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The study of fish populations by the analysis of commercial catches
A statistical review

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Statistically, the study of fish populations from an analysis of commercial catches may be regarded as two successive sampling processes: First, the commercial catch forms a sample from the total population and second, a sample is taken from the catch for scientific examination, e.g. length measurement or age determination. In this paper these two processes will be analysed from the statistical viewpoint, in order to find a method of sampling and subsequent analysis giving the least variance and bias. Roughly speaking, the variance is the scatter, about their mean value, of successive estimates of some quantity, e.g. the average length of fish in the catch. The bias is the amount whereby this mean value of the estimates differs from the true value. Thus the variance will become obvious in any series of observations, while bias may be difficult to detect. The fact that repeated samples give very much the same answer can be no guarantee that there is no bias, or even that the bias is small.

In a particular sampling system, the variance will be approximately inversely proportional to the amount of sampling, that is increasing the sampling will decrease the variance, and vice-versa. Bias cannot be reduced by increasing the amount of sampling, but only by using a correct sampling system. The "best" system of sampling and subsequent analysis, judged on a statistical basis, will be that which is as far as possible free from bias, and which gives the smallest variance for a given sampling effect. Looked at another way, it will require the smallest amount of sampling to reduce the variance to some desired level. The sampling pattern giving the smallest variance for one estimate will not necessarily be that giving the smallest variance for some other estimate; for instance the best sampling design to find the average age may not be the best for finding the ratio of males to females. Therefore the choice of sampling pattern depends, possibly quite critically, on the information ultimately required. In population work the most important estimates are for the fundamental parameters: growth, natural and fishing mortality and recruitment. Of these, the most difficult to estimate, and the most liable to sampling errors, are the mortalities. The methods of estimating them, and the type of information required, are discussed more fully by Beverton and Holt (No. 24). The most powerful estimates are in the form of indices of abundance for each age-group; i.e. numbers proportional to the total numbers of fish of that age in the sea, the coefficient of proportionality being constant from year to year. Less useful is the relative age-composition during each year; e.g. percentage age-composition. It may not be generally realised that a faute de mieux estimate of mortality may also be made, when age-determinations are not available, from similar data on length-composition. Beverton and Holt also discuss methods of estimating fishing mortality alone, which do not directly need sampling of the commercial catch in the manner described here, though catch sampling is needed for estimation of total mortality.

For the ultimate purposes of this paper, therefore, the quantities for which estimates will be made, and bias and variance calculated, will be

* A fuller exposition of this subject by the same author is in Press. (Fishery Investigations, Series II)

indices of abundances for each age and length group. As an intermediate step, but also intrinsically very important, the numbers of fish landed of each age and length group will be estimated. This will also give a relative age and length composition. The latter problem will be discussed in the first part of this paper; the second part will deal with estimation of the composition of the stock.

The direct sampling of the commercial catch for length and age composition presents in general a straightforward statistical problem, and the degree of variance may be readily calculated. Bias may arise both in the choice of the section of the catch from which to sample, and the choice of fish to be measured within this sample. After the fish are landed and sold, a single ship's catch is likely to be divided among several different merchants. Each will tend to buy that size of fish which is particularly suited to his requirements, so that measurements of fish taken at any particular merchant are unlikely to be representative of the whole landings. Therefore, to avoid bias from this cause, the samples have to be taken directly from the landings, before the catch of each ship is split up. Even then bias may occur when the catch is divided into two or more categories, on a basis of size or condition of the fish, unless a sample is taken from every category. This is obvious when the basis of categories is size, but it is also true when the catch is divided according to the condition of the fish. For instance at Lowestoft, the main categories for plaice are large, medium and small, but particularly after the spawning season, thin and damaged fish are sorted out. These last seldom amount in weight to more than a few percent of the total landing, but may contain half the biggest and oldest fish. Obviously the number of old and big fish would be seriously under-estimated if the three main categories were taken as representative of the whole catch. This is illustrated in Table I below.

Table I Hypothetical example of catch by categories of a Lowestoft trawler

		Large	Medium	Small	Thin	Total
Weight landed (stones)	= A	30	100	480	10	620
Weight measured "	= B	10	5	3	10	
Raising Factor	= A/B	3	20	160	1	

Length group (cm)			25-29	30-34	35-39	40-44	45-49	50+	Total
Number Measured	Large	C				16	33	15	64
	Medium	D		2	47	27			76
	Small	E	26	41	8				75
	Thin	F			7	15	14	14	50
Number Landed	Large	C x 3				48	99	45	192
	Medium	D x 20		40	940	540			1,520
	Small	E x 160	4,160	6,560	1,280				12,000
	Thin	F x 1			7	15	14	14	50
	Total		4,160	6,600	2,227	603	113	59	13,762
	Total Less Thin		4,160	6,600	2,220	588	99	45	13,712

In this sample which though imaginery, is realistic, the weight of the thin fish is barely 1% of the whole, but they contain nearly a quarter of those fish above 50 cm.

The choice of sample within a category is probably unimportant, the difference in composition between different parts of the same category being likely to be small. If such a difference does exist, it is likely to be most marked between the first and last fish landed, i.e. probably between the last and first fish caught. During one month at Lowestoft two samples were taken from the same category off a number of different ships, the samples comprising respectively the first and last fish landed. No significant difference was found between samples from the same ship, though there was considerable differences between ships.

Bias may also arise through personal selection within the sample taken for measuring. If only a fraction of the fish available for selection are picked up and measured, this fraction, will for most people, contain rather too many big fish. Often too, the top few fish in a box have been selected and put there to impress the buyers. For instance, a sample of 50 fish picked carelessly off the top of a box of small plaice (containing altogether some 300 fish) may have an average length some half-centimetre greater than the rest. This is an important difference when the whole length range is only a few centimetres. This bias is easily avoided by measuring all the fish in a box, which makes selection impossible, or by taking all the fish from one side, so that the sample measured consists of all the fish originally to one side of the box, and again selection is impossible or difficult. This same problem arises in sampling a haul by a research vessel. Here again it is best, if at all possible, to take the whole catch as a sample. But, because there may be a tendency for the big fish all to go to the side, even taking all the fish in one part of the catch may give an unrepresentative sample. Such selection will be most likely to occur when the size-range of the fish is great. For instance it is more probable in a sample of cod, where the biggest fish may be over 10 times the size (by weight) of the smallest, than for herring where the biggest may be only twice the size of the smallest.

The variance in the length distribution may often be reduced by a suitable choice of sampling method. In a paper read at the last meeting of the I.C.E.S. at Copenhagen (Gulland, 1953), it was shown that the variance using a large number of small samples was considerably less than when the same number of fish were measured in a few big samples. For instance, for medium plaice, the same accuracy can be obtained with a quarter the effort by taking samples of 50 fish in each sample, than with rather fewer samples of 400 fish in each sample. This result, indicating an upper limit to the efficient size of sample of around 50 fish, has been found to be applicable to all species of fish (cod, plaice and hake) for which it has been tested.

The variance may also be reduced, and possible bias eliminated, by stratified sampling. That is, the total landings may be divided up into a number of different strata e.g. by ports, method of capture, time of landing etc. Samples are taken from each separate stratum and estimates made of its length composition. These separate estimates are then combined to give the length composition of the total landings. The more dissimilar the strata, the greater is the benefit gained by using stratified sampling.

The most advantageous stratification is therefore the division provided by market categories based on size. The estimate of the length distribution of the catch of the vessel which is sampled is, of course, obtained by the use of stratified sampling, (see Table I), but the estimates for the landings of all vessels may or may not involve the use of categories. The two methods are demonstrated in Table 2, which shows the further analysis whereby the catch of one ship, given in Table 1, is raised to give the total catch of all ships.

Table 2. Hypothetical example to show the use of categories to obtain total length distribution from that of a single ship.

		Large	Medium	Small	Thin	Total
Total Weight landed	A	750	1,500	3,840	110	6,200
Weight landed by sampled ship	B	30	100	480	10	620
Raising Factor	A/B	25	15	8	11	10

	length (cm)		25-29	30-34	35-39	40-44	45-49	50+	Total
Number in Sample	Large	C				48	99	45	192
	Medium	D		40	940	540			1,520
	Small	E	4,160	6,560	1,280				12,000
	Thin	F			7	15	14	14	50
	Total	G	4,160	6,600	2,227	603	113	59	13,762
Total Number Landed	Large	C x 25				1,200	2,475	1,125	4,800
	Medium	D x 15		600	14,100	8,100			22,800
	Small	E x 8	33,280	52,480	10,240				96,000
	Thin	F x 11			77	165	154	154	550
(i)	Total	G x 10	41,600	66,000	22,270	6,030	1,130	590	137,620
(ii)	Sum of Categs.		33,280	53,080	24,417	9,465	2,629	1,279	124,150

Ignoring categories, the total length composition is obtained by multiplying the catch of the sampled ship (row G)by the ratio of total catch to sample catch. The result is given in the last but one row. The composition of the individual categories may be calculated, and then added together, to give the sums in the last row. Because the sampled ship contained relatively more of the category small and less large, it is to be expected that, by ignoring categories, the numbers in the smaller length-groups would be over-estimated and those in the larger sizes under-estimated. This can be seen at once to be so, by comparing the totals in the last two rows. The gain in accuracy i.e. reduction in variance, by this use of categories is indicated in Table 3. This shows, for the Lowestoft plaice landings of October - December 1950, the estimated numbers landed and their variances, in each 5-cm. length group. Three methods of calculation were used; (i) treating the landings as a whole (ii) dividing the landings according to market categories or (iii) dividing the landings into areas of capture.

Table 3. Estimates and variances of the numbers of plaice in each length group landed by Lowestoft trawlers in October - December, 1950 using three methods of estimation.

Length-Group	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55+
				Estimated Numbers Landed x 10^{-3}				
Method (i)	26.81	2,063	932	276.5	132.6	66.01	35.50	22.22
Method (ii)(categ.)	28.56	2,213	952	267.2	118.6	58.98	31.83	19.46
Method (iii)(Area)	22.62	2,037	975	295.5	128.8	66.62	32.76	18.40
				Variances x 10^{-6}				
Method (i)	42.58	18,294	2,778	392.7	132.5	29.42	16.48	8.78
Method (ii)(categ.)	29.56	2,174	1,320	143.5	30.8	14.73	3.50	2.99
Method (iii)(Area)	32.68	14,224	3,301	626.5	147.3	35.06	10.38	6.56

Besides stratification by market categories, when these are sufficiently well defined to be applicable, the English landings are also divided by ports and by month of capture. While these stratifications do not reduce the variance to anything like the same extent as does the use of market categories, they are of great importance in eliminating possible bias. This is because it is much easier to take a truly random sample at one port for a short period than from landings at several ports and extending over a long period. Thus, without stratification, one section of the landings is very likely to be over-represented in the samples. For instance more plaice from North Sea trawlers are landed at Grimsby than at Lowestoft; at the same time, for practical reasons, more fish can be measured at Lowestoft than at Grimsby. Thus, the Lowestoft landings are over-represented in the samples; they contain, moreover, rather smaller fish, so without stratification by ports, there would be a bias towards under-estimating the average size of fish.

For much theoretical population work the knowledge of the age-composition is rather more important than that of the length-composition (see Beverton and Holt No. 24). Fortunately, the age of most commercial fish in European waters can be determined from scales or otoliths with a fair degree of accuracy. Apart from any definite errors in the age-determinations, a definite bias can be introduced by ignoring in the calculations those otoliths or scales which are difficult, but not impossible, to read. These will generally be the larger or more slowly growing, and hence older fish, and their omission would give a bias towards under-estimating the average age. The degree of this bias for the North Sea plaice age-determinations is indicated in Table 4. This is based on the regular plaice sampling at Lowestoft, for which an age is attached to every otolith read, those which are difficult to read being recorded as doubtful e.g. 8?.

Table 4. Average age of Lowestoft and Grimsby otolith samples, showing difference between definite and doubtful otoliths

Length Group	Number of Fish			Average Age		
	Queries	Definite	Total	Queries	Definite	Total
25-29 cm	22	338	360	4.4	4.1	4.1
30-34 cm	27	332	359	5.7	5.2	5.2
35-39 cm	46	313	359	7.6	6.1	6.3
40-44 cm	70	170	240	8.8	7.0	7.5
45-49 cm	99	139	238	11.0	3.7	9.6
50-54 cm	120	117	237	12.2	10.9	11.6
Total	384	1409	1793	9.8	6.1	6.9

Out of the 1793 otoliths examined, a little under a quarter, (384) were recorded as doubtful, but the proportion of doubtfuls varied greatly with the size of fish. Only 5% of the smallest (25-29 cm) length group, but over half the biggest (50-54 cm), were doubtful.

Taking all the otoliths together, the average age of the queried was nearly four years greater than that of the definite, and their omission would apparently reduce the average age from 6.9 to 6.1 years, a very considerable degree of bias. This difference is partly due to the queried, within any length group, being rather older than the definite, but also to the average size being considerably greater; 44.8 cm against 36.8 cm for the definite. The latter difference must be real, and cannot be the effect of any errors in the age-determination of the difficult otoliths. The former difference may either mean that the age of the slower growing fish is harder to determine, which is quite likely, or that there is a tendency to over-estimate the age when the otolith is difficult to read.

Because they are likely to be perhaps a year or so out either way, the inclusion of doubtful otoliths will tend to blur the differences between adjacent year-classes. The otoliths belonging to a strong year class, but recorded in error as belonging to an adjacent, weak year class will not be balanced by the otoliths in fact belonging to the weak year class, but recorded as belonging to the strong year class. Therefore when there is a particular interest in the comparative strengths of year-classes rather than in a correct overall age-distribution, it may be better to risk a bias in the age composition, and omit the doubtful otoliths.

The age composition may be obtained by sampling directly for age in exactly the same way as for length-distributions. However, because the length of a fish usually gives a good guide to its age, and also many length measurements may be done as quickly as one age-determination, the age composition may be often most easily obtained from a large number of length measurements, and a relatively few age-determinations. The method has been described and used by Fridriksson (1934) and others, and is illustrated in Table 5 taken from Table 1 of Fridriksson.

Table 5. Hypothetical example of age-length key applied to cod (from Fridriksson 1934)

Length	Numbers		$^x/_y$	Number Aged		Total	
	Total (x)	Aged (y)		Age a	Age b	Age a	Age b
100 +	5	1	5		1		5
95-99	20	5	4		5		20
90-94	50	10	5		10		50
85-89	72	18	4	1	17	4	68
80-84	168	42	4	8	34	32	136
75-79	480	12	40	9	3	360	120
70-74	210	7	30	7		210	
69	95	5	19	5		95	
Total	1,100	100		30	70	701	399
		Percentage		30	70	63.7	36.3

Here 100 fish were measured and had their age determined, and a further 1,000 were measured. The difference between the age-composition based on 100 fish, and that based on 1,100 is very marked. This is because there is a big difference between the length composition of the two sets of fish, and also in the age-composition of different length-groups. The practical advantages of the method would therefore be expected to be greatest when there was a big variation in length composition between successive samples, and when the fish grow quickly and fairly uniformly. Both these conditions are satisfied in many commercial fisheries.

Possible bias in the method is small, assuming the length data to be unbiassed. It could arise, not through sampling too many fish of one age, but only by sampling too many fish of one age within a single length-group, which seems unlikely to happen. Any tendency to include too many big, or small, fish in the sample for age, is immediately corrected for. This can be taken advantage of to give better accuracy for the older and scarcer fish. In a random sample, one or two length-groups, and a few age-groups, will usually predominate, and the abundance of these ages will be known reasonably accurately. Conversely the older age-groups will occur only rarely, and their abundance will be only poorly determined. It is often best to know the abundance of most year-classes about equally well, and this may be achieved by using an age-length key and taking samples for age-determination not randomly, but so as to give about equal numbers in each length-group.

The effect on the variance of the age-composition, of the use of an age-length key, and of non-random sampling, is shown in Table 6. This gives, for the Lowestoft plaice landings of January and February 1950, the estimated numbers landed in each age-group, and their variance and coefficient of variation. These have been calculated for two methods; (i) by direct age-sampling and (ii) by use of an age-length key. Thirdly the variance and coefficient of variation, to be expected if, in using an age-length key, the same total number of otoliths had been taken, but with more from big fish, and fewer from small fish, have been calculated.

Table 6. Number and variances of age-groups of plaice landed at Lowestoft in January and February 1950, as estimated by different methods

Age	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII+
Direct Age Sample											
Numbers x 10^{-3}	191	986	1,621	610	290	154	179	148	80	55	123
Variance x 10^{-6}	3,683	98,000	119,000	22,300	3,780	645	4,490	304	1,150	1,660	1,320
Coeff. of Var.	31.8	31.8	21.3	24.4	21.2	16.5	37.4	11.8	42.4	74.0	29.5
Age-Length Key											
Number x 10^{-3}	215	1,114	1,870	689	321	153	172	127	70	52	88
Variance x 10^{-6}	1,545	8,300	13,100	4,340	2,070	875	932	646	378	299	288
Coeff. of Var.	18.3	8.2	6.1	9.6	14.2	19.3	17.7	20.0	27.7	33.3	19.3
Age-Length Key (revised numbers)											
Variance x 10^{-6}	2,990	12,300	17,400	5,400	2,270	671	632	388	232	222	161
Coeff. of Var.	25.4	10.0	7.1	10.7	14.9	16.9	14.6	15.5	21.7	28.7	14.4

As the estimates of variance, particularly for the direct sampling of age, are based on only a few samples, they are not likely to be very accurate. In particular the estimated variances for the VII and IX groups are almost certainly too low, and those for the VIII and XI group too high. Comparison of the figures for the methods show that, because they contained relatively too many large fish, and too few small, the direct age-samples give, for the VII and older age-groups, estimates higher than with the age-length key and consistently lower for ages II to IV. Except for the VII and IX groups the variance using an age-length key is less, and usually considerably less, than that for direct age sampling. Admittedly some of this improvement must be set against the effort involved in the samples measured, but not examined for age, but the greater part of the improvement is due to the change in method, and means a definite reduction in the variance for a given sampling effort. The last two rows of Table 6 show how increasing the proportion of large fish otolithed has increased the accuracy among the older fish, at comparatively small loss of accuracy among the younger fish. The abundance of the latter is still known relatively more accurately, but this effect could, if necessary, be eliminated or even reversed by taking still more otoliths from the older fish.

Because the age-length key depends only on the age-at-length i.e. the growth, which is liable to be less variable than the sample age-composition, it does provide a more or less reliable method whereby results gained from age and length studies on one section of the catch or population may be extended to a section for which length-measurements only are available. For instance, market measurements of the commercial catch may be converted to an age-composition by means of otolith samples taken from the catch of a research vessel. Again, when several countries are fishing one area, it may happen that age and length measurements may be done by only one country, but that length-measurements are done by several. For instance, at present only length-measurements are being carried out on samples of the catches of cod from Iceland landed by English trawlers. For, at least, a first approximation, age-samples from Icelandic catches from similar areas could be used to form an age-length key applicable to the English catches, and thus to determine the number of fish of each age-group in the English landings.

In considering the commercial catch as a sample of the natural population of a species at the ages liable to capture, it is useful to distinguish sampling for the density, or abundance, and sampling for structure, i.e. length or age composition. In assessing the density, each haul may be considered as giving a sample of the density of the fish at the position of the haul, and we will suppose that for a given haul;

$$d_i = cD_i$$

where d_i = catch in i^{th} haul
D_i = density of fish at the position of i^{th} haul
c = constant

that is, a single haul will take, on the average, a fixed proportion of the fish present. This is probably true for such gears as trawls and seines, though other kinds of gear such as long lines, may become saturated in heavy fishing, e.g. when most of the hooks are occupied, and take a smaller proportion when the density is high. However, on our assumption, when the results of several hauls are combined, we have

$$\sum d_i = \sum cD_i$$

or, taking the mean

$$\bar{d} = c\bar{D}$$

$$= c'D$$

where $\bar{d}$ = mean catch per haul, i.e. catch per unit of effort
$\bar{D}$ = average density of fish at the fishing positions
D = average density of fish over the whole region
c' = constant

The constant c' will be different from c, in general larger, because fishing will be done where the fish are most abundant, so that the average density at the fishing positions will be greater than the average over the whole area. As we are only attempting to find a number proportional to the density, or abundance, it is not necessary, or indeed possible, to know the value of c' Strictly then, bias will be impossible, but an analogous effect will be steady long-term changes in the average value of c' particularly from year to year. Possible sources of variation in c' include

(i) Random haul-to-haul variations
(ii) Weather
(iii) Behaviour of the fish
(iv) Skill of the fishermen
(v) Changes in the distribution of the fleet in space and time
(vi) Changes in the power and size of the ship, type of gear etc.

The first of these, though it may be large and give a coefficient of variation of say 60% for a single haul, becomes negligible when the number of hauls is large. For instance, in the mean of 10,000 hauls - not a very large number in relation to the activities of a whole fleet - a coefficient of variation of 60% for a single haul, is reduced to only 0.6%. Thus the variance from this cause may be reduced to a reasonable value, by having catch-per-unit-effort figures for possibly only a small sample of the fleet. Similarly the effects of weather, when averaged over a whole year, may be expected to be small, though possibly important over smaller periods of time. Changes in the behaviour of the fish, particularly for lines or gill-nets, which depend on the fish catching themselves, can have a large effect, particularly between different seasons of the year. However, the behaviour is likely to be the same at a given season, from one year to the next; also changes in behaviour are liable to be difficult to detect and estimate and will not be considered further in this paper. Similarly the skill of the fishermen will be assumed to be constant.

The most important source of variation of c' is formed by changes in the fishing power of the ships or gear, as these may be considerable; and,at least

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The first of these, though it may be large and give a coefficient of variation of say 60% for a single haul, becomes negligible when the number of hauls is large. For instance, in the mean of 10,000 hauls - not a very large number in relation to the activities of a whole fleet - a coefficient of variation of 60% for a single haul, is reduced to only 0.6%. Thus the variance from this cause may be reduced to a reasonable value, by having catch-per-unit-effort figures for possibly only a small sample of the fleet. Similarly the effects of weather, when averaged over a whole year, may be expected to be small, though possibly important over smaller periods of time. Changes in the behaviour of the fish, particularly for lines or gill-nets, which depend on the fish catching themselves, can have a large effect, particularly between different seasons of the year. However, the behaviour is likely to be the same at a given season, from one year to the next; also changes in behaviour are liable to be difficult to detect and estimate and will not be considered further in this paper. Similarly the skill of the fishermen will be assumed to be constant.

The most important source of variation of c' is formed by changes in the fishing power of the ships or gear, as these may be considerable; and, at least as important, they are likely to change consistently and steadily from year to year. For instance, between 1923 and 1927, the introduction of the Vigneron-Dahl gear raised the fishing power of steam trawlers by some 50% (Bowman 1932) and thus, relative to pre-1923, the density of fish after 1927, as estimated from the catch per hour of steam trawlers, will be over-estimated by 50%. Similar changes in the power of ship, have been taking place, over a longer period, in the English distant water trawler fleet. To a fair approximation, the fishing power of these trawlers is proportional to their gross tonnage. In 1930 the average tonnage of newly built distant water trawlers was some 350 tons; this has increased to 450 tons in 1947, and to some 600-700 tons now. The effort statistics on which the catch per unit effort figures are based must therefore be calibrated. This problem is further discussed by Beverton and Parrish in another paper (No. 25) at this meeting.

The relation between c' and c and hence the value of c' will depend on the relative distributions of the fish and the fishing. This is best discussed in two parts. First, on a single fishing ground, there will be a difference between the average density at the actual positions of the ships, and over the whole fishing ground, and secondly there will be a difference between the average density on the fishing grounds, weighted by the amount of fishing on each, and the average over the whole region inhabited by the stock. The first of these is dependent on the ability of the fishermen to find small local concentrations of fish, and is largely a matter of skill, though it may be affected by such items of gear as radar, or Decca, for more accurate navigation, or echo-sounder for better location of the fish. The second difference, which may be termed the concentration, will depend on the decision of the fishermen on which ground to go to, whether, for instance, to go a long way from port for good catches, or to stay nearer port for poorer catches. It is likely to be particularly important when two or more species inhabit more or less separate areas within the same region, e.g. haddock and plaice in the North Sea. Here a real increase in the density of haddock might mean more ships would fish for haddock rather than for plaice. They would thus leave the plaice area; the catch of plaice, for the same total North Sea effort would drop; and the apparent density of plaice would decrease.

The effect of varying distribution of fishing within one fishing ground is difficult to estimate, but the effect of concentration can be estimated and allowed for, provided sufficiently detailed information is available.

Suppose the whole region is divided up into a number of small sub-areas, in each of which the catch and effort are known. Then we can write, for the 1st sub-area.

$$D_i = \frac{1}{c} d_i$$

where D_i = Density in i^{th} sub-area
c = Constant
d_i = catch per unit effort in i^{th} sub-area;
assuming that the effects of non-uniform distribution within the area may be taken as constant.

Then if N_i = total numbers of fish in i^{th} sub-area
a_i = area of i^{th} sub-area
and similar symbols without the sub-script denote the values for the whole region, then

$$N = \sum N_i$$

$$N_i = a_i D_i$$

$$N = aD$$

$$\therefore \quad aD = N = \sum a_i D_i$$

$$= \sum a_i \frac{1}{c} d_i$$

$$\therefore \quad D = \frac{1}{c} \frac{\sum a_i d_i}{a}$$

i.e. the density index is the weighted mean of the catch per unit effort in each sub-area, the weighting factors being the size of the sub-areas. This equation is has increased to 450 tons in 1947, and to some 600-700 tons now. The effort statistics on which the catch per unit effort figures are based must therefore be calibrated. This problem is further discussed by Beverton and Parrish in another paper (No. 25) at this meeting.

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i.e. the density index is the weighted mean of the catch per unit effort in each sub-area, the weighting factors being the size of the sub-areas. This equation is effectively the same as that developed by Beverton and Holt (in Press) and Beverton and Parrish (this meeting) for the effective overall fishing intensity $\bar{f}$.
For if f_i and Y_i are the intensity (i.e. effort per unit area) and catch in the i^{th} sub-area; and Y the total catch,

$$\frac{Y}{a\tilde{f}} = cD = \frac{\sum a_i d_i}{a} = \frac{1}{a}\sum a_i \frac{Y_i}{a_i f_i}$$

$$\therefore \tilde{f} = \frac{Y}{\sum Y_i/f_i}$$

A numerical value for the concentration is given by the ratio of the simple fraction-total catch divided by the total effort - to the weighted index of density.

That is, concentration $= \frac{ad}{\sum a_i d_i} = \frac{c'}{c}$

or if there are n sub-areas, each of equal area

concentration $= \frac{nd}{\sum d_i}$

This ratio has been calculated for British steam trawlers fishing in the central North Sea (region IV b), west of 4°E, for the years 1947 to 1952. The sub-areas used were the usual statistical rectangles, approximately 30 miles square. For plaice the ratio has varied between 1.64 in 1948, and 1.42 in 1950, a decrease of 13%, and for haddock between 0.61 in 1947 and 0.86 in 1949, an increase of 40%. While for plaice, the preferred species in this region, the ratio is greater than unity, that for haddock, inhabiting a very different part of the area, it is rather less than unity. The changes in the concentration imply that the simple ratio of total catch to total effort may change by 13% for plaice, and 40% for haddock purely because of changes in the distribution of the fishing, without any real change in density.

Ideally, the choice of sub-areas should be such, (i) that they cover the whole stock of fish, (ii) that within each the distribution of fish and fishing is regular, and (iii) that some fishing is done in each, so as to provide an index of density. Often the fishing activities of a single country do not cover the whole stock. For instance, the English trawl fishery extends only erratically east of 4°E, so that English statistics alone cannot give a fully accurate index of the whole North Sea plaice stock; nor does the limit of consistent English trawling appear to correspond with any limit of a real biological subdivision of the plaice stock. However, the fishing by all countries taken together does cover pretty well the whole North Sea. Therefore provided the units of effort of each country are properly calibrated, see Beverton and Parrish (this meeting), an accurate index of density for the whole North Sea stock could be obtained by detailed combined international statistics.

A final source of variation in the relation between catch per unit effort and density lies in possible variation in time. This corresponds almost exactly with the effectsin changes in distribution in space and may be corrected in the same way. In many fisheries particularly for pelagic species the catch per unit effort changes, due to changesin behaviour of the fish, e.g. spawning concentrations, from season to season within the year. In general, more fishing will be done at times when the catch per unit effort is high, and if in one year proportionally more fishing is done at this time, the total catch will increase, giving an apparent increase in density. Just as for uneven spatial distribution, the year may be divided into periods, within each of which the catch per unit is more nearly constant. Then, the annual index of density, relatively free from changes in the temporal distribution of fishing, will be given by the mean of the catch per unit effort within each period.

All these corrections may be combined together to give the best index of density for the year. Within each interval of time and sub-area, the density index is the catch per standard unit of effort, and the density index for the year over the whole region, will be the mean of these separate catches per unit effort. The ratio of this index to the average density will be as near as possible constant. The area covered by the stock generally remains constant from year to year, so the index of density will serve equally well as an index of abundance, or total numbers. If the area is variable then the index of abundance will be area×index of density.

In estimating the structure of the population, that is its relative size and age composition, bias is a far bigger problem than variance. Even a small number of hauls on the same spot will give a very consistent composition of the catch, though this may well not be the true composition of the population at that spot. Thus the variance over the very large number of hauls in a commercial fleet's activities will be very small. Bias may be considered in two parts; first the structure of the population at the fishing position may not be typical of that of the whole population; secondly the structure of the catch may not be the same as that of the population at the position of capture. The first of these has the same effect as the uneven distribution of fishing and density of fish, and may be dealt with in a similar way. For instance, in the North Sea plaice fishing, if more ships fished off the continental coast-grounds typically containing small plaice, instead of on the Dogger Bank - typically containing large plaice - then relatively more small plaice would be landed, and the apparent structure of the population would be altered. By dividing the area into sub-areas, and treating the density of each age or length group separately, in the same way as in obtaining a correct density index for the whole population, a correct structure for the whole population may be obtained. This method involves not only estimates of structure, but also of abundance, but this is unavoidable if the structure of the whole population, i.e. the relative abundance of different groups, is to be estimated when they are separated into partly different areas. If no estimates of density can be made, some idea of the structure of the population, particularly of its change, can still be obtained which will not be disturbed by changes in the distribution of the fleet. Suppose the whole region is divided up into areas in each of which the structure is uniform, and hence may be estimated at once from the catches. Then the true structure will be the weighted mean of the structures in each area, the weighting factors being the abundance in each area. This will now not be known, but if some other constant weighting factors are taken, then the resulting estimate for the structure will be unaltered by changes in the distribution of the fishing between the various areas. It will not be the true structure, but will be reasonably close, and in particular will reflect quite well changes in the population structure.

The landings of fish from a particular area will differ in structure from the true population in that area. This may be due to rejection of small fish, selection of small fish through the meshes of the net, or escapement, that is differential capture of large and small fish other than by mesh selection. The first two are only important over a limited and usually easily discovered size range, but the second of these is much more difficult to determine. Escapement will be noticeable when two or more gears operating on the same part of a stock have catches with different structures e.g. the long-line, gill-net and purse-seine catches of cod at Lofoten (Rollefsen, 1953). Then escapement must be taking place for at least two of these gears - probably long-line and gill nets. Though this means that the long-line and gill net catches are no use for direct estimation of the population, it also means that the effect of the gear on the population cannot be represented by the same mortality coefficient for all age-groups. If the non-representative gear takes a fair proportion of the total catch, so that its effect on the population is important, then the catches from it will have to be sampled, to give the catches and hence the mortalities, in each age-group separately. This problem is discussed further by Margetts (No. 28).

The above review is not an exhaustive survey of all sources of bias and variance; also, particularly in estimating the population from the catch, several likely sources of error have been mentioned, but assumed to be small in default of methods of correcting for them. Some comfort however, that the major sources of variation have been accounted for in one fishery may be gained from an analysis of the Lowestoft plaice sampling. For the three biological years April 1950-March 1953, the expected variance in the estimated numbers of each year class were calculated. From these the expected variance in the exponential mortality rates was calculated, and was 0.034. At the same time the actual observed variance for the set of 12 separate estimates of mortality, for the 6 most abundant and fully recruited year-classes for the two pairs of years 1950-51 and 1951-52 was calculated, and was 0.027. The reasonably close agreement between the two is a fair indication that the known and calculable sources of variance are the most important. That is, the sampling of a fish population by a commercial fleet can in some circumstances at least probably give estimates within a predictable and not too large margin of error.

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