1

DYNAMICS OF MATURATION IN LONG-LIVED FISH POPULATIONS

II. NORWEGIAN SPRING SPAWNING HERRING

by

R.J.H.Beverton[1], A.Hylen[2] and O.J.Ostvedt[2]

1) *School of Pure and Applied Biology, University of Cardiff, Wales,*
2) *Institute for Marine Research, Bergen, Norway*

1. INTRODUCTION

1.1 It is well-known that quantitative patterns exist between age and size at first maturity, longevity T_{max} (and hence natural mortality rate M) and the von Bertalanffy growth parameters K and L_{inf} in fish populations (Beverton & Holt, 1959, and many later authors; see review in Beverton, 1992) and also in other vertebrates (Charnov & Berrigan, 1991). These Growth-Maturity-Longevity (GML) patterns between major taxa, species and populations of the same species are mediated by environmental conditions that accord with the criteria for evolutionary fitness (Roff, 1984), age at maturation and longevity being higher and size at maturity being lower relative to the potential growth span in colder conditions, and *vice versa* (Beverton, 1992).

1.2 These characteristics also influence how a population will respond to fishing, but the study of the *dynamics* of these phenomena needed for this purpose is difficult. Thus, depletion by fishing is often followed by a substantial decrease in the mean age (and sometimes size) at maturity. To attempt to determine whether this is associated with an increase in the natural mortality rate and decrease in longevity as would be expected from inter-population and inter-specific comparisons, and to what extent observed maturity trends are purely structural or imply real biological (ie density-dependent) change, is virtually impossible because the population size and structure in these circumstances is dominated by the increased fishing mortality.

1.3 However, the maturation of any one year-class in the longer-lived fish populations is spread over several ages, thus dividing the year-class into what may be called *maturation cohorts*. In sampling the Norwegian spring-spawning herring fishery and the Lofoten fishery for mature Northeast Arctic cod, the Bergen Institute for Marine Research started in the early thirties to record (from the scale or otolith, respectively) not only the actual age of the fish when caught but also the age at which it spawned. The subsequent age-composition and growth of each *maturation cohort* can therefore be followed throughout its mature life after spawning for the first time, thus offering at least the possibility of answering the questions posed in the preceeding paragraph and of testing whether similar GML patterns exist among the maturation cohorts of a given year-class as between whole populations and between species.

1.4 This paper reports the preliminary results of an analysis of the SPRING SPAWNING HERRING data on a maturation-cohort basis. The companion paper by the same authors on the NE ARCTIC COD was presented to the ICES Statutory Meeting in Dublin in September (CCC 1993: Symp/No.59).

2 MATERIAL AND METHODS

2.1 Lea (1928) and Runnstrom (1936) showed that the onset of maturation in the Norwegian herring was visible as a discontinuity in the ring structure of the scale, and from the late 1930's to the mid-1960's both the actual age and the age at maturity of each herring sampled was recorded in the Bergen data base. Ostvedt (1958, 1963) used this information to express the mature stock as "spawning classes", in which all the fish spawning for the first, second,.. etc time in a given year are aggregated separately. He showed that this made better use of the data for estimation of mortality, but in his 1958 paper commented that "....it may be that our presumption of the same mortality rate for all spawning groups of a year-class (when all individuals have attained sexual maturity) does not hold true". This question can now be tested.

2.2 Typically, a very small proportion of any one year-class of Norwegian spring spawning herring matures at 3 years, the majority from 4 to 7 years, and a small proportion (in the earlier years only) at 8 and even 9 years of age.   For the present analysis, the post-maturation age-composition and highest recorded age (T_{max}) of each of these maturation cohorts from 3 to 9 (designated MC-3....MC-9) have been compiled for year-classes 1930-1950. Data for year-classes 1930-1933 are limited and have been used for estimation of maximum age but not (at this stage) for mortality estimation. Year-classes after 1950 could not be used owing to the escalation of fishing after the early 1960's.

2.3 Since a main aim is to detect whether the natural mortality rate differs between the maturation cohorts VPA is inappropriate, at least for this exploratory analysis. Age-compositions have therefore been constructed from purse-seine samples (which were most numerous and can be taken as unselective) raised to gill-net CPUE, which Ostvedt (1964) showed was preferable to purse-seine CPUE as an index of stock abundance.

2.4 The mean length-at age (in cm groups) have also been compiled on a maturation cohort basis for the same run of year-classes, but for this paper only the data for year classes 1945-1953 have been analysed.

3. TOTAL MORTALITY RATE OF MATURATION COHORTS

3.1 A total of 17 year-classes each comprising between five and seven maturation cohorts is a unique data base, but its analysis presents several complications, of which the three most important are as follows.

3.2 Although the fishing rate on the mature stock remained low until 1962 - at about F = 0.15 (assuming an overall natural mortality rate of 0.1, Dragesund et al, 1980), the young herring fishery expanded greatly, thus reducing the proportion of late-maturing cohorts in post-1940 year-classes relative to the early maturers.   Conversely, the

youngest maturing cohorts were poorly represented in year-classes 1934-1940. Maturation cohort mortality rates are therefore given separately for three groups of year-classes, viz:-

(a) 1934-40; MC-8 and MC-9 well represented; MC-3 less well,
(b) 1941-47; MC-3 well represented; MC-8 & MC-9 less well,
(c) 1948-50; MC-3, MC-4 and MC-5 only.

3.3 The total mortality rate (hereafter designated Z) of all maturation cohorts is effectively independent of age up to a threshold of 17 years, after which it appears to increases sharply. This is best seen in the most abundant MC's where old fish are still well represented, as in the log age-compositions of MC's 5, 6 & 7 from certain year-classes shown in Fig. 1. This rapid steepening of the log age-trajectories occurs between ages 17 and 21, as shown by the frequency histogram of Fig 2.

3.4 It is, of course, possible that this phenomenon is an artefact due to erosion of the scale edge or difficulties in counting the outermost rings, notwithstanding the skills of the highly experienced age-readers of the time. For the present paper we have therefore taken advantage of the sharpness of the discontinuity at high ages in the log trajectories of the maturation cohorts to restrict the measurement of mortality to the linear part of the trajectory without undue subjectivity or loss of rigour (see Fig 1). This has the advantage of being able to work with simple instantaneous coefficients to measure mortality in the usual way and avoid the complications of a 2-parameter age-specific function such as the Gompertz (Beverton, 1963; Witten, 1987). The maximum age data are not, however, discarded, but are used as an ancillary source of information.

3.4 The third problem in mortality estimation is that the sample sizes of the youngest and oldest cohorts (MC-3,4,8,9) are always much less than of the medium-aged (MC-5,6,7); there are also considerable differences between the sizes of the whole year-classes in the data set. Inevitably, even although trajectories of three or less data points are discarded, the precision of estimates of the mortality rate (ie the slopes of the log regressions) of individual MCs varies both randomly and systematically. In calculating mean mortality rates for MCs and for groups of year-classes, individual estimates are therefore weighted by the reciprocal of their variances.

3.5 Fig 3 is a scatter plot of the individual estimates of Z for each maturation cohort in the total data set, distinguishing the three groups of year-classes (1934-4 O; 1941-47 O; 1948-50). Most of the outliers are of low precision, and the general picture is sharpened by calculating the weighted mean Z (with +-2SE) of the maturation cohorts in each group of year-classes, as shown in Fig 4. Points to note are:-

i) apart from MC-3, Z decreases from between 0.25-0.35 for MC-4 to 0.05-0.15 for MC-8

ii) estimates of Z for the youngest maturation cohort MC-3 range from 0.1 to 0.25; this is significantly less than Z for MC-4 and, probably, MC-5.

4. LONGEVITY OF MATURATION COHORTS

4.1 However reliable the age-determination procedure, maximum recorded age (T_{max}) depends on sample size as well as the mortality rate. Because sample size necessarily varies greatly between cohorts (being smallest for the youngest and oldest cohorts), it is necessary to normalise observed T_{max} values to a standard sample size before they can be compared.

4.2 Since the MC log age-compositions are not linear at high ages, normalising to log of sample size is inappropriate; the double exponential form of the Gompertz suggests that T_{max} may better be related to loglog of sample size (Beverton, 1963; Hoenig, 1983). That it is so sufficiently well for the present purposes is shown in Fig 5, where the recorded maximum age for each MC in year-classes 1930-1940 is plotted against lnln sample size (omitting, unavoidably, samples of one fish only).

4.3 The slope of the regression (3.64) is highly significant (p<0.001), enabling observed T_{max} to be normalised to the average sample size of the best-sampled MC-6 (300 fish; ie lnln of 1.741) by the equation:_

$$T_{max}(norm) = T_{max}(obs) + 3.64(1.741 - lnln.sample\ nos.) \quad \ldots\ldots\ldots(1)$$

4.4 Fig 6 shows observed T_{max} (O) and normalised T_{max} (O) plotted against MC age. The mean normalised T_{max} increases asymptotically with MC age, reaching 22.6 years with MC-9. The highest individual value of normalised T_{max} is 25 years (2 fish) from MC-9. Fish of this age would be extremely rare, since MC-9 was itself rare (and is non-existent nowadays), but 25 years is not impossible. It is also significant that even although normalisation increases T_{max} for MC-3 from 13 (observed) to a mean of about 18 years, this is still lower than T_{max} of any of the older maturation cohorts (see also paras 6.3.4.& 6.4.1).

5. GROWTH AND LENGTH AT MATURITY OF MATURATION COHORTS

5.1 Estimates of K and L_{inf} for each maturation cohort estimated by non-linear regression are shown plotted against MC age in Fig 7. Values from the smoothed curves have been used to construct the growth-in-length of maturation cohorts of Fig 8. The substantial decrease in K with maturation age has the effect of separating the cohort growth curves up to maturation, the earliest maturers having the fastest growth, after which they converge to nearly the same L_{inf}.

5.2 The *length-maturation envelope*, ie the line joining the length (L_m) at which each maturation cohort reaches maturity, is shown on Fig 8 by the heavy line. There is not a strict length threshold at maturation, but the maturation envelope is much less steep than the growth curve itself over the range of maturation ages.

6. DISCUSSION

6.1 Among the questions arising from the above results are:-

i) what is the best assessment of how the total mortality rate Z varies between the maturation cohorts - in effect, with age at maturity <u>within</u> the year-class?

ii) how much of the change in Z can be attributed to a real change of natural mortality rate with age at maturation?

iii) how does the intra-year-class GML pattern compare with the inter-population and inter-specific patterns for the clupeiformes derived from the literature?

iv) what are the implications to assessing the response of the population to fishing pressure or environmental changes?

6.2 <u>Change of total (Z) and natural (M) mortality rate with age at maturity</u>

6.2.1 The downward slopes (from MC-4 onwards) of the plots of Z against MC-age plots of Figs 3 & 4 persist however the data set is analysed. Being derived from purse-seine data, this can hardly be due to gear selectivity, especially as each MC for most of its adult life covers nearly the same range of size (Fig. 8) and all cohorts are present together in the spawning aggregation. Again, not only was there no corresponding increase in fishing mortality rate during the period but, if there had been, it should have affected all maturation cohorts similarly.

6.2.2 The evidence therefore points to the decrease of Z from MC-4 to MC-9 (ie with increase in maturation age) being both real and due mainly if not wholly to a decrease in the natural mortality rate M. To narrow this down further, the bold curve of Fig 9 shows the "central" trend based on the full set of year-classes (1934-1950); Z decreases from around 0.3 for MC-4 to 0.1 for MC-8. Some of this lowest Z of 0.1 for MC-8 must have been due to fishing; if, say, half of it, then this would make $F = M = 0.05$ for maturation cohort 8. If we are correct in our surmise that F was essentially the same for all maturation cohorts, a natural mortality curve can be constructed that follows the Z curve 0.05 below it and rising to 0.25 for MC-4, as shown by the dotted line of Fig 9.

6.2.3 That adult M should be lower for the older compared with younger maturers makes physiological sense and is in accord with general life-history patterns (see below). What is puzzling is why the mortality rate for the youngest maturing cohort at age 3 should apparently be lower than MC-4 and probably MC-5 also. Two other pieces of evidence are material here; the maximum age data and the growth parameters.

6.3 <u>Longevity</u>

6.3.1 T_{max} and instantaneous mortality coefficient are dimensionally inverse, but only strict reciprocals if the latter is age-independent. This appears not to be the case with the present data, but T_{max} and M ought still to be monotonically related. Fig 10

shows M for Mc's 4-9 from Fig 9 plotted against mean normalised T_{max} from Fig 6. The points are closely linear, a back-projection to the normalised T_{max} of 17.86 for MC-3 giving an estimate of M for MC-3 of 0.36, which is entered on Fig 9.

6.3.2 Fig 10 implies that the product MT_{max} is not constant but also varies with maturation age, as shown in Fig 11. Beverton (1992, Table II) derived from the literature values of MT_{max} for the longer-lived clupeids ranging from 0.25 t0 0.35, with a "central" value of 0.3. This zone is marked on Fig 11, and corresponds to MC-5 and MC-6 which are the main maturation cohorts.

6.4 Growth

6.4.1 The growth parameter K, like M, is a rate variable and the two tend to move together, the ratio M/K being a relatively conservative statistic, at least within a given species group. M/K is not, however, the same for each maturation cohort, as shown in Fig 12 (derived from Figs 7 and 9). The relationship between M/K and maturation age is closely linear, a back-projection to MC-3 giving a predicted M/K = 0.74. With K = 0.51 at MC-3 (Fig 7) this implies a value of M for MC-3 of 0.51*0.74 = 0.38. This value, also entered on Fig 9, is similar to that predicted from T_{max}.

6.4.2 Beverton (1992, Table III) gives M/K for long-lived clupeids from 0.35 to 0.6, with a central value of 0.5. This zone is shown on Fig 12 and also corresponds with values for the main cohorts MC-5 and MC-6, as does MT_{max}.

6.5 Comparison with general GML patterns for the clupeiformes

6.5.1 It has for long been noted (eg Beverton & Holt, 1959 and subsequent authors), that M in the long-lived clupeids is small for their T_{max} and also for their K; ie both MT_{max} and M/K are lower than for all other groups so far examined (except *Sebastes* spp.; Beverton,1992). This gives some grounds for believing that the apparent truncation of the life-span seen in the present herring data (Fig 1), resulting in a smaller T_{max} than would be expected from a projection of the life-span on the basis of the M for younger ages, is real. The consistency between the projections from M/K and MT_{max} trajectories noted above is further support.

6.5.2 Figs 13 and 14 compare the inter-cohort relationships between L_m and L_{inf} and between T_m and T_{max} with those of other *C.harengus* populations in the North Atlantic (from Jennings and Beverton,1991) and with reference to the proportional line for the clupeiformes generally (from Beverton, 1992). In both plots, the maturation-cohort trajectory lies across the general proportional trend, implying that inter-cohort GML pattern is less prounced than that in independent populations which have presumably become adapted to different conditions over many generations.

6.5.3 The maturation cohorts comprising a year-class of Norwegian herring year-class are evidently formed by differential immature growth rates combined with a limited range of size at maturation. This is similar to salmon, where smoltification and maturation is assocated with marked differences in immature growth (eg Thorpe 1989) but contrasts with NE arctic cod, in which all maturation

cohorts as immatures appear to have essentially the same growth rate (see B,H & O;ICES CM1993/H:22).

      6.5.4 The finding that M varies with maturation age in herring has interesting demographic implications. Since additional mortality due to fishing will change the relative contribution of young and old maturation cohorts in the total stock, it means that the overall M is no longer constant but is dependent on the intensity of fishing. Both for assessment and for measurement and interpretation of changes in mean age and size at maturation, whether due to fishing or environmental factors and especially from the standpoint of genetics (Law, 1989), analysis on a cohort basis seems advisable.

REFERENCES

Beverton, R.J.H. (1992). *J. Fish Biol.* 41,(B), 137.
Beverton, R.J.H. & Holt, S.J. (1959) *CIBA Colloquia*, 54.142.
Charnov, E.L. & Berrigan, D. (1991). *Phil.Trans. Roy.Soc.* 332,41.
Hoenig, J. (1983). *Fish Bull.* 81, 898.
Jennings, S. & Beverton, R.J.H. (1991). *ICES J.Mar. Sci.* 48, 117-126.
Law, R. & Grey, D.R. (1989). *Evol. Ecol.* 3, 343-359
Lea, E. (1928). *Arsb. ved. Norges Fisk.*, IV, 3-36.
Ostvedt, O.J. (1958). *ICES R.P-v.* 143, 53.
Ostvedt, O.J (1963) *ICES R.P-v.* 154, 109-117.
Ostvedt, O.J (1964) *ICES R.P-v.* 155, 90-93.
Roff, D.A. (1984). *Can.J.Fish.Aquatic Sci.* 41, 984.
Runnstrom, S. (1936). *Fisk. Skr.* V(2), 1-107.
Thorpe, J.E. (1989) *J.Fish Biol.* 35,(A), 295
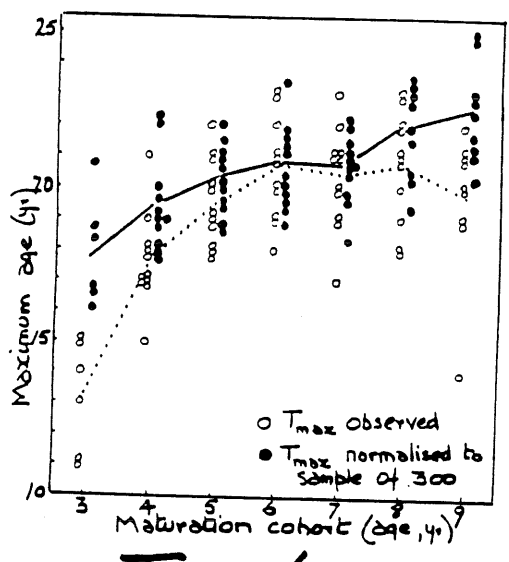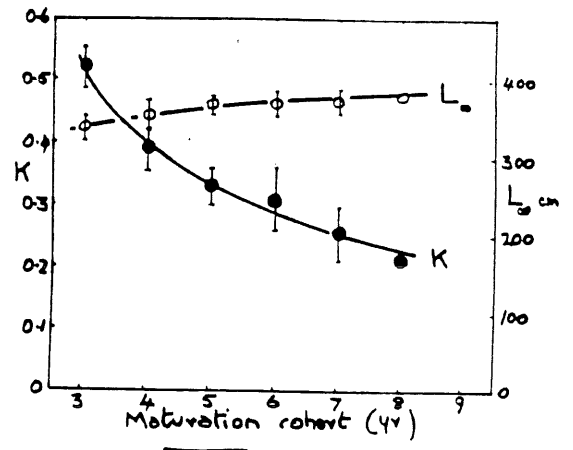Witten, M. (1987) *Basic Life Sciences* 42, Plenum Press
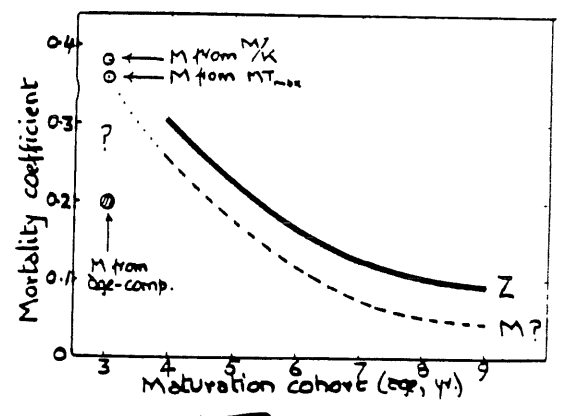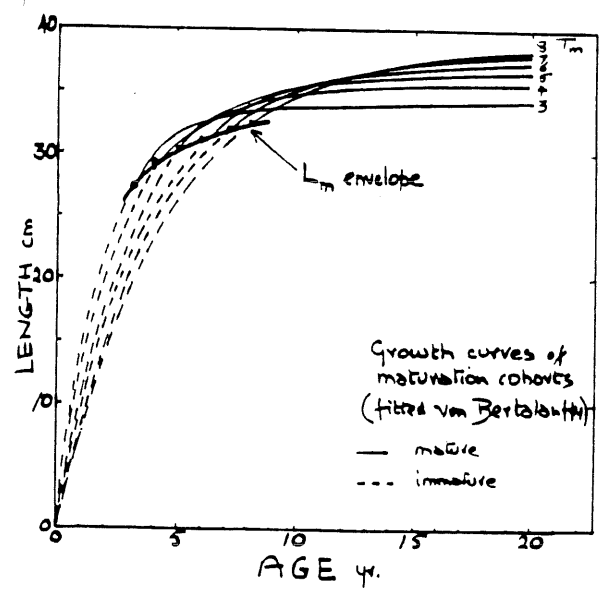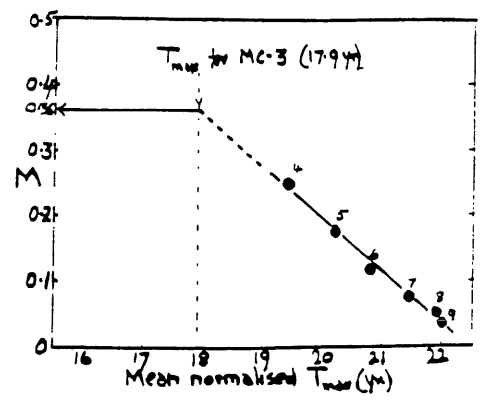
FIGURES
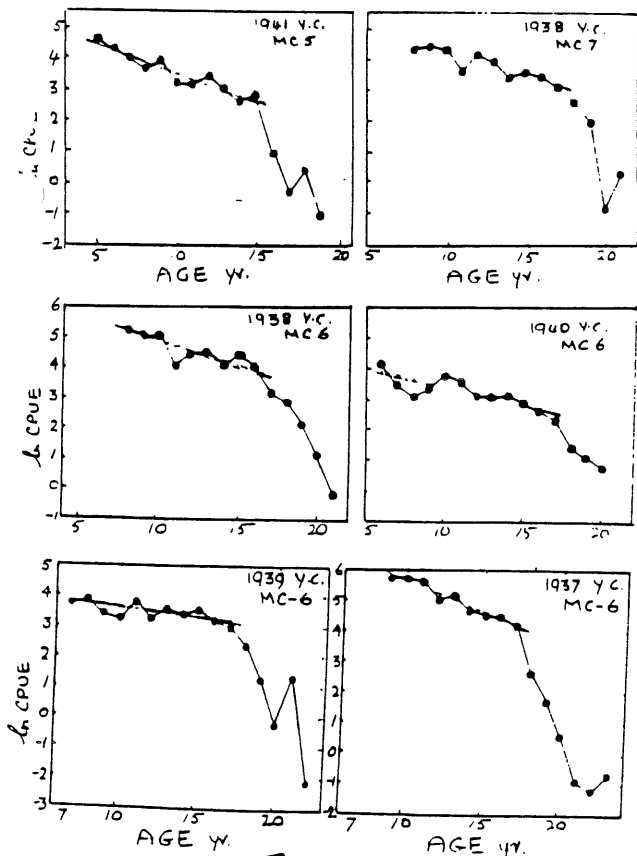
Fig 1
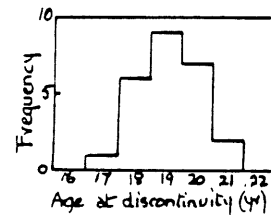
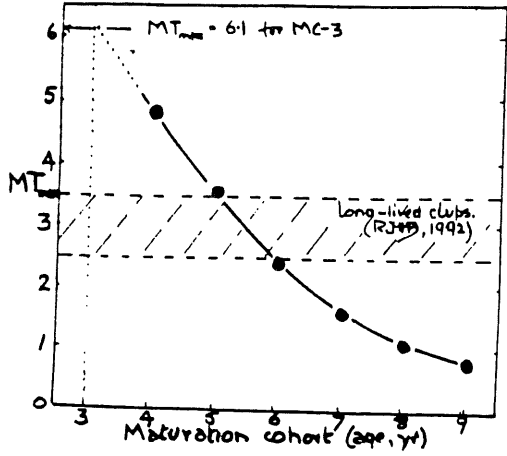

Fig 2
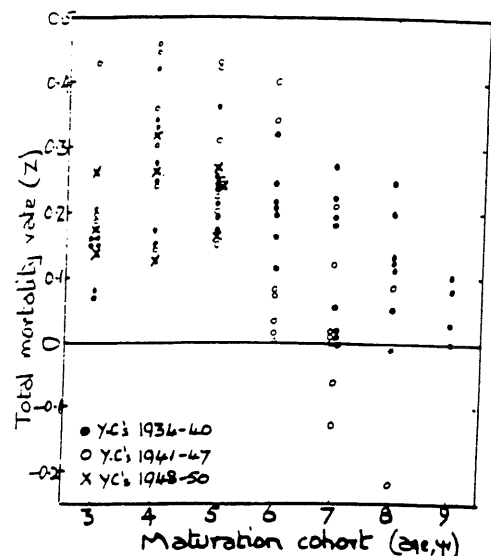
Fig 3
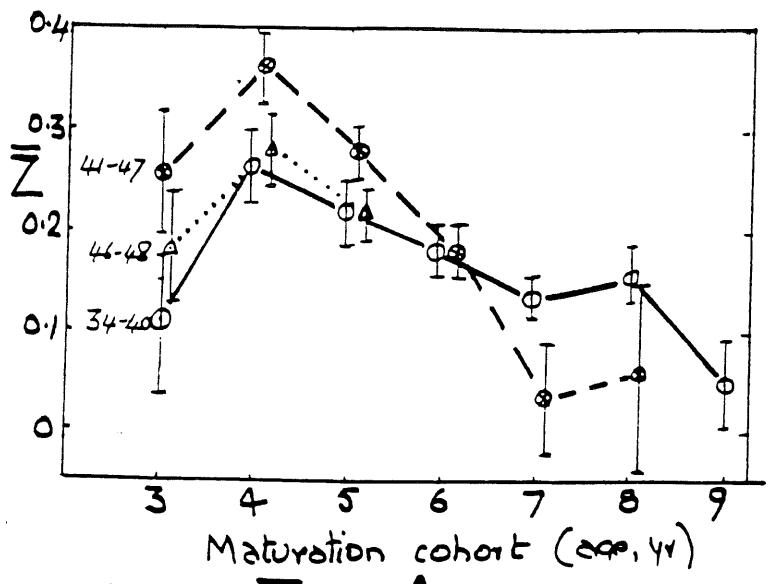
Fig. 4
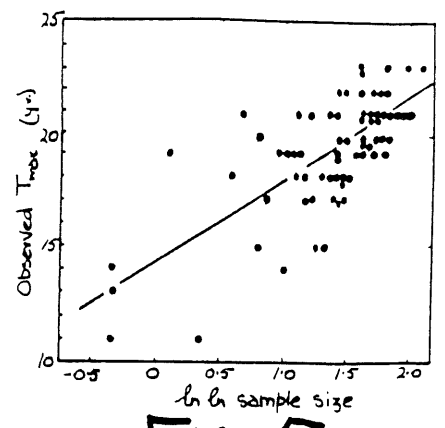
Fig. 5

Fig. 6

Fig. 7

Fig. 8

Fig. 9

Fig 10

Fig. 11

Fig. 12

Fig. 13

Fig. 14