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ANNEX

[GULLAND :] Estimation of Mortality Rates

Introduction

In the previous analysis of the Arctic cod, as presented in the second progress report of the Working Group at ICES in 1959, mortality rates had been estimated in the usual manner as the ratio of the catches per unit effort of the same year-class (or year-classes) in successive years.

As shown in the Figures 15 and 16 in the report, this method gave some extremely variable estimates, though an attempt was made to reduce the variance by omitting certain years where the estimated mortality appeared to be too high. More seriously the method, at least in the simple form, depends on fishing mortality being constant with age. This is clearly not true for the trawl fisheries; thus the 1959 report estimated the fishing mortality (for all gears combined) to be about the same, or even higher, for the immature fish as for the mature fish. As the majority of the mature fish are caught outside the feeding areas, mainly by gears other than trawl, the fishing mortality on mature fish caused by trawlers in the feeding area must be quite small, and certainly much smaller than the corresponding mortality on young fish. Such a change in fishing mortality with age will bias, possibly quite seriously, the estimates of mortality rate.

The present Working Group therefore considered that other methods of estimating mortality should be considered. The method of virtual populations (Fry, 1949; Ricker, 1958) was used. This appears to reduce fluctuations due to changes in availability, and the known catches in the mature fisheries provide useful upper estimates to the fishing mortality in the immature fisheries. Also, using methods analogous to those of Jones (1964) preliminary estimates of natural mortality, and of total mortality among the oldest fish, were used to obtain unbiased estimates of the true mortality among the younger fish.

Methods

The following notation will be used:-

${}_xC_n$ = catch in numbers, during year n, of the year-class born in year x;

${}_xV_n$ = virtual population in year n of the x year-class;

i.e. ${}_xV_n$ = the total number of fish of the x-year-class which will be caught in the year n or later;

${}_xN_n$ = total number of fish of the x-year-class alive at the beginning of year n;

then ${}_xV_n = {}_xE_n \cdot {}_xN_n$, where

${}_xE_n$ = "exploitation ratio", i.e. the proportion of the fish of the x-year-class alive at the beginning of year n which will, at some time, be caught.

(In the simple constant parameter case ${}_xE_n$ = constant = E = $F/_{F+M}$)

In these definitions suffices have been used to denote different years, and prefixes denote different year-classes. In the following symbols it is more convenient to use prefixes for different age-groups, though retaining suffices for years;

${}_tF_n$ = fishing mortality coefficient on fish of age t in year n;

f_n = fishing effort in year n;

${}_tq_n$ = catchability coefficient for fish of age t in year n;

M = natural mortality coefficient (assumed constant).

A first estimate of the survival during year n is given by the ratio of the virtual populations of a year-class at the beginning and end of the year, i.e.

$${}_xS_n = {}_xV_{n+1}/{}_xV_n$$

which if all the mortalities are constant reduces to

$$ {}_xS_n = E_xN_{n+1}/E_xN_n = e^{-(F+M)} $$

The virtual population also provides, in all situations, an upper limit to the rate of exploitation ("u" in Ricker's notation; $\frac{F}{F+M}(1-e^{-F+M})$),

as the rate of exploitation =

$$ {}_xC_n/{}_xN_n > {}_xC_n/{}_xV_n $$, and this upper limit may not infrequently be useful.

More precisely, the catch during any year can be expressed as a function of the fishing and natural mortality rates during the year, and of the population at the end of the year. Thus, in a manner similar to that of Jones (1964), if it is assumed that natural mortality is constant, and some value of fishing mortality among the very old fish is assumed, it is possible for each year-class to proceed year by year backwards from old to young fish estimating the fishing mortality in each year.

Assuming that year-class x is t years old in year n,

let $$ {}_xr_n = {}_xN_{n+1}/{}_xC_n $$

i.e. r is the population at the end of the year, expressed as a proportion of the catch during the year (thus r can be greater or less than unity)

then $$ {}_xr_n = \frac{{}_xN_{n+1}}{{}_xC_n} = \frac{{}_xN_n\, e^{-(F+M)}}{{}_xN_n \frac{F}{F+M}(1-e^{-(F+M)})} $$

where for convenience F has been written for ${}_tF_n$.

Thus ${}_xr_n$ is a simple function of ${}_tF_n$ and M, and if given M, the function

$\frac{(F+M)\ e^{-(F+M)}}{F(1-e^{-F+M})}$ is tabulated for a range of values of F, then once ${}_xr_n$ is determined, ${}_tF_n$ can be at once read off from this table.

Now $$ {}_xr_n = {}_xN_{n+1}/{}_xC_n = \frac{{}_xV_{n+1}}{{}_xE_{n+1} \cdot {}_xC_n} $$

$$ = \frac{1}{{}_xE_{n+1}}\left(\frac{{}_xV_{n+1}}{{}_xV_n - {}_xV_{n+1}}\right) = \frac{1}{{}_xE_{n+1}}\left(\frac{{}_xS_n}{1 - {}_xS_n}\right) $$

i.e. ${}_xr_n$ is a simple fraction of the apparent survival during year n (as estimated from virtual populations) and the exploitation ratio ${}_xE_{n+1}$, applicable to the fish of the x-year-class alive at the end of year n.

The exploitation ratio, ${}_xE_n$, applicable to the fish at the beginning of year n will be the sum of the proportions of fish alive at the beginning of the year caught during the year, and caught later, i.e.

$$ {}_xE_n = \frac{{}_tF_n}{{}_tF_n + M}\left(1 - e^{-({}_tF_n + M)}\right) + e^{-({}_tF_n + M)}\ {}_xE_{n+1} $$

Thus, if values of M and ${}_xE_{n+1}$ are assumed, estimates can be observed in succession of ${}_xr_n$, ${}_tF_n$, ${}_xE_n$, ${}_xr_{n-1}$, ${}_{t-1}F_{n-1}$ ..... etc. The actual steps in the calculation of mortality rates for the 1948 year-class are set out in Table 1 (values of M = 0.20, and E at the 15th birthday of 0.8 were taken).

Table 1. Calculation of true mortality rates for the 1948 year-class.

Age	S	Z'	$\frac{S}{1-S}$	E	r	F	Z	$\frac{F}{Z}(1-e^{-Z})$	Ee^{-Z}
14	.37	.99	.588	.8	.735	.79	.99	.501	.298
13	.39	.94	.640	.799	.801	.75	.95	.484	.309
12	.45	.80	.818	.793	1.03	.62	.82	.423	.349
11	.48	.74	.923	.772	1.20	.56	.76	.392	.361
10	.40	.92	.667	.753	.886	.70	.90	.462	.306
9	.49	.70	.961	.768	1.25	.54	.74	.382	.366
8	.42	.87	.724	.748	.968	.65	.85	.438	.319
7	.51	.67	1.04	.757	1.38	.50	.70	.360	.376
6	.68	.39	2.13	.736	2.89	.27	.47	.215	.460
5	.70	.36	2.33	.675	3.45	.23	.43	.187	.439
4	.78	.24	3.55	.626	5.67	.15	.35	.127	.441
3				.568					

The right-hand columns are determined quickly, using tabulations, for a range of F, of r, $\frac{F}{Z}(1-e^{-Z})$, and e^{-Z}. Included in the table are the values of Z', $(= -\log_e S)$, the first estimate of the total mortality coefficient. In fact, for much of the table Z' is close to the corrected value, Z, though fluctuating rather more widely, and being a distinct under-estimate of Z for the youngest fish.

Results

Table 2 shows Z', the mortality estimated as the ratio of virtual populations at the beginning and end of the year for fish between 4 and 14 years old for the years 1946-1962. (The figures are based on preliminary data on the total catches of each age-group, which have since been revised. It is believed that there revision will not alter the estimates of mortality appreciably). Compared with the estimates obtained from catch per unit data these are much less variable; from the method used no negative values can occur, and for fish less than 10 years old the greatest value is only 1.13. Examination of the table suggests, as does the catch per unit effort data, that the fish are not fully recruited until they are six years old; from eight years old there is some recruitment to the mature fisheries, so that an increasing part of the total fishing mortality occurs outside the feeding areas. Accordingly a first estimate of the division between fishing and natural mortality was obtained by relating the apparent mortality Z' among 6 and 7 years old fish to the total effort in the feeding area (Regions I and IIb). There is no direct estimate of the combined effort in the two regions. The estimate used was the sum of the total international effort in each area, expressed in English units (millions of ton-hours). Alternatively, because the catch per ton-hour is higher in Region IIb than in Region I, by an average factor of 1.5, a better estimate might be

Effort = (Effort in I) + (Effort in IIb) x 1.5.

However, as the trends in effort in the two regions have been similar it is probable that the results would be the same.

Figure 1 shows the plot of apparent mortality of 6 (below) and 7 (above) year old fish against effort; the correlation is very good. As the method tends to under-estimate the mortality when this is low, the total mortality at low levels of effort, and hence the intercept on the y-axis (the estimate of natural mortality) will tend to be low. In Figure 1 the intercepts on the y-axis are 0.05 (for 6 year olds) and 0.20 (for 7 year olds): as these are under-estimates a first estimate of 0.2 for natural mortality was used to calculate by the methods o[illegible] better estimates of Z. These are given in Table 3.

Using these estimates, further plots of total mortality against effort are shown (Figure 2). For both ages the correlation is slightly improved: intercepts (i.e. the estimate of M) are 0.21 and 0.40 for 6 and 7 year olds respectively. The confidence limits of the two estimates of M are 0.15-0.27 and 0.30-0.50, suggesting that there are some real differences in the mortality/effort relation for the two ages. Though the agreement between the estimates from the two ages is not too good, they suggest that M is between 0.2 and 0.4.

A nearly independent estimate can be obtained from the ratio of the catches per unit effort of certain year-classes in the Barents Sea and (four years later) on the Norway coast; the calculations of this ratio were made in the 1959 report(Table 18 and Figures 18a and b). The value of this ratio depends on the effort units used in the two areas as well as on the mortality between the times when the catches per unit effort are measured (4-7 years old in Region I, and 8-11 years old in Region IIa). However, if the effort units remain the same then changes in the ratio will be related directly to changes in the mortality. Figure 18b suggests that at the present high levels of effort the logarithm of the ratio is about 2.0 greater than when fishing was zero, i.e.

$$4\,\overline{F} = 2.0 \qquad \overline{F} = 0.5$$

where $\overline{F}$ is the average fishing mortality between 4 and 11 years old. The average total mortality over the main ages (4-10) and years concerned (1953-57) was 0.71; subtracting an F of 0.5 gives an estimate of natural mortality of 0.21.

Comparison with previous results

The total mortality rates obtained here are, for the immature fish (under say 10 years old) considerably smaller than those given in the previous report. This is due to the real decrease with age in the fishing mortality in the trawl fisheries. The decrease can be estimated by dividing the total fishing mortality on each age into that occurring in the spawning area (Region IIa) and in the feeding areas (Regions I and IIb) in the ratio of the catches in the two areas. That is F^1, the fishing mortality in the trawl fisheries is given by

$$F^1 = F \times \frac{\text{Catch in I and IIb}}{\text{Total catch}}$$

The relevant calculations for the 1948 year-class between 4 and 11 years old is given in Table 4. F^1 increases between 4 and 7 years old, and then decreases. These estimates of F^1 cover the years from 1952 to 1959, during which the effort has changed, and the more important measure is the changes with age of q^1,

where $\quad F^1 = q^1\ f, \quad \text{or } q^1 = F^1/f$

The mortality estimated from catch per unit effort data may differ from the true mortality during the year for two reasons: the decrease in catchability, q, with age, and any change in true mortality rates. The magnitude of these effects can be determined from the equation

$$\log_e n_t/n_{t+1} = Z_t + \log_e \frac{Z_{t+1}(1-e^{-Z_t})}{Z_t\ (1-e^{-Z_{t+1}})} + \log\ {}_tq/{}_{t+1}q$$

where n_t, n_{t+1} are the catches per unit effort of a given year-class in successive years, and ${}_tq$, ${}_{t+1}q$ are the values of q for that year-class in the two years

$$\text{or} \qquad \log_e n_t/n_{t+1} = Z_t + A + B$$

where A = correction for changes in mortality
B = correction for changes in q.

Table 5 shows these corrections, the resulting expected value of the apparent total mortality based on catch per unit effort data, and also the observed apparent mortalities in Regions I and IIb. These last are each the average of the estimates based on English and on U.S.S.R. data. Though the agreement between expected and observed apparent mortalities is not complete, it is reasonably good.

Table 2. Total mortality coefficients "Z" as estimated from the ratio of initial populations at the beginning and end of each year

Age	1946	1947	1948	1949	195o	1951	1952	1953	1954	1955	1956	1957	1958	1959	196o	1961	1962
14			.304	.575	.861	1.185	1.086	.708	1.184	.886	1.020	.815	.174	.409	.787	1.514	.992
13		.638	.525	.835	.866	.945	1.073	.824	.863	.836	1.140	1.135	.491	.476	.51o	.943	.762
12	.536	.769	.705	.743	1.134	.869	1.659	.824	.884	,818	1.194	.928	1.070	.823	.800	1.108	1.342
11	.504	1.006	.720	.802	1.142	.883	1.207	.892	.924	1.110	1.077	.968	.921	.742	.935	1.128	1.191
1o	.500	.643	.550	.625	.582	.710	.952	.671	.839	.954	.882	.735	.924	.940	.898	.979	.889
9	.425	.616	.615	.506	.578	.701	.750	.542	.518	.736	.885	.705	.565	.796	.565	.817	1.13o
8	.234	.239	.435	.424	.523	.564	.581	.467	.524	.727	.874	.839	.572	.597	.580	.793	.919
7	.221	.329	.651	.487	.500	.651	.724	.425	.487	.669	.798	.719	.691	.601	.591	.664	.790
6	.156	.195	.274	.462	.348	.452	.691	.450	.391	.716	.906	.666	.742	.602	.717	.638	.881
5	.067	.182	.107	.276	.124	.355	.499	.362	.370	.408	.621	.288	.472	.568	.533	.586	.666
4	.033	.072	.018	.101	.031	.219	.241	.210	.206	.138	.283	.149	.350	.294	.305	.359	.366
3	.013	.009	.005	.022	.002	.055	.034	.063	.034	.029	.053	.035	.109	.060	.065	.133	?

Table 3. Corrected estimates of total mortality coefficient, assuming M = 0.2

Age	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
14									1.15	.91	1.02	.85	.32	.51	.81	1.45	.99	
13								.86	.89	.87	1.11	1.02	.55	.55	.61	.95	.79	
12							1.62	.84	.90	.85	1.14	.85	1.01	.83	.82	1.07	1.28	
11						.93	1.15	.90	.92	1.10	1.02	.95	.90	.76	.95	1.14	1.19	
10					.65	.76	.94	.72	.87	.94	.90	.74	.90	.94	.92	.99	.93	
9				.57	.65	.73	.77	.61	.58	.76	.88	.74	.63	.83	.64	.85	1.12	
8			.49	.66	.59	.61	.62	.53	.59	.75	.85	.83	.64	.64	.64	.86		
7		.41	.66	.54	.54	.66	.71	.50	.56	.70	.80	.72	.70	.63	.66			
6	.29	.33	.38	.51	.43	.50	.67	.50	.47	.73	.88	.68	.74	.64				
5	.24	.31	.26	.37	.28	.44	.52	.43	.46	.49	.63	.40	.53					
4			.23	.26		.34	.35	.33	.34	.29	.38	.29						

Table 4. Estimation of fishing mortality in feeding areas.

Age	Year	Total F	Numbers caught x 10^{-6}			Trawl F = F^1	Effort	t^q
			I + IIb	Total	% Trawl			
14	1962	.79	57	315	18.1	.143	758	.189
13	1961	.75	285	542	52.6	.394	691	.571
12	1960	.62	363	1,859	19.5	.121	609	.199
11	1959	.56	1,307	3,715	35.2	.197	556	.354
10	1958	.70	3,785	10,772	35.1	.246	657	.374
9	1957	.54	10,297	18,619	55.3	.299	649	.461
8	1956	.65	34,532	50,473	68.4	.445	764	.582
7	1955	.50	78,636	82,534	95.3	.476	616	.773
6	1954	.27	80,382	80,811	99.5	.269	479	.562
5	1953	.23	109,197	109,197	100	.230	455	.505
4	1952	.15	98,068	98,068	100	.150	456	.329

Table 5. Estimation of the apparent total mortality rate in the feeding areas, and comparison with observed values in I and IIb.

Ages	$t^q/_{t+1}q$	B	Z_t	A	Apparent Z	Observed Z	
						I	IIb
8-9	1.263	0.23	.85	- .05	1.03	1.42	1.46
7-8	1.328	0.28	.70	+ .06	1.04	1.12	.82
6-7	.727	- 0.32	.47	+ .10	.23	.44	.73
5-6	.899	- 0.11	.43	+ .02	.34	- .12	.33
4-5	.651	- 0.43	.35	+ .03	- .05	- .33	.05

Note: A = correction for change in mortality = $\dfrac{Z_{t+1}\ (1 - e^{-Z_t})}{Z_t\ (1 - e^{-Z_{t+1}})}$

B = correction for change in catchability = $\log\ {}^{t}q/_{t+1}q$

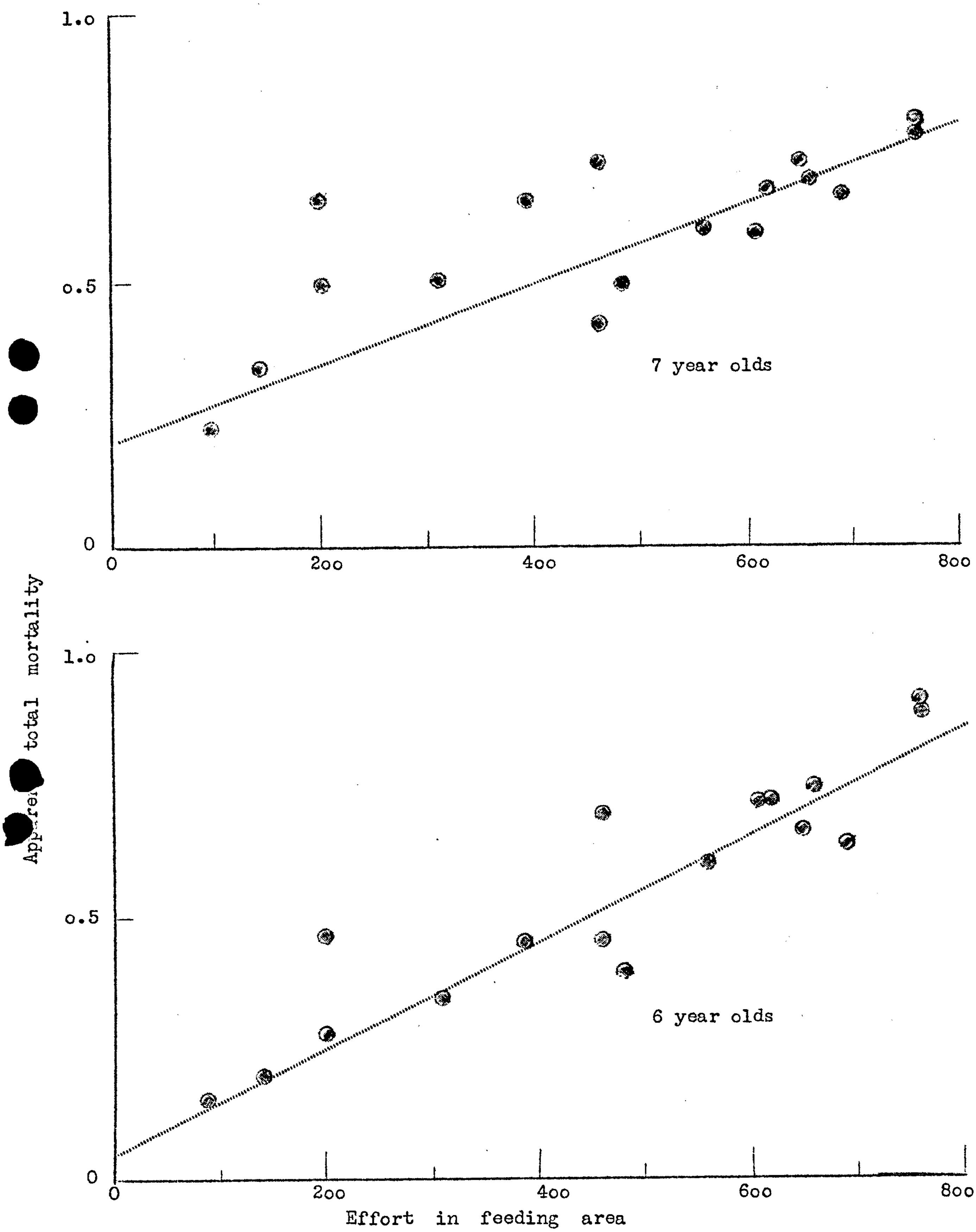

Figure 1. The relation between apparent total mortality and effort in the same year.

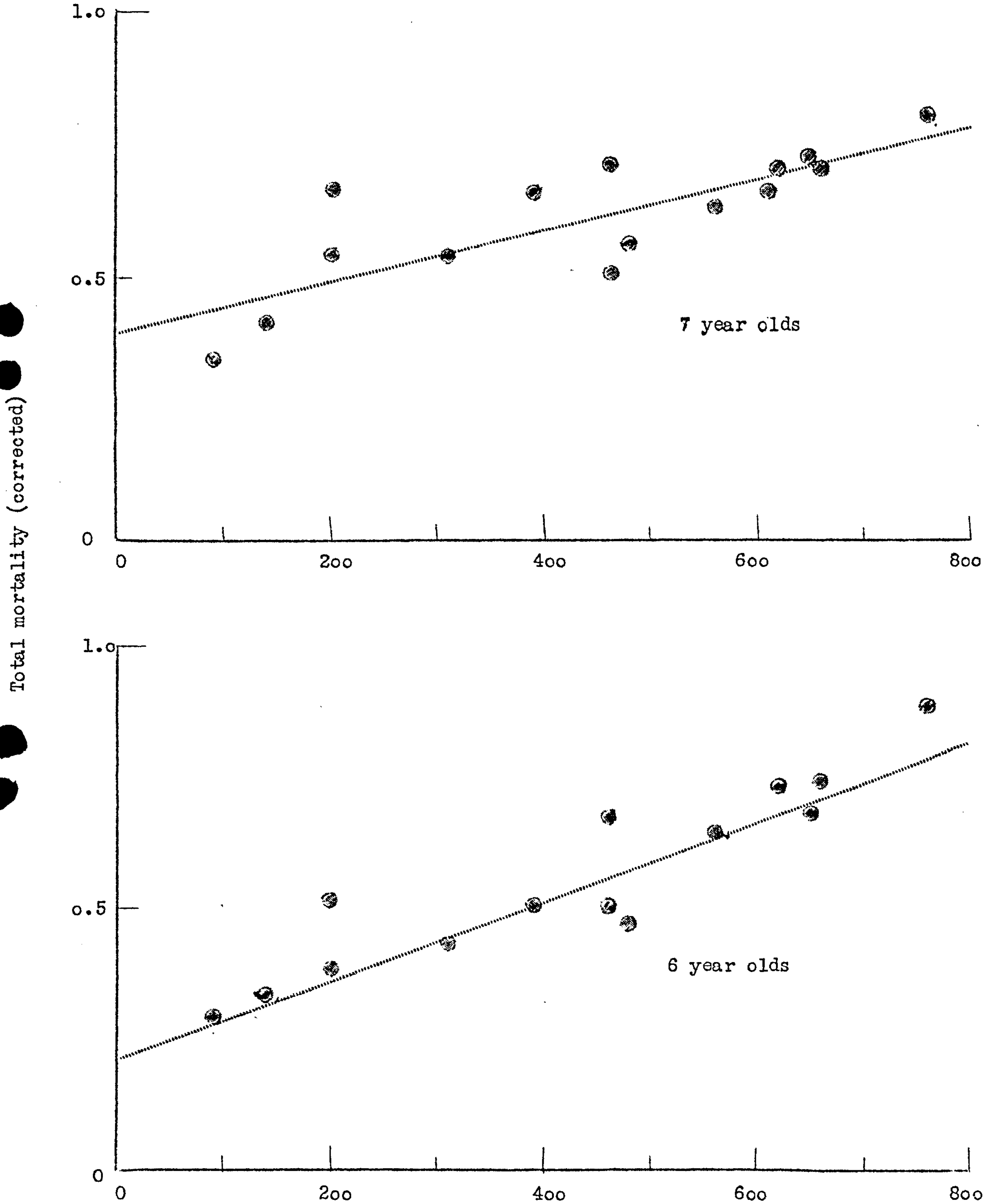

Figure 2. The relation between the corrected estimates of mortality and effort.