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THE BREEDING AND FECUNDITY OF THE LONG ROUGH DAB *HIPPOGLOSSOIDES PLATESSOIDES* (FABR.) AND THE ASSOCIATED CYCLE IN CONDITION

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(Text-figs. 1–11)

Although the Long Rough Dab, *Hippoglossoides platessoides* (Fabr.), is represented by two subspecies, *H. p. limandoides* (Bloch) round the northern European coasts and *H. p. platessoides* on the North American Atlantic seaboard (Norman, 1934) and is often very abundant, little is known about its breeding biology.

The American race has been discussed by Huntsman (1918), and Bigelow & Schroeder (1953), but they do not consider the breeding biology in any detail. For the European race Saemundsson (1908, 1925, 1927) for Icelandic, Krüger (1942) for Baltic, Essipow & Slastnikow (1932) and Milinsky (1944) for Barents Sea fish, refer briefly to the breeding habits. Notes on the occurrence of Long Rough Dab eggs are scattered through the literature (Bal, 1943; Williamson, 1899; Günther, 1888; Rass, 1936; Otterstrøm, 1906; Pertseva, 1939 and others). As to fecundity, Fulton (1891) and Mitchell (1913) have given egg counts for five and eleven fish respectively from British coasts, and Milinsky (1944) for three fish from the Barents Sea.

In this paper the breeding biology of the Clyde population of Long Rough Dabs will be described. Since many aspects of breeding phenomena are closely associated with the condition of the fish, this is also considered (see also Fulton, 1904). Lastly, the fecundity of the species will be considered in relation to the age, length and weight of the fish. Some of these subjects are treated statistically, and details of the analyses, together with discussions of their validity, are given separately in Appendices 1–4. The biological significance of the analyses are given along with the other results of the investigation in the first part of the paper. The growth rate of some of the fish has been considered in previous papers (T. B. Bagenal, 1955*a*, *b*).

My special thanks are due to Mrs Jean Morrison who counted the eggs for the fecundity estimates, Miss Sheila Morris, who did most of the calculations, my wife for advice on statistical treatments, and the officers and crews of the Marine Station's research vessels for the collection of the material.

METHODS AND MATERIALS

The material on which this paper is based was caught in approximately monthly samples taken from October 1953 to May 1955. The dates of capture are given in Table 1. The fish ranged from 5 to 33 cm in length and 0 to 7+ years of age. The samples were obtained with a small-mesh cotton V.D. trawl of the following dimensions: headline, 49 ft.; footrope, 78 ft.; bridles, 15 fathoms; lower wings and belly mesh size, $2\frac{1}{2}$ in. bar, all other meshes, 1 in. bar. It is thought that this trawl took an adequate sample of the population, though the mesh-size selection gave noticeably biased samples of the younger age-groups (see T. B. Bagenal, 1955*a*, *b*). Supplementary hauls (Table 2) were taken with other trawls of various dimensions.

The fish were mostly caught off Mountstuart House on the east side of the Isle of Bute at a depth of about 40 m. Before the final adoption of this sampling area, hauls were taken at various places round the Isle of Cumbrae, though prior to and during the spawning time samples were also obtained from the deeper water between Bute and Cumbrae. During the 1955 spawning season hauls were also taken at other places in the Clyde Sea area (see Table 2 and p. 348). As will be shown later, there is a segregation of mature and immature fish, and the more scattered sampling areas at spawning time were chosen to avoid any bias that this might produce.

The fish were examined fresh in the laboratory. For the purposes of this study the following information was obtained for each individual fish: overall length, sex, stage of maturity, weight of the gonads, and gutted weight; the otoliths were kept for age determination. The overall length was measured from the tip of the lower jaw to the end of the longest caudal fin ray to the nearest 0·5 cm. Later, however, the measurements were grouped into centimetre groups which ranged from $x-0{\cdot}25$ to $x+0{\cdot}75$ cm; these were, however, all classed as x cm rather than $x{\cdot}25$ cm for simplicity in computation. Each fish was assigned to a 'gonad stage' according to an arbitrary classification:

Stage 1. Fish with small translucent, clear or slightly pinkish gonads. It was thought that these fish would not spawn during the next season.

Stage 2. Fish with larger, opaque ovaries in which the eggs were usually visible and opaque. These were thought to be ripening fish that would spawn during the next season.

Stage 3. Fish with at least some translucent eggs in the ovary which had a 'plum-pudding' appearance. These fish were thought to be very close to the time of spawning and included those that were actually ripe and running.

Stage 4. Spent fish with large, blood-shot, empty and flaccid ovaries.

Later, two further stages were introduced, stage 4_1 to include immature fish that had apparently spawned during the previous season, and stage 4_2 for maturing fish which appeared to be recovering from the spent condition. This classification was as far as possible based on what the future breeding condition was supposed to be. It has the advantages of simplicity and of not requiring later regrouping of stages to provide sufficient numbers for analysis.

The classification of the maturity of the males was difficult and no clear stages in gonad development could be found. In any case the numbers caught were so small that analysis of different stages was not practicable.

The gonad weight, and the gutted weight without gonads (in this paper called simply 'weight') were taken to the nearest 0·5 g.

The treatment of the otoliths in age determination has already been described (T. B. Bagenal, 1955*a*).

During the spawning period 20 min hauls were taken with a coarse plankton net at the surface to collect Long Rough Dab eggs. These hauls, taken regularly twice a week in Fairlie Channel, were supplemented by others from elsewhere. Later, hauls were taken for larval and post-larval stages and the young bottom-living fish were caught with a small beam trawl with $\frac{1}{4}$ in. bar cotton netting.

THE LENGTH–WEIGHT RELATION AND CONDITION

Before analysing the data on the breeding and fecundity of the Long Rough Dab it was necessary to consider the condition of the fish; many breeding phenomena might be associated with the well-being of the particular individuals. While there are a number of ways by which the condition of a Long Rough Dab might be measured, the obvious choice with the data available was the weight of the fish for a given length. It seems a reasonable assumption that the heavier fish of a given length are in better general health. In the process of arriving at the relative condition of the Long Rough Dabs, the length–weight relation was analysed, and since this relation is of interest in itself, it will be considered here.

THE LENGTH–WEIGHT RELATION

The details of the analyses of the relation of length to weight for the fish are given in Appendix 1. It is shown that for most groups of fish the weight increases at a rate slightly greater than the cube of the length (Fig. 1). This power was not found to differ between different age-groups or between the males, and immature, maturing and spent females. However, significant differences were found between the powers for immature females caught on different dates. The value of the power ($=b$, the coefficient of the regression of the logarithms of weight on length) is shown in Fig. 2 and appears to vary in an annual cycle. The significance of this would seem to be that if all the fish are gaining in weight and the power is increasing, the larger fish must be putting on weight faster than the small ones, whereas if the power is decreasing the smaller fish must be gaining faster. This aspect of the length–weight relation will be discussed in connexion with the condition of the Long Rough Dabs.

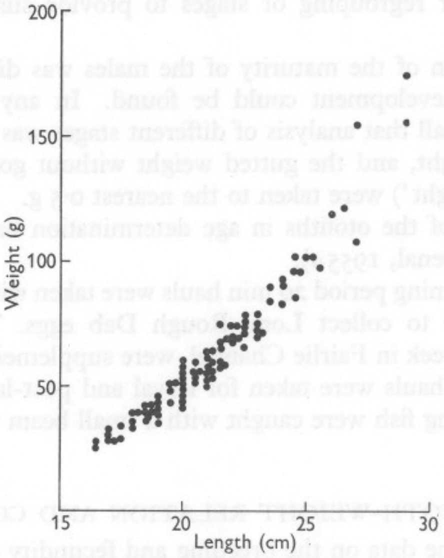

Fig. 1. Scatter diagram of length and weight of maturing (stage 2) female Long Rough Dabs caught on 2 March 1954.

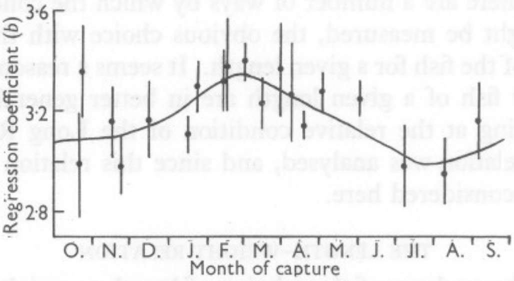

Fig. 2. The regression coefficients (*b*), with their 95 % fiducial limits (vertical lines), for the regressions of log weight on log length of immature female Long Rough Dabs.

THE SEASONAL CYCLE IN CONDITION

The measure of condition has been calculated as the expected weight of a 20 cm Long Rough Dab, derived from analysis of the length–weight relation. The condition of the males, immature, maturing and spent females was found to differ from month to month, and the results are illustrated diagrammatically in Fig. 3. The age-groups within these classes were pooled because on only one of the four dates tested was there a possibly significant difference in their condition.

The data are most complete for the immature female fish. It can be seen that these reach their peak of condition in November–December, and then they lose condition until late April after which there is a recovery. In Fig. 4 are shown the cycles in condition and regression coefficients together. This figure suggests that at first the smaller fish both lose and gain condition faster than larger ones, though later this is reversed and the large fish tend to catch up.

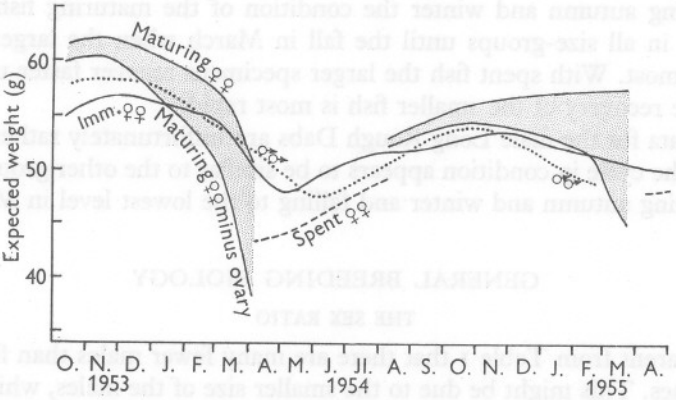

Fig. 3. Diagram of the expected weights of 20 cm male, immature, maturing and spent female Long Rough Dabs from October 1953 to April 1955. The line for spent females continues low in July and August 1954 because those fish that were obviously recovering to spawn again were classified as maturing females.

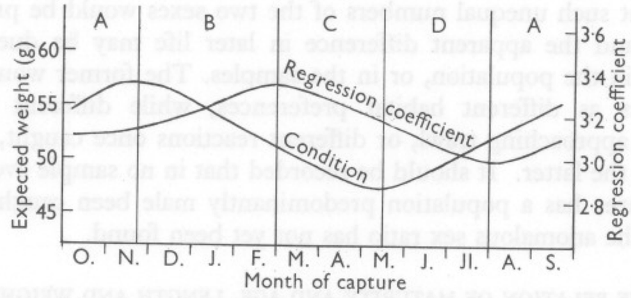

Fig. 4. Diagram of the cycles of regression coefficients (*b*) and condition of immature female Long Rough Dabs, based on Figs. 2 and 3. Period A: August–November; all fish gaining in weight, large fish gaining faster than small fish. Period B: November–February; all fish losing weight, small fish losing faster than large ones. Period C: March–May; all fish still losing, large fish now losing faster. Period D: May–July; all fish gaining in weight again; the small fish gaining faster than the large fish.

The condition of the maturing females is also shown in Fig. 3. It will be realized that any change in condition might be masked by changes in the gonads. The condition has therefore been calculated, both from the total weight including the gonads and from the weights excluding gonads. It can be seen that the total condition (based on weight including gonads) is greater than that of the immature fish, but during March those fish which spawn late lose condition very rapidly and that even earlier the maintenance of the total condition is due to the developing gonads at the expense of the condition of the rest of the fish. The condition of the spent fish is considerably lower than any other group but recovery is rapid, and by August is at approximately the same level as the other groups. The regression coefficients (Table 17) suggest that during autumn and winter the condition of the maturing fish changes similarly in all size-groups until the fall in March when the larger fish are affected most. With spent fish the larger specimens recover faster until May when the recovery of the smaller fish is most rapid.

The data for the male Long Rough Dabs are unfortunately rather meagre, though the cycle in condition appears to be similar to the other groups, being high during autumn and winter and falling to the lowest level in May.

GENERAL BREEDING BIOLOGY

THE SEX RATIO

It is apparent from Table 1 that there are many fewer males than females in the catches. This might be due to the smaller size of the males, which would be able to escape through the net more easily (T. B. Bagenal, 1955*b*), but even for comparable size-groups the males are less numerous than the females, and as the females grow faster, one would expect to find more males in the small size-groups if equal numbers are produced and survive. It seems very unlikely that such unequal numbers of the two sexes would be produced at spawning, and the apparent difference in later life may be due either to differences in the population, or in the samples. The former would include such factors as different habitat preferences, while different behaviour towards an approaching trawl, or different reactions once caught, would be included in the latter. It should be recorded that in no sample ever taken in the Clyde area has a population predominantly male been caught, and the reason for the anomalous sex ratio has not yet been found.

THE RELATION OF MATURITY AND AGE, LENGTH AND WEIGHT

The data are given in Tables 3–7, and are based on the fish caught during the 6 months, October to March, prior to spawning (in 1954 there was no December sample). The two years 1953–54 and 1954–55 are treated separately, though the combined figures are also given, and the data are illustrated in Fig. 5 A–C.

The relation of maturity and age is given in Table 3 and Fig. 5 C. The results for the two years are quite comparable. It will be noticed that there is no definite age at which the fish become mature, for although the percentage mature increases with age, immature specimens of all but the oldest fish have been found. Data concerning the relation of maturity and length are given in Table 4 and Fig. 5 B. The agreement between the two years is again good, and, as with age, there is no length above which all fish are mature. The single immature individual in the 32 cm size-group (6+ years of age) is probably of no significance. The data are re-arranged in Table 5 and Fig. 5 A to illustrate the relation of maturity and weight. The same relationship can be seen, though in this case the agreement between the two years is not apparently so good.

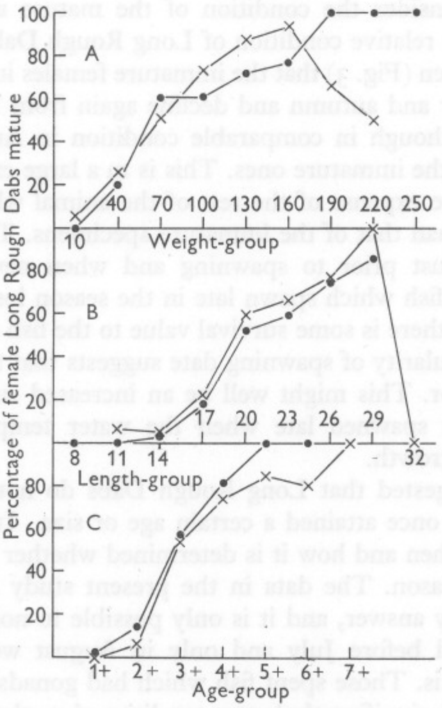

Fig. 5. The relation of percentage maturity to weight (A), length (B) and age (C) of female Long Rough Dabs, based on the 6 months prior to spawning, ●—●, 1953–54; ×—×, 1954–55.

Within a given age-group there is considerable variability in the length and weight of the fish. Tables 6 and 7 give the distribution of mature and immature fish in length- and weight-groups of Long Rough Dabs of the same age. Only in the 3+ and 4+ age-groups were there sufficient fish, well enough divided between mature and immature, to give adequate numbers in each class for comparisons to be possible. The means given in Tables 6 and 7 are based on the original data. An analysis of the percentages of mature fish in subgroups of the same age and length, and of the same age and weight are given in Appendix 2. The results of these tests show that the variability between the percentages for different ages with the same length is significantly greater than that between pairs of groups of fish of the same age and length caught in 1954 and in 1955, though the variability between those for length-groups of the same age is not. This suggests that maturity is more closely linked with the age of the fish than its length. Thompson (1915), working on the Halibut, similarly found 'that the maturity is entirely dependent on age, not on size...'.

A further comparison of the relation of maturity, length and weight is made when we consider the condition of the mature and immature fish. A discussion of the relative condition of Long Rough Dabs has already been given, and it was seen (Fig. 3) that the immature females increase in condition during the summer and autumn and decline again from November to May. The mature fish, though in comparable condition in August, put on total weight faster than the immature ones. This is to a large extent an increase in gonad weight at the expense of the rest of the animal which is relatively in poorer condition than that of the immature specimens. The fish are in their lowest condition just prior to spawning and when newly spent. It also appears that those fish which spawn late in the season lose the most weight. This suggests that there is some survival value to the fish to spawn early, but the maintained regularity of spawning date suggests that there must be some compensating factor. This might well be an increased survival value to the offspring by being spawned late when the water temperatures are more suitable for rapid growth.

It has been suggested that Long Rough Dabs do not necessarily spawn every year, having once attained a certain age or size. It would be of great interest to know when and how it is determined whether the fish will spawn during the next season. The data in the present study are not sufficiently detailed to give any answer, and it is only possible to note that stage 2 fish were not identified before July and only in August were there sufficient numbers for analysis. Those spent fish which had gonads developing for the next season were in significantly better condition than those classed with the immature fish.

THE SEASONAL CYCLE IN GONAD WEIGHT

It was clear from a preliminary examination of the data that the weight of the gonad increased with the size of the fish, but the effect of the age on gonad weight was not apparent. The statistical analysis of the data is given in Appendix 3, where it is shown that for fish of a given length or weight there is no difference in the gonad weights of the different age-groups. After pooling the ages, the expected gonad weights for mature female Long Rough Dabs of 69·98 g were calculated for the months prior to spawning and these, shown in Fig. 6, illustrate the rate of development of the maturing ovaries.

THE SPAWNING TIME

In Table 1 can be found the dates of capture and the numbers of Long Rough Dabs of each maturity stage that were caught. The percentages of immature, ripe and spent of the total mature fish are given in Fig. 7, which also includes a graph of the numbers of Long Rough Dab eggs in 20 min tow-net hauls off Keppel Pier. From this figure it can be seen that the spawning times in 1954 and 1955 were very similar, and lasted from the beginning of March until the end of the second week in April, and half the fish had spawned by 20–22 March. It is at this time too that the fish are in the poorest condition, though the lowest level reached by the males is later than that of the mature females.

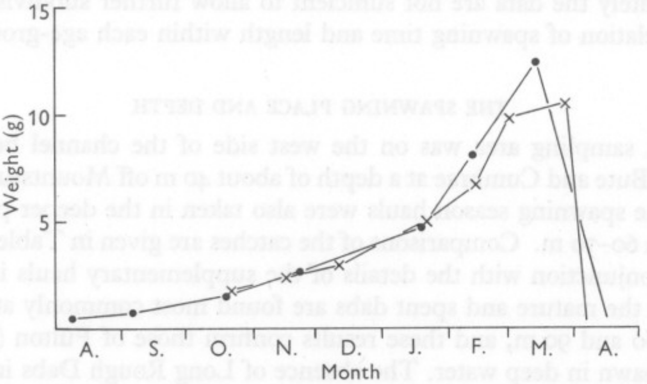

Fig. 6. The expected gonad weight of a female Long Rough Dab 69·98 g in weight, from October 1953 to March 1954 (×—×), and from August 1954 to March 1955 (●—●).

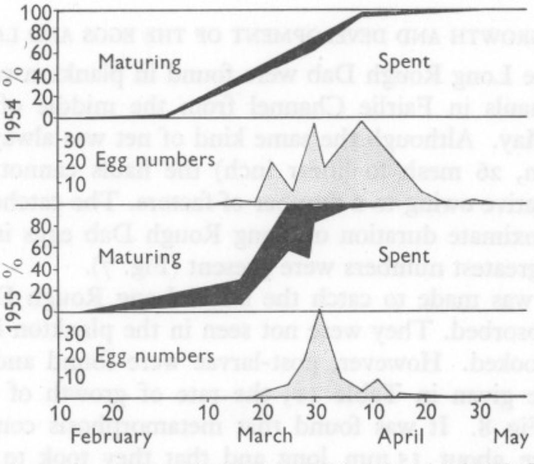

Fig. 7. The percentage of maturing, ripe (solid black) and spent female Long Rough Dabs through the 1954 and 1955 breeding seasons. The numbers of Long Rough Dab eggs in 20 min plankton hauls are also illustrated (stippled frequency diagram).

The egg collections support these conclusions very well. It appears from the small percentage of stage 3 fish caught on each occasion (never more than 50%) that this stage is of short duration for each individual fish, as was found by Fulton (1890). In this respect it is of interest that only one fish (caught on 29 March 1955) was actually fully ripe with running eggs. A comparison with previous studies in other regions, based on egg surveys or the maturity stage of the adult, is given in Table 8.

The relation of spawning time and age is shown by the data in Table 9, which suggests that the older fish spawn first. It has also been found that the larger fish spawn first; the mean length of the spent fish on 30 March 1954 was 22·7 cm compared with 19·5 cm for those that had not yet spawned. Unfortunately the data are not sufficient to allow further subdivision and to test the relation of spawning time and length within each age-group.

THE SPAWNING PLACE AND DEPTH

The main sampling area was on the west side of the channel between the islands of Bute and Cumbrae at a depth of about 40 m off Mountstuart House. During the spawning season hauls were also taken in the deeper parts of the channel in 60–70 m. Comparisons of the catches are given in Table 10. These data, in conjunction with the details of the supplementary hauls in Table 2, show that the mature and spent dabs are found most commonly at depths of between 60 and 90 m, and these results confirm those of Fulton (1890) that the fish spawn in deep water. The absence of Long Rough Dabs in the catch on 6 April 1955 in 150 m confirms the general impression, gained over a number of years, that these fish are very rare in the deepest water of the Clyde area.

THE GROWTH AND DEVELOPMENT OF THE EGGS AND LARVAE

The eggs of the Long Rough Dab were found in plankton catches obtained from 20 min hauls in Fairlie Channel from the middle of March to the beginning of May. Although the same kind of net was always used (mouth diameter 45 cm, 26 mesh to linear inch) the hauls cannot be considered strictly quantitative owing to a number of factors. The catches, however, do show the approximate duration of Long Rough Dab eggs in the plankton, and when the greatest numbers were present (Fig. 7).

No attempt was made to catch the larval Long Rough Dabs before the yolk-sac was absorbed. They were not seen in the plankton hauls, but were probably overlooked. However, post-larvae were found and the details of the catches are given in Table 11; the rate of growth of these larvae is illustrated in Fig. 8. It was found that metamorphosis commenced when the larvae were about 15 mm long and that they took to the bottom as fully metamorphosed fish at about 25 mm in length. There was considerable individual variation about these average sizes.

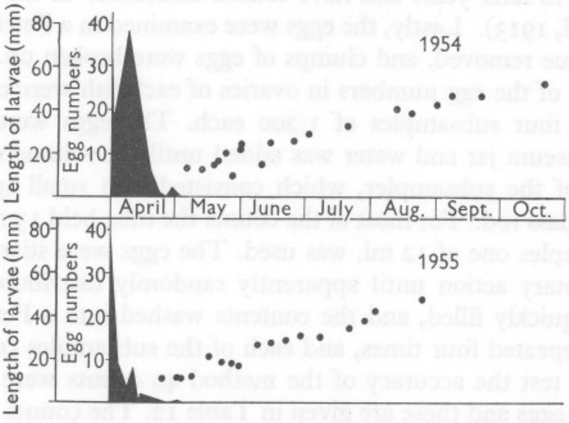

Fig. 8. The lengths of post-larval Long Rough Dabs during the summers of 1954 and 1955. The decline in egg numbers in the plankton hauls is shown in solid black for each year.

FECUNDITY

During the study of the breeding biology, fecundity estimations were made for 119 of the stage 2 Long Rough Dabs. The fish were mainly from two samples, the first consisting of the 25 fish obtained on 15 February 1954, and the second of the 91 fish on 2 March 1954 (see Table 1). On these dates all the maturing female Long Rough Dabs that were caught were examined; and they may be considered as random samples from the population; the stage 3 fish on 2 March 1954 was not included since some of its eggs may have already been shed. The remaining three fish were obtained on 15 and 30 March, and were selected because they represented the smallest size-groups of mature females and were supposed to supplement the two random samples. After the usual treatment of the fish (see p. 340), the gonads were preserved. The full details for each individual were kept separate, and these are given in Table 30.

The method of preservation and subsequent treatment of the ovaries followed that used by Simpson (1951) for plaice. The ovaries were preserved and stored in Gilson's fluid modified by doubling the amount of acetic acid. This not only preserved the eggs but also helped to liberate them by breaking down the ovarian tissue. The process was aided by repeated, though spasmodic, shaking of the bottles in which the ovaries were preserved. Before the eggs were to be counted the ovaries were teased apart and the ovarian tissue removed and any adhering eggs were returned to the bottle. Next the eggs were washed by successive shaking in Gilson's fluid and decanting the supernatant liquid, though if the eggs were to be counted immediately water was used and this was not found to affect the eggs. The decanting removed not only remaining pieces of ovarian tissue, but also those minute eggs which would be laid in later years and have caused difficulties in the past (Fulton, 1891; Mitchell, 1913). Lastly, the eggs were examined in a Petri dish and any remaining tissue removed, and clumps of eggs were broken up.

Estimations of the egg numbers in ovaries of each fish were obtained from the means of four subsamples of 1/200 each. The eggs were placed in a cylindrical museum jar and water was added until the volume was 200 times the capacity of the subsampler, which consisted of a small specimen tube attached to a glass rod. For most of the counts the tube held 13 ml., but in the earlier subsamples one of 12 ml. was used. The eggs were stirred vigorously with a non-rotary action until apparently randomly distributed. The subsampler was quickly filled, and the contents washed into a Petri dish. This process was repeated four times, and each of the subsamples counted.

In order to test the accuracy of the method 40 counts were made on the same batch of eggs and these are given in Table 12. The counts were made in series of four and the subsamples were returned to the jar after each series. The standard deviation of forty observations was 97·308 corresponding to a coefficient of variation of 10·05%. For the means of four the standard deviation is 48·654 ($97·308/\sqrt{4}$) corresponding to a coefficient of variation of 5·03%.

This may be compared with the method given by Simpson who used a 1 ml. stempel pipette from a 150 ml. whirling flask and got a standard deviation for forty observations of 35·393 or $C=9·57\%$ and for means of 4 of 4·78%. The coefficient of variation based on his actual means was 3·64%, and in the present work 7·05%. This indicates that Simpson's actual means were less variable than might be expected by chance from the separate counts, while those given in Table 12 are more variable.

The analyses of the relations of fecundity to age, length, weight and gonad weight are given in Appendix 4.

RESULTS

The data given in Appendix 4 show that the fecundity of the female Long Rough Dabs varies from 25,000 eggs for a fish of *ca.* 15 cm and 20 g to 250,000 for one of *ca.* 30 cm and 200 g. The statistical analysis of the data shows that there is very great variability in the fecundity, and that while the general level can be related to the age, length, weight and gonad weight of the fish, there is still a large amount of variability after these factors have been taken into account. The analyses show that for estimating the fecundity, weight and gonad weight used together are the most accurate. However, since length is so much easier and quicker to measure, if time is limited and the fish are not, it might be more suitable to predict fecundity from a larger sample using only the length data. The variability is shown diagrammatically as scatter diagrams of fecundity and length, weight and gonad weight in Figs. 9–11. The fecundity has been found to increase at a rate slightly above

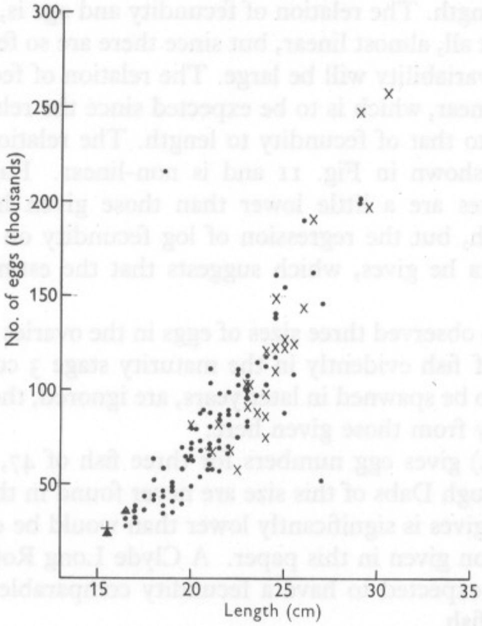

Fig. 9. Scatter diagram showing the relation of fecundity and length of female Long Rough Dabs. ×, 15 February 1954; ●, 2 March 1954; +, 15 March 1954; ▲, 30 March 1954.

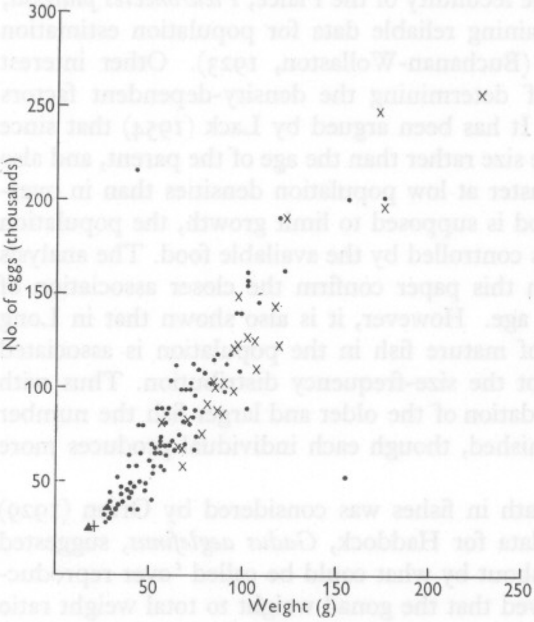

Fig. 10

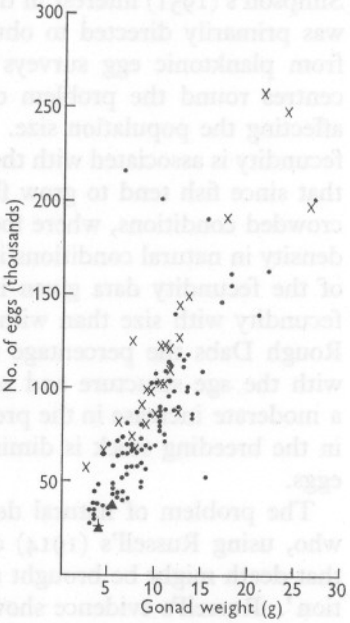

Fig. 11

Fig. 10. Scatter diagram showing the relation of fecundity and weight of female Long Rough Dabs. Symbols as in Fig. 9.

Fig. 11. Scatter diagram showing the relation of fecundity and gonad weight of female Long Rough Dabs. Symbols as in Fig. 9.

the cube of the length. The relation of fecundity and age is, in so far as there is a relationship at all, almost linear, but since there are so few age classes it is obvious that the variability will be large. The relation of fecundity to weight is also probably linear, which is to be expected since the relation of weight to length is similar to that of fecundity to length. The relation of fecundity to gonad weight is shown in Fig. 11 and is non-linear. Fulton's (1891) five fecundity estimates are a little lower than those given here for fish of a comparable length, but the regression of log fecundity on log length is not linear for the data he gives, which suggests that the estimates may not be reliable.

Mitchell (1913) observed three sizes of eggs in the ovaries she examined. If those estimates of fish evidently in the maturity stage 3 condition, and also the minute eggs to be spawned in later years, are ignored, the estimates do not differ significantly from those given here.

Milinsky (1944) gives egg numbers for three fish of 47, 48 and 49 cm in length. Long Rough Dabs of this size are never found in the Clyde area, but the fecundity he gives is significantly lower than would be expected from the regression equation given in this paper. A Clyde Long Rough Dab of about 32 cm would be expected to have a fecundity comparable to that given by Milinsky for his fish.

DISCUSSION

Simpson's (1951) interest in the fecundity of the Plaice, *Pleuronectes platessa*, was primarily directed to obtaining reliable data for population estimation from planktonic egg surveys (Buchanan-Wollaston, 1923). Other interest centres round the problem of determining the density-dependent factors affecting the population size. It has been argued by Lack (1954) that since fecundity is associated with the size rather than the age of the parent, and also that since fish tend to grow faster at low population densities than in overcrowded conditions, where food is supposed to limit growth, the population density in natural conditions is controlled by the available food. The analysis of the fecundity data given in this paper confirm the closer association of fecundity with size than with age. However, it is also shown that in Long Rough Dabs the percentage of mature fish in the population is associated with the age structure and not the size-frequency distribution. Thus with a moderate increase in the predation of the older and larger fish the number in the breeding stock is diminished, though each individual produces more eggs.

The problem of natural death in fishes was considered by Orton (1929) who, using Russell's (1914) data for Haddock, *Gadus aeglefinus*, suggested that death might be brought about by what could be called 'over reproduction'. Russell's evidence showed that the gonad weight to total weight ratio increases with the size of the fish, and Orton suggested that this tendency would produce a size limit above which the fish could not survive. In the breeding data on the Long Rough Dab analysed in this paper it has been shown that relation of gonad weight to weight is linear and no trend was found in the relation with increasing age (p. 373). However, another aspect of the same problem is seen when we consider the fecundity. Milinsky's very large dabs did not produce the egg numbers expected from their size. Furthermore, from a consideration of the regression of log fecundity on log gonad weight (Fig. 11), it appears that the number of eggs in the gonad does not increase in proportion to the weight. This result was unexpected since the larger gonads will have a proportionally smaller surface area and so, not only should carry less surface moisture when they are weighed, but also less ovarian tissue should be found surrounding the eggs in the larger gonads. We can only suppose that the heavier gonads produce fewer eggs per gram than do the lighter ones, so the eggs are presumably larger and heavier. In future work an analysis of the eggs is needed to show how the fecundity is related to the food reserves in the eggs themselves, and so perhaps to their viability. To a large extent in fish, significance of the fecundity is obscured by the enormous numbers of eggs laid and its dependence on the size of the parent, but the significance of clutch-size in birds and litter-size in mammals have been discussed by Lack (1947, 1948*a*, *b*). It would appear that, as in these other groups, if other factors are equal the eggs from the more fecund parents would have greater chances of survival than those from the less fecund. Unless there were some compensating factor, a mutation tending to produce greater fecundity would pass through the whole population. It has, in the past (Simpson, 1951), been suggested that the factors governing the fecundity of individual fish might be: (*a*) the condition of the fish when the germinal epithelium is laid down during the first year of life; and (*b*) the condition of the fish either when the eggs to be laid each year are separated from the mass of developing ova, or when the new primary oocytes are being formed each year. The condition of the fish at these critical times is expected to be closely associated with the food supply and the temperature of the environment. These environmental factors may indeed be expected to influence the fecundity of individual fish within limits set by their hereditary characteristics. A mutation, tending to increase the general level of fecundity, would still be expected to spread through the entire population were it not for some compensating factors, which reduce the chances of survival of the entire progeny of a particularly fecund individual. Such compensating factors may act on the parent or the eggs. After spawning the female fish are in the poorest condition reached during the whole year. If fecundity and post-spawning condition were inversely correlated and the condition of the fish critical to their survival, the more fecund fish might not live to spawn again or only to spawn two seasons hence. With the data available there is no evidence of the more fecund fish being in poorer condition (Appendix 4, p. 375).

It is clear from the earlier section that some fish do not spawn every year having once reached sexual maturity. It is, however, difficult to say if this is associated with greater fecundity in the previous season.

Factors associated with the survival of the progeny would include the possibility of the eggs being smaller, and containing less food reserves.

While it is not possible at this present stage to suggest which of these factors is the most likely to control the fecundity of a given species of fish, these are the lines on which future work might profitably be directed.

SUMMARY

Details are given of the breeding biology, including the fecundity, of the Long Rough Dab deduced from samples taken in the Clyde Sea area from October 1953 to April 1955. Where possible breeding is related to the condition of the fish; the index of condition is based on the length–weight relation.

The weight of Long Rough Dabs of each sex and stage in maturity increases as a power, slightly greater than the cube, of the length. An annual cycle of fluctuations of this power is seen in the immature females, and indicates how changes in condition at different seasons affect the different size-groups. The measure of condition is taken as the expected weight of a 20 cm Long Rough Dab, and the changes in this weight are followed through the sampling period for males and for immature, maturing and spent females. All groups tend to be in best condition during November and December followed by a decline to the spawning time, in March and April, after which there is a slow recovery.

The scarcity of males in the samples cannot be satisfactorily explained. There is no definite age, length or weight above which all the female fish become mature, but the percentage of mature fish is more closely linked to the age structure than to the size-distribution. The condition of the mature and immature fish is compared; mature females are initially in better condition, and as the breeding season approaches this is maintained by the gonads developing at the expense of the flesh. The relations of the gonad weight to length and to weight appear to be similar in all age-groups, and the pre-spawning increase in gonad weight is discussed.

The spawning season was determined from the disappearance of mature fish from the samples and their replacement by spent females, and by the appearance of eggs in the plankton; it extends from the beginning of March to the middle of April. The older and larger fish have been found to spawn first; spawning takes place predominantly at depths of 60–90 m. The eggs remain in the plankton in quantity for 3–4 weeks. The larvae metamorphose at about 15 mm, take to the bottom at approximately 25 mm and for the first 6 months grow at about 10 mm per month.

The fecundity was estimated from four subsamples of 1/200 of the eggs from each of 119 fish, mostly caught on two dates. The egg numbers varied from 25,000 for a fish of 15 cm to over 250,000 for a 30 cm fish. The data were subjected to multiple regression analyses and it is seen that the fecundity is most accurately estimated from the weight and gonad weight together, and the addition of length to these measurements does not increase the efficiency significantly. The fecundity was found to be related to weight linearly, to the length at a power greater than the cube and to the gonad weight at a power less than unity. The significance of these relations and a discussion of the wider implications of the paper is given.

REFERENCES

BAGENAL, M., 1955. A note on the relations of certain parameters following a logarithmic transformation. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 289–96.

BAGENAL, T. B., 1955*a*. The growth rate of the Long Rough Dab *Hippoglossoides platessoides* (Fabr.). *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 297–311.

—— 1955*b*). The growth rate of the Long Rough Dab *Hippoglossoides platessoides* (Fabr.)—a correction. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 643–7.

BAL, D. V. 1943. A study of fish eggs and larvae from Manx waters. I. Observations on the fish eggs. *J. Univ. Bombay*, N.S. 11 B (5), pp. 54–90.

BIGELOW, H. B. & SCHROEDER, W. C., 1953. Fishes of the Gulf of Maine. *Fish. Bull., U.S.*, Vol. 53, No. 74, 577 pp.

BUCHANAN-WOLLASTON, H. J., 1923. The spawning of plaice in the southern part of the North Sea in 1913–14. *Fish. Invest., Lond.*, Ser. 2, Vol. 5, No. 2, 36 pp.

COCHRAN, W. G., 1947. Some consequences when the assumptions for the analysis of variance are not satisfied. *Biometrics*, Vol. 3, pp. 22–38.

ESSIPOW, W. J. & SLASTNIKOW, G., 1932. Zur Biologie des Kambalajorsch (*Drepanopsetta platessoides* O. Fabr.) im Barentsmeer. *Wiss. Fischereiuntersuchungen am Murman (Barents Sea)*, pp. 191–8. (In Russian: German summary.)

EWART, J. C. & FULTON, T. W., 1889. Report on the spawning of the British marine food-fishes. *Rep. Fish. Bd Scot.*, Vol. 7, pp. 186–221.

FULTON, T. W., 1890. The spawning and spawning place of marine food-fishes. *Rep. Fish. Bd Scot.*, 8 (1889), Part III, pp. 257–69.

—— 1891. On the comparative fecundity of sea fish. *Rep. Fish. Bd Scot.*, 9 (1890), Part III, pp. 243–68.

—— 1904. The rate of growth of fishes. *Rep. Fish. Bd Scot.*, 22 (1903), Part III, pp. 141–241.

GÜNTHER, A., 1888. Report on the fishes obtained by Mr J. Murray in deep water on the north-west coast of Scotland between April 1887 and March 1888. *Proc. roy. Soc. Edinb.*, Vol. 25, pp. 205–20.

HUNTSMAN, A. G., 1918. Histories of new food fishes. 1. The Canadian plaice. *Bull. biol. Bd Can.*, No. 1, 32 pp.

KRÜGER, K. VON, 1942. Erneutes Auftreten der Scharbzunge, *Drepanopsetta platessoides* Fabr. in der westlichen Ostsee. *Kieler Meeresforsch.*, Bd. 4, pp. 18–37.

LACK, D., 1947. The significance of clutch size. *Ibis*, Vol. 89, pp. 302–52.

—— 1948*a*. The significance of clutch size. *Ibis*, Vol. 90, pp. 25–45.

—— 1948*b*. The significance of litter size. *J. Anim. Ecol.*, Vol. 17, pp. 45–50.

—— 1954. *The Natural Regulation of Animal Numbers*. 343 pp. Oxford.

LECREN, E. D., 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the Perch (*Perca fluviatilis*). *J. Anim. Ecol.*, Vol. 20, pp. 201–19.

MATHER, K., 1946. *Statistical Analysis in Biology*. Second edition. London: Methuen.

MILINSKY, G. I., 1944. On the biology and fisheries of the long rough dab of the Barents Sea. *Trans. Knipovich polyar. sci. Inst.*, Vol. 8, pp. 388–415. (In Russian: English summary.)

MITCHELL, A. M., 1913. On the egg production of certain fishes. *Rep. N. Sea Fish. Invest. Comm.*, 5th Report (Northern Area), pp. 191–204.

NORMAN, J. R., 1934. *A Systematic Monograph of the Flatfishes (Heterostomata)*. Vol. 1. London.

ORTON, J. H., 1929. Reproduction and death in invertebrates and fish. *Nature, Lond.*, Vol. 123, pp. 14–15.

OTTERSTRØM, A., 1906. Eggs and young of fishes in the Danish waters. *Rep. Danish biol. Sta.*, Vol. 13, 85 pp.

PEARSON, E. S. & HARTLEY, H. O., 1954. *Biometrika Tables for Statisticians*, Vol. 1. Cambridge University Press.

PERTSEVA, T. A., 1939. Spawning, eggs and fry of fish in the Motovski Bay. *Trans. Inst. mar. Fish. USSR.*, Vol. 4, pp. 417–70. (In Russian: English summary and table headings.)

RASS, T. S., 1936. Spawning, eggs and fry of the food-fishes of the Barents Sea. Breeding and development of fish in the subarctic. *Int. Rev. Hydrobiol.*, Vol. 33, pp. 250–70.

RUSSELL, E. S., 1914. Report on the market measurements in relation to the English haddock fishery during the years 1909–1911. *Fish. Invest., Lond.*, Ser. 2, Vol. 1, No. 1, 134 pp.

SAEMUNDSSON, B., 1908. Oversigt over Islands Fiske med oplysninger om deres forekomst vigtigste biologiske forhold og okonomiske betydning. *Skr. Komm. Havunders, Kbh.*, No. 5, 140 pp.

—— 1925. Fiskirannsoknir 1923–1924. *Andvari, Reykjavik*, pp. 33–71.

—— 1927. Synopsis of the fishes of Iceland. *Rit Visind. Isl.*, Vol. 2, 66 pp.

—— 1949. Marine Pisces. *Zoology of Iceland*, Vol. 4, Pt. 72, 150 pp.

SIMPSON, A. C., 1951. The fecundity of the plaice. *Fish. Invest., Lond.*, Ser. 2, Vol. 17, No. 5, 27 pp.

SNEDECOR, G. W., 1946. *Statistical Methods*. Fourth edition. Iowa State College Press.

THOMPSON, W. F., 1915. A preliminary report on the life-history of the halibut. *Rep. Comm. Fish. B.C.*, 1914, pp. 76–120.

WILLIAMSON, H. C., 1899. On the pelagic fish-eggs and larvae of Loch Fyne. *Rep. Fish. Bd Scot.*, 17 (1898), Part III, pp. 79–131.

TABLE 1. DETAILS OF CATCHES

Date		Females				Total	Grand
1953	Males	Stage 1	Stage 2	Stage 3	Stage 4	females	total
23. x.	7	30	35	—	—	65	72
19. xi.	10	26	30	—	—	56	66
15. xii.	5	27	21	—	—	48	53
1954							
21. i. 26. i.	5	46	40	—	—	86	91
15. ii.	—	24	25	—	—	49	49
2. iii.	10	176	91	1	—	268	278
30. iii.	—	68	9	4	21	102	102
8. iv.	—	67	3	3	74	147	147
3. v.	5	74	—	—	43	117	122
2. vi.	30	111	—	1	64	176	206
8. vii.	16	57	5	—	17	79	95
9. viii.	37	46	61	—	9	116	153
7. ix.	12	31	36	—	1	68	80
21. x.	12	31	22	—	—	53	65
25. xi.	8	76	86	—	1	163	171
1955							
20. i.	3	69	41	—	—	110	113
14. ii.	5	35	36	—	—	71	76
16. iii.	2	51	12	4	1	68	70
18. iv.	2	73	—	—	36	109	111

TABLE 2. DETAILS OF CATCHES IN SUPPLEMENTARY HAULS

Date		Depth		Females				Total	Grand
1955	Position	(m)	Males	Stage 1	Stage 2	Stage 3	Stage 4	females	total
14. ii.	Bute Channel	60–70	1	18	15	—	—	33	34
	Mountstuart	40–50	—	27	12	—	—	39	39
25. iii.	Skelmorlie	35–45	—	7	—	1	1	9	9
	Bute Channel	50–70	—	4	—	4	6	14	14
29. iii.	Bute Channel	60–70	—	—	—	2	1	3	3
	Bute Channel	60–70	—	1	—	—	—	1	1
	Mountstuart	40–50	—	27	—	7	6	40	40
	Mountstuart	40–50	2	35	—	4	6	45	47
30. iii.	Off Lady Isle	40–50	1	61	—	7	33	101	102
	Off Ardrossan	50–70	—	29	1	2	16	48	48
6. iv.	Off Sannox Arran 1 m	150	—	—	—	—	—	—	—
	Sannox Arran 2 m	*ca.* 90	—	54	—	1	13	68	68
	Sannox Arran 2 m	*ca.* 90	—	17	—	—	14	31	31
	S.W. Garroch Head	*ca.* 60	—	27	—	—	11	38	38

TABLE 3. THE RELATION OF MATURITY AND AGE

Age-	1953–54			1954–55			Both years
group	Immature	Mature	% mature	Immature	Mature	% mature	% mature
1+	30	1	3·2	3	—	0	2·9
2+	202	35	14·8	147	10	6·4	11·4
3+	81	109	57·4	83	97	53·9	55·7
4+	16	70	81·4	24	69	74·2	77·7
5+	—	27	100	4	22	84·6	92·5
6+	—	1	100	1	4	80·0	83·3
7+	—	—	—	—	1	100	100
Total	329	243	42·48	262	203	43·66	43·01

TABLE 4. THE RELATION OF MATURITY AND LENGTH

Length-group	1953–54 Immature	1953–54 Mature	1953–54 % mature	1954–55 Immature	1954–55 Mature	1954–55 % mature	Both years % mature
8	5	—	0	—	—	—	0
11	16	—	0	13	1	7·1	3·3
14	40	1	2·4	95	5	5·0	4·3
17	119	25	17·4	59	17	22·4	19·1
20	80	88	52·4	49	73	59·8	55·5
23	55	82	59·9	34	68	66·7	62·8
26	12	35	74·5	11	38	77·6	76·0
29	2	12	85·7	—	1	100	86·7
32	—	—	—	1	—	0	0
Total	329	243	—	262	203	—	—

TABLE 5. THE RELATION OF MATURITY AND WEIGHT

Weight-group	1953–54 Immature	1953–54 Mature	1953–54 % mature	1954–55 Immature	1954–55 Mature	1954–55 % mature	Both years % mature
10	61	—	0	101	6	5·6	3·6
40	157	41	20·7	83	29	25·9	22·6
70	58	91	61·1	46	48	51·1	57·2
100	40	63	61·2	24	67	73·6	67·0
130	10	26	72·2	5	35	87·5	80·3
160	3	10	76·9	1	15	93·8	86·2
190	—	8	100	1	2	66·6	90·9
220	—	3	100	1	1	50·0	80·0
250	—	1	100	—	—	—	100
Total	329	243		262	203		

TABLE 6. THE RELATION OF MATURITY AND LENGTH WITHIN AGES 3+ AND 4+

	1953–54				1954–55			
Age …	3+		4+		3+		4+	
Length-group	Immature	Mature	Immature	Mature	Immature	Mature	Immature	Mature
14	—	—	—	—	2	—	—	—
17	2	6	—	3	19	13	—	—
20	26	52	2	16	40	60	4	11
23	50	47	3	31	21	23	13	32
26	3	3	9	19	1	1	7	26
29	—	1	2	1	—	—	—	—
Total	81	109	16	70	83	97	24	69
Mean	22·16	21·45	24·69	22·97	19·90	20·35	23·25	23·58

TABLE 7. THE RELATION OF MATURITY AND WEIGHT WITHIN AGES 3+ AND 4+

	1953–54				1954–55			
Age …	3+		4+		3+		4+	
Weight-group	Immature	Mature	Immature	Mature	Immature	Mature	Immature	Mature
10	—	—	—	—	1	—	—	—
40	7	15	1	5	33	22	—	3
70	35	54	2	20	33	39	11	9
100	36	34	3	25	15	30	7	23
130	3	5	7	16	1	5	4	24
160	—	—	3	2	—	1	1	9
190	—	1	—	1	—	—	1	1
220	—	—	—	1	—	—	—	—
Total	81	109	16	70	83	97	24	69
Mean	82·96	80·46	115·63	99·71	56·87	66·29	89·58	98·99

TABLE 8. THE SPAWNING TIME OF THE LONG ROUGH DAB

Authority	Region	Range of spawning time	Maximum spawning
Bagenal (this paper)	Clyde	Feb.–Apr.	Mar.
Williamson (1899)	Loch Fyne	Mar.–June	Apr.
Günther (1888)	W. Scotland	Feb.–Mar.	Early Mar.
Bal (1943)	Irish Sea	Mar.–Aug.	Apr.
Ewart & Fulton (1889)	Firth of Forth	Dec.–May	Mar.
Ewart & Fulton (1889)	Moray Firth	Jan.–Feb.	—
Fulton (1890)	Moray Firth	—	Mainly Mar.
Otterstrøm (1906)	Kattegat & Baltic	—	Mar. only
Pertseva (1939)	Barents Sea	Mar.–June	End of Apr.
Rass (1936)	Barents Sea	Mar.–June	May
Saemundsson (1949)	Iceland	May–June	—
Huntsman (1918)	Bay of Fundy	Apr.–May	—
Huntsman (1918)	Gulf of St Lawrence	May–June	—
Huntsman (1918)	Newfoundland	July	—

TABLE 9. THE AGE AND MATURITY-STAGE DISTRIBUTION AT SPAWNING

		Maturity stage			
Date	Age	2	3	4	Total
30. iii. 54	3	5	1	1	7
	4	2	3	5	10
	5	1	1	12	14
	6	—	—	3	3
	Total	9	4	21	34
16. iii. 55	3	1	—	—	1
	4	8	3	—	11
	5	3	1	1	5
	Total	12	4	1	17
25. iii. 55	3	—	3	—	3
	4	—	2	5	7
	5	—	—	1	1
	6	—	—	1	1
	Total	—	5	7	12

TABLE 10. COMPARISON OF NUMBERS OF IMMATURE AND MATURE LONG ROUGH DABS IN DEEP AND SHALLOW WATER

		Depth			
		40–50 m		60–70 m	
Date		Haul III	Haul IV	Haul I	Haul II
14. ii. 55	Stage 1	31	27	15	8
	Stage 2	14	12	19	22
2. iii. 54	Stage 1	84		92	
	Stage 2	18		74	
	Stage 3			1	
8. iv. 54	Stage 1	55		12	
	Stage 2	—		3	
	Stage 3	1		2	
	Stage 4	11		63	
	Total non-breeding	197		127	
	Total breeding	56		184	
	Total	253		311	

TABLE 11. DETAILS OF CATCHES OF POST-LARVAL LONG ROUGH DABS

1954					1955				
Date	No.	Mean (mm)	S.D.	Gear	Date	No.	Mean (mm)	S.D.	Gear
6. v.	6	13·2	3·2	Plankton net	25. iv.	9	10·8	2·4	Plankton net
13. v.	7	12·7	2·6	Plankton net	2. v.	3	11·3	—	Plankton net
19. v.	86	15·2	3·8	Plankton net	4. v.	64	10·8	2·5	Plankton net
20. v.	16	15·9	4·4	Plankton net	9. v.	254	12·2	2·6	Plankton net
24. v.	1	20	—	Plankton net	17. v.	48	21·2	4·5	Plankton net
27. v.	1	10	—	Plankton net	23. v.	4	18·5	—	Plankton net
31. v.	1	22	—	Plankton net	28. v.	1	18	—	Plankton net
31. v.	69	23·7	1·8	Beam trawl	1. vi.	10	17·2	3·4	Plankton net
10. vi.	28	15·1	4·8	Plankton net	9. vi.	46	26·7	2·4	Beam trawl
14. vi.	26	24·8	2·7	Beam trawl	15. vi.	42	27·8	3·3	Beam trawl
25. vi.	13	26·1	2·8	Beam trawl	22. vi.	44	28·5	2·7	Beam trawl
2. vii.	22	29·0	2·8	Beam trawl	30. vi.	61	30·9	3·4	Beam trawl
20. vii.	56	33·0	3·9	Beam trawl	8. vii.	11	30·5	2·5	Beam trawl
12. viii.	26	40·8	3·5	Beam trawl	22. vii.	31	34·5	4·7	Beam trawl
19. viii.	38	38·6	4·5	Beam trawl	29. vii.	31	37·7	4·7	Beam trawl
31. viii.	33	43·1	4·1	Beam trawl	3. viii.	39	41·8	4·4	Beam trawl
7. ix.	21	47·1	4·9	Beam trawl	25. viii.	49	48·2	5·2	Beam trawl
21. ix.	37	46·8	3·6	Beam trawl					
21. x.	62	53·3	5·2	Beam trawl					

TABLE 12. DETAILS OF REPLICATE COUNTS OF LONG ROUGH DAB EGGS

Series no.	1	2	3	4	5	6	7	8	9	10
Count no. 1	1046	940	1051	917	858	1006	919	1032	1038	902
2	851	1069	1006	995	777	933	1153	1044	1009	1016
3	970	994	881	1037	844	796	931	875	1012	935
4	1114	1183	966	985	808	762	1077	960	978	1048
Mean	995·25	1046·5	976·0	983·5	821·75	874·25	1020·0	977·75	1009·25	975·25

Grand mean of 40 observations = 967·95
S.D. = 97·308
Coefficient of variation = 10·05 %

Mean of 10 means = 967·95
S.D. = 68·264
Coefficient of variation = 7·05 %

TABLE 13

Subgroup	s.s.l.	s.s.w.	s. products l.w.	Regression coefficient b	s.s. due to regression	Residual s.s.	Degrees of freedom
Age 1+	0·003397	0·054392	0·011935	3·513394	0·041932	0·012460	6
2+	0·223974	2·827187	0·764614	3·413852	2·610279	0·216908	124
3+	0·040840	0·535860	0·137443	3·365402	0·462551	0·063309	33
4+	0·008973	0·118283	0·032089	3·576173	0·114756	0·003527	4
					Total	0·296204	167
Total within ages	0·277184	3·535722	0·946081	3·413188	3·229152	0·306570	170
					Difference	0·010366	3
Between ages	0·964671	11·123082	3·274817	3·394750	11·117185	0·005897	2
					Sum	0·312467	172
Total	1·241855	14·658804	4·220898	3·398865	14·346264	0·312540	173
					Difference	0·000073	1

TABLE 14

Line	Source	Sums of squares	Degrees of freedom	Mean square	Variance ratio	Significance
1	Due to total regression	14·346264	1	14·346264	7939·272	**
2	Difference between 'means regression' and 'average within ages regressions'	0·000073	1	0·000073	—	—
3	Deviations of means about 'means regression'	0·005897	2	0·002948	1·635	N.S.
4	Between adjusted subgroup means	0·005970	3	0·001990	1·122	N.S.
5	Between subgroup regression coefficients	0·010366	3	0·003455	1·948	N.S.
6	Total deviations about subgroup regressions	0·296204	167	0·001774	.	.
7	Average within subgroups regression	0·306570	170	0·001803	.	.
8	Deviations about total regression	0·312540	173	0·001807	.	.
9	Total	14·658804	174	.	.	.

Line 1 is tested against line 8.

Lines 2 and 3 are tested against line 7.

Lines 4 and 5 are tested against line 6.

** indicates significance at 1 % probability level.

* indicates significance at 5 % probability level.

N.S. indicates not significant.

— indicates mean square less than that against which it is tested.

TABLE 15. SUMMARY OF THE ANALYSES OF VARIANCE TESTING THE DIFFERENCES IN LENGTH–WEIGHT RELATION BETWEEN AGE-GROUPS OF LONG ROUGH DABS IN 1954

	Females							
	Immature		Maturing		Spent		Males	
Source	2. iii.	2. vi.	2. iii.	25. xi.	8. iv.	2. vi.	2. vi.	9. ix.
Due to total regression	**	**	**	**	**	**	**	**
Difference between 'means regression' and 'average within subgroups regression'	—	—	—	N.S.	—	—	—	—
Deviations of means about 'means regression'	N.S.	**	N.S.	N.S.	—	—	—	—
Between adjusted subgroup means	N.S.	*	—	N.S.	—	—	—	—
Between subgroup regression coefficients	N.S.	—	—	—	—	—	N.S.	—

TABLE 16. SUMMARY OF THE ANALYSES OF VARIANCE TESTING THE DIFFERENCES IN LENGTH–WEIGHT RELATION OF GROUPS OF LONG ROUGH DABS IN SUBGROUPS BY DATES OF CAPTURE

	Females			
Source	Immature	Maturing	Spent	Males
Due to total regression	**	**	**	**
Difference between 'means regression' and 'average within subgroups regression'	**	**	**	N.S.
Deviations of means about 'means regression'	**	**	**	**
Between adjusted subgroup means	**	**	**	**
Between subgroup regression coefficients	**	N.S.	—	N.S.

TABLE 17. REGRESSION COEFFICIENTS (*b*) OF THE REGRESSIONS OF LOG WEIGHT ON LOG LENGTH TOGETHER WITH THEIR 95% FIDUCIAL LIMITS

	Females											
	Immature			Maturing			Spent			Males		
Date	Lower limit	*b*	Upper limit	Lower limit	*b*	Upper limit	Lower limit	*b*	Upper limit	Lower limit	*b*	Upper limit
1953 Oct.	3·18	3·36	3·54	2·25	2·75	3·24	—	—	—	2·75	3·16	3·57
Nov.	3·02	3·16	3·30	3·02	3·25	3·48	—	—	—	3·10	3·38	3·66
Dec.	3·01	3·17	3·32	2·91	3·19	3·46	—	—	—	2·23	3·18	4·12
1954 Jan.	3·20	3·30	3·40	3·00	3·20	3·41	—	—	—	2·92	3·55	4·18
Feb.	3·20	3·39	3·57	2·86	3·20	3·54	—	—	—	—	—	—
Mar.	3·32	3·40	3·47	2·98	3·15	3·32	—	—	—	1·96	3·01	4·06
Mar.	3·18	3·37	3·55	1·68	2·36	3·04	2·65	3·08	3·52	—	—	—
Apr.	3·08	3·28	3·47	—	—	—	3·02	3·31	3·59	—	—	—
May	3·21	3·28	3·35	—	—	—	3·17	3·34	3·51	2·39	3·97	5·56
June	3·18	3·25	3·32	—	—	—	2·97	3·11	3·25	2·75	3·00	3·25
July	2·82	2·98	3·14	—	—	—	2·70	3·33	3·95	2·82	3·11	3·40
Aug.	2·83	2·96	3·09	2·93	3·09	3·26	2·48	3·04	3·61	2·71	2·92	3·14
Sept.	3·01	3·16	3·31	2·71	3·19	3·67	—	—	—	2·65	2·99	3·32
Oct.	2·78	2·99	3·19	2·86	3·15	3·43	—	—	—	2·71	3·35	3·99
Nov.	2·87	2·99	3·10	2·87	2·98	3·10	—	—	—	2·41	2·84	3·26
1955 Jan.	3·04	3·11	3·18	2·86	3·12	3·38	—	—	—	2·25	2·89	3·54
Feb.	3·21	3·32	3·44	2·86	3·03	3·21	—	—	—			
Mar.	3·13	3·23	3·33	2·49	3·07	3·66	—	—	—			
Apr.	3·09	3·14	3·19	—	—	—	2·85	3·13	3·42	—	—	—
Total	3·14	3·17	3·20	3·04	3·11	3·18	3·04	3·14	3·23	2·95	3·07	3·18

TABLE 18. SUMMARY OF ANALYSIS OF VARIANCE TESTING DIFFERENCES OF REGRESSIONS OF LOG WEIGHT ON LOG LENGTH OF THE MAIN GROUPS (SEX AND MATURITY STAGE) OF LONG ROUGH DABS

Source	Significance
Due to total regression	**
Difference between 'means regression' and 'average within groups regression'	*
Deviations of means about 'means regression'	**
Between adjusted group means	**
Between group regression coefficients	N.S.

TABLE 19. THE EXPECTED WEIGHTS (g) FOR THE DIFFERENT MATURITY STAGES OF LONG ROUGH DABS 20·0 cm IN LENGTH FOR EACH MONTH OF CAPTURE, WITH THEIR 95% FIDUCIAL LIMITS

	Females								
	Immature			Maturing			Spent		
Date	Lower limit	$\hat{W}$	Upper limit	Lower limit	$\hat{W}$	Upper limit	Lower limit	$\hat{W}$	Upper limit
1953 Oct.	53·70	55·34	57·02	59·84	61·94	64·12	—	—	—
Nov.	55·08	57·02	59·02	60·81	62·52	64·27	—	—	—
Dec.	54·08	55·85	57·68	58·75	60·81	62·95	—	—	—
1954 Jan.	53·33	54·70	56·10	58·34	59·98	61·66	—	—	—
Feb.	51·76	53·95	56·23	56·89	59·70	62·66	—	—	—
Mar.	54·20	54·95	55·72	58·21	59·57	60·95	—	—	—
Mar.	48·53	50·23	52·00	43·85	49·77	56·49	40·09	43·25	46·67
Apr.	48·53	50·35	52·24	—	—	—	42·36	44·36	46·45
May	47·21	47·95	48·75	—	—	—	41·98	43·35	44·77
June	48·98	49·77	50·58	—	—	—	45·92	47·10	48·31
July	51·17	52·97	54·83	—	—	—	44·77	48·64	52·84
Aug.	48·75	50·23	51·76	51·76	52·97	54·20	45·50	48·08	50·82
Sept.	51·76	53·21	54·70	51·64	54·45	57·41	—	—	—
Oct.	49·09	51·29	53·58	54·33	56·10	57·94	—	—	—
Nov.	52·36	53·70	55·08	56·36	57·41	58·48	—	—	—
1955 Jan.	51·29	52·12	52·97	53·21	55·59	58·08	—	—	—
Feb.	50·47	51·64	52·84	60·53	61·80	63·10	—	—	—
Mar.	50·00	51·05	52·12	52·36	55·98	59·84	—	—	—
Apr.	49·77	50·35	50·93	—	—	—	44·16	48·19	52·60

	Males			Maturing females without gonads		
Date	Lower limit	$\hat{W}$	Upper limit	Lower limit	$\hat{W}$	Upper limit
1953 Oct.	43·05	56·75	74·82	55·59	60·39	65·61
Nov.	54·45	61·24	68·87	58·61	60·53	62·52
Dec.	35·89	56·75	89·74	56·23	58·48	60·81
1954 Jan.	45·50	59·84	78·70	53·46	55·21	57·02
Feb.	—	—	—	50·47	53·95	57·68
Mar.	36·73	52·97	76·38	50·47	51·40	52·36
Mar.	—	—	—	34·12	39·54	45·81
Apr.	—	—	—	—	—	—
May	33·73	51·76	79·43	—	—	—
June	41·11	45·19	49·66	—	—	—
July	47·42	52·60	58·34	—	—	—
Aug.	45·19	48·42	51·88	50·93	52·24	53·58
Sept.	47·42	53·21	59·70	49·55	53·46	57·68
Oct.	43·15	56·36	73·62	48·19	54·58	61·80
Nov.	43·25	51·88	62·23	49·66	52·97	56·49
1955 Jan.	37·58	48·75	63·24	49·43	52·00	54·70
Feb.				49·77	51·05	52·36
Mar.				42·85	45·92	49·20

TABLE 20. DISTRIBUTION OF PERCENTAGE MATURE FEMALE FISH IN GROUPS CLASSIFIED BY AGE AND LENGTH. ONLY PERCENTAGES BASED ON MORE THAN TEN FISH GIVEN

Age-group ...	1+		2+		3+		4+		5+	
Year	53–54	54–55	53–54	54–55	53–54	54–55	53–54	54–55	53–54	54–55
Length-group										
11	—	0	16·74	—	—	—	—	—	—	—
14	—	—	13·05	0	—	—	—	—	—	—
17	—	—	15·34	20·27	39·58	—	—	—	—	—
20	—	—	—	30·46	50·77	54·76	58·89	70·54	—	—
23	—	—	—	—	46·32	44·14	57·48	72·74	90·00	—
26	—	—	—	—	—	—	62·58	55·49	—	90·00

TABLE 21. DISTRIBUTION OF PERCENTAGE MATURE FEMALE FISH IN GROUPS CLASSIFIED BY AGE AND WEIGHT. ONLY PERCENTAGES BASED ON MORE THAN TEN FISH GIVEN

Age-group ...	1+		2+		3+		4+		5+	
Year	53–54	54–55	53–54	54–55	53–54	54–55	53–54	54–55	53–54	54–55
Weight-group										
10	0	—	0	13·94	—	—	—	—	—	—
40	—	—	20·09	15·79	55·67	39·23	—	—	—	—
70	—	—	40·22	—	51·18	47·41	72·44	42·13	—	—
100	—	—	—	—	44·20	54·76	70·91	61·14	—	73·26
130	—	—	—	—	—	—	56·54	67·78	—	—
160	—	—	—	—	—	—	—	71·56	—	—

TABLE 22. ANALYSIS OF VARIANCE OF PERCENTAGE MATURITY WITH LENGTH, WEIGHT AND AGE. ONLY PERCENTAGES BASED ON MORE THAN TEN INDIVIDUALS ANALYSED

Source	Sums of squares	Degrees of freedom	Mean square	Variance ratio	Significance
Between ages within lengths	3244·2618	7	463·466	$F=10{\cdot}2$	Significant at 1 %
Between lengths within ages	570·1470	8	71·268	$F=1{\cdot}6$	Not significant
Within ages and lengths	316·5692	7	45·224	—	
Between ages within weights	1537·4635	6	256·244	$F=2{\cdot}3$	Not significant
Between weights within ages	900·0838	7	128·583	$F=1{\cdot}2$	Not significant
Within ages and weights	874·6500	8	109·331	—	—

TABLE 23. ANALYSIS OF REGRESSION OF GONAD WEIGHT ON LENGTH, AND OF GONAD WEIGHT ON WEIGHT FOR DIFFERENT AGES, FOR DATA OF TWO DATES

	Length (cm)		Weight (g)	
Source	15. ii.	2. iii.	15. ii.	2. iii.
Due to total regression	**	**	**	**
Difference between 'means regression' and 'average within age regression'	N.S.	N.S.	N.S.	*
Deviations of means about 'means regression'	N.S.	—	—	—
Between adjusted means	N.S.	—	N.S.	N.S.
Between regression coefficients	N.S.	**	N.S.	N.S.

TABLE 24. THE VALUES OF THE COEFFICIENTS FOR THE REGRESSIONS OF LOG GONAD WEIGHT ON LOG LENGTH AND ON LOG WEIGHT

	Length (cm)		Weight (g)	
Age	15. ii.	2. iii.	15. ii.	2. iii.
2+	—	3·408	—	0·881
3+	2·747	3·175	0·862	0·880
4+	5·845	2·339	2·082	0·650
5+	4·876	−0·797	1·092	0·076
Total regression	3·829	3·162	1·242	0·954

TABLE 25. THE EXPECTED GONAD WEIGHT OF A FEMALE LONG ROUGH DAB OF 69·98 g (THE GRAND MEAN WEIGHT)

	1953–54 (g)	1954–55 (g)
Aug.	—	0·64
Sept.	—	0·81
Oct.	1·88	1·61
Nov.	2·36	2·75
Dec.	2·99	—
Jan.	5·08	4·66
Feb.	6·70	8·13
Mar.	9·75	12·39
Mar.	10·50	—

TABLE 26. SUMMARY OF ANALYSES OF REGRESSIONS OF FECUNDITY ON LENGTH AND ON WEIGHT OF FISH IN DIFFERENT AGE-GROUPS

	Length		Weight	
Source	15. ii.	2. iii.	15. ii.	2. iii.
Due to total regression	**	**	**	**
Difference between 'means regression' and 'average within ages regressions'	—	—	—	N.S.
Deviations of means about 'means regression'	—	—	—	
Between adjusted age means	—	—	—	N.S.
Between subgroup regression coefficients	N.S.	N.S.	N.S.	N.S.

TABLE 27. THE ABOUT REGRESSION MEAN SQUARES FROM THE ANALYSES OF THE REGRESSIONS OF LOG FECUNDITY (*F*) ON THE LOGS OF AGE (*A*) LENGTH (*L*) WEIGHT (*W*) AND GONAD WEIGHT (*G*)

F on	15. ii. 54	2. iii. 54
A	0·0949	0·1057
L	0·0233	0·0534
W	0·0161	0·0543
G	0·0272	0·0541
A and *L*	0·0240	0·0540
A and *W*	0·0168	0·0542
A and *G*	0·0195	0·0539
L and *W*	0·0166	0·0533
L and *G*	0·0128	0·0443
W and *G*	0·0103	0·0433
L, *W* and *G*	0·0108	0·0438

TABLE 28. EQUATIONS FOR ESTIMATING THE FECUNDITY (*F*) FROM LENGTH (*L*) WEIGHT (*W*) AND GONAD WEIGHT (*G*) OF LONG ROUGH DABS

Factor	Equation	Standard error of estimate (eggs)
	15. ii. 54	
L	$\hat{F}=1{\cdot}4333\ L^{3{\cdot}5533}$	±39,070
W	$\hat{F}=626{\cdot}71\ W^{1{\cdot}1388}$	±38,880
W and *G*	$\hat{F}=1674\ W^{0{\cdot}7699}\ G^{0{\cdot}2970}$	±38,750
L, *W* and *G*	$\hat{F}=3709\ L^{0{\cdot}2077}\ W^{0{\cdot}8350}\ G^{0{\cdot}2949}$	±38,750
	2. iii. 54	
L	$\hat{F}=7{\cdot}154\ L^{3{\cdot}0621}$	±26,890
W	$\hat{F}=1603\ W^{0{\cdot}9461}$	±26,910
W and *G*	$\hat{F}=3458\ W^{0{\cdot}5192}\ G^{0{\cdot}4481}$	±26,700
L, *W* and *G*	$\hat{F}=2111\ L^{0{\cdot}2556}\ W^{0{\cdot}4486}\ G^{0{\cdot}4403}$	±26,720

TABLE 29. THE 95 % FIDUCIAL LIMITS OF THE REGRESSION COEFFICIENTS (*b*) OF THE REGRESSIONS OF LOGARITHMS OF FECUNDITY ON THE LOGARITHMS OF AGE, LENGTH, WEIGHT AND GONAD WEIGHT

	15. ii. 54			2. iii. 54			
Factor	*b*	Lower limit	Upper limit	*b*	Lower limit	Upper limit	Remarks
Age	1·0033	0·6212	1·3854	1·0328	0·8894	1·1762	Linear
Length (mm)	3·5533	3·4304	3·6762	3·0621	2·8337	3·2905	>Cubic
Weight (g)	1·1388	1·1058	1·1718	0·9461	0·9235	0·9686	*ca.* linear
Gonad weight (g)	0·6907	0·6645	0·7169	0·8117	0·7806	0·8428	<Linear

TABLE 30. THE LENGTH, WEIGHT, GONAD WEIGHT, AGE AND EGG COUNTS OF FEMALE LONG ROUGH DABS

Fish no.	Total length (cm)	Flesh wt. (g)	Ovary wt. (g)	Age	Egg count				Fecundity estimate
					I	2	3	4	
15 February 1954									
324	295	175·0	26·5	4+	940	1069	994	1183	209,300
325	230	84·0	10·5	3+	509	510	518	525	103,100
326	230	81·0	8·5	3+	471	430	510	408	90,950
327	245	106·5	11·5	3+	505	584	561	558	110,400
329	230	90·0	10·5	3+	515	519	520	506	103,000
330	250	101·5	12·5	3+	563	606	667	707	127,150
333	245	96·5	13·5	4+	703	730	814	731	148,900
334	240	95·0	11·5	4+	717	682	503	520	121,100
335	260	117·0	12·5	4+	767	700	693	772	146,600
337	210	65·0	4·5	3+	345	295	359	346	67,250
338	235	85·5	12·5	3+	437	406	412	508	88,150
339	255	106·0	7·5	4+	667	610	627	600	125,200
341	230	84·5	9·0	3+	538	491	513	450	99,600
342	250	118·5	10·5	3+	570	588	654	641	122,650
343	240	89·0	10·0	3+	392	383	401	553	86,450
348	215	69·5	6·0	4+	448	421	380	388	81,850
351	225	68·0	2·5	4+	268	267	342	273	57,500
354	240	95·0	9·5	4+	492	550	449	475	98,300
355	245	96·5	11·0	3+	653	573	587	646	122,950
359	290	172·0	24·0	5+	1340	1300	1245	1078	248,150
360	265	123·0	17·5	4+	967	1076	869	912	191,200
363	305	226·5	21·5	5+	1383	1256	1240	1281	258,000
365	240	78·0	7·5	5+	436	348	388	318	74,500
366	220	66·5	7·5	3+	356	310	396	307	68,450
370	200	57·0	9·0	3+	415	346	411	448	81,000
Mean	243·6	101·88	11·5	3·6	606·34				121,268
2 March 1954									
379	190	35·0	8·5	3+	253	255	199	229	46,800
380	220	69·0	5·0	3+	354	331	366	348	69,950
381	235	83·5	13·0	4+	459	625	643	573	115,000
383	210	53·5	12·5	3+	489	399	537	347	88,600
385	245	85·5	13·5	4+	636	646	604	478	118,200
386	215	67·0	12·0	3+	558	504	447	461	98,500
387	195	50·5	6·5	3+	208	172	186	239	40,250
388	205	101·5	12·0	4+	374	464	474	458	88,500
389	220	69·0	13·5	4+	506	535	424	510	98,750
390	250	101·5	18·0	4+	873	773	780	681	155,350
391	200	47·5	5·5	3+	244	276	245	221	49,300
392	175	28·5	5·5	2+	247	242	181	202	43,600
398	290	156·0	10·5	5+	950	1025	1057	992	201,200
399	205	52·5	9·5	3+	349	345	382	286	68,100
400	215	65·5	14·0	4+	436	444	373	476	86,450
401	195	47·5	6·5	3+	250	233	216	191	44,500
402	225	65·5	11·0	4+	395	310	387	413	75,250
403	180	39·0	3·5	2+	208	219	252	213	44,600
404	200	56·0	11·0	4+	302	396	386	348	71,600
420	190	44·5	8·5	2+	266	214	285	237	50,100
421	225	73·0	13·0	3+	537	582	593	523	111,750
422	225	72·0	10·0	3+	474	537	543	506	103,000
423	190	43·5	3·0	3+	168	181	201	151	35,050
424	190	39·0	7·0	3+	189	238	172	227	41,300
425	225	77·5	11·0	3+	635	498	546	517	109,800
426	210	58·0	10·5	3+	363	435	452	360	80,500
427	210	60·5	11·5	3+	540	531	467	550	104,400
428	205	55·5	8·5	4+	416	335	363	345	72,950
429	230	73·5	11·5	3+	489	458	506	462	95,750
430	185	35·5	3·5	2+	218	190	187	177	38,600
431	200	53·5	6·5	2+	348	322	306	324	65,000
432	200	45·5	8·5	4+	401	402	428	325	77,800
433	210	64·0	11·5	3+	551	509	594	582	111,800
469	200	54·5	7·0	2+	299	370	321	312	65,100

TABLE 30 (*continued*)

Fish no.	Total length (cm)	Flesh wt. (g)	Ovary wt. (g)	Age	Egg count				Fecundity estimate
					1	2	3	4	
470	185	40·0	3·5	2+	161	188	174	173	34,800
471	210	55·5	10·0	3+	348	298	379	367	69,600
472	240	83·0	10·0	3+	485	520	509	546	103,000
473	200	44·0	10·5	3+	375	420	415	381	79,550
474	230	68·5	13·5	3+	517	514	503	453	99,350
475	205	52·0	7·0	4+	267	253	284	271	53,750
476	185	42·0	6·5	3+	1107	1112	1050	1057	216,300
477	175	34·0	4·5	3+	180	187	197	174	36,900
482	170	29·0	3·5	2+	166	197	210	199	38,600
483	180	32·5	6·5	2+	223	259	291	261	51,700
485	210	63·5	7·5	2+	288	336	363	347	66,700
486	215	59·0	9·5	4+	465	430	449	368	85,600
487	220	74·0	8·5	4+	368	396	369	408	77,050
488	235	90·0	14·5	3+	534	478	512	430	97,700
489	270	155·0	15·5	4+	258	270	249	273	52,500
490	200	60·0	7·5	3+	284	313	381	402	69,000
491	210	50·0	8·5	3+	280	292	351	292	60,750
492	195	42·5	7·0	3+	290	287	269	320	58,300
493	210	51·5	8·0	4+	296	266	302	305	58,450
494	180	39·0	6·0	2+	308	286	350	327	63,550
495	185	38·5	5·5	3+	271	270	346	280	58,350
496	185	40·0	6·0	3+	248	236	198	189	43,550
497	165	25·5	3·5	2+	170	191	142	141	32,200
503	245	102·0	18·0	3+	700	801	940	794	161,750
504	260	119·0	15·5	4+	1027	908	922	957	190,700
505	245	96·0	12·0	3+	700	701	701	698	140,000
506	240	93·0	12·5	4+	589	598	543	629	117,950
507	230	79·0	10·0	3+	549	510	613	492	108,200
512	220	73·5	10·5	3+	449	483	442	385	87,950
513	220	68·0	10·5	2+	377	426	380	454	81,850
514	220	68·5	11·0	3+	426	475	434	439	88,700
515	205	56·0	10·5	2+	484	421	411	454	88,500
516	215	58·0	9·0	3+	344	366	329	352	69,550
517	180	34·5	6·0	2+	236	170	229	218	42,650
518	185	41·5	5·5	2+	242	200	262	226	46,500
519	170	30·0	5·0	2+	154	172	151	175	32,600
520	170	33·0	5·0	2+	219	180	146	178	36,150
521	170	29·0	3·5	2+	150	148	130	169	29,850
522	165	27·0	3·0	2+	133	117	145	168	28,150
552	290	173·0	27·0	5+	1050	972	1055	953	201,500
553	270	107·5	17·0	5+	770	674	814	674	146,600
554	245	96·0	21·0	5+	729	662	792	610	139,650
555	255	97·5	15·0	5+	552	552	518	558	109,000
556	215	74·5	6·5	3+	347	374	360	391	73,600
557	210	62·0	6·0	3+	365	372	364	329	71,500
558	200	44·5	8·0	4+	365	316	301	326	65,400
559	195	50·5	7·0	2+	401	378	265	349	69,650
560	205	60·0	10·5	3+	476	442	387	469	88,700
561	210	55·5	7·5	3+	311	271	314	263	57,950
562	230	73·0	14·0	3+	415	403	414	445	83,850
563	225	78·0	8·0	3+	508	457	355	429	87,450
564	265	121·5	22·0	5+	872	786	752	850	163,000
565	230	70·5	7·0	3+	454	371	385	408	80,900
566	215	57·5	9·0	4+	280	288	302	268	56,900
567	240	90·5	11·5	4+	553	584	588	538	113,150
568	190	40·0	4·0	3+	272	241	199	260	48,600
569	200	59·0	4·5	2+	307	307	346	334	64,700
Mean	21·16	63·87	9·44	3·1	409·22				81,844
15 March 1954									
669	155	21	4·0	.	102	158	136	121	25,850
30 March 1954									
691	165	28	5·5	2+	197	202	156	191	37,300
692	150	18	4·0	2+	127	139	118	130	25,700

APPENDIX 1

THE ANALYSIS OF THE LENGTH–WEIGHT RELATION AND CONDITION

The data used in this analysis were obtained from the samples listed in Table 1. The methods of obtaining the data have been given, but it must be remembered that there is no evidence available as to the selectivity of the trawl with regard to the length–weight relation. We may suppose that the fatter and heavier fish of a given length would be more easily retained by trawl meshes of a given size.

A preliminary scatter diagram (Fig. 1) of length and weight suggested that their relationship was of the form

$$W = aL^n,$$

where W = weight, L = length, a is constant and n an exponent approximately = 3. The analysis of the data could best be accomplished by using logarithms and fitting the straight line regression of log weight on log length,

$$\log W = \log a + n \log W$$

to the data by the method of least squares.

The data were divided into four groups according to sex and maturity as follows: (1) males; (2) immature females (stage 1); (3) maturing females (stage 2); (4) spent females (stage 4). These groups were further divided into subgroups by month of capture. Although it was originally proposed to further divide the subgroups into their respective age-classes, this was not found to be practicable owing to the small numbers that would be in each division. The two largest subgroups from each main group were chosen and a preliminary analysis carried out to see if the length–weight relation differed in the different age-classes. This was carried out by an analysis of covariance in a manner similar to that used by LeCren (1951). For an account of the statistical methods see Snedecor (1946, pp. 318–29) and Mather (1946, pp. 119–28). As an example of the calculations, the data for the immature females in the sample caught on 2 March 1954 are given in Tables 13 and 14. The two most important tests (apart from line 1, Table 14) are those of lines 4 and 5 (Table 14). The first tests the significance of the differences between the expected weights in each subgroup corresponding to the grand mean length. This is therefore a test of the differences in condition between the different subgroups (see next section). The second tests the difference between the subgroup regression coefficients and is therefore a test of the difference in length–weight relation of the subgroups. The other tests are of less interest. Line 3 tests the significance of the regression of the means of the subgroups, while line 2 tests whether there is a significant difference between the average of the subgroup regressions and the regression of their means. It is obvious that if line 3 is significant, line 2 can have no meaning.

Various tests were performed on the data before the regression analyses were carried out, in order to see to what extent the assumptions made were in fact valid. Bartlett's test of homogeneity was applied to the residual variances (Pearson & Hartley, 1954); because in order that the tests of significance may be valid the data must be homogeneous. These tests showed that the data were heterogeneous. The heterogeneity was not removed by considering the age-groups separately and it was thought that Bartlett's test might have revealed non-normality in the log length and log weight frequency distributions. Tests for normality were carried out on a large number of these distributions and the majority were found to be significantly non-normal. It is clear that if the lengths are normally distributed, the weights will not be, if the length–weight relation approximates to $W = aL^3$. Although taking logarithms helps to normalize the weights, it simultaneously tends to skew the lengths. For a critical discussion a considerably more complicated form of analysis is required, and it was not thought that such an analysis was justified with the present data. It should be borne in mind, however, first that the effects of non-normality do not invalidate the estimates of the regression; the equation found is still the 'best straight line' (by the method of least squares) for the data; it is only the tests of significance that are less reliable than would be the case with strictly normal and homogeneous data. Secondly, the effect of non-normality is usually to produce more significant results than would otherwise be found (Cochran, 1947). In this work on Long Rough Dabs it was found (for example in Tables 5 and 6) that the comparisons being tested were mostly either not significant ($P > 0{\cdot}05$) or highly significant ($P < 0{\cdot}01$), and in only a few cases would the conclusions be changed by using the 0·01 level of probability as a basis for rejection of a hypothesis rather than the more usual level of 0·05, and the more severe test may be used for these data.

THE LENGTH–WEIGHT RELATION

The analyses of the regressions of log weight on log length were first carried out on different age-groups of otherwise comparable fish (Table 15). These 'between ages' comparisons were made on the two subgroups from each main group that contained the most individuals. It can be seen that in one case there was no definite trend in the means of the different ages, and in this case too the differences in 'condition' of the fish are possibly significant. It will be noted that in no case was there a significant difference in the length–weight relation of the different ages as shown by the regression coefficients. This evidence suggests that the age-groups may be pooled and the analysis continued to test the differences on different dates of collection.

The results of these analyses are given in Table 16 and the regression coefficients for the regressions are given in Table 17 together with their 95% fiducial limits.

These limits were calculated as

$$b \pm t[1/Sx^2 \text{ (residual s.s.}/n-2)]^{\frac{1}{2}},$$

where t = Student's 't' for $n-2$ degrees of freedom, Sx^2 = sum of squares for length, residual s.s. = residual sum of squares (e.g. from Table 13). In Table 16 it will be noted that only for the immature females are there significant differences between the coefficients for different dates.

It is usual in studies of the length–weight relation of fish to test if the regression coefficients are significantly different from 3, to see if the fish in question obey the 'cube law'. It can be seen from Table 17 that 3 is within the 95% fiducial limits for most subgroups except those of the immature females, for which the coefficients are mostly significantly greater than 3. However, with the total regressions, based on all the points summed over dates, only with the males do the fiducial limits include 3. It is usually assumed that differences in the regression coefficients at different times are not of interest and are only estimates of the overall value. However, the fluctuations in the coefficient may be of interest since they indicate how different size-groups are behaving in their length–weight relation. For example, if all fish are putting on weight and the large fish do so relatively faster, the coefficient increases, whereas if the coefficient decreases it is indicative of relatively faster weight increase by the smaller fish. In this way the study of the regression coefficient should be closely linked with the analysis of the condition.

It has been noted that only the immature females showed significant differences in the regression coefficients of different dates. These are shown graphically in Fig. 2, where it can be seen that there appears to be a yearly cycle in the value of b. The biological significance of this cycle has already been discussed. With maturing and spent Long Rough Dabs the differences in the coefficients are not significant, but even so they may be of interest. The values of the coefficients for the total regression (pooled over dates for each group) are also given in Table 17, and the significance of their differences are shown in Table 18. The data for the immature fish are included even though not homogeneous.

In Table 16 can be found the significance of the differences in the adjusted means for the different subgroups (dates) of the main groups of Long Rough Dabs. These adjusted means for each subgroup are the expected mean weights of fish of the grand mean length (for each main group). They are, therefore, a test of the condition between the subgroups of fish and it will be noticed that in each case the differences are significant. Within each group the adjusted weights are comparable, but in order to compare the condition of the different groups one with another it is necessary to adjust the weights not to the mean length of the group but to a length more suitable for all the groups.

An arbitrary length of 20 cm was chosen as being conveniently within the range of all the groups and sufficiently near the grand mean length. While male Long Rough Dabs as large as 20 cm are rare, this length is at the lower end of the range of mature females. The weights expected ($\hat{W}$) for fish of 20 cm calculated from the regression equations for each month are given in Table 19 together with their 95 % fiducial limits, and are shown diagrammatically in Fig. 3. The differences found to be significant in Table 6 can be taken as equally applying to these variations. A discussion of the results is given earlier in the paper.

The expected weights are given by

$$\hat{W} = \overline{W} . L^b / \bar{l}^b,$$

where $L = 20$ cm, and $\overline{W}$ and $\bar{l}$ are the arithmetic means of the weights and lengths obtained from the raw data. This equation is derived from

$$\log \hat{W} = \log \overline{W} + b(\log L - \log \bar{l}),$$

but for estimating the weight from the lengths, the antilog of log $\hat{w}$ gives a biased result since it is based on the mean of the logarithms (= geometric mean) and the arithmetic mean should be used (M. Bagenal, 1955). The 95 % fiducial limits of estimated weight ($\hat{W}$) are given by

$$\text{Antilog}\ [\log \hat{W} \pm t[(1/n + (L - \bar{l})^2/Sx^2) \text{ residual s.s.}/n - 2]^{\frac{1}{2}}].$$

In this case the limits may be calculated on the logarithmic values and the antilogarithm taken to give the limits in grams.

APPENDIX 2

THE ANALYSIS OF MATURITY AND AGE, LENGTH AND WEIGHT

The data for the percentage of mature fish were grouped into two tables for length and weight (Tables 20 and 21). It will be seen that in some cases the two years 1953–54 and 1954–55 provided pairs of percentages of the same age and length. The variability between these pairs provided a standard against which it was possible to test (after a transformation of percentages into angles) (Snedecor, 1946, p. 447 and table 16·8) the variability between ages within length-groups, and between length-groups within ages; and similarly for ages and weights.

The result of this test is given in Table 22, where it is seen that the variability between different ages with the same length is significantly greater than that between years, though the variability between length-groups of the same age is not.

A comparable analysis for age and weight is also given in Table 22. Here the variance between ages, although double that of the 'between weights' is not statistically significantly greater than that of the 'between pairs' variance.

APPENDIX 3

THE ANALYSES OF GONAD WEIGHT

The effect of the age of the female Long Rough Dab on gonad development was examined in preliminary regression analyses of the logarithms of the gonad weights on lengths and on weights for different ages carried out on the data of 15 February and 2 March 1954. The results of these analyses are summarized in Table 23. Full details of method and data are given in Appendix 1.

The coefficients for the regressions of gonad weight on length for the different ages were found to differ significantly for the 2 March data. To a large extent this variability was due to the inclusion of the data from the six 5-year-old fish, which were widely scattered; but even without these fish the coefficients were significantly different at the 5% level. Since in the analysis of regression on weight the regression coefficients were not significantly different it is probably safe to ignore this anomalous result. The values for the regression coefficients are given in Table 24. There is no clear trend in the coefficients with increasing age and those for the regressions of gonad weight on weight may be taken to indicate a linear relationship; that is, the data suggest that there is no difference in the gonad weight/flesh weight ratio in the different age-groups.

The analyses summarized in Table 23 indicate that either length or weight may be used in the further analysis of the gonad weight annual cycle, and that the different ages may be pooled. The standard error of estimates of gonad weight are very comparable for the length and weight regressions, being 0·112 g for the former and 0·119 g for the latter for the March data, and 0·146 g for both length and weight for February. For further analysis the regression of log gonad weight on log weight was used. The values for the regression coefficients did not appear to change from month to month in any ordered manner, showing there was no obvious difference in the time of gonad development of fish of different sizes. The adjusted gonad weights were calculated for fish of a grand mean weight of 69·98 g and are shown in Table 25 and Fig. 6.

APPENDIX 4

THE ANALYSIS OF FECUNDITY

In Fig. 9 the fecundity and length data are given as a scatter diagram for the 119 observations, and in Fig. 10 the fecundity and weight are shown. While the latter figure suggests that the relation of fecundity and weight may be linear, Fig. 9 suggests that the relation with length would be of the form

$$F = aL^n,$$

or

$$\log F = \log a + n \log L,$$

where F = fecundity, L = length and a and n are a constant and exponent to be obtained from the data. Both these suggestions were examined by analyses of the regressions of logarithm of fecundity on the logarithm of the independent factor. First, however, analyses of covariance were carried out to determine whether the relations of fecundity and length and weight changed significantly with age. These analyses were essentially similar to those shown in Tables 3 and 4 for the length-weight relation. The results of these analyses are shown in Table 26.

The regressions analysed were those of log fecundity on log length and log weight; the values for the fecundity were the arithmetic means of the four original estimates for each fish. Since the differences between the ages were not significant, the data were pooled and the regressions of log fecundity on log age, length, flesh weight and gonad weight were analysed. Later multiple regression analyses of fecundity on combinations of these characters were also carried out. In each analysis the 'due to regression' mean square was tested against the 'about regression' variance to test the validity of the regression in question. From the four estimates of the fecundity for each fish, the 'within fish' variance could be calculated ($=\Sigma F_i^2-4\Sigma\overline{F}^2$, where Fi for $i=1$, 2, 3 and 4 are the logarithms of the four fecundity estimates and $\overline{F}$ their mean) and was taken as a measure of the errors inherent in the counting and subsampling method. This 'within fish' variance is the appropriate mean square for testing the 'about regression' variance, since it is hoped to reduce the variability about the regression plane (by the most suitable combination of characters for estimation) until it is no longer significantly larger than the variability of the laboratory technique. The 'within fish' variance, however, was not large (0·0019 with 273 degrees of freedom, on 2 March 1954 and with 75 degrees of freedom on 15 February 1954), and the 'about regression' variances were always significantly greater than this. The more highly statistical method outlined above for finding the most suitable factors for use in estimating fecundity seems more satisfactory than that used by Simpson (1951) for Plaice. Although Simpson also counted four subsamples of the eggs from each fish, he used these not as a measure of his experimental error, but only to arrive at a more reliable estimate of the fecundity (the standard deviation of the estimate would be reduced by $\sqrt{4}$ of that of a single count). His estimate of the errors in the laboratory method was based on his count of forty subsamples taken specially for the purpose. With the methods given here one may easily measure which factors are the most reliable for estimating fecundity, and test their significances.

After the analyses of covariance and tests of significance had been carried out, the regression equations for estimation were transformed back from logarithms to actual values, and the standard errors of estimate of the real fecundity were calculated. This (by rearrangement of equation 5, M. Bagenal, 1955) is given by the standard error of estimate

$$=\sigma_{\hat{F}}=200\overline{F}[\text{antilog }(\sigma_y^2/\log_{10}e)-1]^{\frac{1}{2}},$$

where $\sigma_y^2=$ the total 'about regression' residual variance in logs and $\overline{F}=$ the arithmetic mean fecundity from all the estimates. Using the above formula to obtain the 'between counts' errors for the two sets of data one obtains $\sigma_{\text{counts}}=61{\cdot}240$ for the mean count of 606·34 eggs for 15 February and $\sigma_{\text{counts}}=41{\cdot}331$ for the mean count of 409·22 eggs of the 2 March collection. These both correspond to a coefficient of variation of 0·1010 or 10·10% (since the within fish variance was the same for both dates); this closely approximates to the value obtained from the 40 replicate counts. Of the standard errors of estimate given later for each regression equation ± 12,248 eggs and ± 8266 eggs can be accounted for by the variability in laboratory method of the February and March collections respectively.

The 'about regression' mean squares, obtained from the analyses of the regressions and multiple regressions of log fecundity on the logs of age, length, weight and gonad weight are given in Table 27. In all cases these are significantly greater than the 'within fish' mean square, showing that the great variability between fish cannot be due to experimental technique alone.

Of the single factors, age alone is of little use for estimating fecundity and, indeed, for the 15 February data, the 'due to regression' mean square is only significant at the 5% level. Furthermore, the addition of age to the other factors does not produce any significant improvement, except to gonad weight with the February data. Age is not therefore considered in any three factor analyses.

On neither date does the addition of length to the regression of fecundity on weight significantly decrease the 'about regression' sums of squares, and for the March data weight does not significantly improve length alone for prediction purposes. In all other cases the addition of a second variate significantly reduces the 'about regression' sums of squares.

From the two variate analyses it is seen that for both dates weight and gonad weight together are the best for fecundity prediction purposes, and the addition of length as a third variate does not produce a significant improvement. The most useful equations for predicting fecundity are given in Table 28, together with the standard errors of estimate. The equations were obtained, in the case of the relation with length for example, in the form

$$\hat{F} = 200\bar{f}\,.\,L^b/\bar{l}^b,$$

where $\hat{F}$ is the expected fecundity for a given length (L) and $\bar{f}$ and $\bar{l}$ are the arithmetic means of the egg counts and lengths obtained from the raw data. This is similar to the equation used for estimating 'condition' from the length–weight relation (p. 372).

The choice of the measurement to be used for estimating fecundity should not of course be dictated solely by a consideration of Table 27. The lengths of fish are so much easier and quicker to obtain than the corresponding weights and gonad weights that if time is limited and the fish are not, greater accuracy in estimating the mean fecundity might be obtained by measuring length alone since the standard error of estimate would be reduced by increasing the sample size.

The values of the fiducial limits at the 95 % probability level for the coefficients of the regressions of the logarithms are given in Table 29.

A further aspect of the relation of fecundity to length and weight was examined by a consideration of the correlation of fecundity and condition. The correlation ($r = 0{\cdot}12$) between the log condition ($= \log W - \log \hat{W}$) and the logarithms of the deviations of the fecundities from their expected values ($= \log F - \log \hat{F}$) was not found to be significant ($\hat{W}$ = expected weight and $\hat{F}$ = expected fecundity). In other words, it was found that there was no association between the deviations of the fecundities from the line of their regression on length, and the deviations of the weights from their regression line on length.