# Ecological studies in Korsfjorden, Western Norway.
# The generations and stocks of *Calanus hyperboreus* and *C. finmarchicus* in 1971-1974

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ABSTRACT

The annual cycles of *Calanus hyperboreus* and *C. finmarchicus* are interpreted from data on the numerical abundance of the last four developmental stages (copepodid and adult). Estimates of the numbers of recruits to each stage, the timing of recruitment and its spread in time, and the instantaneous mortality rate have been obtained for each of the three sampled generations (one per year) of *C. hyperboreus* and for each of the six generations (two per year) of *C. finmarchicus*, using the model proposed by Manly (1974). The calculated curves fit the observed data well, though there are some inconsistencies in the estimated numbers of recruits to successive stages, due to the complementary effect of varying recruitment and mortality rate.

*C. hyperboreus* is shown to have a consistently low mortality rate (0.003-0.007) except at the end of its life span. Predation pressure on this species seems to be low and an appreciable portion of its biomass seems free to pass to the decomposers. *C. finmarchicus*, on the other hand, has a much higher mortality rate (0.02-0.4) throughout its development, at least from copepodid III onwards. Virtually the whole population appears to fall prey to carnivores.

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RÉSUMÉ

Études écologiques dans le fjord de Kors, Norvège occidentale.
Générations et stocks de *Calanus hyperboreus* et *C. finmarchicus* de 1971 à 1974.

Les cycles annuels de *Calanus hyperboreus* et *C. finmarchicus* sont interprétés à partir de données sur l'abondance numérique des quatre derniers stades de développement (Copépodites et adulte).
Les estimations du nombre de recrues pour chaque stade, la chronologie et l'étendue dans le temps des périodes de recrutement et le taux de mortalité instantanée ont été obtenus pour chacune des six générations (deux par année) de *C. finmarchicus*, par application du modèle de Manly (1974). Les courbes calculées s'accordent bien avec les données d'observation, bien qu'il y ait quelques discordances dans les nombres estimés de recrues pour les stades successifs, en raison de l'effet complémentaire des variations du recrutement et du taux de mortalité.

*C. hyperboreus* présente un taux de mortalité particulièrement bas (0,003-0,007) sauf à la fin de son développement. La pression de prédation semble être faible chez cette espèce et une portion appréciable de sa biomasse semble disponible pour les décomposeurs. On trouve chez *C. finmarchicus*, au contraire, un taux de mortalité beaucoup plus élevé (0,02-0,4) pendant tout son développement, tout du moins à partir du copépodite III. L'ensemble de la population paraît virtuellement destiné à constituer des proies pour les carnivores.

## INTRODUCTION

Interpopulational studies require estimates of recruitment, growth, and mortality of the various populations. Growth can be estimated by direct observation. Recruitment and mortality, however, are parameters which operate, in opposite directions, on one and the same stock and can be difficult to distinguish. Models in which these are recognized as separate parameters build on various assumptions regarding the nature of the mortality rate. A model proposed by Manly (1974) for the dynamics of successive instars of insects assumes (*a*) a normal distribution for recruitment, and (*b*) a constant mortality rate. The equation for the model is

$$N_t = M^* \, e^{-\theta t} \int_{-\infty}^{(t-\mu^*)/\sigma} \frac{e-(1/2)\,x^2 \cdot dx}{\sqrt{2\Pi}},$$ (1)

where $N_t$, the number of individuals at time $t$; $M^*=M \cdot e^{\theta\,(\mu+(1/2)\,\theta\sigma^2)}$; $\mu^*=\mu+\theta\sigma^2$; M, the total number of recruits; $\theta$, the instant mortality rate (daily mortality rate $=1-e^{-\theta}$); $\mu$, the mean time of recruitment; and $\sigma$, the standard deviation about $\mu$.

In fitting this equation to a given set of data the best possible estimates of M, $\mu$, $\sigma$, and $\theta$ are required. These estimates are determined using a least squares algorithm. The algorithm determines the "best" parameter values which minimize the deviations between the populations predicted by equation 1 and the observed populations. It is essential for success, however, that the starting values for the various parameters be as good as possible. Since sample variability is great in plankton investigations (Cassie, 1968), we have found it necessary to improve the method of estimating the starting values.

Differentiating equation 1 and converting to natural logarithms, we obtain

$$\ln\left(\frac{dN_t}{dt}+\theta N_t\right)=\ln\left(\frac{M}{\sqrt{2\pi}}\right)-\frac{1}{2}\left(\frac{t-\mu}{\sigma}\right)^2.$$ (2)

We estimate $dN_t/dt$ from observed values. $\theta$ is estimated by regression analysis of the observed values from the period when recruitment is considered to have ceased, i.e. when $(t-\mu)/\sigma>2$. Under this condition more than 95 % recruitment has occurred and the integral in equation 1 becomes approximately unity. Hence,

$$\ln N_t \approx \ln M^* - \theta t.$$ (3)

$\theta$ is varied within the range (0.1, 10 $\tilde\theta$) where $\tilde\theta$ is the value obtained by regression. For each of these values of $\theta$, substituted in equation 2, a set of estimates of M, $\mu$ and $\sigma$ is obtained. The set of estimates of all four

parameters so obtained which gives the least sum of squared deviations when fitted to the observed data is then chosen as the set of starting values for obtaining best fit by iterative convergence (see Matthews, Hestad, 1977). Although recruitment can virtually cease early in the duration of a given stage, it is important in the equation that $(dN_t/dt)+\theta N_t>0$. When this is not the case, the particular values must be ignored or adjusted to give a small positive value.

The possibility of estimating satisfactory starting values is ultimately dependent on the consistency of the data. The sampled populations considered in this article often showed such variability that convergence seemed impossible to achieve. In these cases we have chosen to use the starting values themselves and have termed these "best estimates" in the following text.

*Calanus hyperboreus* (Kröyer) is an arctic/boreal epiplanktonic copepod which in more temperate regions is distributed in deep waters (Östvedt, 1953; Grainger, 1965). The structure of its mouthparts is suitable for feeding on phytoplankton (Conover, 1966), though it must have an alternative diet where the population is permanently below the euphotic zone, as seems to be the case in Korsfjorden (P. Johannessen, pers. comm.). As the species is represented all the year round and is known to have a fairly simple annual cycle, it was chosen as the subject for a test of the applicability of Manly's model to a planktonic population. When this test proved successful, the study was extended to include a related species, *C. finmarchicus* (Gunnerus), which fulfils a very important role as a herbivore and as food for carnivores in the Korsfjord plankton.

The material was obtained at approximately fortnightly intervals between February 1971 and February 1974 using the Longhurst frame net (see Matthews, Sands, 1973). Most of the water column was sampled by an oblique haul on each occasion and the results have been standardized to represent the numbers present in the whole water column, 1 m² in cross section and 690 m deep.

## RESULTS

### Calanus hyperboreus

The occurrence of copepodids III-V and of adult males and females (Fig. 1) shows a clear annual cycle with some difference in detail and in stock size from year to year. As the species spends most of its developmental time at stages IV and V, the generation cycle is more clearly seen in the timing of other, shorter-lived stages, particularly
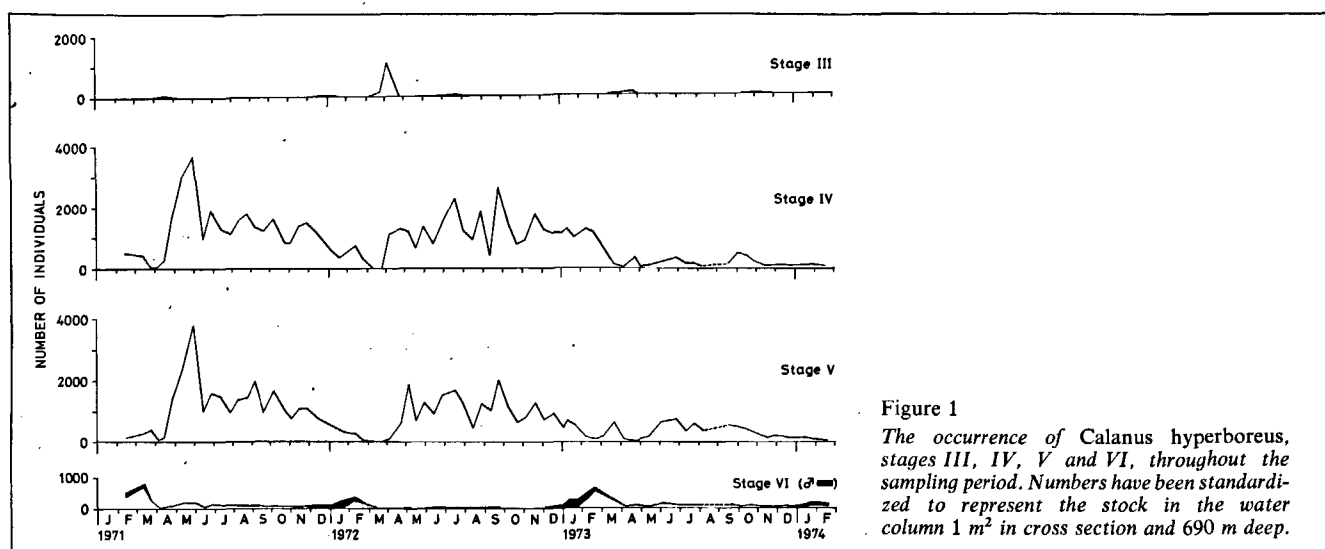
Figure 1

*The occurrence of* Calanus hyperboreus, *stages III, IV, V and VI, throughout the sampling period. Numbers have been standardized to represent the stock in the water column 1 $m^2$ in cross section and 690 m deep.*

the adult males. These only occur during a brief period between the middle of December and early March, quite consistently in each of the 3 years of sampling. At their peak in January they can considerably outnumber the adult females. The females, which are much less limited in time, tend to reach a peak in numbers a little after the males, at which time the majority is gravid. There is also a secondary peak around June or July, accompanied by a very few adult males.

Relatively few stage III copepodids have been obtained and stages I and II were only recorded in the spring of 1973. The timing of all three stages, however, is consistent with late winter spawning and fairly rapid development through the naupliar stages. Judging by the scarcity of young copepodids and the early increase in numbers of stage IV, development continues to be rapid until that stage is reached. Although stage IV remains quite abundant until late in the year, the numbers of stage V also build up around May and stay fairly high until the end of the year. This pattern is repeated in the 3 years of sampling and is taken to indicate a period of prolonged — or delayed — development in which the species spends some 8 months mostly at either stage IV or stage V. A few of those which pass rapidly through stage IV seem also to pass rapidly through stage V and appear as the summer "generation" just visible in June-July. In the subsequent analysis, however, these adults are considered rare enough to ignore and the generation cycle is treated as an annual one.

The population data need to be re-presented in a form suitable for Manly's model. Since recruitment is defined as the entry of individuals into a given developmental stage, numbers of individuals in stages junior to the one being considered are excluded. Mortality, on the other hand, refers to the decrease in numbers due to death and does not include loss from a given stage due to moulting to the next, so the numbers of individuals in any senior stage are added to the one being considered.

The cumulated data for the successive stages are presented in Figure 2. In the summer and autumn months there are some quite wide fluctuations, the timing of which is not the same from year to year. They are considered to be due to sampling error or to show the effect of extrinsic factors operating on the populations and have not been taken into account when fitting Manly curves.

The estimated parameters for the successive stages of the three generations are given in Table 1. Stage III is so much more scarce than stages IV and V in the samples that the parameters estimated for that stage are inevitably affected by the numbers and timing of the later stages. Because the model assumes a normal distribution for the time of recruitment to each stage, it cannot take account of alternative delays at stage IV or stage V. The estimated time of peak recruitment, $\mu$, therefore refers only to the rapidly developing section of the juvenile populations, and the spread in time, $\sigma$, is thus underestimated for stage V. The estimated number of

Table 1

Calanus hyperboreus. *Total number of recruits (M) to the* 1 $m^2$ *water column, day of peak recruitment ($\mu$) in days from the start of the calendar year, spread of recruitment ($\sigma$), and instantaneous mortality rate ($\theta$), excluding senile mortality in the case of the copepodids, for stages III, IV, V and VI (males and females combined), in the three generations sampled. Values in brackets are uncertain for reasons discussed in the text.*

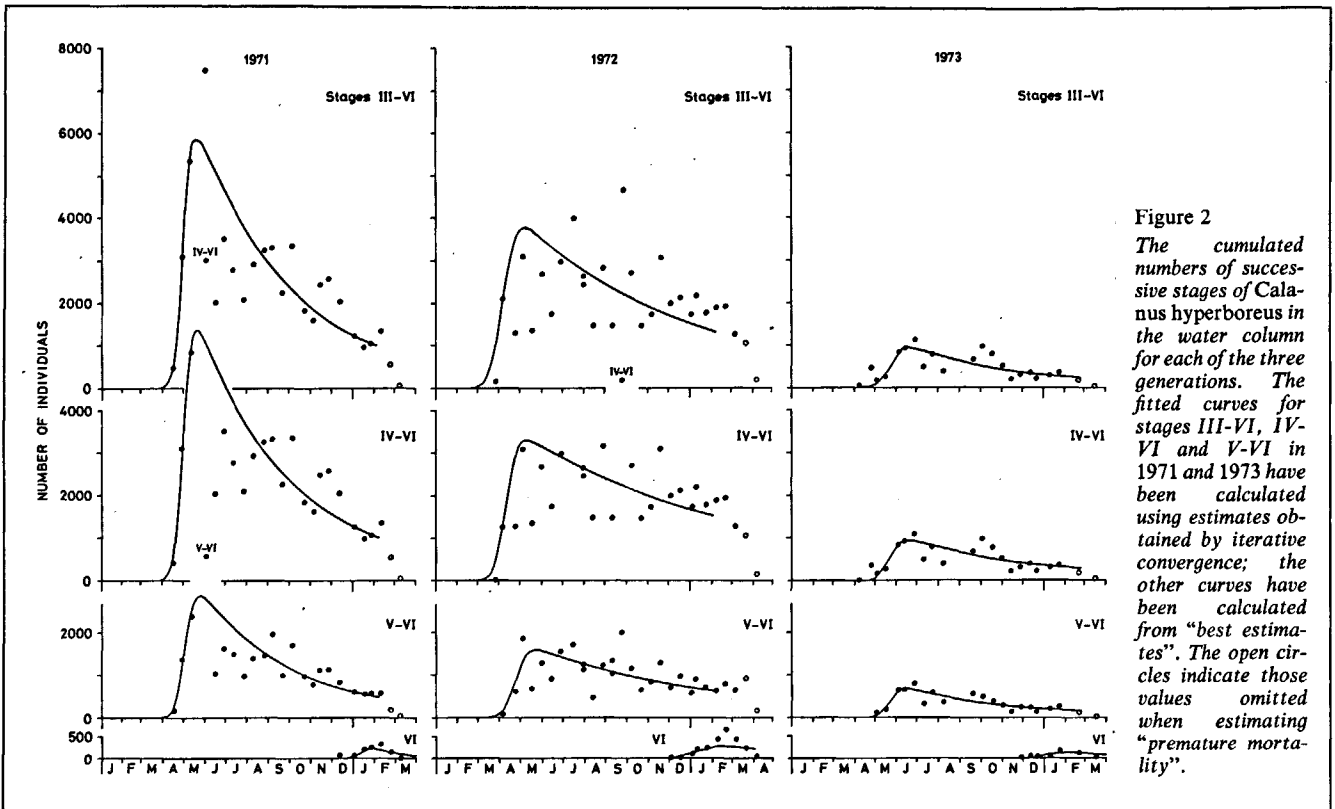| | 1971 | | | | 1972 | | | | 1973 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | III | IV | V | VI | III | IV | V | VI | III | IV | V | VI |
| M | 7 690 | 7 680 | (3 830) | 1 700 | 6 650 | 5 420 | (3 020) | 900 | 1 220 | 1 210 | (890) | 220 |
| $\mu$ | 119.7 | 119.8 | (122.2) | 379.6 | 97.4 | 102.1 | (115.3) | 386.4 | 143.0 | 143.5 | (143.4) | 375.4 |
| $\sigma$ | 10.9 | 10.7 | (12.2) | 11.6 | 15.6 | 13.3 | (14.0) | 23.3 | 14.5 | 13.4 | (12.1) | 13.9 |
| $\theta$ | 0.007 | 0.007 | (0.007) | 0.019 | 0.004 | 0.003 | (0.004) | 0.008 | 0.005 | 0.005 | (0.006) | 0.006 |

Figure 2

*The cumulated numbers of successive stages of Calanus hyperboreus in the water column for each of the three generations. The fitted curves for stages III-VI, IV-VI and V-VI in 1971 and 1973 have been calculated using estimates obtained by iterative convergence; the other curves have been calculated from "best estimates". The open circles indicate those values omitted when estimating "premature mortality".*

recruits to this stage does not therefore include the slow developers, and in consequence mortality is also underestimated. While the parameters obtained for stages V-VI must thus be treated with caution, those given for stages IV-VI should be reasonable estimates for the combined stages, likewise those given for stage VI alone.

As stated above (p. 278), the model estimates a single mortality rate, though in reality at least two rates probably apply, namely the "premature mortality rate" of individuals which do not complete their life cycle, and the "senile mortality rate" of spent adults which is apparent in the rapid decline over the last few observations of each generation. Senile mortality has been excluded from the estimates of juvenile mortality by ignoring the last two observations of each generation. The senile mortality rate could be calculated empirically and incorporated as a terminal function in the model.

Convergence was achieved for the three juvenile curves of 1971 and 1973 (see Fig. 2), in some cases after calculating running averages of three observations for the declining phase. For adults in 1971 and 1973 and all stages in 1972, the fitted curves in Figure 2 represent the "best estimates". In 1973, when the copepodid cycles were delayed some three to five weeks relative to 1971 and 1972, the number of recruits was one-fifth to one-sixth that of the other years (see Table 1). The generation cycle seems to have recovered its usual timing by the time the adults appeared in the winter of 1973-1974. Mortality is low and remarkably constant for all juveniles. The estimated mortality of adults, though higher, is too low to fit the observed decline, despite the fact that all observations have been taken into account.

*Calanus finmarchicus*

The mesh size of the Longhurst frame net was not suitable for catching the first two copepodid stages of this species; the third and probably the fourth were also considerably undersampled. The various stages that were caught show, collectively and individually, a very marked annual cycle, but within this cycle it is evident that there are more than one generation per year in Korsfjorden.

A visual cohort analysis of the population (Fig. 3) has provided the basis for distinguishing the generations before application of Manly's model. Cohorts are in general not difficult to distinguish except at stage V, where it is evident that the population tends to spend much of its developmental time; there is almost certainly considerable individual variation with consequent overlapping of generations. Peaks in adult numbers, when males tend to precede females slightly, followed by peaks of juveniles (stages III and IV) indicate successful spawning periods in early spring and early summer. A smaller peak of adults in late summer/early autumn is not followed by any distinct peak in juveniles, so a third generation is considered to be insignificant; only a small proportion of the population is involved and there seems to be no effect on recruitment. It has therefore only been necessary to divide the mass of individuals at stage V into two generations in the year. This has been done by assuming the rise and the first peak of the year (in May) to consist exclusively of spring-spawned individuals and then describing a symmetrical distribution about the peak. The remainder have been assigned to the second generation.

The problem of estimating recruitment to stage V does not arise in the case of *C. finmarchicus* since delayed
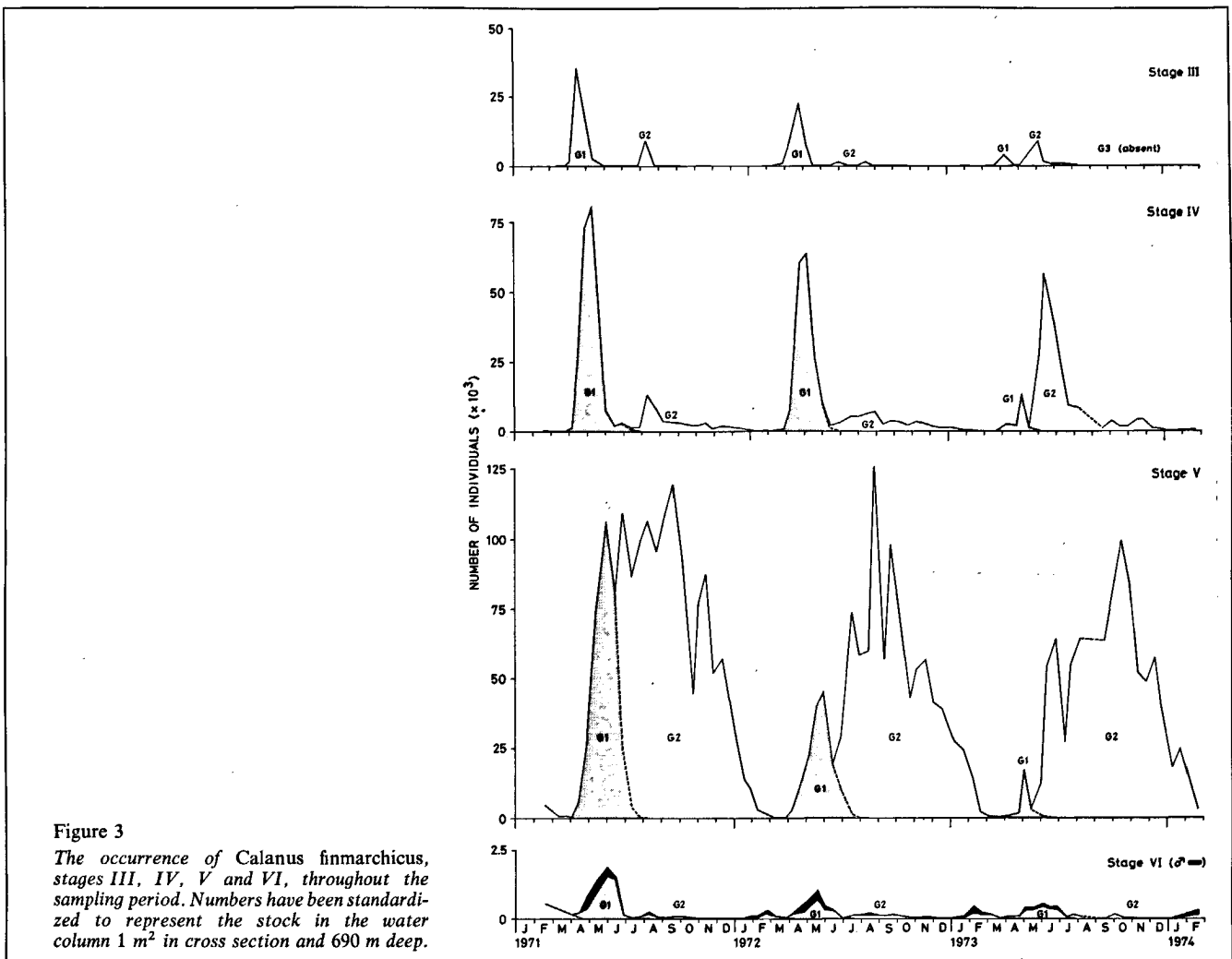
**Figure 3**

*The occurrence of Calanus finmarchicus, stages III, IV, V and VI, throughout the sampling period. Numbers have been standardized to represent the stock in the water column 1 $m^2$ in cross section and 690 m deep.*

development does not seem to occur in stage IV as it did in *C. hyperboreus*. There is instead a problem with the adults of the second generation of each year, which clearly do not satisfy the requirement of the model that recruitment be normally distributed in time (see Fig. 3). As the early autumn adults seem not to spawn successfully — or significantly — they have been excluded from the adult stocks as analyzed, though they have been included in the cumulations with younger stages in order not to exaggerate the mortality rates of these younger stages.

Five generations are completely represented in the sampling period and a sixth has been completed by extrapolating to a nominal single adult at the end of March 1974, in conformity with the pattern seen in 1971-1972 and 1972-1973. The cumulated data for each generation are presented in Figure 4. The fitted curves in the figures are described by "best estimates" of the various parameters (Table 2).

The first generation of each year is much more concentrated in time than is the second (*cf.* values of σ). This can result, as in 1971, in a standing stock which is not much less than the stock present later in the year (see Fig. 3), though the number of recruits is always considerably less (*cf.* values of M for stage III). If the generations have been correctly identified, peak recruitment (see values of μ) to the later copepodid stages

of generations 1 occurs in the last week of April and the first week or 10 days of May, and of generations 2 in the last two weeks of August. Adult recruitment occurs soon afterwards in the case of generations 1, but there is a delay of some five months in the case of generations 2.

Since the final few observations of each generation of *C. finmarchicus* do not show the same sudden decline in numbers as occurs with *C. hyperboreus*, a constant rate of mortality seems to be an acceptable assumption. Nevertheless, tests were run to estimate mortality without the last three observations of each generation. The example of such a curve given for stages IV-VI generation 2 of 1971 (see Fig. 4) shows little or no improvement over the curve where all observations have been included. Other such curves gave distinctly poorer fits to the observed data.

The various estimates of mortality vary considerably, from a mere 2 % per day for the copepodids of one of the long-lived second generations to almost 50%, i.e. $(1 - e^{-0.492}).100$, per day for the adults of the brief generation 1 in 1972.

## DISCUSSION

The plankton of the Norwegian coast has been the subject of numerous investigations, in most of which the biology of *Calanus* spp. has figured prominently
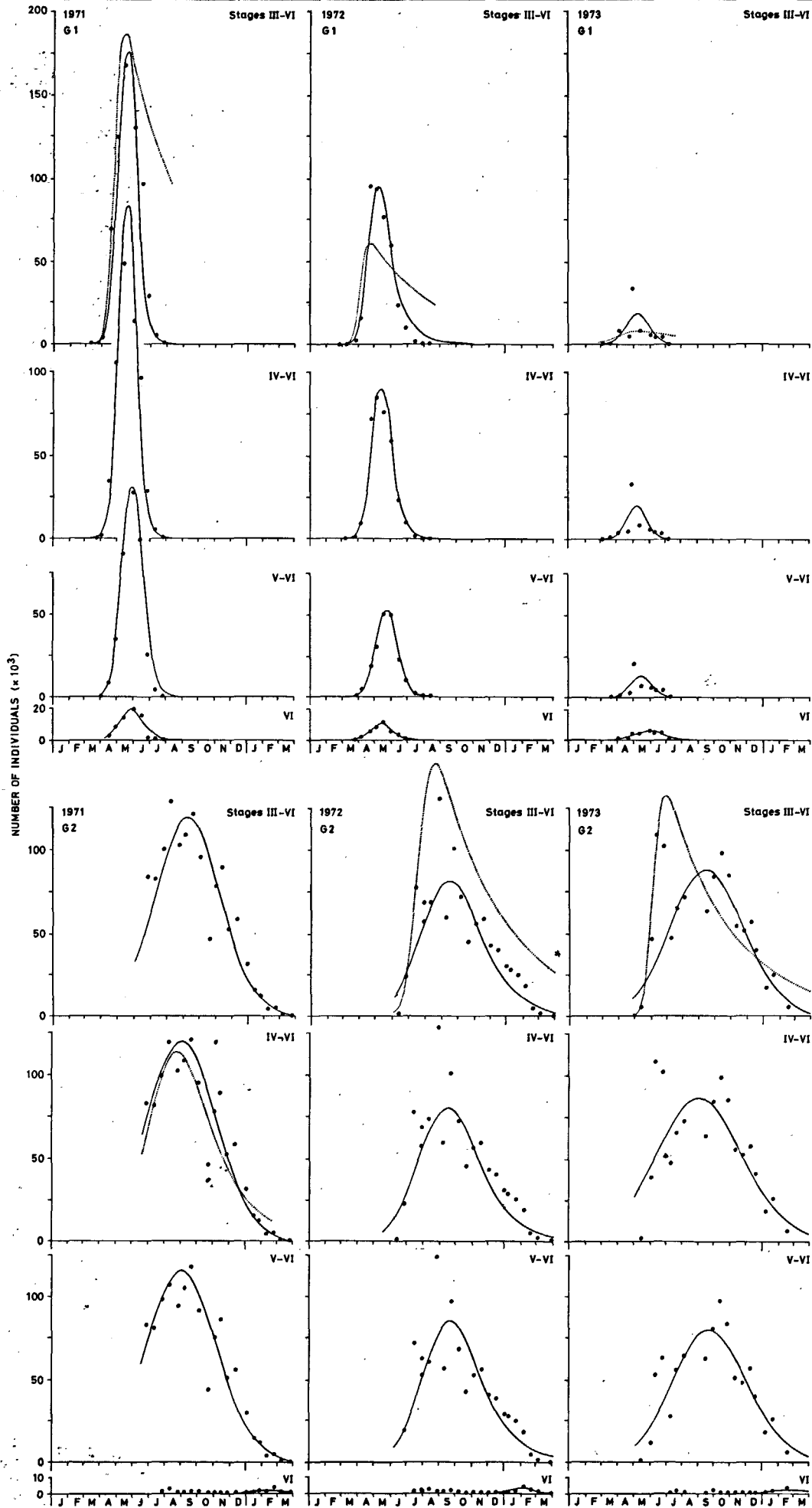
Figure 4

*The cumulated numbers of successive stages of* Calanus finmarchicus *in the water column for each of the six generations. The fitted curves have been calculated from "best estimates". The last three observations have been excluded in calculating the stippled curve for the combined stages IV-VI of generation 2 of 1971. The mortality rate has been fixed at 0.008 in calculating the stippled curves superimposed on the figures for the combined stages III-VI of the other generations.*

Table 2

Calanus finmarchicus. *Total number of recruits* (M) *to the* 1 $m^2$ *water column, time of peak recruitment* ($\mu$) *in days from the start of the calendar year, spread of recruitment* ($\sigma$), *and instantaneous mortality rate* ($\theta$) *for stages* III, IV, V *and* VI *(males and females combined) in the six generations sampled.*

| | G 1, 1971 | | | | G 2, 1971 | | | | G 1, 1972 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | III | IV | V | VI | III | IV | V | VI | III | IV | V | VI |
| M | 1 078 900 | 1 303 300 | 866 300 | 100 100 | 2 129 800 | 3 699 200 | 3 518 500 | 3 600 | 236 600 | 367 000 | 1 327 200 | 243 700 |
| $\mu$ | 130.8 | 133.5 | 143.1 | 138.3 | 245.5 | 239.4 | 238.8 | 394.6 | 114.6 | 123.8 | 145.5 | 133.6 |
| $\sigma$ | 16.2 | 15.8 | 18.5 | 20.5 | 61.4 | 66.7 | 66.9 | 19.8 | 15.0 | 17.0 | 20.0 | 19.1 |
| $\theta$ | 0.122 | 0.136 | 0.122 | 0.087 | 0.104 | 0.164 | 0.162 | 0.029 | 0.037 | 0.071 | 0.457 | 0.492 |

| | G 2, 1972 | | | | G 1, 1973 | | | | G 2, 1973 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | III | IV | V | VI | III | IV | V | VI | III | IV | V | VI |
| M | 300 800 | 295 900 | 301 100 | 22 200 | 149 600 | 246 400 | 307 100 | 46 900 | 801 300 | 1 221 300 | 600 600 | 8 400 |
| $\mu$ | 229.3 | 229.7 | 234.5 | 395.0 | 125.1 | 127.5 | 132.7 | 145.4 | 241.6 | 233.6 | 244.3 | 403.2 |
| $\sigma$ | 47.5 | 47.4 | 44.8 | 17.5 | 19.5 | 18.3 | 19.6 | 27.4 | 68.4 | 81.1 | 67.9 | 24.0 |
| $\theta$ | 0.022 | 0.022 | 0.022 | 0.145 | 0.143 | 0.232 | 0.430 | 0.111 | 0.046 | 0.061 | 0.037 | 0.056 |

(e. g. Ruud, 1929; Sömme, 1934; Östvedt, 1953; Wiborg, 1954; Lie, 1965) and it is to be expected that the present investigation should produce no surprises as far as the annual cycle is concerned. There is general agreement that there is a single generation of *C. hyperboreus* in the year, though opinions have varied as to whether maturity is achieved after 1 or 2 years. The uncertainty arises partly from the effect of extrinsic factors operating on the population which can effectively eliminate certain developmental stages from the samples. This emphasizes the fact that a sampling programme, even in a semi-enclosed system like a fjord, is not necessarily operating with constant populations. What can be assumed is that the sampled system is in long-term equilibrium, if not between birth and death, then between entry and departure. Though the juveniles of *C. hyperboreus* may not be the actual progeny of the adults seen beforehand, they can be considered to represent the succeeding generation, hence the interpretation of the data as indicating a 1-year cycle of spawning, development, and maturation.

In the case of *C. finmarchicus*, generations have only been distinguished when significant recruitment seems to have ensued. Two such generations per year have been identified, though breeding activity is not entirely confined to these (*cf.* Wiborg, 1954; Lie, 1965). The developmental strategies followed by the populations in spring and in summer/autumn are different. The present model offers some precise information on the lengths of time spent at the various developmental stages and quantifies the period of consolidation, almost hibernation, undergone by the stage V copepodids in the autumn/winter stock.

The various short-term fluctuations in the number of stage V, in particular, probably reflect interchange between stocks on a local scale and indicate that recruitment to the Korsfjord stock is not solely due to spawning by the parent population in the area. The apparent mortality may likewise be influenced by gain from or loss to surrounding areas. Nevertheless, the long-term picture is of a stock in equilibrium.

The fact that convergence was achieved in six out of twelve sets of data for *C. hyperboreus* (three of the other sets, for the adults alone, consisted of very low counts) is an indication that the calculated parameters are realistic estimates of recruitment and its timing, and of mortality. The fit of some of the curves to the observed data for *C. finmarchicus* may, however, be too good. The data for the declining phase of generations 1 and the recruitment phase of generations 2 are themselves the result of a decision on splitting the generations and have therefore a built-in regularity. Moreover, the remarkable fit in the case of generation 1 in 1972 involves an *increase* in the estimated number of recruits to successive copepodid stages; paradoxical increases in M from stage to stage also occur in other generations. Manly's model appears to allow undue simultaneous change in M and $\theta$, with the result that high estimates of both or low estimates of both produce expressions which in some cases can describe observed data almost equally well; the main effect of lower recruitment and mortality is greater skewness of the curve.

In order to check whether this lack of sensitivity in the model could nullify the apparent difference between the mortality rates of *C. hyperboreus* and *C. finmarchicus*, estimation of recruitment (M) and its timing ($\mu$ and $\sigma$) have been obtained for each generation of *C. finmarchicus* assuming a fixed mortality rate, $\theta$, of 0.008, which is slightly higher than was obtained for any copepodid stage of *C. hyperboreus*. The resulting curves for *C. finmarchicus*, stages III-VI combined, in each generation have been superimposed in Figure 4. In each case, the curve gives a worse description of the observed data than does the curve described by the "best estimates". It can be concluded that, though some of the freely estimated values of $\theta$ for *C. finmarchicus* may be too high, the difference in the level of mortality between the two species is a real one. The surprise is not that *C. finmarchicus* suffers a daily mortality rate of around 10% ($\theta = 0.02 - 0.4$) — it is a favourite food of many pelagic carnivores — but that *C. hyperboreus* should have such a low premature daily mortality rate of

283

around 0.5 % ($\theta = 0.003 - 0.007$). If this is representative of prey organisms in the deep-water community, the rate of transfer of organic matter must be very low. This transfer seems in large measure to be to the decomposers in the system. As adult females are not likely to become suddenly more vulnerable to predation just after the height of the spawning season, they probably die. Senile mortality would release material and energy to decomposers rather than to higher trophic levels. No such senile mortality was discerned among the adults of *C. finmarchicus*, so it seems likely that virtually the whole population falls prey to carnivores.

## Acknowledgements

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