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Differential Catchability of Male and Female Plaice in the North Sea and its Effect on Estimates of Stock Abundance

by

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Introduction

A very general, though not quite universal, characteristic of fish is that the female of the species grows to a larger size than the male and also lives longer. Among fish of commercial importance these features are especially marked in many species of flatfish. For example, the limiting size (L_∞) attained by male plaice (Pleuronectes platessa L.) in the North Sea is about 45 cm while that by females is nearly 7o cm; similarly, female plaice are sometimes recorded from this area up to 2o years of age and more, despite fairly intensive fishing, but male plaice older than 14 years are very rare.

While there is good reason to believe that the natural mortality rate of mature females is indeed lower than that of mature males, in other species as well as plaice, this is not a sufficient explanation of the observed porportions of the two sexes in the catches. Thus, typically, males exceed females in the younger age-groups and it is only among the older fish that the sex-ratio (defined here as the number of males divided by the number of females) falls below unity. The predominance of males is especially marked among the younger mature fish at spawning time, and various theories have been advanced to explain it (Simpson, 1959). This will be referred to again later; here it is enough to note that whatever may be the cause of the seasonal changes in sex-ratio of the catches, the consequence is that the effective "catchability" (an ungainly but appropriate term for the constant of proportionality (q) relating fishing effort to fishing mortality in the equation $F = qf$) of males is likely to differ from that of females. Therefore the relation between catch per unit effort and abundance for the stock as a whole (sexes combined) will depend on the sex-ratio which, in turn, will be influenced by the amount of fishing.

In another contribution to this Symposium, Gulland has shown that the increase in gross (i.e. sexes combined) catch per unit effort of North Sea plaice from 1939 to 1945 in the English trawl fishery, even when calculated on a sub-area basis, probably overestimates the true increase in stock abundance. In this contribution the data are analysed by sexes in an attempt to measure the difference if any, in the catchability of males and females, and hence to see to what extent this could account for the bias in the gross catch per unit effort as a measure of stock abundance. The sex-ratio in the commercial catches does not, of course, give a direct measure of the relative catchability of males and females unless the true sex-ratio in the fished stock is also known. The method employed is therefore to estimate from catch and effort data the fishing mortality of males and females separately, the ratio of which defines the relative catchability of males to females (q^m/q_f), and hence to measure the true sex-ratio of the pre-war and post-war stocks.

Natural Mortality of Male and Female Plaice

From the survival of certain year-classes present in the commercial catch samples both in 1939 and again in 1945, Beverton and Holt (1957) estimated the average natural mortality coefficient during the war period as roughly 0.1. This is consistent with the difference in total mortality coefficient (Z) under steady but different levels of fishing intensity in the 193o's and 195o's (Gulland, No.14, this Symposium). Further analysis of the data for the 1932, 1933, and 1934 year-classes by sexes gives estimates of M for male and female plaice separately, the estimated catch per unit effort of these year-classes in June 1939 and June 1945 being shown by sexes in Table 1.

Table 1. Catch per unit effort (Nos. per 100 hrs fishing) of males and females of the 1932, 1933 and 1934 year-classes in June 1939 and 1945. The values for June 1945 are estimated by back-extrapolation from sample data starting in December, 1945, as described in the text in connection with the estimation of Z in the immediate post-war fishery.

Year-class	June 1939			June 1945		
	Age-group	Males	Females	Age-group	Males	Females
1932	V	652	750	XI	252	365
1933	VI	302	376	XII	76	147
1934	VII	111	192	XIII	31	110
T o t a l		1065	1318		359	622

Assuming the catchability of each sex to be the same at the lower ages (i.e. in 1939) as at the higher (i.e. in 1945), these data give estimates of total mortality coefficient between June 1939 and 1945 of

$$6\ Z_m = 1.09$$

$$6\ Z_f = 0.75$$

There was, however, an appreciable amount of fishing in the western North Sea in the second half of 1939 (Margetts and Holt, 1948); no precise allowance can be made for this but it probably generated an F of not less than 0.2 to 0.3. Subtracting 0.25 from the above values and dividing by six gives estimates of M during the war period of

$$M_m = 0.14$$

$$M_f = 0.08$$

The precision of these values to the second decimal place cannot be relied upon, but the important thing in the present context is that the difference between M_m and M_f is much less than that between Z_m and Z_f in both post-war and pre-war fisheries, as will now be shown.

Total Mortality and Relative Catchability of Male and Female Plaice in the Post-War and Pre-War Fisheries

The high catch (in weight) per unit effort of plaice in the English fishery when fishing was resumed on the main plaice fishing grounds of the western North Sea in the summer of 1945, and its rapid decline thereafter, has been documented by Margetts and Holt (1948). From July 1945 onwards an estimate can be made of the total number of fish caught per 100 hrs trawling. In Figure 1 is plotted, as natural logarithms, the number caught per 100 hrs (Lowestoft and Grimsby combined) in each month as a ratio of the average number in the corresponding month and rectangles during the pre-war years 1931-38. This procedure, which gives an index of numbers caught per unit effort comparable to that of weight shown in the lower curve of Gulland's Figure 1, minimises that part of the seasonal and regional variation in catch per unit effort common to both the pre- and post-war fisheries, and so clarifies the underlying trends. During the first year of fishing the relative rate of decrease is effectively constant, giving an estimate of total Z of about 1.3 (cf. Holt, 1949).

Otolith sampling began in December 1945, and from then onwards the decrease of males and females of the constituent year-classes can be followed separately, the total catch per unit index of Figure 1 being apportioned accordingly. It is not practicable to show all the data graphically in this way, but an example is shown in Figure 2 for the 1939 year-class, which comprised age-group VI in December 1945 and was the dominant year-class in the catches, both by numbers and weights; it can be taken as being effectively unfished until the summer of that year.

The data for both males and females are graduated well by linear regressions, that for males being considerably steeper than that for females; the total mortality coefficients estimated from the slopes of these regressions fitted by least squares are

$$Z_m = 1.84$$

$$Z_f = 1.08$$

Subtracting the above values of M_m and M_f gives

$$F_m = 1.70$$

$$F_f = 1.00$$

and hence a relative catchability of males to females (denoted by γ_q) of

$$\gamma_q = {}^{1.7}/_{1.0} = 1.7$$

Estimates of Z_m, Z_f and r_q for the other fully-recruited year-classes (1938 to 1932) obtained in the same way are given in Table 2, the values of Z being shown in Figure 3 plotted against the age of the year-class in the summer of 1945.

Table 2. Estimates of Z and F by sexes for the fully-recruited age-groups in the immediate post-war fishery, and the relative catchability of males to females (γ_q)

Year-class	Age-group	Z_m	Z_f	F_m	F_f	γ_q
1939	VI-VII	1.84	1.08	1.70	1.00	1.70
1938	VII-VIII	1.75	1.14	1.61	1.06	1.52
1937	VIII-IX	1.62	1.06	1.48	0.98	1.51
1936	IX-X	1.62	0.89	1.48	0.81	1.83
1935	X-XI	1.66	0.97	1.52	0.89	1.71
1934	XI-XII	1.44	0.89	1.30	0.81	1.60
1933	XII-XIII	0.92	0.74	0.78	0.66	1.18
1932	XIII-XIV	0.67	0.98	0.53	0.90	0.59
1931	XIV-XV	-	0.30	-	0.22	-
1930	XV-XVI	-	0.34	-	0.26	-

It will be seen that Z_m is consistently higher than Z_f except among the oldest fish. The monthly abundance indices for the 1940 year-class (age-group V in 1945) are not linear but fall on a curve which steepens with time, indicating that the year-class was not fully-recruited in 1945; even so, the average slope for males is steeper than for females, rough estimates being Z_m = 0.9 and Z_f = 0.4. The 1941, 1942, and 1943 year-classes were certainly recruiting during the period 1945-47 and cannot be used to estimate total mortality directly.

Estimates of the average total mortality coefficient by age and sex from catch per unit effort data for Lowestoft and Grimsby during the period 1931-38 are given in Table 3, page 4, and shown graphically in Figure 3 for comparison with pre-war estimates. Values of F_m, F_f and γ_q for this period, obtained by subtracting the same values of M_m and M_f as before, are also given in the table. Again Z_m is considerably greater than Z_f, but both are lower than in the post-war fishery except for females older than XIV years.

There are therefore two general features emerging from Figure 3 and Tables 3 and 4. One is that the fishing mortality coefficient of male plaice is higher than that for females, and secondly that the coefficient for both sexes was higher in the immediate post-war fishery than pre-war. It is, however, only the first of these that is immediately relevant in the present context, and it confirms that the effective catchability of males is indeed higher than that of females. The average ratio of r_q for the main fully-recruited age-groups (V-X in the pre-war fishery and VI-XI in the post-war) is about 1.6 in both periods.

Table 3. Estimates of Z and F by sexes for the fully-recruited age-groups in the pre-war fishery (1931-38), and the relative catchability of males to females (r_q).

Age-group	Z_m	Z_f	F_m	F_f	r_q
V-VI	o.75	o.72	o.61	o.64	o.95
VI-VII	o.91	o.68	o.77	o.6o	1.28
VII-VIII	o.86	o.54	o.72	o.46	1.56
VIII-IX	1.14	o.58	1.oo	o.5o	2.oo
IX-X	o.83	o.43	o.69	o.35	1.97
X-XI	1.28	o.52	1.14	o.44	2.59
XI-XII	o.89	o.22	o.75	o.14	5.35
XII-XIII	o.7o	o.37	o.56	o.29	1.93
XIII-XIV	-	o.32	-	o.24	-
XIV-XV	-	o.52	-	o.44	-
XV-XVI	-	o.39	-	o.31	-

In detail, however, there appear to be some differences in the relative catchability of the sexes between the two periods. Thus r_q for the youngest fully-recruited age-groups in the pre-war fishery (age-groups V and VI) is apparently not much different from unity and substantially less than in the post-war fishery. If this difference is real it could mean either that males of these age-groups were more catchable relative to females, or females less catchable relative to males, in the post-war compared with the pre-war fishery.

There is no way of proving from these data alone which explanation is the correct one. However, the fact that the greater effective catchability of males is certainly caused partly - if not mainly - by their greater catchability at spawning time (as is discussed later), suggests that the effective catchability of males is more likely to be sensitive to a change in the seasonal distribution of fishing than is that of females. For example, if the post-war fishery concentrated more on or near the spawning grounds than did the pre-war one (and there are some indications that this was the case (Margetts and Holt, 1948)), it could have resulted in more males being caught relative to females. On this hypothesis, the interpretation of the pre-war/post-war differences of Figure 3 is that while the pattern of distribution of F_f with age for females remained the same (even though its level increased, for other reasons), that of F_m for males increased relatively more among the youngest age-groups.

In order to calculate the changes in the effective catchability of the pre- and post-war stocks two procedures will therefore be used. One is to disregard the apparent changes of F with age in both sexes (which are in any event of somewhat dubious interpretation from this evidence alone) and to use the same average value of $r_q = 1.6$ for both periods and for all age-groups. The other is to accept the values of r_q shown in Tables 3 and 4 for each age-grpup as real, and to assume that it is the male catchability which has changed. Because r_q increased in the younger age-groups which contribute to the catch, this second procedure results in something like a maximum estimate of the change in catchability of the post-war stock compared with pre-war.

The Sex-ratio and effective Catchability of the Pre- and Post-War Stocks compared

To calculate the effective catchability of the stock, in so far as this depends on its sex composition, it is necessary to know not only the relative catchability of males to females but also the true ratio of the sexes in the stock. This latter can be determined by dividing the sex-ratio in the catch by the relative catchability factor r_q. If the sex-ratio of the catches is denoted by r_c and that of the stock by r_s, the effective catchability of the stock (in numbers), taking the catchability of females as unity, is

$$\frac{r_s \times r_q + 1}{r_s + 1} \qquad \ldots\ldots\ldots\ldots\ldots \quad (1)$$

where $r_s = r_c / r_q$

Table 4 therefore summarises the catch sex-ratios for the pre-war years 1931-38 and in the immediate post-war fishery. The values for December 1945, 1946 and 1947 are taken from the fitted regressions for the fully-recruited age-groups (e.g. Figure 2) or from free-hand curves for the younger age-groups; they therefore reflect, intentionally at this stage, only the general trend in sex-ratio as the accumulated stock was fished down, not its seasonal variation. Data for the younger age-groups in the post-war fishery are highly variable and only rough values can be given; these are shown in parenthesis.

Table 4. Sex-ratio in the age-groups comprising the catch and fished stock during 1931-38 and in the immediate post-war period, the latter being calculated from the values of r_q given in Tables 3 and 4. Values in paranthesis are rough estimates only (see text).

	Sex-ratio in catch					Sex-ratio in stock				
Age-group	Average 1931-38	June 1945	Dec. 1945	Dec. 1946	Dec. 1947	Average 1931-38	June 1945	Dec. 1945	Dec. 1946	Dec. 1947
III	o.93	-	(1.5)	(1.5)	(1.4)	(o.93)	-	(o.91)	(o.91)	(o.85)
IV	1.o2	(1.7)	(1.6)	(1.5)	(1.6)	(1.o2)	(1.o3)	(o.97)	(o.91)	(o.97)
V	1.o3	(3.4)	2.7o	1.64	1.45	1.o8	(2.o6)	1.64	o.99	o.88
VI	1.1o	3.76	2.59	1.83	1.49	o.86	2.21	1.52	1.o8	o.88
VII	1.1o	1.85	1.36	1.22	1.11	o.7o	1.22	o.9o	o.8o	o.73
VIII	o.7o	1.5o	1.15	o.74	o.55	o.35	o.99	o.76	o.49	o.36
IX	o.33	1.54	1.o6	o.64	o.39	o.17	o.84	o.58	o.35	o.22
X	o.23	1.16	o.78	o.51	o.37	o.o9o	o.68	o.46	o.3o	o.22
XI	o.o9	o.68	o.5o	o.43	o.24	o.o17	o.42	o.31	o.27	o.15
XII	o.o4	o.43	o.38	o.29	o.21	o.o2o	o.36	o.33	o.25	o.18
XIII	o.o3	o.24	o.28	o.34	o.17	o.o15	o.41	o.48	o.57	o.29
XIV	o.oo2	-	-	o.36	o.27	o.oo1	-	-	o.61	o.46
Total	o.97	2.21				o.61	1.38			

It is evident from this table that the faster rate of decline of males compared with females caused the sex-ratio in the catches to change rapidly in the immediate post-war period, so that the sex-ratio in June 1945 when fishing started would have differed appreciably from that in December when detailed sampling began. The fact that the decrease of both the total numbers and of the constituent age-groups and sexes was progressive, even on a monthly basis (see Figures 1 and 2), suggests that sex-ratio of the fully-recruited year-classes in the catches in June 1945 can be estimated reasonably well by extrapolating the linear regressions back to that date, as shown by the broken lines of Figure 2. Thus the sex-ratio of the 1939 year-class in the catches in June 1945 is predicted in this way as 3.76 compared with the interpolated ratio in December of 2.59.

With the simpler procedure outlined above, in which the relative catchability of males to females for the fished stock as a whole is taken to be $r_q = 1.6$ in both the pre- and post-war periods, it is sufficient to use simply the total catch sex-ratios shown at the foot of Table 4. These are o.97 in the pre-war fishery and 2.21 in June 1945; in other words, males and females were present in about equal numbers in the pre-war catches but males outnumbered females by two to one in the immediate post-war catches. The sex-ratios in the fished stocks are therefore calculated as

$$r_s = {}^{o.97}/_{1.6} = o.61$$

in the pre-war stock, and as

$$r_s = {}^{2.21}/_{1.6} = 1.38$$

in the June 1945 stock. Using equation (1), the effective catchability of the pre-war stock is

$$\frac{0.61 \times 1.6 + 1}{1.61} = 1.22$$

and of the June 1945 stock is

$$\frac{1.38 \times 1.6 + 1}{2.38} = 1.35$$

Therefore the June 1945 stock was

$$1.35/1.28 = 1.11 = +11\%$$

times more catchable, in numbers, than the pre-war stock, due to the differential catchability of the sexes and the change in sex-ratio.

The second procedure is to accept the values of r_q for the various age-groups given in Tables 3 and 4 as real and to assume that where r_q in the post-war fishery differs from the pre-war, it is due to a change in the relative catchability of males, that of females remaining unchanged. The calculation in this case is similar, but is performed for each age-group separately, the resulting catchabilities being weighted by the percentage contribution of the year-class to the total catch and then summed. The second part of Table 4 shows the stock sex-ratios calculated by dividing the catch sex-ratios at each age by the corresponding value of r_q. For the partially recruited age-groups, for which no direct estimate of mortality rate is available, r_q has been taken as unity in the pre-war fishery and 1.6 in the post-war fishery, which is consistent with the hypothesis that there was a real increase in the catchability of the youngest males in the post-war fishery. From here, the calculation of effective catchability can be illustrated by taking age-group VI as an example. Its sex-ratio in the pre-war stock is estimated as 0.86 with a relative catchability of $r_q = 1.28$; its effective catchability was, therefore, from equation (1)

$$\frac{0.86 \times 1.28 + 1}{1.86} = 1.13$$

The sex-ratio of age-group VI in the post-war stock is, however, estimated as 2.21 with a relative catchability of 1.70, giving an effective catchability of

$$\frac{2.21 \times 1.7 + 1}{3.21} = 1.48$$

On this basis, age-group VI was therefore

$$1.48/1.13 = 1.31$$

times more catchable in the post-war fishery than the pre-war one. Performing similar calculations for the other age-groups, weighting by the percentage age-composition in the pre-war and June 1945 fisheries shown in Table 5, page 7, and summing, gives an effective catchability for the whole pre-war stock of 1.03 and for the June 1945 stock of 1.36, the change between the two periods being

$$1.36/1.03 = 1.33 = +33\%$$

These two estimates of change in effective catchability, + 11% and + 33%, are measures of the extent to which gross catch per unit effort (in numbers) overestimates the true increase in the number of fish in the fishable stock in June 1945 compared with pre-war due to sex differences. A further bias, opposite in direction, arises in the use of catch in weight per unit effort as a measure of the change in stock biomass in such circumstances. This is because the weight of mature male plaice becomes progressively less than that of mature females with increasing age; therefore the gross average weight of an individual fish (sexes combined) in the post-war catches was less than in the pre-war ones because the proportion of mature

males was higher. From the catch sex-ratios of Table 4, the ratio of weight of male to female plaice at each age are given in Table 5, and the percentage composition by weight of the age-groups comprising the pre- and post-war catches also given in Table 5, the average weight of an individual fish in the post-war catches is found to be about 6% less than in the pre-war ones because of the higher proportion of males.

Table 5. Percentage age-composition by numbers and weight of pre- and post-war catches, and average weight of males to females at each age. Mean of Lowestoft and Grimsby samples.

	% by numbers		Average weight male/female		% by weight	
Age-group	1931-38	June 1945	1931-38	1945-46	1931-38	June 1945
II	2.1	-	1.oo	o.97	1.1	-
III	18.9	-	o.94	1.oo	11.8	+
IV	34.4	2.3	o.91	1.o3	26.3	1.3
V	24.6	7.4	o.86	1.oo	25.5	5.2
VI	1o.9	36.o	o.78	o.93	14.6	31.o
VII	4.6	24.2	o.73	o.77	8.o	24.5
VIII	1.9	13.2	o.68	o.72	4.1	15.o
IX	1.o	7.8	o.63	o.69	2.7	9.7
X	o.7	5.5	o.59	o.63	2.1	7.6
XI	o.4	2.3	o.57	o.57	1.5	3.5
XII	o.3	o.8	o.63	o.56	1.3	1.3
XIII	o.2	o.5	o.59	o.53	1.o	o.9

The resultant bias in gross catch (in weight) per unit effort in June 1945 as a measure of the change in stock biomass compared with pre-war is therefore either

$$1.11 \times o.94 = 1.o4 = + 4\%$$

or

$$1.33 \times o.94 = 1.25 = + 25\%$$

according to whether it is assumed that the relative catchability of the younger males remained the same or increased. The first of those biasses is so small that it can for all practical purposes be neglected, this despite the considerable difference in catchability of the sexes and the marked increase in sex-ratio in the post-war catches. The second could be a more substantial error, but is clearly generated by the unproven assumption that the catchability of the younger males in the post-war fishery had increased relative to females, and as such is a maximum estimate of error. Strictly speaking, the opposite assumption, that the change in r_q was due to a relative decrease in the catchability of females, is equally valid on the evidence available, in which case the effective catchability of the post-war stock would have been less than the pre-war, not greater. In view of these uncertainties it is therefore of relevance to review briefly some other evidence bearing on the relative catchability of male and female plaice.

The Phenomenon of Differential Catchability of Male and Female Plaice

The predominance of males in catches at spawning time has of course long been recognised as a feature of plaice fisheries. Early writers (e.g. Hefford, 1916) were inclined to the view that this was sufficient to explain the gradual decline of the proportion of males in the older age-groups, and assumed that the sexes were equally catchable at other times of year. More recently, Simpson (1959) has recorded sex-ratios as high as 5o in age-group II, and between 5 and 1o in age-groups IV and V on the Southern Bight spawning grounds in 1948-5o. How much this is due to the earlier maturation of males than females, or because they stay longer on the spawning grounds, or possibly because their reaction to the approaching gear makes them more intrinsically "catchable", remains unresolved by such evidence alone; there is, however, some inferential evidence to suggest that the greater catchability may not be confined to the spawning season or even to fish which have reached maturity.

A peak in the sex ratio at spawning time is present in the commercial catch data analysed here. Figure 5 shows the proportion of males, on a logarithmic scale, in the catches of age-groups V and VIII at Lowestoft (solid circles) and Grimsby (open circles) separately in 1946-47, which brings out two interesting features. One is that although the sex-ratios are usually highest at spawning time (December to February) the seasonal trend does not appear to be strictly confined to those months, and there is a suggestion of a secondary peak in the summer, especially in the Lowestoft catches. The other is that the sex-ratio in the Grimsby catches is usually lower than in the Lowestoft ones, the difference being more marked among the older fish than the younger and occurring in both winter and summer. Probably this is due, mainly at least, to a difference in the areas fished by the two fleets, although this is unlikely to have been very marked in the immediate post-war fishery.

If true differential catchability is in fact confined to the spawning season it might be expected that it would be also restricted to mature fish. It is therefore relevant to examine briefly the data from the lines of trawling stations running roughly at right angles to the Dutch coast into the southern North Sea which were worked by Dutch and English research vessels in 1950-53, since the catches were of mainly immature fish. Figure 6 shows the total number of male and female plaice of age-groups II, III and IV caught at each station of the Texel Line in 1950 and 1951, which were worked in the same month of each quarter excepting July 1951. A complication is that the mean distance from the coast of males at each age is a little greater (1-6 miles, on average) than that of females. Even so, it is clear that there is a preponderance of males at all except the innermost stations, and it seems unlikely from the general shape of the distributions that there could in reality have been a concentration of females close to the coast sufficient to make much difference to the overall sex-ratios. The full evidence is not, however, entirely consistent. Thus, included in Table 6, page 9, are sex-ratios from the other two occasions when the Texel Line was worked (April 1952 and January 1953), and from the parallel IJmuiden Line which was worked in April of the years 1950-52. Of the 39 ratios, 23 are significantly greater than unity at the 0.05 probability level (underlined in Table 6), 14 do not differ significantly from unity, and 2 (parenthesised, both in age-group II) are significantly less than unity. The data as a whole are therefore consistent with the hypothesis that males, throughout the year and even when immature, are generally speaking more readily caught by a trawl than are females. Other possible explanations are that the true sex-ratio has usually been altered in favour of males at a still earlier stage of the life-history - perhaps even at birth or that there has usually been a segregation of the sexes laterally along the coast during the first two years of life. Some such phenomena could be the cause of the two sex-ratios of Table 6 which are significantly less than unity, but in any event there is sufficient variability of the sex-ratio to imply differences in either the true or apparent abundances of the sexes which are rather remarkable at such an early age and which cannot be related to maturation.[x]

The limitation of all evidence from catches alone is that the true sex-ratio on the grounds can only be inferred or guessed. Estimation of the differential fishing mortality rate of the sexes, as employed here, is a somewhat roundabout way of overcoming the difficulty; the more direct approach would seem to be by tagging experiments. Given a representative distribution of tagged fish in time and space, and assuming that practical complications such as the unreliability of reporting from spawning grounds noted by de Veen (1962) (a crucial point in this context) can be dealt with, the ratio of the recapture rate of males to females should give a direct measure of the relative catchability factor S_q as defined here, especially if the data are analysed by methods such as Gulland's (1961) which is specifically concerned with estimation of q. Recent tagging studies do not seem to have been much concerned with this question, but Borley (1916) analysed the early English plaice tagging data from the North Sea with particular reference to differences in the recapture rate of the sexes. He concluded that the recapture rate of males was higher than that of females at all times of year, although the difference was greatest at spawning time. From Borley's summary Table 7, the mean ratio of male to female recapture rate is 1.62 in the winter (January to March) and 1.04 in the summer (July to September), which latter does not appear likely to differ significantly from unity.

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x) A possible cause of this variability is diurnal variation in the catches affecting males and females unequally, but the information to test this was not available to the author at the time of preparation of this paper.

Table 6. Sex-ratio in catches of age-groups II, III and IV on Texel and IJmuiden Lines of trawl stations.

Line	Date	II			III			IV		
		F	M	S_c	F	M	S_c	F	M	S_c
Texel	Jan. 1950	323	214	1.51	295	173	1.71	125	5o	2.5o
	Apr. 1950	182	169	1.o8	359	3o2	1.19	336	266	1.26
	July 1950	178	137	1.3o	158	132	1.2o	1o5	96	1.o9
	Oct. 1950	11o	87	1.26	16o	1o5	1.43	92	66	1.39
	Jan. 1951	262	144	1.82	312	133	2.35	174	72	2.42
	Apr. 1951	142	134	1.o6	214	168	1.27	257	2o4	1.26
	Oct. 1951	247	188	1.31	114	1o4	1.1o	14o	117	1.2o
	Apr. 1952	473	811	(o.58)	679	563	1.21	269	2o3	1.33
	Jan. 1953	258	276	o.93	176	2o2	o.87	44	42	1.o5
	Mean ratio			1.21			1.37			1.5o
IJmuiden	Apr. 195o	382	464	(o.82)	248	166	1.49	158	14o	1.13
	Apr. 1951	86o	624	1.38	317	146	2.17	199	115	1.73
	Apr. 1952	331	311	1.o7	219	162	1.35	49	51	o.96
	Apr. 1953	259	2o2	1.28	196	156	1.26	82	7o	1.17
	Mean ratio			1.14			1.57			1.25

However,
the summer value is affected by two particularly low ratios from small numbers of fish; if the individual ratios are weighted roughly by the square root of numbers, the weighted mean summer ratio becomes 1.1o, the winter ratio being 1.67; this is suggestive but no more. In view of the major changes in plaice fishing methods and gear which have occurred in the past (e.g. the introduction of the Danish seine) and are still happening (e.g. the re-introduction of the beam trawl), a better understanding of the intrinsic catchability of the sexes would be worth having, and properly designed tagging experiments seem likely to offer a fruitful line of investigation.

Conclusions

The changes that had occurred in the sex-ratio in the North Sea plaice stock when fishing resumed in 1945, and the immediately following trends, are broadly consistent with what would be expected if males were normally more catchable than females. Thus the scarcity of males in the older age-groups of the pre-war stock is evidently due, partly at least, to them being "fished-out" more rapidly than females owing to their greater catchability; as would also be expected, their abundance had increased much more than had that of females in 1945 after six years' respite from fishing. Figure 4 shows in graphical form the estimated changes in sex-ratio of the fished stock from Table 4, where it can be seen that by the end of 1947 the sex-ratio in all except the oldest age-groups of the stock had become nearly the same as in the pre-war stock. Certain other features of this diagram are less easy to explain. The uncertainty attaching to the relative catchability in the younger age-groups has been referred to previously; the assumptions made in Table 4 and Figure 4 result in stock sex-ratios in these age-groups which are about unity and similar in both the pre- and post-war fisheries, but imply a substantial difference in catchability between the two periods. This apparently greater relative catchability of

males in the post-war fishery also extends to age-groups V and VI, and may have been partly due to a greater concentration of fishing in the south-eastern North Sea than pre-war (see Margetts and Holt, ibid.). More surprising are stock sex-ratios appreciably greater than unity in the previously unfished age-groups V and VI in June 1945 and even in December. This may reflect a later onset of maturity than in the pre-war stock, and while there does not seem to be direct evidence to test this, it is certainly the case that the average age at recruitment to the post-war fishery was at least a year higher than pre-war.

A proper interpretation of peculiarities such as these would require a more detailed analysis of the data than is possible here; it would need to take account, amongst other things, of the differences in the magnitude, sex-ratio and distribution of the catches of the Lowestoft and Grimsby fleets separately, instead of combining them rather superficially by simply averaging their catch per unit efforts, as has been done here. This mean, in effect, treating males and females throughout as separate populations - which indeed they are in all important respects excepting, presumably, that their initial year-class strength is the same, although it is their differential catchability which is likely to be responsible for the biggest discrepancies if sexes are combined, especially if this is sensitive to changes in fleet distribution or type of gear. Nevertheless, the answer to the main question which it was intended to explore seems to emerge clearly enough. It is, that of the total bias in catch per unit effort as an index of abundance in the immediate post-war fishery, which Gulland (No. 14, this Symposium) estimates as at least 75% in June 1945, only a minor part, at the most about one-third, can be attributed to differences in catchability and relative abundance of the sexes. The main peculiarity of the post-war fishery compared with the pre-war is that the total mortality rate of both sexes (except the oldest fish) was apparently much higher than can be accounted for by the amount of fishing (Figure 3). Different reasons must be sought to explain this, such as a greater concentration of fishing on the medium sizes and ages of fish (for which there is some indication from Table 5), or changes in the local distribution of fish and fishing within the smallest statistical unit of area, as suggested by Gulland.

Summary

1. A feature of the English North Sea plaice fishery during the immediate post-war period (1945-47) was a marked increase in the proportion of males to females in the catches compared with the pre-war fishery, suggesting that males are more "catchable" than females. This was confirmed by finding that the fishing mortality coefficient for males (and hence their relative catchability) was some 5o% higher than that for females in both the pre- and post-war fisheries.

2. The sex-ratio of the fished stocks in the two periods was calculated by dividing the sex-ratio in the catches by the relative catchability of males to females. In this way it is estimated that stock as fished in June 1945 might have been up to 33% more "catchable" in numbers, and 25% more by weight, purely through differences in the proportions and catchability of the sexes, although these are maximum figures.

3. "Catch per unit effort" (sexes combined) therefore overestimates the true increase in stock in June 1945 compared with pre-war for this reason alone, but this can account, at most, for only about one-third of the bias detected by Gulland (No. 14, this Symposium). There remains the anomaly that the fishing mortality rate of both males and females was considerably higher in the post-war fishery than pre-war without there being, apparently, a corresponding increase in fishing intensity to account for it.

4. Some evidence is discussed which suggests that male plaice, at all times of year and whether mature or immature, may be intrinsically more readily captured by a trawl than females, although the effect is most marked among mature fish at spawning time. It may be worth while to revive something of the interest in this phenomenon shown by the pioneer fisheries scientists, using modern tagging techniques and with reference to various types of fishing gear.

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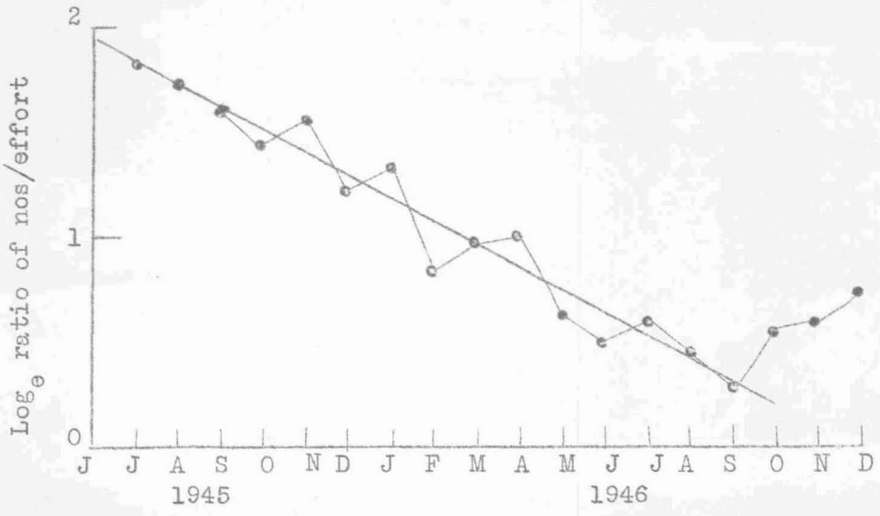

Figure 1. Monthly index (log$_e$ units) of number of North Sea plaice landed per unit effort during the immediate post-war fishery. The relative rate of decline is about 1.3

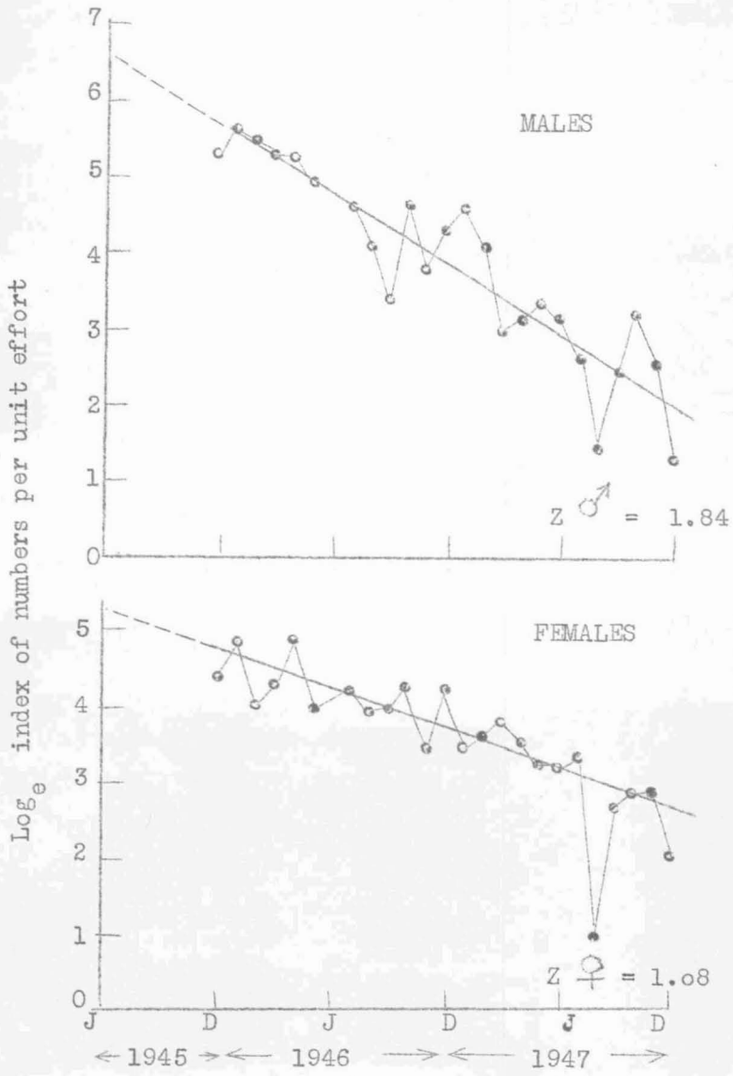

Figure 2. Monthly index of abundance of the 1939 year-class of plaice in the immediate post-war fishery to show rate of decrease of males and females separetely.

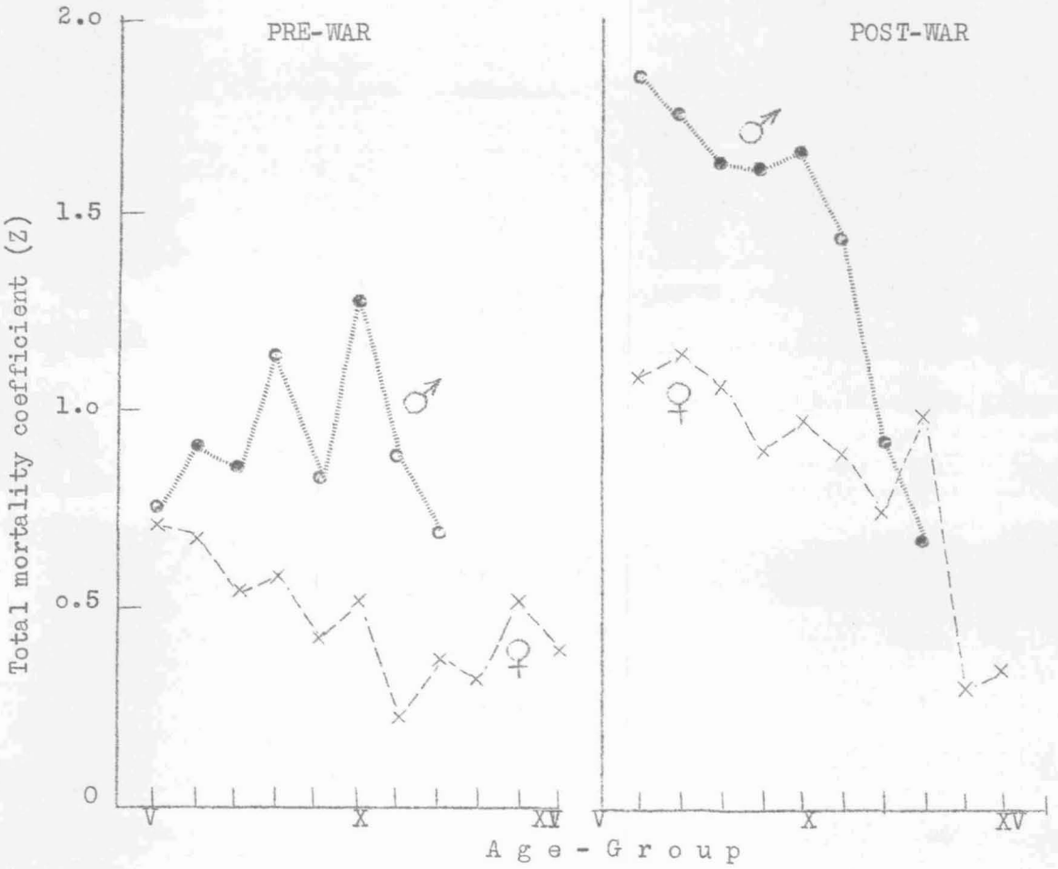

Figure 3. Total mortality co-efficients in fully-recruited age-groups of male and female plaice in the pre- and post-war fisheries.

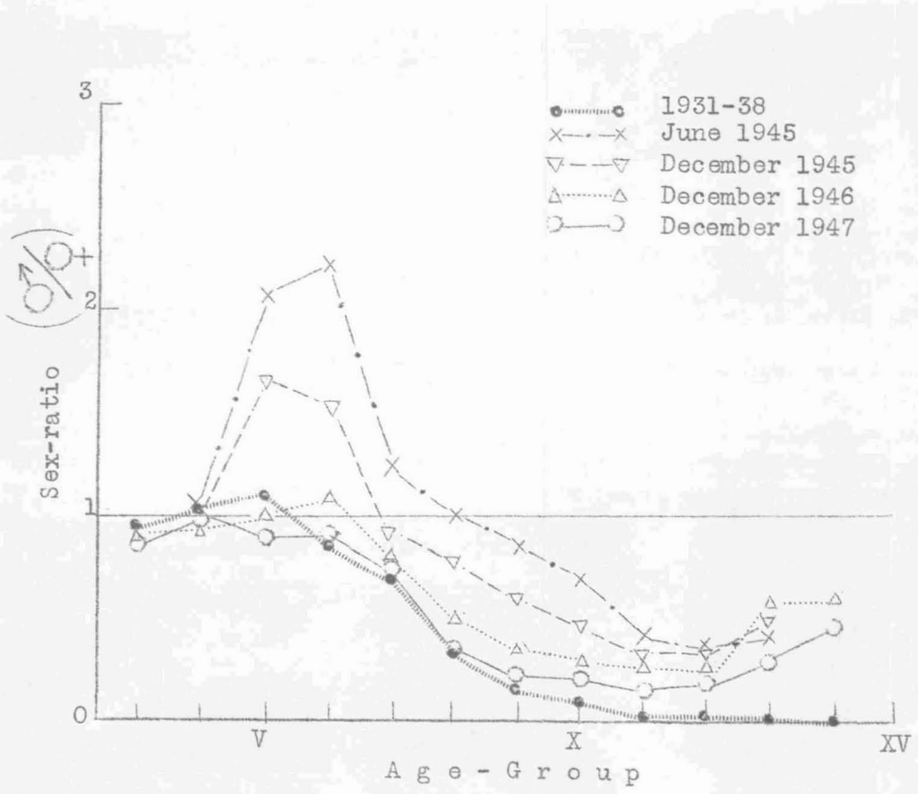

Figure 4. Estimated sex-ratio in age-groups comprising the fished stock of plaice in the pre-war fishery and at various times during the immediate post-war period.

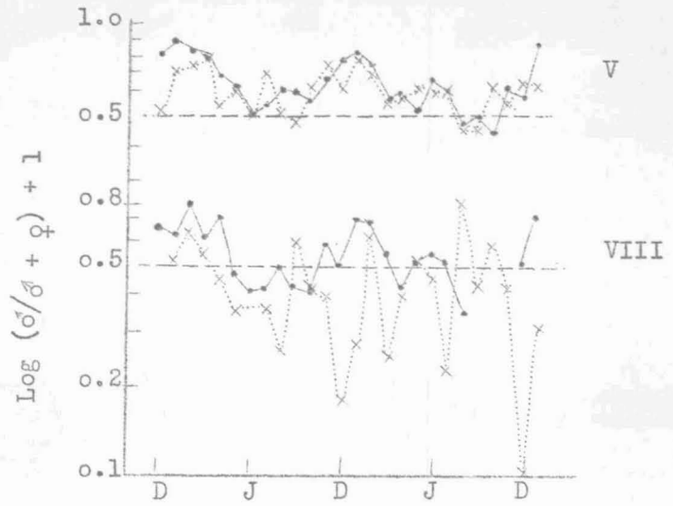

Figure 5. Sex-ratio in landings of plaice of age-groups V and VIII at Lowestoft and Grimsby.

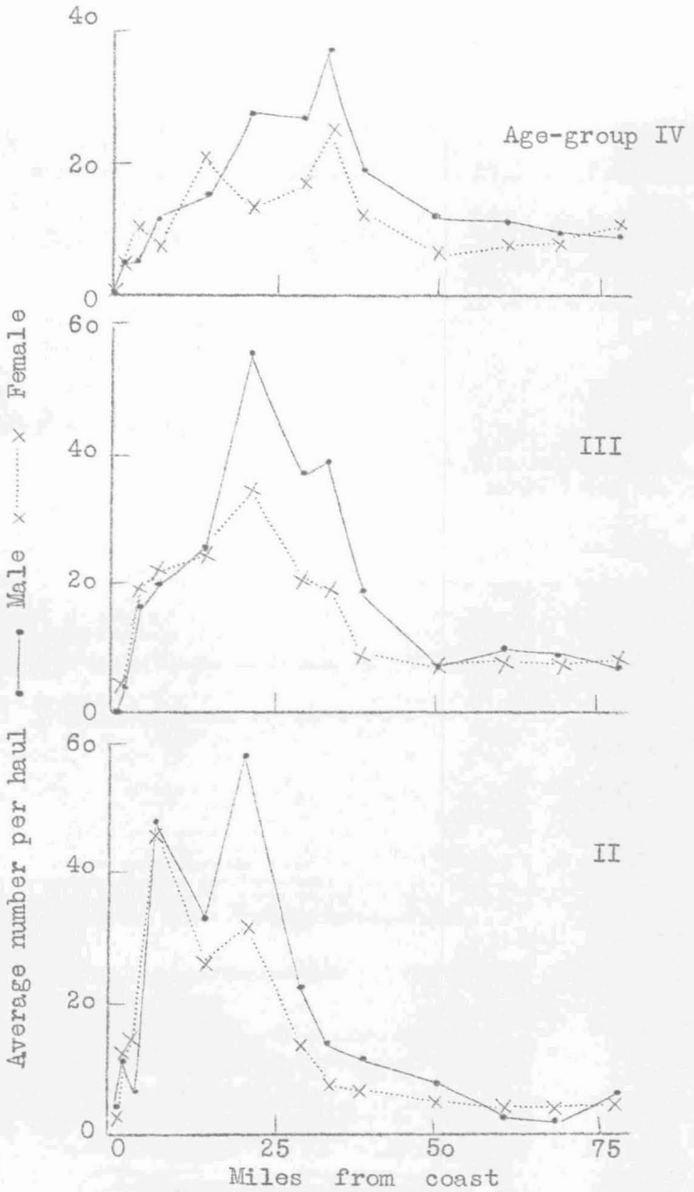

Figure 6. Length composition of research vessel catches of male and female plaice of age-groups II, III and IV taken on Texel Line, 1950-51.