Dogger spawners, September 1964. 20 eggs per female. The results of the routine weighings of 100 eggs are given for comparison

length (cm)	age (years)	dry weight of 100 eggs (mg)	20 individual weighings per female: mean dry weight n = 20 (mg)	total range (mg)
25·5	3	17·3	0·174 ± 0·0083	0·143 – 0·187
26·0	3	20·4	0·199 ± 0·0089	0·176 – 0·215
26·5	3	22·5	0·224 ± 0·0106	0·195 – 0·245
30·5	8	24·6	0·243 ± 0·0135	0·185 – 0·265
30·5	4	40·9	0·414 ± 0·0101	0·388 – 0·436

Materials and Methods

Samples of ripe eggs from most of the main spawning groups in the north-eastern Atlantic were collected in the period from 1961 to 1964. The positions of the samples, from about 25 spawning grounds and from all months of the year except July, are shown in Figure 1. This extensive coverage was made possible only by the help of several scientists from laboratories in various countries, listed in Table 1. Their collaboration is much appreciated.

The number of fish taken in each group varied widely; in some cases it was possible to sample extensively in successive years, whereas in others the sampling was rather restricted and did not cover the whole range of size and age. The herring were sampled from research or commercial fishing vessels. If fish were plentiful, sampling was made selective to include fish of all size-groups. As soon as possible after capture, 1 to 2 ml of ripe eggs were stripped into 4% formalin in diluted seawater (S 15‰). After preserving the eggs, the total length of each female was recorded and scales or otoliths taken for age-determination.

For dry weight determinations, 100 fixed eggs per female were rinsed with distilled water, dried to constant weight in a desiccator at 50°C for one or two days and weighed to an accuracy of 0·05 to 0·1 mg.

PETERS (1963) showed small increases in the wet weight of *Tilapia* eggs after fixation in formalin. In order to determine whether fixation in formalin-seawater causes a change in dry matter of the herring egg the following test was made. Ten samples of 50 eggs were taken from a Buchan spawner and immediately dried to constant weight when fresh. Further samples were fixed in the usual way. After about ten weeks fixation a further ten samples of 50 eggs

Table 3

Variation of average dry weight in ten samples (100 eggs each) for each of three females of different origin

Spawning group	average of ten samples of 100 eggs each (mg)	total range (mg)
Norway, March 1962	35·52 ± 0·087	35·2 – 36·1
Dogger, Sept. 1964	23·09 ± 0·37	21·4 – 25·8
Kiel, April 1964..............	20·76 ± 0·36	18·8 – 22·3

were dried and the weights compared with those of the samples dried fresh. The fresh samples had an average dry weight of 17·84 mg/100 eggs and the fixed samples 17·97 mg/100 eggs, representing a non-significant difference of under 1%.

The variation of egg weight within a single sample was determined in five samples of Dogger herring only; in each of these samples, 20 eggs were weighed individually on a micro-analytical balance to an accuracy of 0·005 mg. Means and variances for the individual weights and also the total weight of the normal sample of 100 eggs are given in Table 2. Very close agreement was found between the means of the individual weighings (4th column) and the mean weights/100 eggs normally measured (3rd column). The variance of individual egg weights was much lower than the variance of mean egg weights between females in the Dogger population. The latter variance is, however, unusually high compared with many other groups. In general the smallest egg out of a sample of 20 was 11–33% (average 20%) lighter than the heaviest egg of the sample. Further studies are under way in relation to the suggestion by ANOKHINA (1963) and NIKOLSKY (1962) that egg size is more variable in poorly-fed females.

As an additional test of the variation in egg weight within a female, 10 replicate samples of 100 eggs were weighed from a single female of Kiel, Dogger and Norwegian herring respectively. Table 3 shows the very low variance between the 10 samples taken from the Norwegian female where the lowest weight was only 3% less than the highest. In the other two females, of Dogger and Kiel origin, the lowest sample weights were respectively 17% and 16% less than the highest sample weights of the same female.

Results

Variation in egg weight within spawning groups

Within each group the mean dry weight of eggs varied considerably. The variation between females was much higher than the variation between replicate samples taken from a single female. In most spawning groups the 95% confidence limits were one-half to two-thirds as great as the mean egg weight of the group. Only in Buchan and Minch herring were the 95% confidence limits less than half the mean egg weight of the group.

In order to check how far this variance was due to differences in *sizes* of the mothers, mean dry weights of the eggs of individual females of each group were plotted against the total length of the female. The results are shown as scatter diagrams in Figure 2 for all groups. In the main the graphs do not suggest any close relationship of egg weight to total length of the mother. The correlations were statistically significant in only a few instances, as shown in Table 4.

It seems that in those groups which consisted mainly of small, fast-growing fish, egg weight was positively related to the size of the mother, whereas in those groups in which the majority of the fish were older, with slower growth, such correlations disappeared. In two groups it was even found that very large fish tended to have smaller eggs, although this was not significant statistically. These were Buchan autumn spawners of 1962 and Donegal spring spawners of 1963. Both consisted mainly of exceptionally large fish.

To check the effect of age rather than length a grouping of females according

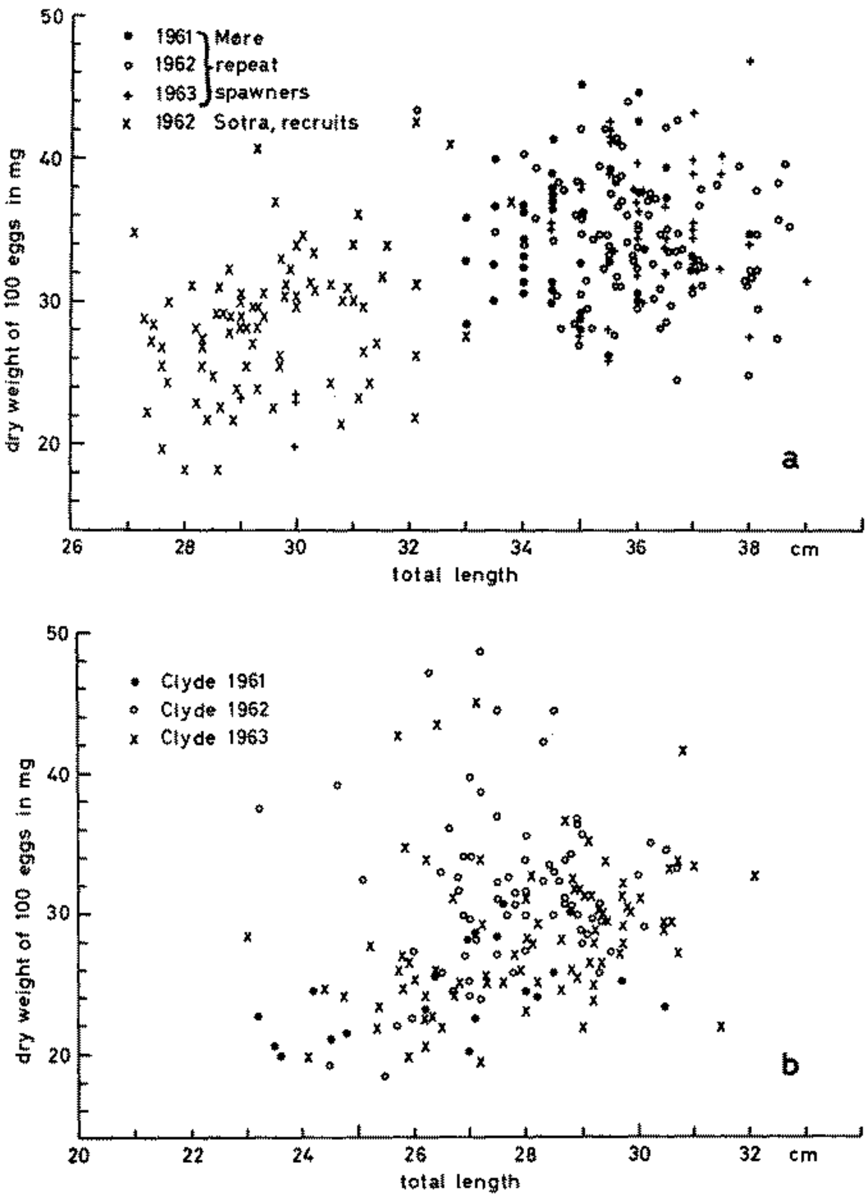


Figure 2. Dry weight of 100 eggs against total length of the mother in various spawning groups: a. Norwegian. b. Clyde.

to *age* is given in Table 5 for all samples for which age data are available. The coverage of the range of age within the various groups was not satisfactory in several instances due to the scarcity of old fish or to the prevalence of single strong year-classes. The average egg weight of various age-groups is shown in

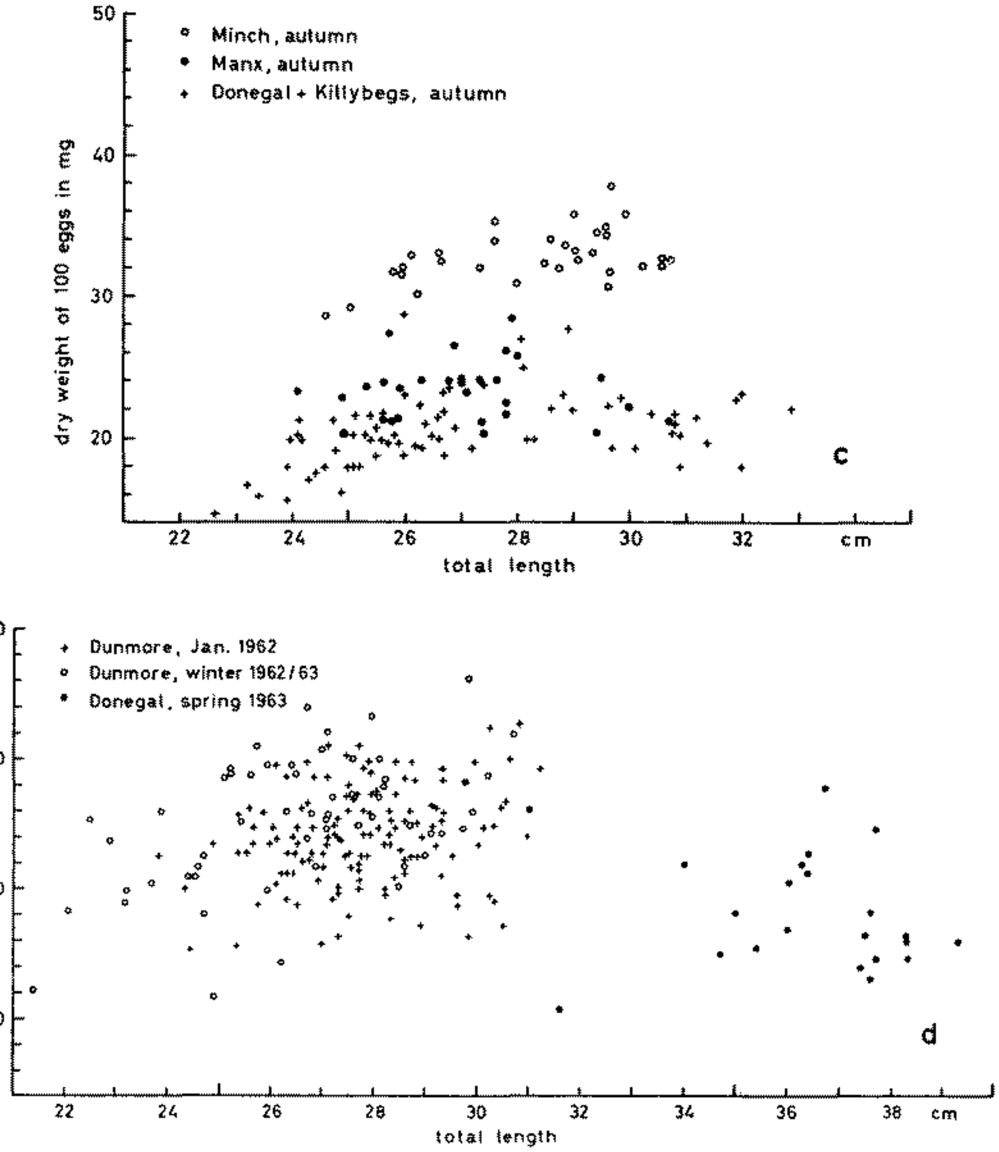


Figure 2. Dry weight of 100 eggs against total length of the mother in various spawning groups: c. Minch, Manx and Donegal autumn. d. Dunmore and Donegal winter-spring.

Figure 3a–c. No statistical tests were applied. Those age-groups which consisted of 10 or more females are marked by circles, age-groups represented by less than four fish being omitted from the graphs.

As already suggested by the relationship to length, Norwegian recruit spawners of 3–4 years of age, caught in the skerries south of Bergen, had eggs

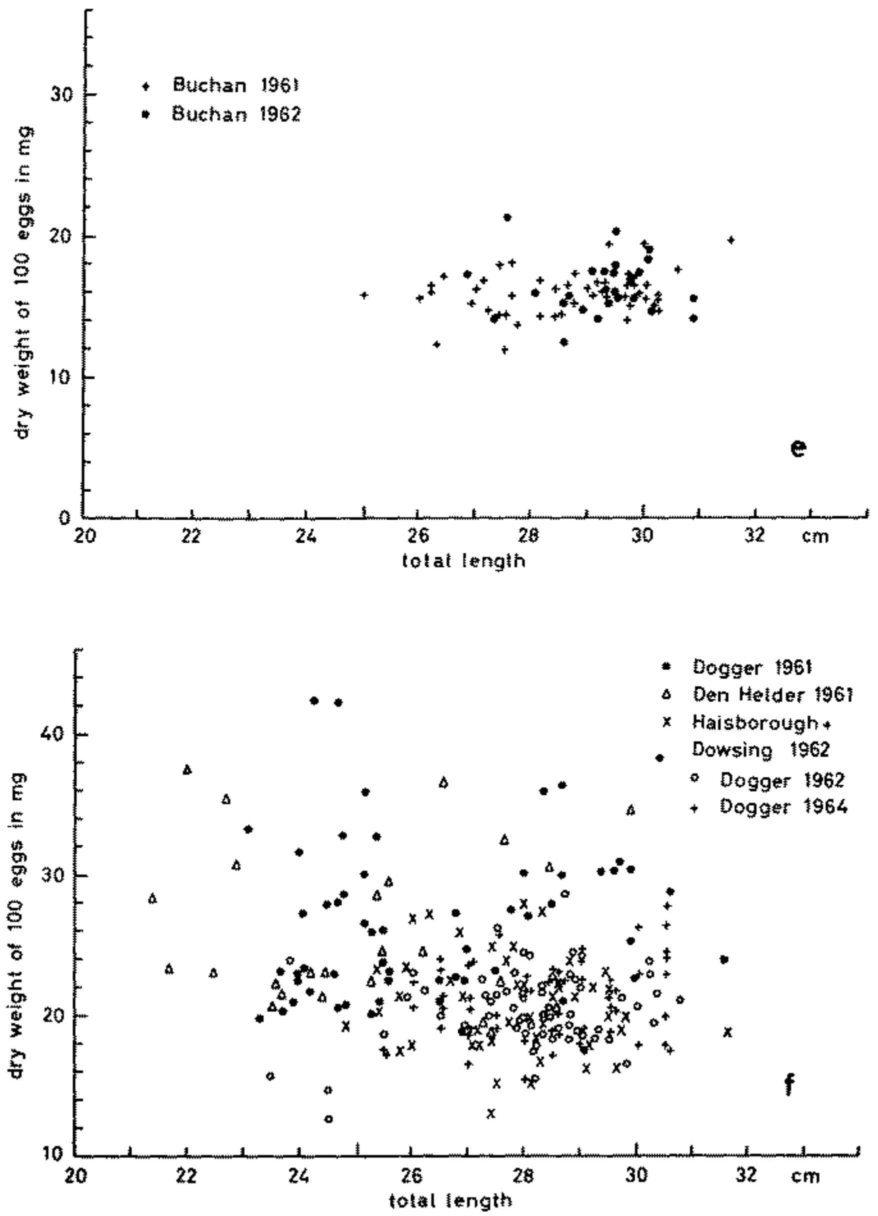


Figure 2. Dry weight of 100 eggs against total length of the mother in various spawning groups: e. Buchan. f. Dogger.

about 14% lighter than the older fish (30 mg/100 eggs and 35 mg/100 eggs respectively). These fish, however, cannot be taken as typical Norwegian spring spawners, which normally recruit at a somewhat higher age (4–6 years). For

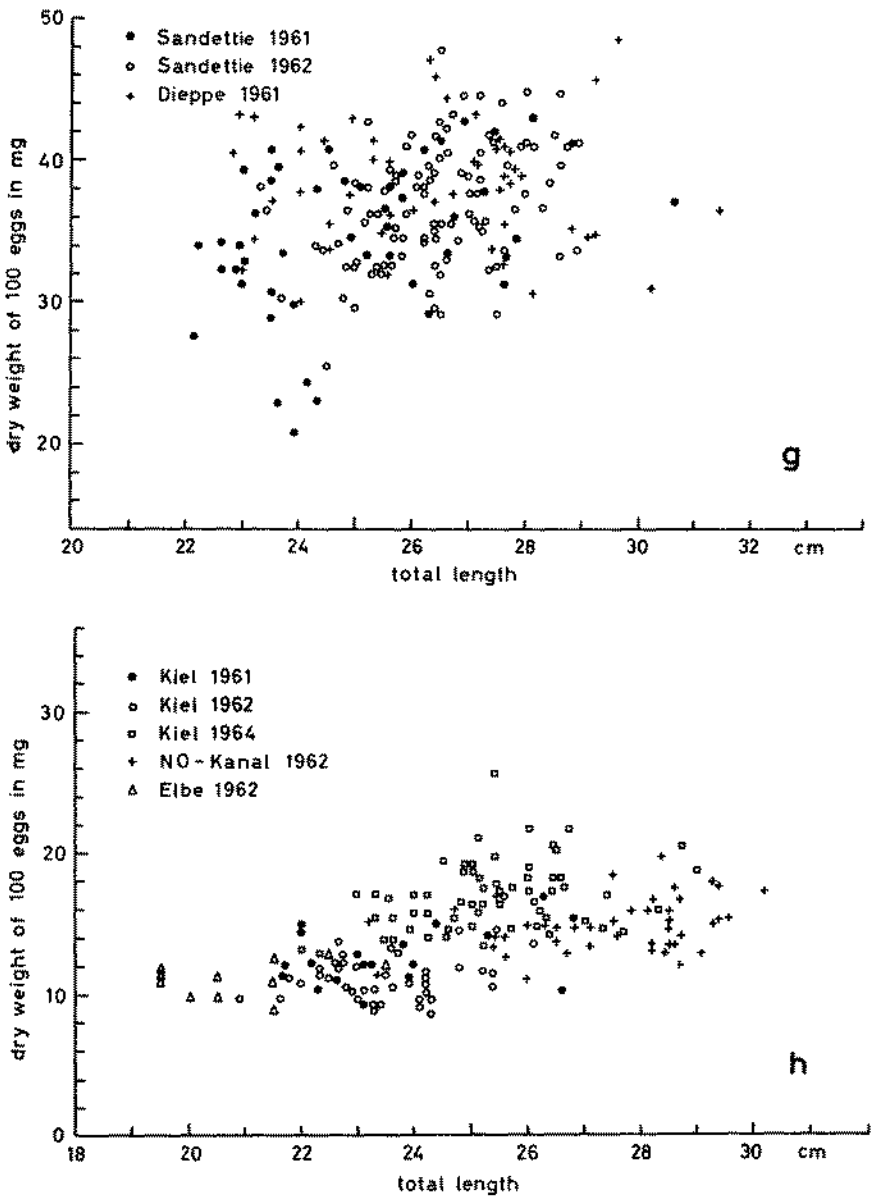


Figure 2. Dry weight of 100 eggs against total length of the mother in various spawning groups: g. Downs. h. Kiel and Elbe.

the older herring of 8–14 years, no further increase of egg weight with age of the mother was observed. The strong year-class of 1950 was sampled in three successive years at an age of 11–13 years. The mean egg weight during this period was stable at 35 mg/100 eggs. The numbers of very old herring were too

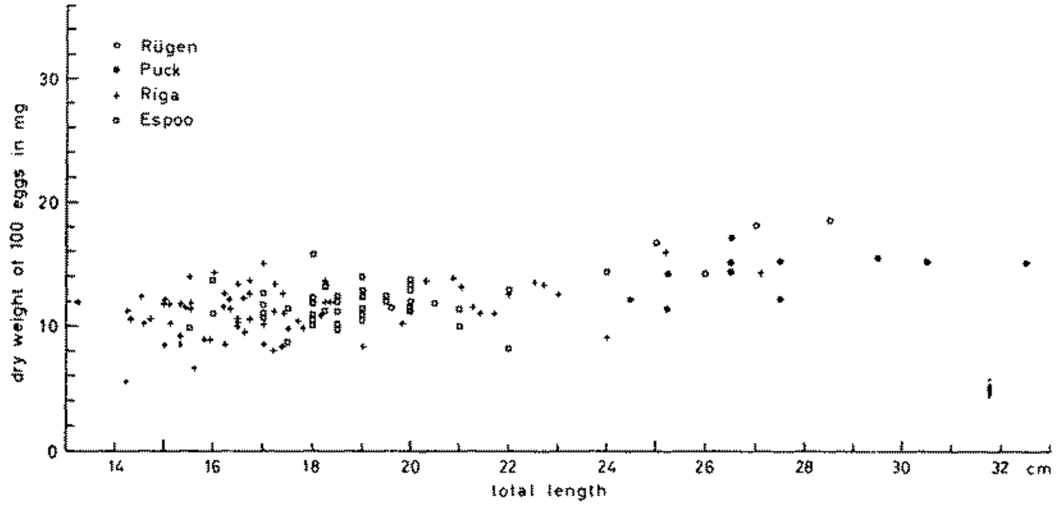


Figure 2. Dry weight of 100 eggs against total length of the mother in various spawning groups: i. Baltic.

Table 4

Correlation between length of the mother and dry weight of eggs

Origin	year	number of fish	mean dry weight of 100 eggs (mg)	correlation coefficient (r)	P
Møre	1961	46	34·5	0·131	n.s.
Møre	1962	92	34·5	0·133	n.s.
Sotra	1962	83	28·9	0·361	$P < 0·001$
Clyde	1961	20	24·2	0·582	$P < 0·01$
Clyde	1962	72	31·7	0·111	n.s.
Clyde	1963	84	28·2	0·296	n.s.
Donegal spr.	1963	23	28·8	−0·389	$P \sim 0·06$
Manx	1962	27	23·4	0·200	n.s.
Minch	1962	34	18·7	0·464	$P < 0·01$
Donegal aut.	1962	20	21·7	0·420	$P \sim 0·05$
Donegal aut.	1962	52	20·0	0·840	$P < 0·001$
Dunmore Jan.	1962	56	35·3	0·491	$P < 0·001$
Dunmore Nov.	1962	46	32·1	0·010	n.s.
Dunmore Jan.	1963	97	34·6	0·080	n.s.
Buchan	1961	47	15·8	0·282	$P \sim 0·05$
Buchan	1962	27	16·2	−0·028	n.s.
Haisborough	1962	50	20·9	0·040	n.s.
Dogger	1961	60	26·7	0·099	n.s.
Dogger	1962	19	18·5	0·645	$P < 0·01$
Dogger	1962	66	21·2	0·070	n.s.
Den Helder	1961	24	26·2	0·118	n.s.
Downs	1961	103	36·6	0·338	$P < 0·001$
Downs	1962	100	36·9	0·358	$P < 0·001$
Kiel	1961	20	12·6	0·500	$P < 0·05$
Kiel + Elbe	1962	92	12·8	0·699	$P < 0·001$
Puck	1964	11	14·4	0·460	n.s.
Espoo	1962	40	11·8	0·191	n.s.

n.s. = not significant

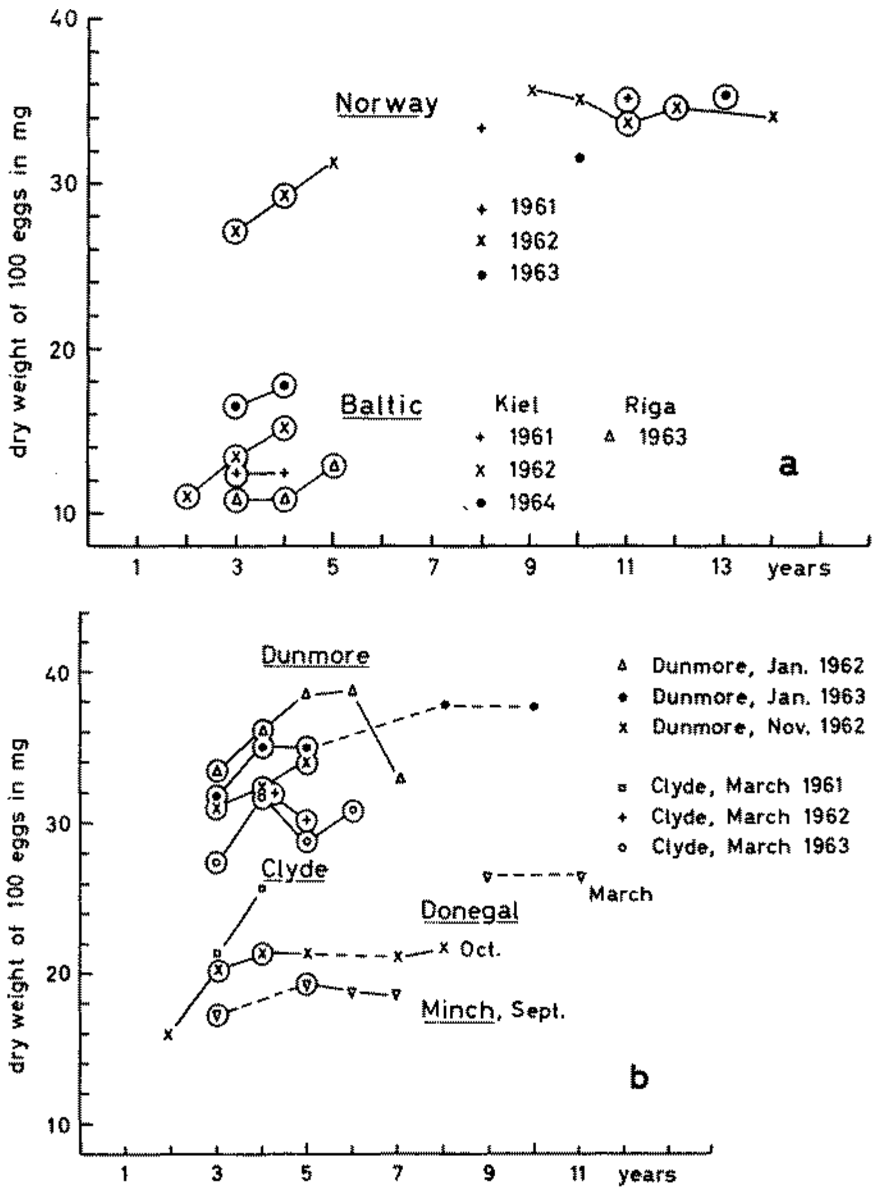


Figure 3. Average dry weight of 100 eggs in successive age-groups. a. Norwegian and Baltic spring. b. West coast of British Isles.

small to permit any conclusion as to whether egg weight decreases at an advanced age of the mother. FARRAN (1938) and POLDER and ZIJLSTRA (1959), however, found indications of a decrease in fecundity in some older age-groups of herring.

In contrast to Norwegian spawners, those of the Clyde are only available at

Table

Average dry weight of 100 eggs in relation to

Origin	years 2	3	4	5	6	7	8
Møre March 1961					30·0(1)	32·8(1)	33·3(5)
Møre March 1962					28·1(1)		38·3(2)
Sotra March 1962		27·1(38)	29·3(35)	31·4(5)			
Sklinna March 1963			25·5(3)				
Clyde March 1961		21·4(8)	26·0(37)	28·8(1)	27·6(1)	23·3(1)	
Clyde March 1962	19·2(1)	38·3(2)	32·3(53)	30·4(14)			
Clyde March 1963	19·8(2)	26·6(37)	32·1(6)	28·9(26)	31·1(13)		
Donegal March 1963			37·2(2)	28·0(1)	23·3(2)		33·9(3)
Manx Sept. 1962		22·4(7)	24·3(11)	24·1(4)	23·4(10)		23·3(2)
Minch Sept. 1961		17·4(11)	18·2(1)	19·6(12)	19·1(5)	18·8(5)	
Donegal Oct. 1962	16·0(5)	20·2(29)	21·2(18)	21·3(5)	23·5(2)	21·1(7)	21·7(6)
Dunmore Jan. 1962	24·6(3)	33·5(10)	36·1(25)	38·4(5)	38·7(4)	32·8(4)	38·6(2)
Dunmore Nov. 1962		31·2(13)	32·3(15)	34·0(10)	29·6(3)	31·7(2)	32·3(3)
Dunmore Jan. 1963		31·6(18)	35·2(18)	34·9(42)	35·5(3)	29·6(1)	37·8(7)
Buchan Aug. 1961		16·0(5)	15·7(10)	15·3(25)	16·9(2)	17·2(6)	
Buchan Aug. 1962	17·0(1)			15·8(6)	16·3(19)		
Whitby Sept. 1962		20·3(2)	17·8(1)	21·5(28)	20·3(3)	20·1(16)	
Dogger Sept./Oct. 1961		26·2(35)	26·8(5)	27·2(10)	28·2(5)	38·0(1)	
Dogger Sept. 1962	16·2(13)	22·1(2)	20·8(37)	20·9(6)	21·0(18)	21·9(6)	
Dogger Sept. 1964	21·0(1)	20·7(19)	21·3(32)	19·5(2)	20·9(6)	22·6(3)	23·7(3)
Den Helder Nov. 1961		25·5(19)	27·7(4)				
Dieppe Nov. 1961		38·8(21)	38·2(12)	38·2(12)	35·8(2)		46·9(2)
Sandettié Nov./Dec. 1961		33·8(36)	36·1(10)	42·3(2)	40·9(1)		
Sandettié Nov. 1962		35·3(25)	37·4(55)	36·0(12)	42·4(3)	39·8(1)	
Elbe April 1962	11·0(7)	11·6(4)					
Kiel April/May 1961	11·0(1)	12·6(12)	12·4(6)		16·9(1)		
Kiel May 1962	11·0(32)	13·3(19)	15·0(23)	17·7(2)	16·2(2)		
Kiel April 1964		16·5(36)	17·7(25)	16·1(1)	18·7(1)		
Riga May/June 1963		10·9(26)	10·9(29)	13·0(12)	13·3(4)		14·1(2)

a young age, the samples mainly consisting of recruit spawners of 3 and 4 years. The egg weights were on average lower in 1961 than in 1962. The youngest of the recruits, at 3 years of age, had rather small eggs; the highest values were found at 4 years, followed by a decrease in 5 year-old fish. If this decrease is typical, one might consider whether the 5 year-olds spawning in the Clyde were abnormal in their reproduction, other fish reaching maturity at 3–4 years and leaving the Clyde soon afterwards for other spawning grounds.

Data for 8 to 13 year-old herring were available from Donegal spring spawners. One might consider the old Donegal herring and the young Clyde herring as members of the same spawning group. In Dunmore winter spawners, as also in Minch and Donegal autumn spawners, where a wider range of age-groups was available, egg weight increased somewhat in the first one or two years of mature life, but fluctuated later on without a trend. The data available for Baltic herring were limited to young fish only. They showed an increase in egg weight with age of the mother. In Dogger and in Sandettié herring some initial increases were also obvious.

In summarizing the results for the various spawning groups, it may be stated that egg size is far less dependent on the size and age of the mother than is fecundity, although very young recruits do tend to have smaller eggs than older recruits and repeat-spawners. In some groups, the increase levels off after one year; in others (Norwegian, Baltic) it continues for longer. The

5

age of the mother. Number of females in parentheses

9	10	11	12	13	14	15	16	17
32·3(3)	37·5(1)	34·8(26)	38·7(2)	37·8(1)	33·2(1)	37·3(1)		
35·7(6)	35·1(5)	33·7(10)	34·7(54)	34·9(3)	34·1(5)	36·5(2)	28·5(2)	34·2(2)
	26·7(1)	30·8(2)	43·5(1)					
	31·7(7)		26·3(2)	35·4(38)	35·8(1)	36·2(5)	37·8(2)	
26·5(4)	26·0(1)	26·9(6)	31·2(3)	23·9(1)				
	21·2(1)							
	35·5(3)							
33·9(3)	37·7(5)							
30·0(1)	23·9(1)							
	36·3(1)							
	36·8(1)							

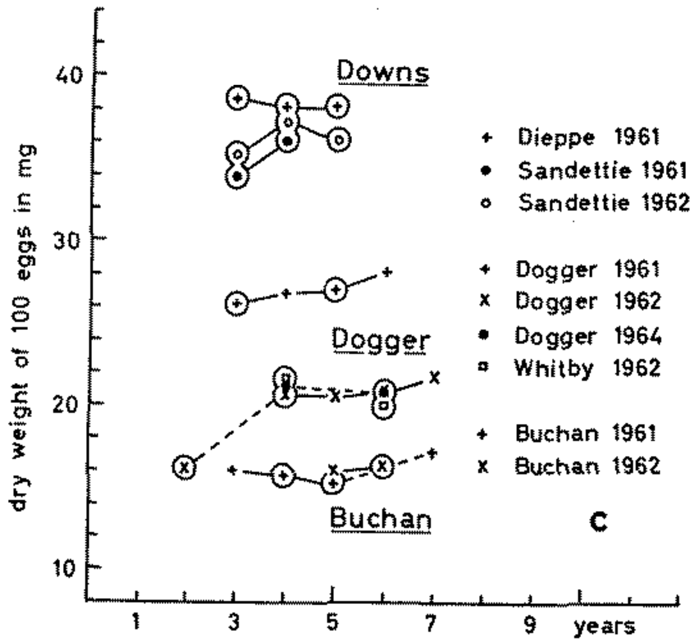


Figure 3c. Average dry weight of 100 eggs in successive age-groups. North Sea.

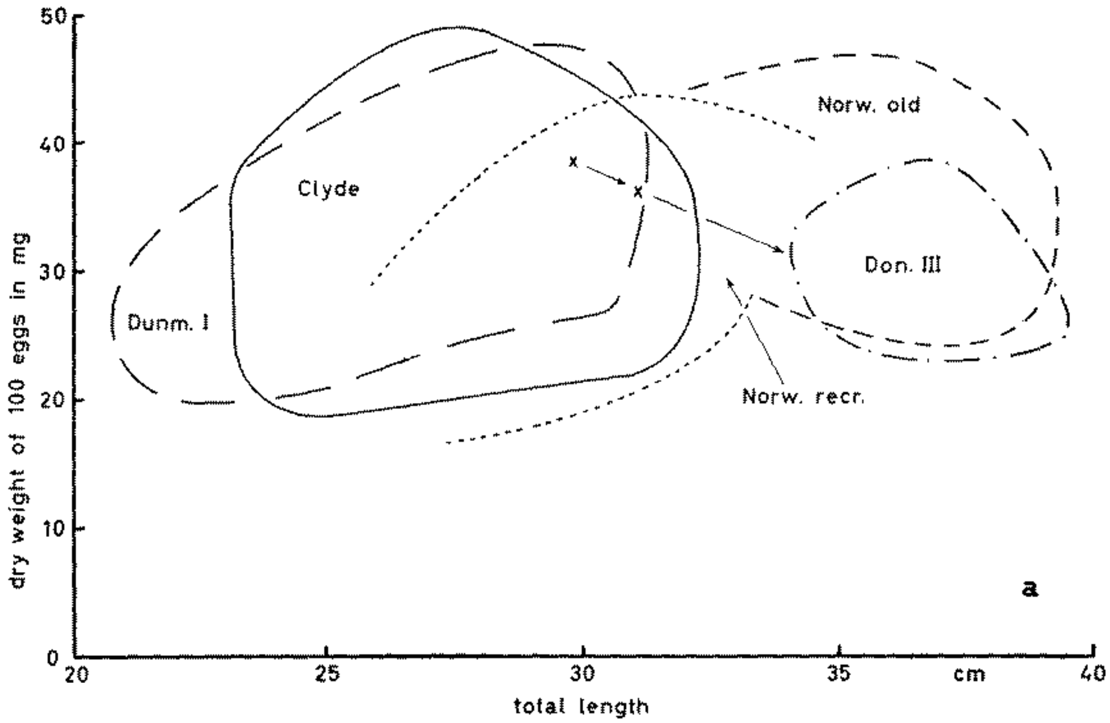


Figure 4a-g. "Areas" covered by the scatter diagrams of egg weight against length of the mother (see Figure 2) in various spawning groups (Roman numerals give month). a. Norwegian, Clyde, Dunmore and Donegal winter-spring.

increase between two successive age-groups may reach or exceed 10% in Norwegian, Baltic and Clyde herring, about 5–6% in Minch and Sandettié herring, and about 2% in Dogger herring. In Dieppe and Buchan herring no increase was noticed.

Variation in egg weight between spawning groups

The differences in average egg weight between various groups were examined in two ways, firstly by the use of egg weight as a character for discriminating "races" and secondly by the relationship of egg weight to spawning time and place.

(1) Egg size as a "racial" character.

The high variability of egg weight within a spawning group and the relationship to age and size of the mother amongst younger fish limit the value of egg dry weight as a discriminating character in herring "racial" studies *i.e.* when trying to show genetical distinctions. In addition to the means and variances listed in Table 4, the plots of egg weight against length of the mother, as given in Figure 2, were used to show the overlap between the groups. In Figure 4 the area of variation for each spawning group is shown surrounded by a line. In

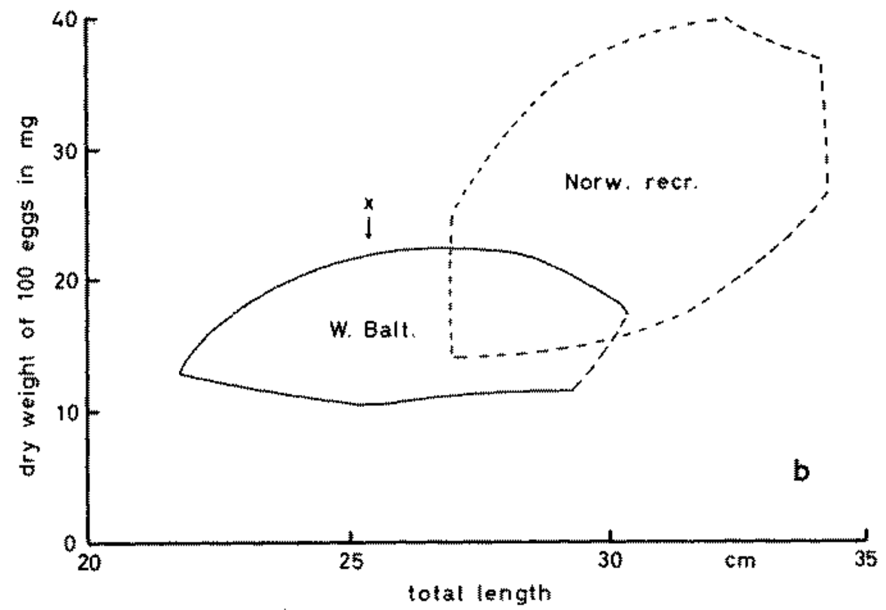


Figure 4. Eggweight against length of mother. b. Norwegian recruits and western Baltic, both spring.

a few cases the values for one or two fish were so far out that it seemed unreasonable to include them in this area.

In Figure 4a the Norwegian spring spawners are compared with other winter/spring spawners from various localities west of the British Isles. The average dry weights for the recruit spawners of Norwegian herring and for the Clyde and Dunmore herring, in which recruits were also dominant, lay between 26 and 30 mg/100 eggs; those for old herring caught off the Norwegian and west coast of Ireland (Donegal) were somewhat higher, 35–36 mg/100 eggs. In spite of this difference in the averages, it seems obvious from Figure 4a that Norwegian, Dunmore, Donegal and Clyde winter/spring herring cannot easily be distinguished by the dry weight of their ripe eggs.

Considerable differences exist, however, between Norwegian and Baltic spring spawners. In Figure 4b those Baltic and Norwegian herring which were not very different in age and spawning time are compared, that is young Norwegian herring (average age 4. 0 years) which were caught in late March and herring of the western Baltic (3·6 years) caught in mid-April.

Although the Norwegian herring were exclusively recruit spawners, whereas most of the Baltic herring were presumably spawning for the second time, the eggs of the Norwegian herring were in general considerably heavier than those of Baltic herring. Apart from differences in growth pattern and maturation rate, substantial differences in terms of egg weight seem to exist between Atlanto-Scandian and Baltic herring, but not between Norwegian herring and winter/spring spawners off the west coast of the British Isles.

Within the various groups of herring spawning in spring from the western bays of the Baltic to the Gulf of Finland, no differences in egg weight could be

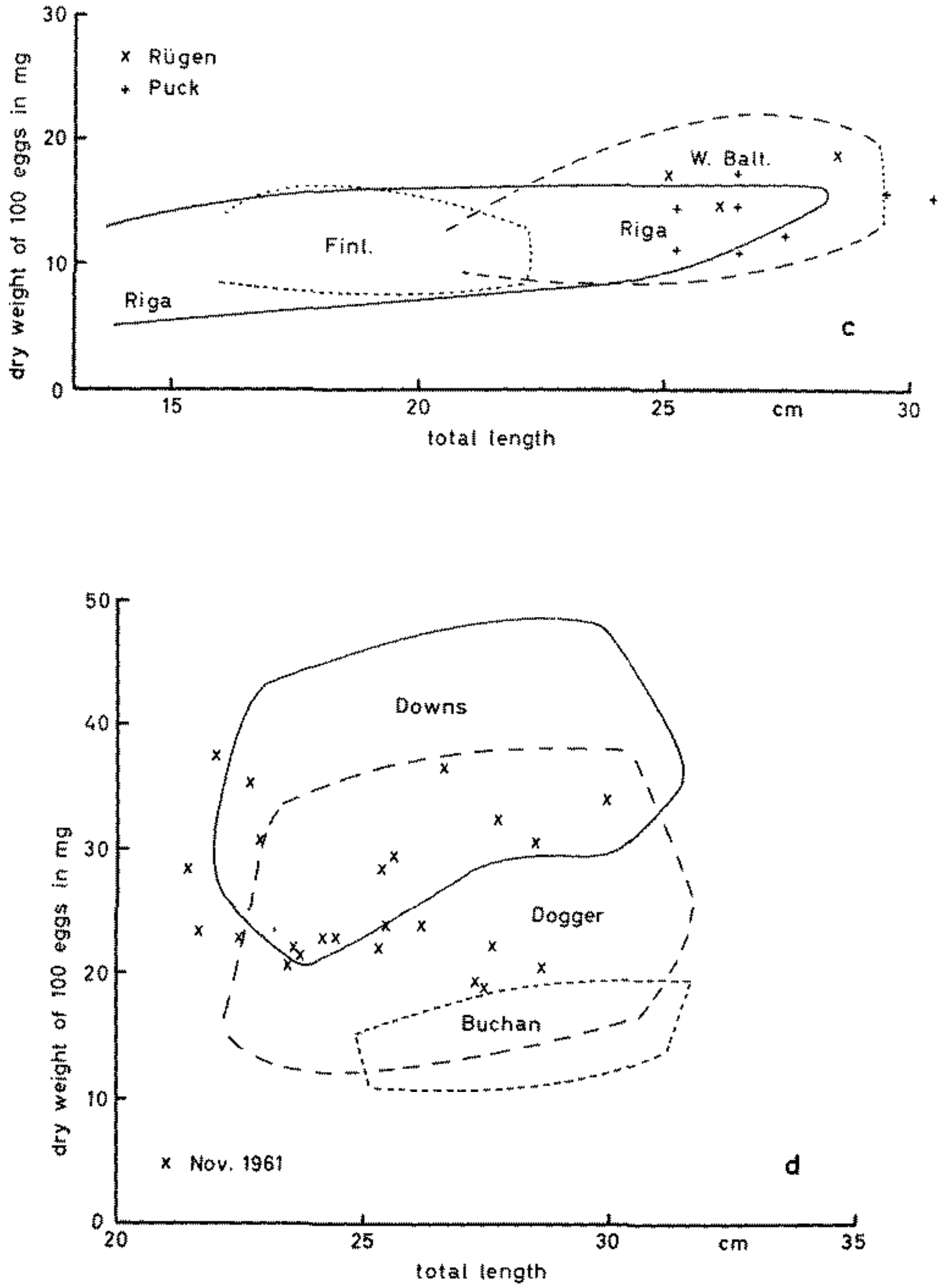
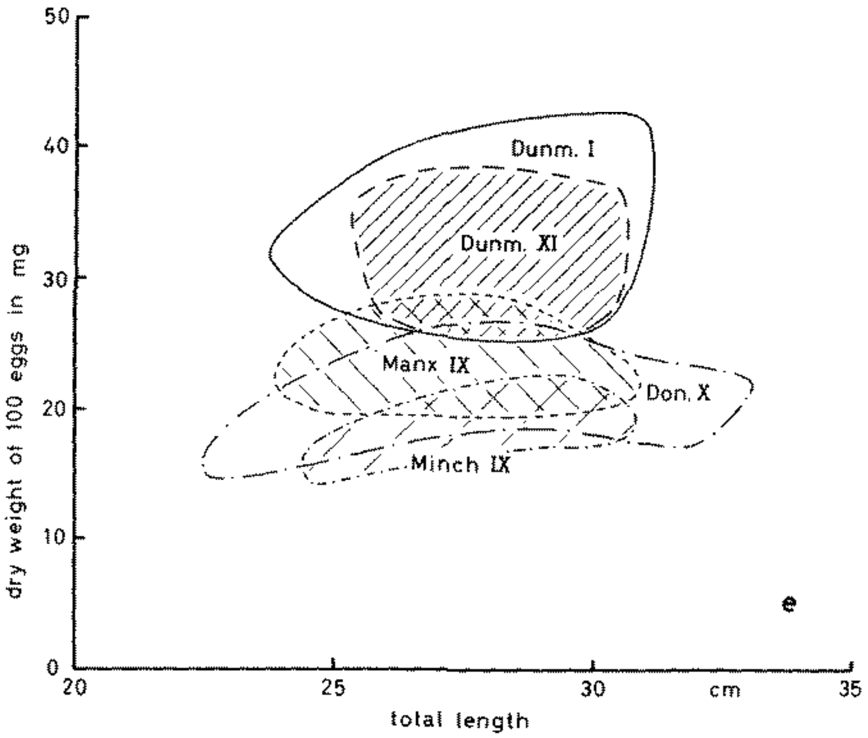


Figure 4. Egg weight against length of mother. c. Baltic. d. North Sea (herring caught off Den Helder in November 1961 are marked by x).



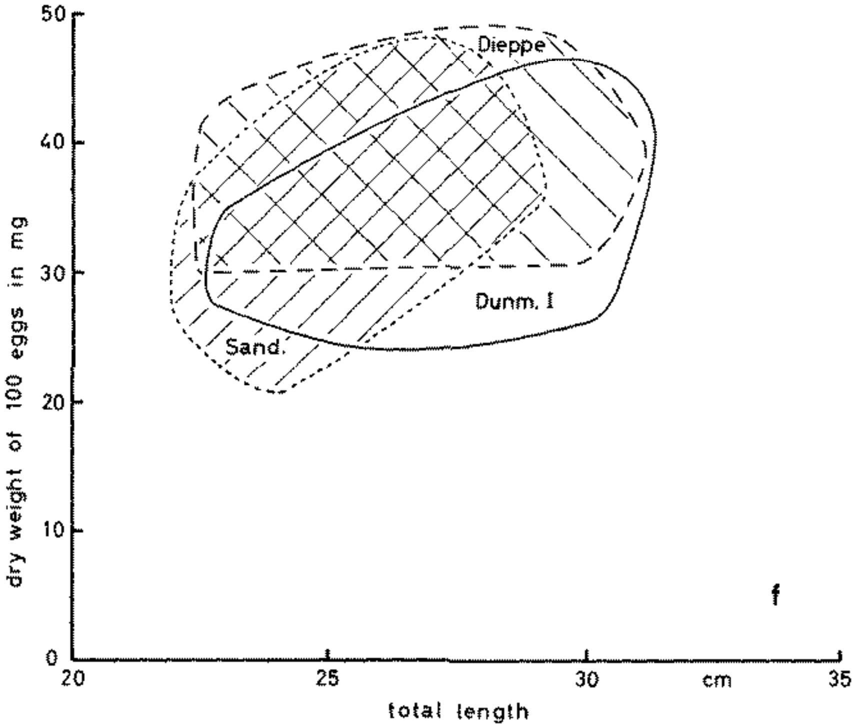


Figure 4. Egg weight against length of mother. e. West coast of British Isles, autumn. f. Downs and Dunmore winter.

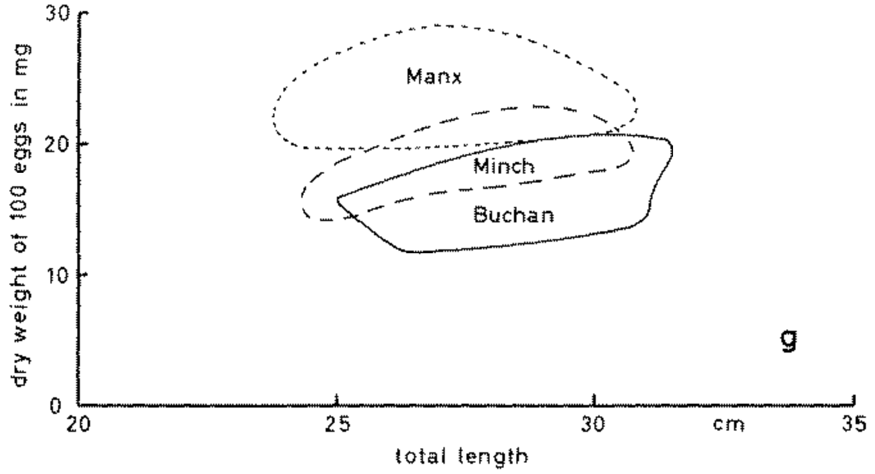


Figure 4. Egg weight against lenght of mother. g. East and west coast of North Britain August–September.

observed over a wide range of lengths, (see Figure 4c). The spring-spawning herring of the Elbe, which belong to the group of small populations of the North Sea coastal waters, were similar to the Baltic herring.

In North Sea herring (Figure 4d) three main groups could be distinguished, all spawning in the second half of the year: Buchan herring spawning in the north-western North Sea in August–September, Dogger herring spawning in the western part of the central North Sea in September–October, and Downs herring spawning in the Southern Bight and in the easternmost part of the English Channel in November–December. The average egg weight of these three groups differed markedly. Downs herring, with a low fecundity, had eggs which were, on average, more than twice as heavy as those of Buchan fish (35–38 mg/100 eggs and about 16 mg/100 eggs respectively). The gap between Buchan and Downs herring was bridged by Dogger herring, whose egg weight overlapped considerably those of the other two groups. The mean dry weight of the eggs of Dogger herring was rather low (about 21 mg/100 eggs) in 1962 and 1964, with little difference between the various spawning places (North of Dogger, Whitby, south-western Dogger, Haisborough, Dowsing), whereas in 1961 it was higher (26·7 mg/100 eggs).

Various groups of autumn spawners are also found off the west coast of the British Isles. Their distribution in terms of egg size is shown in Figure 4e. In order to make the data as comparable as possible only samples from September 1962 to January 1963 were used, whereas in Figure 4a all Dunmore data from 1962 and 1963 were taken together. The smallest eggs were found in Minch herring, spawning in September. Manx herring, spawning at the same time further to the south in the vicinity of Isle of Man, and Donegal autumn spawners caught on the west coast of Ireland in October, were fairly similar in their egg weights, which on average were higher than in Minch herring, although the overlap between the values for Donegal and Minch herring was considerable. Samples taken in the Dunmore fishery off the south coast of Ireland in November showed a considerably higher egg weight than the other groups. In January some fish had larger eggs than any caught in November. It is obvious that Dunmore late autumn and winter spawners were quite distinct from Minch autumn spawners in their egg weight, their eggs being on average twice as heavy as those of Minch herring. Egg weights of Manx and Donegal herring overlapped those of both the other groups; in this way the pattern is similar to that in North Sea autumn spawners.

It is an open question as to how the herring of the waters west of Britain are racially connected with Atlanto-Scandian and North Sea herring. In Figure 4a no consistent difference in egg weight between Clyde, Dunmore, Donegal and Norwegian winter-spring spawners was found. In Figure 4f, Dunmore herring caught in January 1962 and 1963 are compared with the two main components of Downs herring, spawning off Dieppe and at Sandettié. The Dunmore herring had about the same range of variance as the two components of Downs herring. A comparison between North Sea Buchan herring and Minch and Manx herring (Figure 4g) shows considerable separation between these population, with very little overlap between Buchan and Manx fish.

Discussion

Variation in egg weight within spawning groups

Within a spawning group there is little tendency for a *general* increase in egg weight with age of the mother, such as is found with egg number (fecundity). The only striking fact is the small eggs produced by very young recruit spawners (two or three year-olds). It is this which influences the tests of significance (see Table 4) to the extent that a positive relationship between egg weight and length of the mother is statistically significant only when the eggs of these very young recruits are present in the sample.

The question is how such differences affect the viability of the offspring of very young recruit spawners compared with older fish. For instance the Norwegian recruits have eggs as much as 14% lighter than older fish (30 mg/100 eggs compared with 35 mg/100 eggs). This results (see Blaxter and Hempel, 1963) in the larvae from such recruits surviving on their yolk supply for about two days less than those larvae from older fish (39 compared with 41 days from fertilization, at the temperatures prevailing after spawning). Consequently, larvae from recruit spawners will have about two days less aggregate time to achieve the change from internal to external food sources. In addition, the maximum body weight and length attained on the yolk supply will be slightly less in the larvae from recruits (0·13 mg, 10·0 mm) than in the larvae from older parents (0·15 mg, 10·5 mm). This could affect such factors as swimming speed, liability to predation and dependence on physical factors in the environment.

Bridger (1960, 1961) and Cushing and Bridger (1964) obtained evidence which suggested that recruit herring in the southern North Sea were producing less viable larvae than older herring. If the weights of eggs produced by spawners in the Sandettié area are extracted from Table 5 it is found that the recruits have eggs which are 6 to 7% lighter than older spawners, whereas for Dieppe herring no difference in egg size in older fish was found. Blaxter and Hempel (1963) have already estimated the effect of this order of difference* on the

* Difference of 9% as given in Blaxter and Hempel (1963) is an overestimate based on a mixture of older Dieppe and younger Sandettié herring.

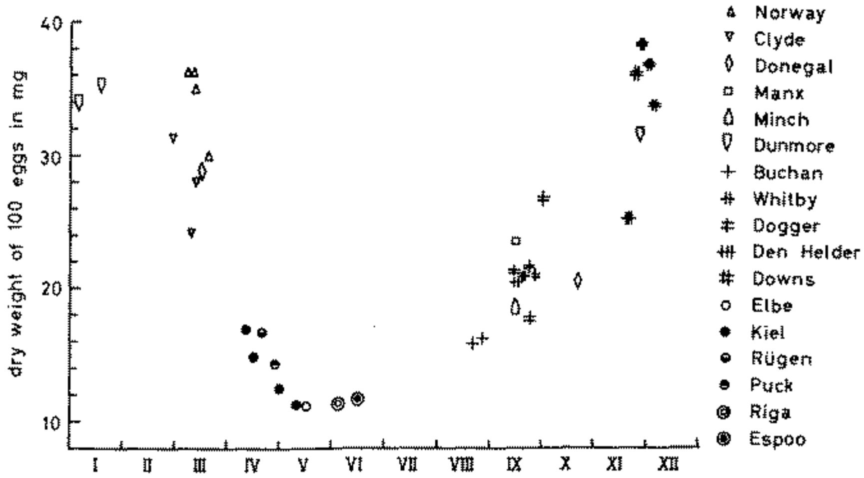


Figure 5. Average dry weight of eggs in various spawning groups against month of spawning.

viability of the larvae. The larvae from recruits might be expected to survive one day less than those from older fish (27 compared with 28 days at the prevailing temperature). The larvae would attain a slightly lower maximum weight and length on the yolk supply (0·16 mg, 10·7 mm for larvae from recruits, 0·17 mg, 11·1 mm for larvae from older fish). The disadvantage to the larvae in the Sandettié area of the southern North Sea is a little less than to those from Norwegian fish. As CUSHING and BRIDGER (1964) comment, the significance of such differences in terms of viability remains in question.

Variation in egg weight between spawning groups

(1) "*Racial*" *differences*

Egg weight clearly varies so much from group to group, that it should be considered as a useful "racial" character and should be included in the lists of the characteristic features of each herring group. Egg weight (and fecundity) may shed some light on the present problems of the interrelationships between groups whose identity is in some doubt. Such a technique has recently been adopted by PARRISH and SAVILLE (1965). For instance the Buchan – Dogger – Downs progression in spawning is shown to be even more distinct than the space and time factors suggest. The large differences in mean egg weight and fecundity support the thesis that Buchan and Downs herring are distinct, although the latter may possibly consist of two sub-groups. Mixing due to accelerated or late spawning may only affect the Dogger group. However, the extent to which egg weight is an inherited factor, independent of the environment, is still open to question and "genetical" affinities and differences based on this character should only be suggested with caution.

Perhaps more definitely, the inherited distinction between the Buchan, Minch and Manx summer spawners can be put forward. Here spawning season and the events leading up to it (such as the "temperature and feeding history" of the parents) are similar and less likely to have had an influence on the egg weight. A similar distinctness may be postulated in the Downs and Dunmore fish spawning in November. The Dunmore herring spawning in January are, however, very similar in egg weight to the November spawners of the southern North Sea.

Egg weight would be a more valuable character if it could be used at times of year other than the spawning season. In contrast to fecundity (BAXTER, 1963) it does not permit an assessment of percentage mixing (and therefore of percentage exploitation) of different groups on the feeding grounds well before spawning.

(2) *Egg weight in relation to spawning time and place*

From the ecological point of view the material can be divided into three main groups according to the season of spawning. This can be seen in Figure 5, although any grouping according to months must be somewhat artificial when comparing fish from different areas, *e.g.* in the eastern Baltic, spring occurs very late so that the conditions in the Gulf of Riga and the Gulf of Finland in June might be comparable with those in Kiel Bay in May. Egg weight in eastern Baltic herring was almost the same as that of late spawners in Kiel Bay.

a. Herring spawning in winter and early spring at a time when adults are existing mainly on their body reserves. The eggs develop at relatively low temperatures and the young larvae meet poor supplies of food, especially larval zooplankton; on the other hand, the predator population may also be scarce. The Norwegian, Clyde and Donegal herring spawning in March belong to this group. All of them have heavy eggs and the larvae hatch with very large yolk-sacs on which they grow to a size which enable, them to feed on relatively large plankton organisms (BLAXTER and HEMPEL, 1963; BLAXTER, 1965).

b. Herring spawning in spring after increases in abundance of zooplankton. The fish of this type may have commenced feeding after the over-wintering period before they spawn. The larvae hatch under favourable feeding conditions, especially those hatching late in the spring. This group is mainly represented by Baltic herring. Their eggs are very small, even smaller than those of Norwegian recruits which spawn only a few weeks earlier, but the warming-up of the water in the western Baltic is much faster than on the Norwegian coast. The Baltic larvae hatching at the end of April or in May may, therefore, meet more favourable feeding conditions than the larvae off Bergen in April. If the average dry weights of the various samples of western Baltic herring are plotted against the date of capture a decrease of egg size with progressing season becomes apparent. This might be due partly to the increasing percentage of recruits in the catch, in the later part of the season, but it might be also an adaptation to the environmental conditions which change rapidly with the progressing season.

c. Herring spawning in summer and autumn which either interrupt their feeding season in order to spawn or which have just finished feeding. The larvae hatch under favourable feeding conditions if spawning takes place in July to September, but the supply of suitable small zooplankton will decrease later. This group is represented by the North Sea Bank (Buchan) herring and by the autumn spawners west of the British Isles. For both areas there is a striking increase in egg size with the progress of

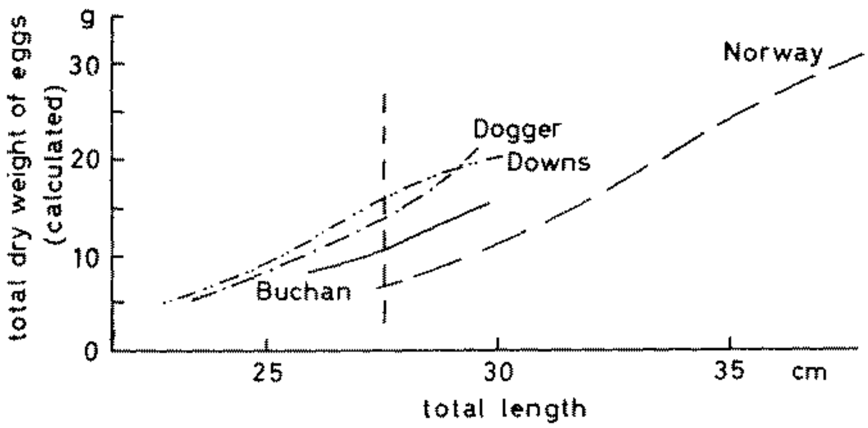


Figure 6. Annual total egg weight production in relation to length of the mother in three spawning groups of North Sea herring and in Norwegian herring. The figures are calculated from published fecundity data multiplied by the average dry weight of eggs in successive centimetre groups.

season, the Buchan herring spawning in August (16 mg/100 eggs) having the same small egg size as Baltic herring caught in April. Dogger, Whitby, Minch, Manx and Donegal herring, spawning in September–October, have somewhat heavier eggs (18–27 mg/100 eggs). Downs herring, which are otherwise closely related to the North Sea autumn spawners, are ecologically of the winter type with very large eggs.

Spawning "strain"

The fact that egg weight and number are inversely related in different groups does not necessarily imply that the total weight of ripe eggs just before spawning is the same in all the groups. Size at first maturity is different in some groups and the increase in total egg mass with length may also vary. In Figure 6 curves are given showing the increase in dry weight of the total ripe egg mass with length of the mother, for both North Sea and Norwegian herring. The total ripe egg mass for each length group (cm) of fish is calculated from the dry weight data of the present paper and fecundity figures given by KÄNDLER and DUTT (1958), POLDER and ZIJLSTRA (1959) and BAXTER (1959). Within the North Sea herring the total ripe egg mass for any given length of fish was highest in the later and more southerly spawners. For example, a Downs herring of 27·5 cm produced 7·3 g dry weight of eggs and a Buchan herring of the same length only 5 g. This can be considered, at least partly, as a consequence of the longer feeding period before spawning; it could also be considered as a greater spawning "strain" on the Downs fish. The Norwegian herring, which first mature at a greater length and age, show a low total egg mass at a given length compared with North Sea herring. On the other hand their life span is longer and over this the aggregate egg mass produced by a fish may well be as high, or higher, than in the North Sea.

PETERS (1963) reported both a similar inverse correlation between egg size and fecundity in *Tilapia* and a similar increase in spawning "strain" with increasing length. These factors could be related to the type of incubation, whether the species in question were "substrate-" or "mouth-brooders".

Factors affecting egg weight

Superimposed on general group differences, which are probably genetically determined, are occasional year-to-year differences which may result from environmental conditions. This was found in the Clyde in 1961 and 1962. It was not possible to make concomitant studies of fecundity, which might also have varied, because it is not certain during the spawning season what proportion of the eggs have been shed. BAXTER (1963) mentioned that fecundity did not seem to vary noticeably on a yearly basis in North Sea herring, though ANOKHINA (1963) reported such variations in the White Sea.

It is of interest that BAGENAL (1963a, b; 1965) reported annual variations in the fecundity of flatfish in the Clyde sea area. In one species there was some evidence for the fecundity being density-dependent, that is higher when the population was reduced in numbers. It is desirable in herring to measure changes in egg weight over a number of years, at the same time measuring fecundity shortly before spawning and trying to assess population density, food supply and environmental conditions over the preceding months.

Further sources of variation in egg size lie in changes with age, there being a tendency for an increase between first-spawners (especially when very young) and repeat-spawners. In addition, there are differences between the mean egg weight of females of a given age and group as well as individual differences in the eggs coming from a single female.

General

Egg size is clearly a "racial" character of some diagnostic value. With fecundity it also has important ecological implications in terms of survival and recruitment, in particular because such large differences are found *within* a single species. There are some other instances where egg size has been found to be variable, for example in *Acanthias* (TEMPLEMAN, 1944) and in *Tilapia* (PETERS, 1963). It would be valuable to extend the study to other fish species with less specialised reproduction where it has, up to the present, been considerably neglected.

Acknowledgements

This paper completes a series giving the results of work by the two authors over the past six years. In addition to the help provided by individuals and laboratories mentioned in Table 1, it is a pleasure to thank Professor A. BÜCKMANN of the University of Hamburg and Dr. C. E. LUCAS and Mr. B. B. PARRISH of the Marine Laboratory, Aberdeen, for their support and advice throughout this period of international co-operation. Mr. J. A. POPE, also of the Marine Laboratory, Aberdeen, has been most co-operative in supplying statistical help during the analysis of many of the results, and for this we are most grateful.

Summary

1. Samples of ripe eggs were collected from different spawning groups of herring in the north-eastern Atlantic and adjacent seas (Figure 1 and Table 1) and for each female the dry weight per 100 eggs was determined.

2. Weighings of single eggs and of replicate samples from one female showed that the variation within a female was smaller than between the females of a spawning group and also smaller than the variation between group means.

3. The variation in egg weight within a group was dependent, to a slight extent, on differences of length and age of the mother. In very young recruits the eggs were significantly lighter than in fish recruiting at an older age and in repeat-spawners. The difference in egg weight between the youngest recruit spawners and the next age-group was about 10–14% in Norwegian, Baltic and Clyde herring, 5–6% in Minch and Sandettié herring and 2% in Dogger herring. In Buchan and Dieppe herring no increase in egg weight from two to three year-old spawners was found. For older fish no relationship of egg weight to age or size of the mother was established. In contrast to the increase in fecundity, the egg weight seems to remain constant over the main part of the mature life in herring.

4. Dry weight of eggs can be taken as a character for discriminating between various groups of herring and is closely related to the spawning season. Spring spawners from Norway, western Scotland, and from western and southern Ireland had large eggs though Baltic spring spawners produced eggs which were less than half the weight of Norwegian herring spawning about the same time. There was no difference in egg weight between spring spawners of the Elbe estuary and the western and the eastern Baltic. In spawners of the North Sea, and in the waters west of the British Isles, the egg weight increased as spawning became later from North to South. Late summer spawners of the Buchan and Minch areas had less than half the egg weight of the late autumn to winter spawners in the Downs and Dunmore fisheries. Autumn spawners of the Dogger and Manx areas showed intermediate egg weights. The difference in egg weight between the different groups of herring in the North Sea was almost as high as between Norwegian and Baltic herring.

5. The ecological importance of winter/early spring spawners producing fewer but large eggs, and late spring/summer spawners producing many rather small eggs, is discussed in the light of previous experimental results on the different viability of larvae hatching from small and large eggs.

6. The total dry weight of all eggs produced at spawning by a female of a given length was calculated for some groups from published fecundity data and from the average egg weight. The production of ripe eggs per season, and thus the "spawning strain" on fish of a given length, was different for various groups, being higher in Downs herring than in Buchan herring. It seemed to be particularly low in Norwegian spring spawners.

References

ANOKHINA, L. E., 1961. "Relationship between the fertility, fat content and the variations in the size of ova in clupeid fishes". Trudy Soveshch. ikhtiol. Kom., **13**: 290–5.

ANOKHINA, L. E., 1962. "On the relationship between fat content in salaka females (*Clupea harengus membras* L.) and quality of its eggs." ICES CM 1962, Doc. No. 151 (mimeo.) 12 pp.

ANOKHINA, L. E., 1963. "Some aspects of the fecundity of the herring in the White Sea." Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, **154**: 123–7.

BAGENAL, T. B., 1963a. "Variations in plaice fecundity in the Clyde area". J. mar. biol. Ass. U.K., **43**: 391–9.

BAGENAL, T. B., 1963b. "The fecundity of witches in the Firth of Clyde." J. mar. biol. Ass. U.K., **43**: 401–7.

BAGENAL, T. B., 1965. "The fecundity of long rough dabs in the Clyde Sea area." J. mar. biol. Ass. U.K., **45**: 599–606.

BAXTER, I. G., 1959. "Fecundities of winter-spring and summer-autumn herring spawners". J. Cons. perm. int. Explor. Mer, **25**: 73–80.

BAXTER, I. G., 1963. "A comparison of fecundities of early and late maturity stages of herring in the north-western North Sea". Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, **154**: 170–4.

BLAXTER, J. H. S., 1965. " The feeding of herring larvae and their ecology in relation to feeding". Rep. Calif. coop. oceanic Fish. Invest., **10**: 79–88.

BLAXTER, J. H. S., and HEMPEL, G., 1963. "The influence of egg size on herring larvae (*Clupea harengus* L)". J. Cons. perm. int. Explor. Mer, **28**: 211–40.

BLAXTER, J. H. S. and HEMPEL, G., 1966. "Utilization of yolk by herring larvae". J. mar. biol. Ass. U.K., **46**: 219–34.

BRIDGER, J. P., 1960. "On the relationship between stock, larvae and recruits in the "Downs" herring". ICES CM 1960, Doc. No. 159 (mimeo.) 11 pp.

BRIDGER, J. P., 1961. "On fecundity and larval abundance of "Downs" herring". Fishery Invest., Lond., Ser. 2, **23**: (3) 30 pp.

CUSHING, D. H. and BRIDGER, J. P., 1964. "The present state of the Bridger Hypothesis relating larval mortality of herring to recruitment". ICES CM 1964, Doc. No. 99 (mimeo.) 6 pp.

FARRAN, G. P., 1938. "On the size and number of the ova of Irish herring". J. Cons. perm. int. Explor. Mer, **13**: 91–100.

FRIDRIKSSON, A. and TIMMERMANN, G., 1951. "Some remarks on the eggs of herring (*Clupea harengus* L.) and capelin (*Mallotus mallotus* (O. F. Müll.)) in Icelandic waters". J. Cons. perm. int. Explor. Mer, **17**: 261–3.

HEMPEL, G., 1965. "On the importance of larval survival for the population dynamics of marine food fish". Rep. Calif. coop. oceanic Fish. Invest., **10**: 13–23.

HEMPEL, G. and BLAXTER, J. H. S., 1963. "On the condition of herring larvae". Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, **154**: 35–40.

ILES, T. D., 1964. "The duration of maturity stages in herring". J. Cons. perm. int. Explor. Mer, **29**: 166–88.

KÄNDLER, R. and DUTT, S., 1958. "Fecundity of Baltic herring". Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, **143**: 99–108.

LIAMIN, K. A., 1959. "Investigations into the life cycle of summer-spawning herring of Iceland". Spec. scient. Rep. U.S. Fish Wildl. Serv., (327) 166–202.

NIKOLSKY, G. V., 1962. "On some adaptations to the regulation of population density in fish species with different types of stock structure". In: "The Exploitation of Natural Animal Populations". Ed. by E. D. LE CREN and W. HOLDGATE, pp. 265–82, Blackwell, Oxford.

PARRISH, B. B. and SAVILLE, A., 1965. "The biology of the north-east Atlantic herring populations". Oceanogr. Mar. Biol. Ann. Rev., **3**: 323–73.

PETERS, H. M., 1963. "Eizahl, Eigewicht und Gelegeentwicklung in der Gattung *Tilapia* (Cichlidae, Teleostei)". Int. Revue ges. Hydrobiol. Hydrogr., **48**: 547–76.

POLDER, J. J. W. and ZIJLSTRA, J. J., 1959. "Fecundity in the North Sea herring". ICES CM 1959, Doc. No. 84 (mimeo.) 10 pp.

RANNAK, L. A., 1958. "Quantitative study of the Baltic herring eggs and larvae in the northern part of the Gulf of Riga and principle factors determining their survival". Trudy vses. nauchno-issled. Inst. morsk. ryb. Khoz. Okeanogr., **34**: 7–18. (In Russian, translation by Fish. Res. Bd Can., No. 238).

STRZYZEWSKA, K., 1960. "Fecundity of the Baltic herring in the Gulf of Gdansk region". ICES CM 1960, Doc. No. 69 (mimeo.) 6 pp.

TEMPLEMAN, W., 1944. "The life history of the Spur dogfish *Squalus acanthias* and the Vitamin A values of dogfish liver oil". Res. Bull. Dept. nat. Res. (15) 102 pp.