The Experimental Modification of Meristic Characters in Herring (*Clupea harengus* L.)

By

G. Hempel*

Biologische Anstalt Helgoland

and

J. H. S. Blaxter

Marine Laboratory, Aberdeen

Introduction

The plasticity of meristic characters in fish under the influence of the external environment is now well known. Meristic counts have been shown to vary with such factors as temperature, salinity, and light conditions during early life. The experimental evidence has been reviewed by TÅNING (1952), while both the experimental and circumstantial evidence, with special respect to the herring, has been reviewed by BLAXTER (1958).

A number of recent papers should be mentioned to bring these reviews up-to-date. Some further experiments have been done on marine fish, a section of work which has been rather neglected in the past due to the greater difficulty of rearing them. MOLANDER and MOLANDER-SWEDMARK (1957) reared plaice and found that the mean vertebral count increased at incubation temperatures above and below 8°C. (This may be called the "Tåning effect.") ITAZAWA (1960) found a "Tåning effect" in *Channa argus*, the mean vertebral count increasing at incubation temperatures above and below 22–25°C. He also found a strong parental effect on the vertebral counts. MCHUGH (1954) working on *Leuresthes tenuis* and LINDSEY (1958) on *Oncorhynchus nerka* found that the light conditions during incubation also affected the mean vertebral count.

Of particular relevance to the plasticity of the meristic characters in *Clupea harengus* is some post-war work. BÜCKMANN (1950) and BÜCKMANN and HEMPEL (1957) in accordance with MCHUGH's (1942) findings on the offspring of *Clupea pallasii* correlated the mean vertebral count of herring larvae caught near the German coast with temperature at the spawning time and found a negative correlation. DAY (1957) described a similar correlation in adult herring off the Canadian coast.

* Present address Institut für Fischereibiologie, Universität Hamburg, Holstenwall 24, Hamburg 36.

Some experimental work has been done on herring. The larvae are difficult to rear to the stage where vertebrae are formed and although this has been done by a number of workers (MEYER, 1878; SCHACH, 1939; DANNEVIG, 1948; and DANNEVIG and HANSEN, 1952) no strict temperature control was maintained nor have any counts of vertebrae been published. KOTTHAUS (1939) suggested that myotome counts would be correlated with vertebral counts and could be substituted for them. Both HEMPEL (1953), working on German coastal herring from Cuxhaven, and BLAXTER (1957) on Scottish east and west coast herring have counted the myotomes of larvae soon after hatching and found negative correlations between temperature of incubation and mean myotome count. HEMPEL reported mean myotome counts rather lower than those of Scottish herring and also lower than those of the larvae of German coastal herring given later in this paper. He used a different counting technique in which the myotomes in the extreme caudal region were not detected.

As the results of a joint investigation between the authors of this report at the Biologische Anstalt, on Helgoland in 1960, further experimental evidence of the plasticity of the meristic characters in herring is now available. Myotome counts have been obtained from larvae reared under different conditions of temperature and salinity. By rearing larvae beyond the yolk-sac stage, in a few cases to metamorphosis (see BLAXTER and HEMPEL, 1961), later meristic counts have also been obtained.

In addition to this work, other data on meristic counts obtained in Aberdeen by the second author in 1957 are also given.

Methods

Apparatus

In the Helgoland experiments, eggs and sperm were obtained by dissecting the gonads from spring spawning herring caught in the approaches to Kiel Harbour and near Cuxhaven at the mouth of the Elbe. These gonads were stored in jars (see BLAXTER, 1955) at about 4°C and taken by ship to Helgoland where the eggs were artificially fertilized. Additionally deep-frozen sperm obtained from a Clyde spring spawning herring were used for cross fertilizations. The eggs were incubated in different ways which are described in detail by BLAXTER and HEMPEL (1961).

1. The eggs were incubated in circulated water at different temperatures in 120 litre tanks. They were kept in darkness until hatching, the hatched larvae then being kept in artificial light. The mean temperatures with standard deviations are given in Table 2.

Some further eggs were incubated in 100 litre tanks in daylight. These tanks had a variable water circulation and no strict temperature control.

A "temperature shock" experiment was also done in which a series of plates of eggs were kept at 10°C, but each day one plate was transferred to 4°C for 24 hours.

2. Further fertilized eggs were incubated in 2 litre glass jars in different salinities from 5–50‰, but in a constant temperature of about 10°C.

3. Larvae from experiments done in Aberdeen prior to the Helgoland work were treated in the way described by BLAXTER (1961).

Table 1

Details of experiments

Parents with length in cm and vertebral count*	Date of fertilization	Experiments
Cuxhaven ♂ (1) × Cuxhaven ♀ (1) 27·4, 56 25·0, 56	26. Apr. 60	Different temperatures, about 5, 8, 11, 14°C
Cuxhaven ♂ (2) × Cuxhaven ♀ (2) 25·0, 57 25·5, 56	26. Apr. 60	Different salinities 5–50 ‰
Cuxhaven ♂ (3) × Cuxhaven ♀ (3) 26·5, 56 29·3, 55 25·5, 56	29. Apr. 60	Temperature shock experiment
Kiel ♂ (1) × Kiel ♀ (1) 24·0, 57 25·3, 56	29. Apr. 60	Different temperatures, about 5, 8, 11, 14°C
Clyde (Scotland) ♂ × Kiel ♀ (1) 27·3, 57 25·3, 56	29. Apr. 60	Different temperatures, about 5, 8, 11, 14°C

* The numbers of the parents in brackets are the same as in Table 1 (BLAXTER and HEMPEL, 1961).

Sampling

Samples were taken of 50 larvae from the different experiments (a) when 50% had hatched and (b) at the end of the yolk-sac stage, which was taken to be about 60 day degrees (taking biological zero as −1°C) after 50% hatching. The larvae were anaesthetized in 2% urethane in sea water and fixed in 2% formalin. Larvae at later stages of development were removed from the tanks when they became moribund. They were also fixed in 2% formalin, but no urethane was used.

Table 2

Significance of myotome counts at different temperatures

Parents (date of fertilization)	Mean incubation temperature (°C)	Standard deviation	Mean myotome count and S. E. (with number in sample)	Variance ratio	Level of probability
Kiel ♂ × Kiel ♀ 29. April	4·51	± 0·68	61·20 ± 0·125 (50)	13·72 3 and 383 d.f. (temperature effect)	P <0·001
	7·46	± 0·54	61·02 ± 0·125 (50)		
	10·76	± 0·36	60·67 ± 0·128 (48)		
	14·38	± 0·63	60·52 ± 0·125 (50)		
Clyde ♂ × Kiel ♀ 29. April	4·51	± 0·68	61·60 ± 0·125 (50)	10·26 1 and 383 d.f. (parental effect)	P < 0·01
	7·46	± 0·54	61·04 ± 0·125 (50)		
	10·76	± 0·36	61·14 ± 0.125 (50)		
	14·38	± 0·63	60·70 ± 0·135 (43)		
Cuxhaven ♂ × Cuxhaven ♀ 26. April	5·15	± 1·20	61·36 ± 0·132 (50)	3·06 3 and 182 d.f.	P < 0·05
	7·56	± 0·50	* 61·40 ± 0·132 (50)		
	7·75	± 0·40			
	10·86	± 0·34	61·24 ± 0·132 (50)		
	13·70	± 1·16	60·83 ± 0·155 (36)		

* Eggs incubated in two tanks for first nine days.

Counting of meristic characters

The myotomes of all larvae were counted under a binocular microscope using polarized light. The older larvae were stained with alizarin using TÅNING's (1944) technique (but without bleaching) for counting vertebrae and fin rays.

In all cases an attempt was made to count the number of *whole* myotomes. In the caudal region the myotomes may be indistinct and in order to avoid bias the samples were counted, usually without knowing their origin, by two observers. While one counted the myotomes of half the sample, the other one checked which was the last myotome. The observers changed over for the second half of each sample. Some samples were later recounted. When this was done it was found that the means obtained in repeat counts agreed closely (within 0·1) with those of the original counts, only with larvae at hatching. At the end of the yolk-sac stage there were sometimes differences between original and repeated counts, though in this case the trend was usually the same, i.e., a high or low count was confirmed by a high or low recount. The difficulty of getting agreement between counts at the end of the yolk-sac stage is probably due to the larvae becoming starved and the tails thin, with a resultant loss in clarity of the myotomes. The results of these counts are not given here for this reason. It would be worth noting in any future work that counts of myotomes at hatching are the more satisfactory.

The number of myotomes in the very young larvae was greater than the number of vertebrae that might have been expected, by 5–9 myotomes. In the older larvae, once the tail had turned up at about 16 mm length, it was possible to count the number of myotomes which positioned the vertebrae themselves, because at this stage the urostyle is partly formed. These counts are therefore termed "vertebral myotomes" as they should be the same as the future number of vertebrae. In still older larvae, over 22–24 mm in length, and including those that reached metamorphosis, it was possible to count some or all of the vertebrae themselves.

Design of experiments

Larvae from the crosses shown in Table 1 were sampled in these experiments for counts of meristic characters.

Results

Myotome counts

1. Effect of temperature

The mean myotome counts of larvae at hatching after incubation in different temperatures are shown in Figure 1. It will be seen that there is a general negative correlation between temperature and mean myotome count. Analyses of variance showed that there were significant differences between the mean myotome counts at the different temperatures (see Table 2).

2. Effect of salinity

The mean myotome counts of larvae at hatching from eggs fertilized and hatched in different salinities are shown in Figure 2. There were two sets of

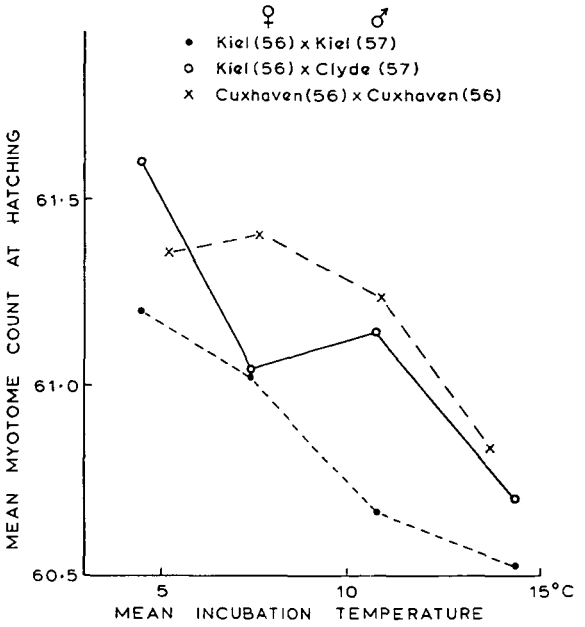

Figure 1. Showing the effect of incubation temperature on mean myotome count.

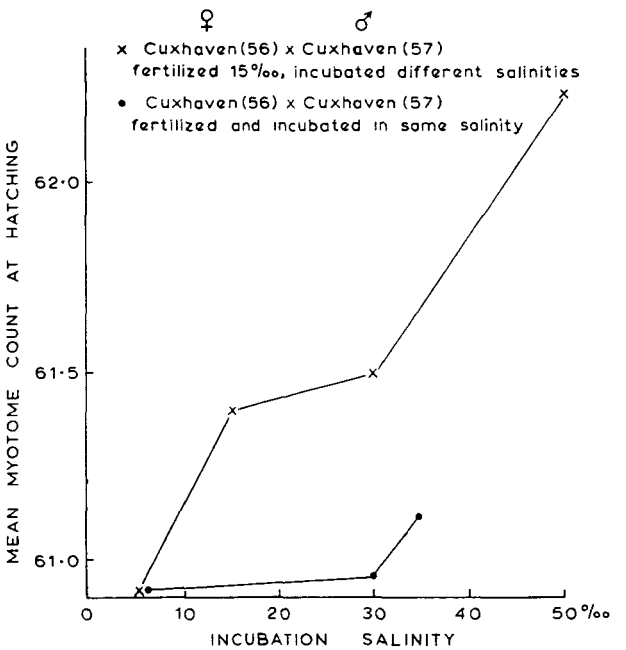

Figure 2. Showing the effect of incubation salinity on mean myotome count.

experiments using the same parents. In one set the eggs were fertilized at 15 ‰ and then transferred to salinities of 5, 15, 30, and 50 ‰. In the other, which was less complete, the salinity at fertilization and later salinities were the same, viz. 5, 30, and 35 ‰. In this experiment the hatching rate was lower and two of the samples taken were necessarily poorer. This could account for the lower values found.

There was a general positive correlation between salinity and myotome count in both experiments. Analyses of variance (Table 3) showed that only in the first was this significant.

Table 3

Significance of myotome counts at different salinities (temperature constant at 10°C)

Parents	Incubation salinity (with fertilization salinity) (‰)	Mean myotome count and S. E. (with number in sample)	Variance ratio	Level of probability
Cuxhaven ♂ × Cuxhaven ♀ 26. April	5 (15)	60·92 ± 0·122 (50)	20·28 3 and 196 d.f.	P < 0·001
	15 (15)	61·40 ± 0·122 (50)		
	30 (15)	61·48 ± 0·122 (50)		
	50 (15)	62·24 ± 0·122 (50)		
Cuxhaven ♂ × Cuxhaven ♀ 26. April	5 (5)	60·92 ± 0·113 (39)	0·64 2 and 111 d.f.	not significant
	30 (30)	60·96 ± 0·100 (50)		
	35 (35)	61·12 ± 0·141 (25)		

3. Effect of length and growth in the yolk-sac stage

Although details will not be given here, there was no obvious correlation between length of larvae and their myotome counts within any one sample. Comparing the data on mean length (BLAXTER and HEMPEL, 1961, Fig. 4) and mean myotome counts at hatching in temperature experiments a positive correlation between size and myotome counts is obvious. In contrast to this the salinity experiments yielded a negative correlation between length and myotome counts: the larvae reared at 50 ‰ were the smallest but had the highest number of myotomes. During the yolk-sac stage there was a general "addition" of visible myotomes with growth in length – the mean myotome count at hatching being lower than at the end of the yolk-sac stage. This "adding on" is presumably due to the myocommata in the extreme caudal region becoming visible in polarized light after hatching.

4. Effect of race and parents

It was also intended to use the myotome counts to test whether the meristic characters of the offspring were dependent on the vertebral counts of the parents or of the race as a whole. BLAXTER (1957) found no significant racial or parental effect on the myotome counts of offspring from Clyde × Clyde, Clyde × North Sea (Banks), and North Sea × North Sea herring. The data reported here give no clear answer to this question.

(*a*) *Racial effect.* The mean vertebral counts of the Kiel and the Cuxhaven herring races are about 55·4; the mean count of the Clyde herring race is about 57·0. The cross fertilization experiments were done with the following parents (individual vertebral count in brackets): —

$$\text{Kiel } ♀(56) \times \begin{cases} \text{Kiel } ♂(57) \\ \text{Clyde } ♂(57) \end{cases}$$

The hybrid larvae (Kiel × Clyde) had mean myotome counts which were significantly higher ($P < 0{\cdot}01$) than the control larvae (Kiel × Kiel) at all temperatures used. This difference might be a measure of the effect due to the males. Unfortunately there is no Clyde × Clyde control (due to the difficulty of storing eggs) reared under the same conditions with which to make a comparison. The only Clyde × Clyde myotome counts available are those of BLAXTER (1957) and the rearing conditions he used (other than temperature) were rather different, so that a fair comparison can not be made with the Helgoland results.

In contrast to the above it is striking that the mean myotome counts of the larvae from the Cuxhaven × Cuxhaven experiments are higher in nearly all cases than both Kiel × Kiel and even Kiel × Clyde larvae, in spite of the similarity of the vertebral counts of the Kiel and Cuxhaven herring groups. It should be mentioned that the larvae from the Cuxhaven experiments were considerably larger at hatching than the Kiel larvae (BLAXTER and HEMPEL, 1961).

(*b*) *Parental effect.* Comparison of the Kiel × Kiel and Cuxhaven × Cuxhaven crosses gives some evidence that the actual counts of the individual parents are unimportant in the determination of the metamerism in their offspring. Thus, while the Cuxhaven × Cuxhaven herrings both have 56 vertebrae and the Kiel × Kiel herrings 56 and 57, the Cuxhaven offspring have higher mean myotome counts. Clearly a very elaborate set of experiments would be required to test this further.

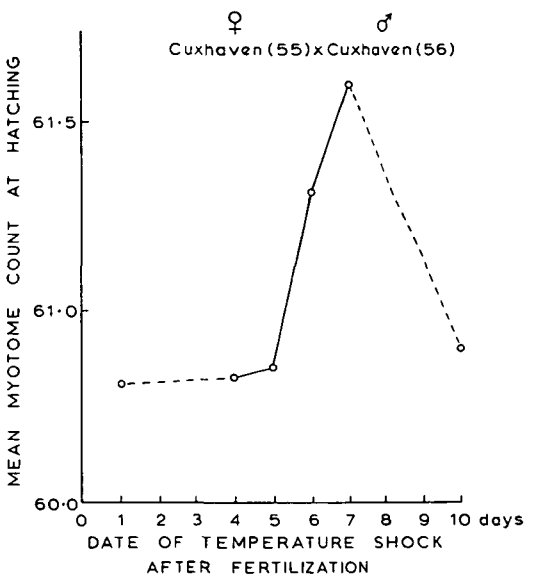

Figure 3. Showing the effect of a temperature shock (transferring from the usual temperature of 10°C to 4°C for 24 hours at different times after fertilization).

Table 4

Mean myotome counts in temperature shock experiment (Cuxhaven ♂ × Cuxhaven ♀, 29. April 1960)

Days after fertilization when shock given	Mean myotome count and S.E. (with number in sample)	Variance ratio	Level of probability
1	60·81 ± 0·134 (36)		
2	No sample		
3	No sample		
4	60·82 ± 0·127 (40)		
5	60·85 ± 0·180 (20)	6·59*	P < 0·001
6	61·32 ± 0·161 (25)	5 and 191 d.f.	
7	61·60 ± 0·117 (47)		
8	No sample		
9	No sample		
10	60·90 ± 0·149 (29)		

* A "t" test between the pooled results of days 1, 4, 5, and 10 against days 6 and 7 gives t = 5·55 (d.f. = 191) P < 0·001.

5. Effect of temperature shock

The results are shown in Figure 3 and Table 4. It will be seen that only a cold shock given 6–7 days after fertilization resulted in an upward trend in the mean myotome count. The level of myotome count before and after this period was about what might be expected for eggs incubated at 10°C (the usual temperature of the experiment) while the level of the myotome count at 6–7 days shock was what might be expected for eggs incubated at 4–5°C (the temperature of the shock). This upward trend is significant. It appears therefore that there is a particular sensitive period during incubation when the number of myotomes is susceptible to the effects of abrupt lowering of temperature.

Later meristic counts

1. Fin rays

After the end of the yolk-sac stage, counts were made of dorsal and anal fin rays once these became stainable with alizarin. However, it was seen immediately that the number gradually increased with growth and as it was not apparent when the final number had been reached, the results of these counts are not given.

Table 5

Counts of vertebrae and "vertebral myotomes"

Parents	Incubation temperature °C	Number of vertebrae 53	54	55	56	57	58	59	60	Total	Mean and S.E.	Variance ratio or "t"	Level of probability
German Coastal Herring 1960 racial mean vertebral count ≏ 55·4	8	–	–	6	2	–	–	–	–	8	55·25 ± 0·237	3·86 2 and 34 d.f.	P < 0·05
	11	–	4	10	1	–	–	–	–	15	54·80 ± 0·173		
	14	2	5	6	1	–	–	–	–	14	54·43 ± 0·179		
Clyde Herring 1957 racial mean vertebral count ≏ 57·0	7	–	–	–	–	–	6	7	1	14	58·64 ± 0·192	t = 2·10 70 d.f.	P < 0·05
	11	–	–	–	–	8	34	13	3	58	58·19 ± 0·094		
	15	–	–	–	–	–	1	–	–	1	58·0		

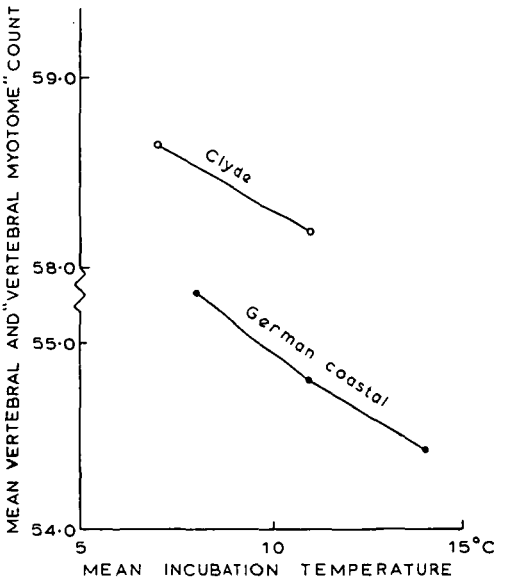

Figure 4. Showing the effect of incubation temperature on mean vertebral and "vertebral myotome" counts.

2. Vertebral and "vertebral myotome" counts

The counts are shown in Table 5 and Figure 4. Both the experiments on German coastal herring and Clyde herring show a significant negative correlation between the counts and temperature. Unfortunately no data are available for either larvae hatched in different salinities or for a Kiel × Clyde cross. The counts of the Clyde offspring were much higher than those of the German coastal larvae. This may be partly due to a genetical effect. However, while the German coastal herring have counts similar to those of the parent race, the Clyde counts are much higher than expected. This could be caused by slightly less favourable conditions prevailing in the Clyde experiments where fresh sea water was not continuously available. GABRIEL (1944) showed that killifish reared in the laboratory had higher vertebral counts than those of wild fish.

Discussion

These results go further than the earlier work of HEMPEL (1953) and BLAXTER (1957) on the experimental modification of meristic characters in herring. Not only do they confirm this earlier work in that incubation temperature has a modifying influence on myotome counts; they also show that salinity before hatching also has such an influence. Further, they suggest that there is a particular sensitive phase before hatching when the myotome count is determined. Perhaps more important, these results give reason to suppose that the vertebral number itself is modified by incubation temperature. Hitherto, this could only be inferred. There is also a suggestion that the difference in mean vertebral counts of Scottish and German spring spawners is genetically based.

So far no evidence has been obtained of a "Tåning effect" in herring, that is the meristic counts being lowest at intermediate temperatures.

Further crossings would be desirable to test the basis of metamerism. For instance crosses should be made between: —

1. Herring of the same area with the same vertebral counts.
2. Herring of the same area with different vertebral counts.
3. Herring of different areas with the same vertebral counts.
4. Herring of different areas with different vertebral counts.

Other experiments are needed to test the sensitive period during incubation when the meristic characters are determined and whether it is the same in all herring groups.

While the influence of the environmental conditions on the meristic characters in herring seems certain, the value of these characters in racial work need not be jeopardized, for as long as the environmental conditions at spawning remain within certain limits the meristic characters will still act as a "label" giving the origin of the herring. One cannot help being struck by the difference in the meristic characters of Scottish and German coastal spring spawners. This difference may be ascribed mainly to genetical causes, for the main difference in environmental conditions for the spawning of these populations, apart from topography, is one of salinity and there is no evidence of this causing a drop in the mean of the vertebral count of about 1·6 vertebrae. This view is confirmed by the results of vertebral and "vertebral myotome" counts described in this paper. There can be no doubt that these German coastal spawners, both in their meristic characters and to some extent in their ecology, have much in common with *Clupea pallasii*.

Acknowledgements

Our thanks are due to Professor A. BÜCKMANN, Dr. C. E. LUCAS, and Mr. B. B. PARRISH for arranging this collaboration and for the valuable discussions we have had with them. We are also grateful to Mr. W. HALL of the Marine Laboratory, Aberdeen for his help with the statistical treatment of the results.

Summary

1. Rearing experiments were done on herring at Helgoland in 1960, using eggs and sperm from spring spawning herring of the Elbe estuary and Kiel Bight. A successful cross fertilization was also made between the eggs from a Kiel female and the sperm of a Scottish (Clyde) spring spawning male, the sperm having been stored frozen for six weeks. Results are also given of some work done at Aberdeen in 1957, using a Clyde male and female.

2. The eggs were incubated and the larvae reared in the early stage at different temperatures (about 5, 8, 11, and 14°C) and different salinities (5–50 ‰). Samples of larvae were taken at hatching and at the end of the yolk-sac stage for counts to be made of their myotomes. Larvae which survived beyond the yolk-sac stage (a few of which metamorphosed) were fixed on death and counts made of other meristic characters which developed after yolk-sac absorption. In particular counts were made of vertebrae and "vertebral myotomes". The latter are the myotomes which are connected with the formation of vertebrae and which are detectable once the urostylar elements are formed.

3. A significant negative correlation was found between mean myotome count at hatching and incubation temperature, and a significant positive correlation between mean myotome count at hatching and incubation salinity. The mean myotome counts of the Kiel ♀ × Clyde ♂ cross were significantly higher than the Kiel ♀ × Kiel ♂ controls. A sensitive phase was found 6–7 days after

fertilization at an incubation temperature of 10°C when a temperature shock (placing the eggs for 24 hours in 4°C) resulted in a much increased mean myotome count.

4. Significant negative correlations were found between mean vertebral and "vertebral myotome" counts and temperature of incubation in larvae which survived well beyond the end of the yolk-sac stage, both where the parents were German coastal spawners (work done at Helgoland) and where they were Clyde spawners (work done earlier at Aberdeen). There appeared to be a considerable difference between these counts for Clyde and German coastal spawners, which strongly suggested a genetical difference between the groups.

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