# Stage-specific mortality of *Calanus* spp. under different predation regimes

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*Abstract*

We have applied the population surface method to estimate the mortality rates of eggs, nauplii, and copepodids of *Calanus* spp. in two Norwegian fjords with contrasting predator guilds. Efforts were concentrated in Lurefjorden on the western coast (sampled weekly from late February to mid-June), an unusual fjord dominated by invertebrate (tactile) planktivores. In addition, monthly sampling in Sørfjorden was carried out for comparisons. The latter fjord resembles most Western Norwegian fjords in that it contains populations of vertebrate (visual) planktivores but lower abundance of the invertebrate planktivores. In Lurefjorden, mortality of *Calanus* spp. was high early in life (~0.35 d$^{-1}$), but significantly lower (~0.00 d$^{-1}$) in the early copepodid stages. In Sørfjorden, mortality was rather uniform throughout ontogeny (~0.08 d$^{-1}$). The noted differences are consistent with different patterns of selective predation between the two fjords. Visual predation in Sørfjorden gave rise to persistent high mortality over the life cycle. Tactile predation in Lurefjorden gave rise to a concave mortality curve for the later developmental stages. Our results indicate that mortality patterns suffered by natural zooplankton populations may differ greatly over short geographical distances, and we suggest that the predator community and mortality patterns must be considered when addressing the spatial and temporal dynamics of zooplankton populations.

To gain mechanistic understanding of the processes structuring pelagic ecosystems, it is essential to know the underlying vital rates of zooplankton populations (Ohman 1988; Aksnes et al. 1997). Traditionally, the quest for mechanisms has focused on bottom-up control of populations (Ohman and Wood 1995; Verity and Smetacek 1996), and models of ocean physics and primary production have reached a high level of precision. But because of the lack of reliable data on vital rates for zooplankton populations, unifying such models with models for higher trophic levels has not succeeded (Bryant et al. 1997). During the last decade top-down control has received increased attention in marine ecology. For instance, insight into how zooplankton may reduce the risk of predation is crucial for understanding how they adapt to life in the water column by their choice of habitat (Fiksen

and Giske 1995), behavior (Ohman et al. 1983; Aksnes 1996; Kaartvedt et al. 1996), and life cycles (Verity and Smetacek 1996). This suggests that the combined effects of bottom up and top-down mechanisms must be considered when addressing the dynamics of marine populations (Peterson and Wroblewski 1984; Ohman 1986; Peterson and Kimmerer 1994; Ohman and Wood 1995; Eiane et al. 1999).

Estimating loss rates from natural populations of zooplankton is complicated and nontrivial. In the pelagic environment, organisms tend to drift with ocean currents, and vertical shear over the depth distribution of a species suggest that time series data obtained at a fixed geographic location reflect much less clearly defined populations than one would wish (Aksnes and Ohman 1996). For this reason, most estimates of zooplankton mortality tend to be obtained from semienclosed parcels of water where the advective transport of organisms is limited (Aksnes and Magnesen 1988; Ohman and Wood 1996; *but see* Ohman and Hirche 2001).

Census data from natural zooplankton populations often include a series of reproduction events and thus may reflect a number of overlapping generations. This adds to the complexity of interpretation because current techniques for handling population dynamics require knowledge about the age and generation times of individuals (Aksnes et al. 1997).

In the study of pelagic food webs, it has proved fruitful to differentiate between vertebrate and invertebrate predators because it has been shown that the two predator types tend to exert different selective pressures on the prey community (Brooks and Dodson 1965; Pastorok 1981). Vertebrate predators of the water column (usually fish) generally use vision in their search for prey and therefore tend to select the larger or more conspicuous forms (Brooks and Dodson 1965; Checkley 1982). Some invertebrate predators (e.g., jellyfish) rely on passive encounters with prey, whereas others (e.g., carnivorous copepods and chaetognaths) generally respond to hydrodynamic disturbances generated by swimming prey (Feigenbaum and Maris 1984; Yen and Strickler 1996). These nonvisual modes of prey search, together with the smaller size of many of the numerically dominating invertebrate predators, is likely to lead to higher predation pressure on smaller to intermediate sized forms of zooplankton.

The dominant zooplankton in the northern Atlantic (*Calanus* spp.) develop from eggs of diameter ~0.15–5 mm total length as adult females. Thus it is likely that *Calanus* spp. over its ontogeny will face differences in mortality regimes.

The way zooplankton utilize the spatial dimension of the water column is also under influence of predator abundance. Ohman (1990) showed that *Pseudocalanus newmani* in Dabob Bay alters vertical migratory behavior in response to changes in the prevailing predation pressure from fish to invertebrates. He demonstrated that at stations where planktivorous fish prevailed, *P. newmani* performs nightly excursions to the food-rich surface waters, whereas at stations where invertebrates (carnivorous copepods and chaetognaths) dominated, the pattern of vertical migration was reversed.

Effects of predation on the dynamics of natural zooplankton populations thus can be threefold: (1) it can reduce the abundance of prey organisms; (2) it can have a size structuring effect on the zooplankton community, thereby affecting the size and age compositions of prey populations; and (3) it can affect the horizontal or vertical distribution of populations.

In the present study, we estimate the stage-specific mortality rates suffered by a natural population of *Calanus* spp. under predominantly invertebrate predation pressure. In addition, mortality estimates are made for a nearby population that is affected principally by vertebrate predation but to a lesser degree experiences invertebrate predation pressure. In comparing the mortality patterns, we discuss the implications that variations in predator regime may have on prey population dynamics.

## Materials and methods

*The study area*—During cruises with R/V *Hans Brattstrøm* throughout the spring and early summer of 1996, two fjords on the western coast of Norway were studied. In Lurefjorden (60°40′N, 5°10′E; maximum depth = 430 m; surface area ≈ 30 km²) populations of mesopelagic fish are absent. The fjord houses a large standing stock of the jellyfish *Periphylla periphylla* (Fosså 1992). In contrast, Sørfjorden (60°25′N, 5°30′E; maximum depth = 360 m; sur-

face area ≈ 25 km²) sustains populations of the mesopelagic fishes *Maurolicus muelleri* and *Benthosema glaciale* and has negligible populations of jellyfish. In both fjords, the zooplankton community is dominated by herbivorous calanoid copepods previously understood to be *Calanus finmarchicus* (Fosså 1992). However, recent findings suggest that fjords on the west coast of Norway may sustain a mixture of *Calanus* species, including at least *C. finmarchicus, C. glacialis,* and *C. helgolandicus* (Bucklin et al. 2000; P. Lindeque pers. comm.). Because we did not differentiate species in this study, we apply the term *Calanus* spp.

*Sampling*—At every station, the salinity and temperature were measured by a Seabird CTD (conductivity, temperature, depth). Water samples (collected in 10-liter Niskin bottles) taken at 5-m intervals from 45 m to the surface were used to monitor the concentrations of chlorophyll *a* (Chl *a*) by filtering 100 ml from each sample on 0.45-$\mu$m Sartorius cellulose nitrate filters, deep frozen at $-18°C$, and analyzed on a Turner Designs fluorometer (Strickland and Parsons 1972). From late February to mid-June, zooplankton were sampled by a Multinett (180 $\mu$m mesh size; Hydrobios, Kiel) applied in the vertical mode in the following sampling scheme. In Lurefjorden, once a week at following depth intervals: 430–300 m, 300–200 m, 200–100 m, 100–50 m, and 50 m to surface; in Sørfjorden, once every month at the following depth intervals: 360–300 m, 300–200 m, 200–100 m, 100–50 m, and 50 m to surface. The upper 50 m of the water column was also sampled (in both fjords and using the same apparatus) in 10-m intervals. Small zooplankton (i.e., <180 $\mu$m) were sampled by pumping (860 L min$^{-1}$) water at 5-m intervals, from 30 m to the surface, into a 60-$\mu$m mesh size net. Every month, both fjords were sampled day and night. Zooplankton samples were fixed in a 4% formaldehyde-in-seawater solution before they were staged and counted. For randomly selected subsamples, the prosome lengths of all developmental stages of *Calanus* spp. were measured.

Sampling all developmental stages of *Calanus* spp. is complicated because of differences in size, swimming ability, and presumably avoidance. To gain insight into what tool (net or pump) is suitable for each developmental stage, we compared estimates of abundance made from depth-integrated net hauls with a combination of nets and plankton pump (Fig. 1). A combination of pump (upper 30 m) and nets (below 30 m) proved to give higher estimates than nets for the smallest stages, and we used this approach for eggs and nauplii stages N1 and N2. No significant difference in abundances were detected for developmental stages N3 and older, but integrated net samples generally gave somewhat higher estimates. Because it is probable that older stages of *Calanus* spp. are capable of some avoidance of pumps, we assumed that integrated net samples were most appropriate for these stages.

*Mortality estimation*—The population surface method (PSM) for age-structured populations (Wood 1994) was used to solve for mortality rates for *Calanus* spp. By assuming smooth population dynamics, this method fits a continuous surface to age-structured population data representing the
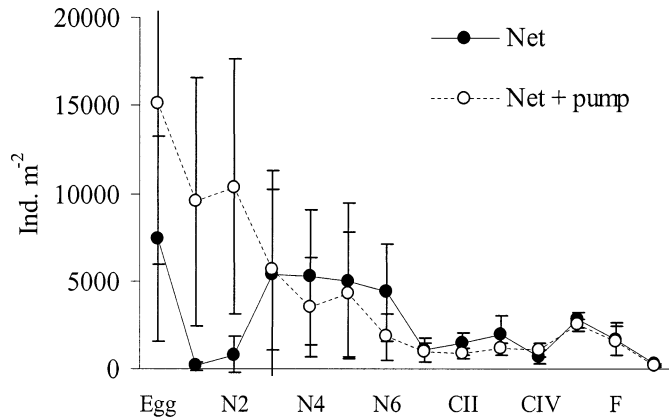
Fig. 1. Estimates of abundance of all stages of *Calanus* spp. from depth-integrated net hauls (180-μm mesh size) and from integrated net hauls from bottom to 30 m plus plankton pump samples from 30 m to the surface. Bars denote 95% confidence limits. Samples are from Lurefjorden on three separate dates in April.

Table 1. Estimated size groups of primary prey of *P. norvegica* based on the assumption that optimal prey size scales to the prosome length of *P. norvegica* times 0.2.

| *P. norvegica* developmental stage | Prosome lengths (mm)* | Prosome length of primary prey (mm) | Corresponding developmental stage of *Calanus* spp.† |
|---|---|---|---|
| CI | 0.9 | 0.2 | N1–N2 |
| CII | 1.3 | 0.3 | N2–N3 |
| CIII | 1.9 | 0.4 | N3–N5 |
| CIV | 2.9 | 0.6 | N5–N6 |
| CV | 4.3 | 0.9 | CI–CII |
| Adult female | 5.3 | 1.1 | CII–CIII |

* Bakke (1977).
† Greene and Landry (1985), Blom et al. (1991).

population per unit age interval at any age and time. Instantaneous mortality rates are calculated from this surface (*see* Wood 1994 for a detailed description). PSM requires the duration of each developmental stage (age) to be determined separately. Estimates of the duration of each developmental stage were obtained by the temperature functions (Corkett et al. 1986) for duration of developmental stages of copepods.

$$D = a(T + 9.11)^{-2.05} \qquad (1)$$

*D* is developmental time, *T* is ambient temperature, and a is a stage-specific, empirically determined constant. To estimate developmental duration for *Calanus* spp., we applied the a parameters derived for *C. finmarchicus* (Campbell et al. 2001) and forced the equation with the observed vertical temperature fields.

The weekly sampling frequency in Lurefjorden is assumed adequate for resolving mortality of all developmental stages. To determine whether the longer sampling interval employed in Sørfjorden was also adequate, we performed a sensitivity analysis on the data from Lurefjorden to assess bias in mortality estimates as sampling interval increased from 1 week to 1 month. This analysis indicated that sampling intervals of 1 month did not adequately resolve mortality rates for young and short-lived developmental stages. For older and longer lived stages (CI onward), mortality estimates obtained from monthly sampling converged with the results obtained from weekly samples. Therefore, in estimating mortality rates from Sørfjorden, we combined all nauplii into a single aggregated stage for which we estimate the mortality rate assumed to be associated with development from hatching to the end of N6. Aggregating the data from Lurefjorden in this same manner gave no significant difference ($P < 0.05$) from the mortality rates obtained for individual stages.

*Quantification of potential predation*—In net samples the dominant predators (by numbers) were the carnivorous copepod *Paraeuchaeta norvegica* and the chaetognath *Eukrohnia hamata*. A detailed account of the plankton community in both fjords has been assembled by Bagøien et al. (2001). In addition, the late copepodid stages of *Calanus* and related genera have been shown to prey on the younger developmental stages of its own species (Landry 1978, 1981; Hada and Uye 1991); therefore, we have included cannibalism as a potential source of predator-induced mortality on young developmental stages. We have treated these groups separately. Based on predation rates reported in the literature, we derive maximum estimates of their predation and compare these with estimates of natural mortality rates of *Calanus* spp.

*Paraeuchaeta* species may prey on all developmental stages of *Calanus,* but laboratory studies indicate that their preferred prey size increases with predator size or developmental stage (Yen 1983). This size-selective predation probably is a function of differential vulnerability of prey stage or age (Greene and Landry 1985) and the size of appendages used for handling prey (Yen 1983). Optimal prey size for *P. elongata* is ~70% of the length of the second basipod segment of the maxilliped, which scales to the prosome length by approximately 0.3 (Yen 1985). For adult females and copepodid stages CV and CIV, the ratio between prosome length and (prosome) length of the preferred prey is 0.2 for *P. elongata* (0.22, 0.21, and 0.21, respectively; Yen 1985). By assuming this relationship for the slightly larger copepodid stages of *P. norvegica,* we suggest that the predation pressure exerted by copepodids of this predator should peak on early developmental stages of *Calanus* spp. (Table 1).

In the absence of feeding rates of *P. norvegica,* we have assumed the Holling type 2 functional response curve (Holling 1959) parameterized for *P. elongata* preying on optimally sized prey (Yen 1983):

$$M = \sum_{i=1}^{k} 2.8 N_i P_i D_i (1 + 0.175 N_i)^{-1} \qquad (2)$$

where *M* is the number of prey eaten in the water column (individuals $d^{-1}\ m^{-2}$), $N_i$ (individuals $m^{-3}$) is the density of prey available in depth interval *i*, $P_i$ (individuals $m^{-3}$) is the density of predators in depth interval *i*, $D_i$ (m) is the thickness of interval *i,* 0.175 is the product of $T_h$ (handling time = 0.0625 d; Yen 1983) and a (attack coefficient = 2.8 $d^{-1}$;

Table 2. Frequency of copepod size classes in the diet of juvenile and adult *Maurolicus muelleri* (calculated from data on gut contents of *M. muelleri* from Herdlefjorden, January–June 1994; based on Skagseth 1999).

|  | Prey size classes (mm) | | | |
| --- | --- | --- | --- | --- |
|  | <1 | 1–2 | 2–3 | >3 |
| Juveniles | 0.41 | 0.39 | 0.14 | 0.06 |
| Adults | 0.24 | 0.38 | 0.30 | 0.09 |

Yen 1983). Equation 1 enables us to make estimates of the predation pressure from each copepodid stage of *P. norvegica*. No attempt was made to quantify the predation pressure exerted by *P. norvegica* nauplii.

To estimate the maximum predation pressure exerted on the *Calanus* community by chaetognaths, we assumed the higher range of predation rates reported for *Eukrohnia hamata* of 0.64 d$^{-1}$ (average = 0.3, range = 0.15–0.64) foraging for small copepods (Øresland 1990, 1995). The maximum attainable predation rates for all *E. hamata* (both juveniles and mature individuals) were computed as

$$M = \sum_{i=1}^{k} C_i D_i 0.64 \qquad (3)$$

where $C_i$ is the density of *E. hamata* in depth interval $i$.

Many planktonic organisms are omnivores at some stage of, or throughout, their life cycles (Isaacs 1977), and several copepods have been reported to prey on young stages of their own species (Landry 1978, 1981; Hada and Uye 1991). Clearance rates of copepods differ considerably with diet (Ohman and Runge 1994) and food concentration (Gamble 1978; Landry 1981), and *Calanus* clearance rates reportedly vary from <1 to >100 ml copepod$^{-1}$ h$^{-1}$ (Gamble 1978). We have assumed the maximum clearance rate of late copepodids of *Calanus* spp. to be 25 ml h$^{-1}$ (Ohman and Runge 1994). Assuming late stages of *Calanus* spp. (CIV to adult females) do not avoid eggs and early nauplii (N1–N3) of its own species when feeding and subsequently ingest (or kill) all encountered organisms (assumed evenly distributed within each depth interval), we have computed the potential predation pressure on these young developmental stages.

$$M = \left[ \sum_{i=1}^{k} (C_i F_i D_i)(N_i D_i) \right] \left( \sum_{i=1}^{k} D_i \right)^{-1} \qquad (4)$$

$C_i$ is the density of late copepodids of *Calanus* spp. (individuals m$^{-3}$) in depth interval $i$, $F_i$ is the *Calanus* spp. clearance rate (0.0006 m$^3$ individual$^{-1}$ d$^{-1}$).

From acoustic surveys (average values for 9.3-km transects), Bagøien et al. (2001) report *M. muelleri* densities of ~13.4 individuals m$^{-2}$ for juveniles and ~4.1 individuals m$^{-2}$ for adults. Selection among size classes of copepod prey is assumed to follow the gut content study over a spring period (January–June) of Skagseth (1999). We averaged her data into a juvenile and an adult age class (Table 2) assuming individuals <40 mm standard length are juveniles and individuals >40 mm are adults (Gjøsæter 1981).

Foraging rates reported from the literature indicate adult *M. muelleri* is capable of feeding on large copepodids at ~750 μg d$^{-1}$ or ~150 μg dry wt d$^{-1}$, and juveniles feed at rates approximately four times higher (~600 μg dry wt d$^{-1}$), but on appreciable smaller copepodids (Giske and Aksnes 1992). The diet of *M. muelleri* typically consists of ~50% copepods by weight (Bjelland 1995) and >50% by numbers of identifiable prey in guts most of spring and summer (Skagseth 1999). From this assumption, we have estimated the effect of predation from mesopelagic fish.

$$M = \sum_{j=1}^{4} (C_J S_{Jj} K_j \beta_J) + (C_A S_{Aj} K_j \beta_A) \qquad (5)$$

$C_J$, $C_A$, and $\beta_J$, $\beta_A$ denote concentration (individuals m$^{-2}$) and daily consumption (μg dry wt d$^{-1}$ individual$^{-1}$) for juvenile (J) and adult (A) fish, respectively. $S_{Jj}$ and $S_{Aj}$ are the fractions of food intake in each of the size categories ($j = 4$) in Table 2. $K$ is the assumed conversion factor from dry weight to number of copepods in each size group assuming the length to weight relationship for copepodid stages of *C. finmarchicus* provided by Blom et al. (1991) ($K_1 = 1/10$, $K_2 = 1/30$, $K_4 = 1/95$, and $K_4 = 1/155$).

For each predator–prey relation (Eqs. 2–5) the maximum estimate of organisms killed can then be related to the corresponding maximum estimate of instantaneous mortality rate ($m$) by

$$m = -\ln(1 - MN^{-1}) \qquad (6)$$

where $M$ is defined by Eqs. 2–5, and $N$ is an estimate of the prey abundance (individuals m$^{-2}$).

The euphausiid populations in the two fjords have not been estimated in this study because the larger krill avoided the equipment used for sampling. We only remark that both fjords sustain krill (as suggested by high numbers of larval krill caught; *see below*). Furthermore, the krill larvae appeared to be found at highest numbers in the upper parts of the water column of both fjords.

## Results

*Seasonal changes*—The first signs of a thermocline developed in mid-April at about 30 m in Lurefjorden (Fig. 2a). Chl *a* levels were low (<1 μg L$^{-1}$) throughout the water column until early April. Peak phytoplankton biomass occurred between 10 and 20 m from mid-April to the end of May (Fig. 2b). Eggs and nauplii were found in high abundance in the upper 50 m of the water column from mid-March until late April in Lurefjorden. In addition, a secondary peak in egg and nauplii abundance appeared from mid-May to early June. Copepodids (CI–CIV) occurred in the upper layers shortly after the increase in egg and nauplii numbers. Copepodids (CV) developed from ca. 20 April, but did not dominate before ca. 5 May, when they were found deep in the water column. From ca. 15 May through 5 June, the population of *Calanus* spp. was dominated by copepodids (CV) aggregating between 100 and 200 m. Adults were present high in the water column from the beginning of the study until mid-March, after which they were almost absent
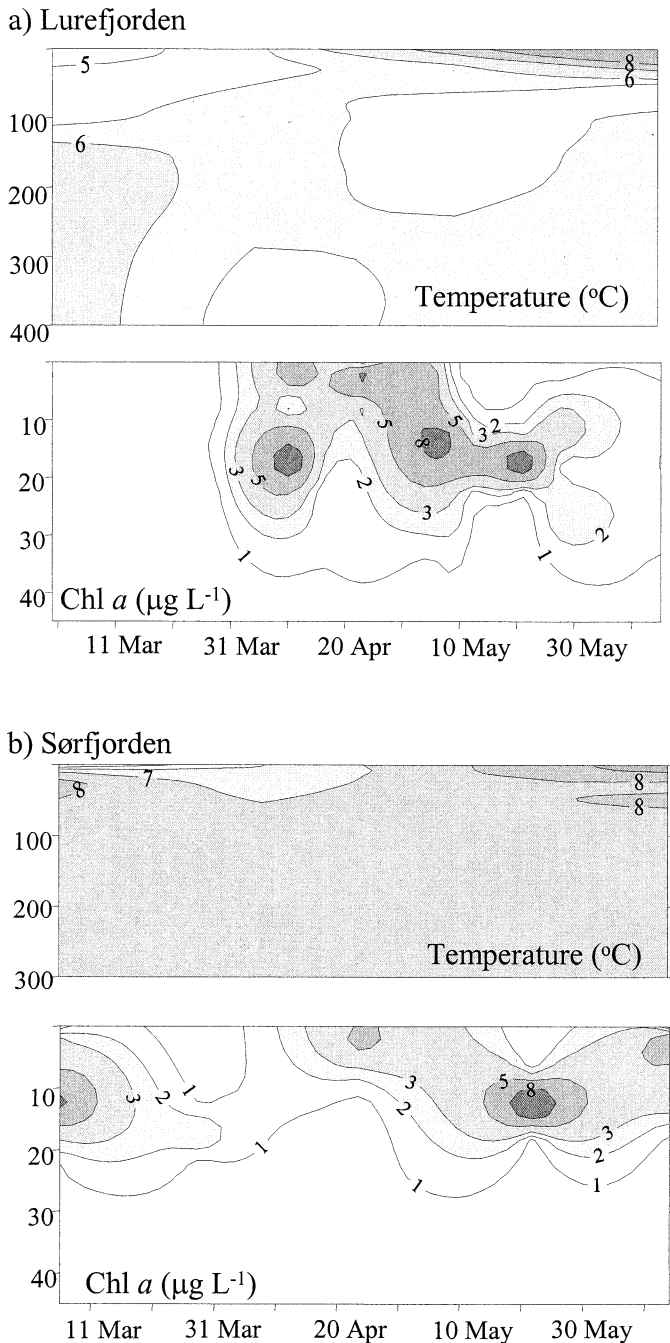
a) Lurefjorden



Temperature (°C)

Chl $a$ (μg L$^{-1}$)

11 Mar     31 Mar     20 Apr     10 May     30 May

b) Sørfjorden



Temperature (°C)

Chl $a$ (μg L$^{-1}$)

11 Mar     31 Mar     20 Apr     10 May     30 May

Fig. 2. Seasonal variations of temperature and Chl $a$ at the stations in (a) Sørfjorden (5 March–12 June 1996) and (b) Lurefjorden (27 February–12 June 1996). Temperatures were measured from the surface to 330 m in Sørfjorden and from the surface to 430 m in Lurefjorden. Chl $a$ was measured in the upper 45 m in both fjords.
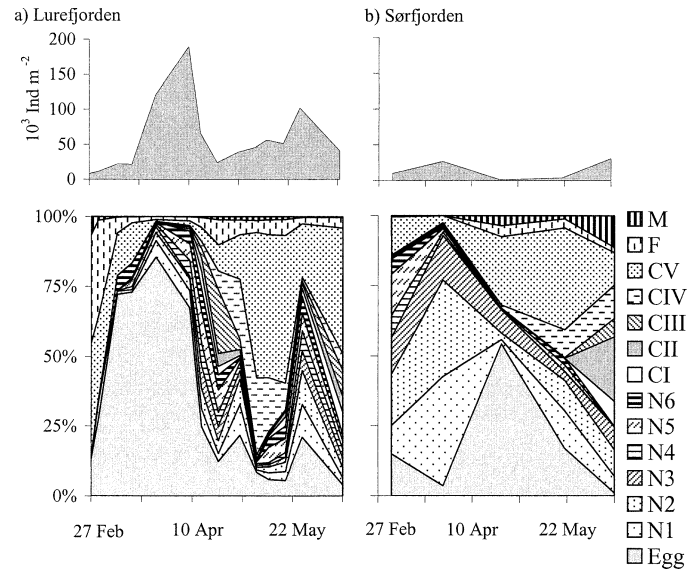


Fig. 3. Seasonal variation of *Calanus* spp. in (a) Lurefjorden, and (b) Sørfjorden. Upper panels show the total abundance of *Calanus* spp. (individuals m$^{-2}$). Lower panels show the abundance of each developmental stage as a percentage of the total population.

until encountered again deep in the water column from mid-April as the next generation developed. From low numbers (~8,000 ind. m$^{-2}$) in February, before peak egg production, the population grew until the first peak (~200,000 individuals m$^{-2}$) in early April (Fig. 3), after which the abundance declined before a second increase in mid-May.

In Sørfjorden, a cold brackish upper layer was present throughout the sampling period (Fig 2b). Although Chl $a$

levels in the top 25 m never dropped below 1 μg L$^{-1}$ during the study period, two distinct bloom events could be identified (Fig. 2a). Eggs and nauplii were already present at high abundance in the upper 50 m of the water column in Sørfjorden at the initiation of sampling, indicating an earlier initiation of the reproductive period in this fjord. Two peaks in abundance may be identified: one in early March and another in early June. Copepodids and adults accumulated in the upper 150 m from ca. 20 May with a peak in abundance at approximately 80 m. In Sørfjorden, the abundance of *Calanus* was lower than in Lurefjorden, never exceeding 30,000 individuals m$^{-2}$ over the sampling period (Fig. 3).

*Estimated predation effects—Paraeuchaeta norvegica* was present at high to moderate densities throughout the water column in Lurefjorden. Whereas nauplii were found below 200 m, the copepodids were distributed throughout the water column. A bimodal distribution was indicated because few individuals were encountered between 100 and 200 m (Fig. 4). The distribution data did not indicate diel vertical migration to be prominent in the fjord, although asynchronous migrations cannot be ruled out. Depth distributions of *P. norvegica* copepodids overlapped all stages of *Calanus* spp. in the fjord, and estimates of potential effect of predation on the *Calanus* suggested that *P. norvegica* predation was important, particularly during the early life history (Table 3).

In Sørfjorden, *P. norvegica* was less abundant. Average density of all stages peaked at ~1 individual m$^{-3}$ in the upper 50 m (Fig. 4). This is reflected by the low potential predation effect estimated on *Calanus* spp. in Sørfjorden by *P. norvegica* (Table 3).

*Eukrohnia hamata* was the most common arrow worm found in these waters. A few specimens of other species (primarily *Sagitta elegans*) were recorded in both fjords, but at much lower densities than *E. hamata,* and they were there-
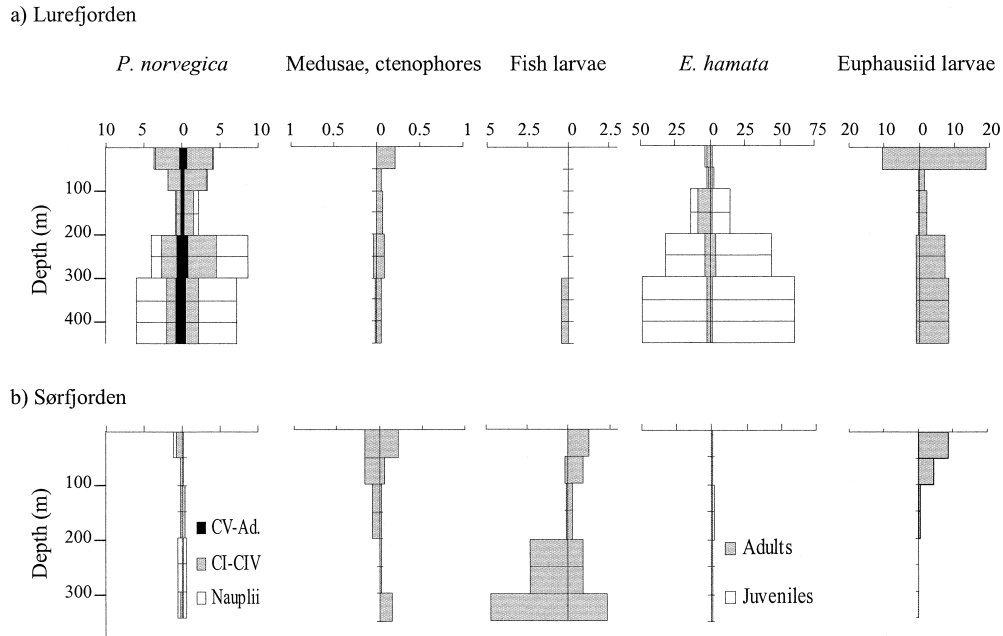
a) Lurefjorden



b) Sørfjorden



Fig. 4. Day- and nighttime distributions of net-caught potential predators on the *Calanus* spp. community in Lurefjorden and Sørfjorden. Values given are averaged for four dates over the sampling period (daily average distributions on 5 March, 23 April, 21 May, and 12 June). In each panel, bars on the left-hand side denote nighttime distributions and bars on the right-hand side denote daytime distributions (individuals m$^{-3}$). Data are missing for nighttime distribution of euphausiid larvae in Sørfjorden.

fore excluded from estimates of predation effect. *E. hamata* was found at increasing densities with depth in Lurefjorden (in excess of 50 individuals m$^{-3}$ below 300 m early in the sampling period). Sørfjorden supported a comparably small population of this planktivore (on average <2 individuals m$^{-3}$) (Fig. 4). Estimated potential mortality effect on *Calanus* spp. accounted for by this predator was markedly higher in Lurefjorden than in Sørfjorden (Table 3).

Larval fish were found almost exclusively in Sørfjorden (Fig. 4). They tend to be found at increasing numbers with depth (average peak abundance = 5 individuals m$^{-3}$ at 300 m). The few fish larvae recorded from Lurefjorden (average ~0.4 individuals m$^{-3}$) were also located at depth (Fig. 4). No attempt was made to classify the fish larvae found during

this study, but both depth distribution and timing coincides with that reported for mesopelagic myctophid larvae (John and Kloppmann 1989).

Over the study period, medusae and ctenophores never became a numerically dominant group in the zooplankton (Fig. 4). They peaked in abundance in the upper 50 m, but average density was as low as 0.25 individuals m$^{-3}$. Because this is a diverse group, no attempt was made to estimate mortality resulting from this source.

*Calanus* spp. egg and early nauplii (N1–N3) were found almost exclusively (≈95%) in the upper 50 m of the water column. The volume of water cleared by the late copepodid stages CIV and CV and mature females could reach ~1.5% d$^{-1}$ of the water volume in the upper 50 m in Sørfjorden,

Table 3. Potential predation pressure (d$^{-1}$) due to *P. norvegica, E. hamata,* late copepodids of *Calanus* spp., and mesopelagic fish (*M. muelleri* and *B. glaciale*) in the two fjords. Estimates of mortality rates of *Calanus* spp. by PSM (Wood 1994) are given in the last column.

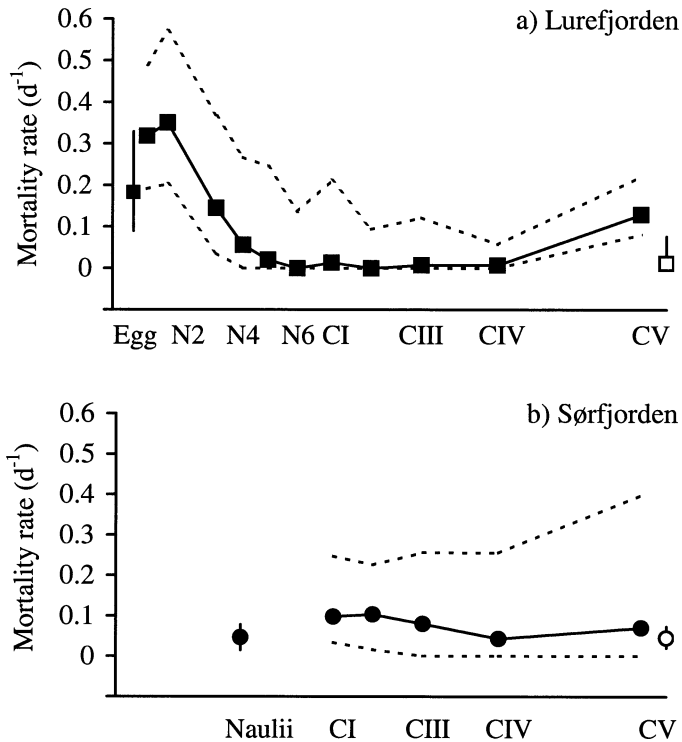| | *P. norvegica* | *E. hamata* | *Calanus* spp. (CIV–adult) | Mesopelagic fish | Total | Estimated mortality (averaged for groups) |
|---|---|---|---|---|---|---|
| Sørfjorden | | | | | | |
| Egg–N3 | 0.01 | 0.01 | 0.02 | 0.02 | 0.06 | 0.08 |
| N4–N6 | 0.00 | 0.05 | — | 0.02 | 0.07 | 0.08 |
| CI–CIV | 0.00 | 0.01 | — | 0.02 | 0.03 | 0.08 |
| Lurefjorden | | | | | | |
| Egg–N3 | 0.11 | 0.01 | 0.03 | — | 0.15 | 0.25 |
| N4–N6 | 0.04 | 0.10 | — | — | 0.14 | 0.02 |
| CI–CIV | 0.01 | 0.06 | — | — | 0.07 | 0.00 |

Fig. 5. Estimated stage-specific mortality rates ($d^{-1}$) of the *Calanus* spp. communities in (a) Lurefjorden and (b) Sørfjorden. Symbols illustrate mean values averaged over the sampling period; dotted lines denote 95% confidence intervals. Open symbols for CV copepodids show mortality estimates assuming none enter dormancy; closed symbols assume all enter dormancy. Egg mortality rates in Lurefjorden are thought to be underestimates (*see text*).

and ~3% $d^{-1}$ of the volume of water above 50 m in Lurefjorden. If *Calanus* spp. kills eggs and early nauplii, it could therefore account for a mortality rate of up to 0.03 $d^{-1}$ in Lurefjorden and up to 0.02 $d^{-1}$ in Sørfjorden (Table 3).

Calanus *mortality*—Mortality of *Calanus* spp. in Lurefjorden was significantly higher for the early life stages (eggs through N2) than for later developmental stages (Fig. 5). In Sørfjorden, a different pattern emerged as the estimated mortality was rather uniform (around 0.08 $d^{-1}$) over the life-history of the animals (Fig. 5). We were not able to distinguish between CV copepodids entering diapause and those continuing to molt into adults. This affects the developmental times of the stage dramatically and subsequently affects estimated mortality rates. Results presented by closed symbols in Fig. 5 were obtained assuming all CV copepodids continued their development. In reality, however, a component of the population enters a state of dormancy in early summer, which involves arrested development (Hirche 1996). This implies that developmental times for part of the season are longer than assumed and, thus, that the mortality rate for CV copepodids (Fig. 5) has been overestimated. An alternative analysis where we assumed animals did not molt from developmental stage CV to adults during the sampling period resulted in a reduction of mortality rates of this developmental stage (open symbols in Fig. 5). Because the

number of individuals developing from stage CV to adults was not clear, it was not possible with any degree of precision to estimate the mortality rates experienced by the adult stages.

We note that egg mortality rates are almost certainly underestimated and should be interpreted with caution because we measured ambient egg concentrations rather than the daily production of eggs into the water column.

Discussion

Sørfjorden and Lurefjorden differ substantially with respect to the planktonic predator community. The dominant carnivorous zooplankton species in Lurefjorden (*P. norvegica* and *E. hamata)* are much reduced in Sørfjorden. Perhaps even more striking is the absence of mesopelagic fish in Lurefjorden (Fosså 1992), although only the larvae are reflected in our present net samples. Both *M. muelleri* and *B. glaciale* are commonly found in fjords and waters off the western coast of Norway (Gjøsæter 1981) and seem to thrive in Sørfjorden (Bagøien et al. 2001).

Chaetognaths are generally viewed as too ineffective as predators to regulate plankton populations (Feigenbaum and Maris 1984), perhaps apart from tropical environments. The diet of the principal species in the fjords studied here (*E. hamata*) tends to be dominated by intermediate-to-small zooplankton (Sullivan 1980), and Pearre (1980) suggested that the mouth width of chaetognaths sets an upper limit to the size classes of prey they can handle effectively. The relationship between body length and mouth width for *E. hamata* is given as 0.062 (Pearre 1982). Thus for the larger *E. hamata,* it should be possible to handle prey up to the size of at least CV *Calanus* spp. (maximum width ≈ 0.64 mm; Sullivan 1980). However, over the duration of the present study, the *E. hamata* population is dominated by smaller individuals, which presumably capture smaller forms of *Calanus*. In our study, chaetognaths accounted for an appreciable part of the mortality of late naupliar stages in both fjords and a major portion of copepodid mortality in Lurefjorden.

According to Yen (1985), *P. elongata* preys most effectively on intermediate size classes of prey. Prey detection in *Paraeuchaeta* sp. probably depends primarily on mechanical stimuli caused by the swimming or feeding currents generated by its prey (Yen 1985). It does not detect and encounter eggs as easily as actively swimming developmental stages (Bailey and Yen 1983). This could possibly account for the higher mortality rate of early nauplii compared to eggs in Lurefjorden (Fig. 5), however a bias in our approach to estimating egg mortality could produce the same effect. Functional response curves for *P. elongata* derived from lab experiments start leveling off only at relatively high prey concentrations (tens of individuals per liter), irrespective of prey size or species used (Yen 1983). Such prey concentrations are orders of magnitude higher than indicated by the net sampling in the present work. This suggests that *P. norvegica* may not be limited by handling when foraging on *Calanus* spp., unless the predators encounter vertical layers of prey undetected by our sampling methods. A further problem arises as juvenile stages of *Paraeuchaeta* (CIV and CV) not

only tend to prey on smaller prey classes than adult females, but also do so at a lower rate (Yen 1985). Nevertheless, the lack of data available from the literature prevents us from making a more thorough examination, and we stress that the calculated predation effect reflects a maximum estimate.

Our data do not offer support for the view that cannibalism is a major contributor to the high mortality on young stages in Lurefjorden (Table 3). It should be kept in mind however that our results are averaged over the total census period. It is not unlikely that during episodes of high abundance of late copepodids the effect will become more pronounced. For instance, the volume cleared during the episode of high abundance of all copepodids combined in the beginning of May in Lurefjorden approaches 10% of the water volume above 50 m per day. Furthermore, cannibalism is an interesting factor to consider because it offers a density dependent mechanism capable of explaining high loss rates on young stages (Ohman and Hirche 2001). Because it affects the populations of other marine copepods (Landry 1978, 1981; Peterson and Kimmerer 1994), the effects of cannibalism on the population dynamics of *Calanus* should be studied in more detail than we have done here.

It seems likely that the different mortality patterns in the two fjords reflect the different predation communities. In Sørfjorden, estimated mortality of *Calanus* spp. is rather uniform over the ontogeny of the organisms, and no clear peaks can be detected. *Calanus* in Lurefjorden on the other hand suffer a peak in mortality early in life (eggs through N3), after which mortality rates are low throughout the rest of development. We find this difference in the ontogenetic mortality pattern consistent with the notion that the high numbers of small or juvenile invertebrate planktivores, particularly *E. hamata* and *P. norvegica,* feed primarily on smaller developmental stages of prey (Pearre 1980; Sullivan 1980; Yen 1985).

The presence of visually searching fish in Sørfjorden probably reduces the number of tactile invertebrate predators, particularly the large carnivorous copepods abundant in Lurefjorden, thus leading to lower predation pressure on the smaller forms of *Calanus* in the fjord. The mesopelagic fish however, probably account for the sustained high mortality rates of the copepodid stages in Sørfjorden. From our estimates, the high abundance of carnivorous zooplankton in Lurefjorden results in high predation pressure on the abundant younger developmental stages of *Calanus* spp. Older and larger developmental stages appear to face lower mortality risk in this fjord, probably because of the absence of visually searching planktivores.

Recent studies of overwintering populations of *Calanus* spp. in fjords on the western coast of Norway lend support to our view. During winter, the populations are dominated by CV copepodids, which suffer higher mortality in Sørfjorden ($\sim$0.012 d$^{-1}$), as well as in other fjords supporting mesopelagic fish, than in Lurefjorden ($\sim$0.008 d$^{-1}$; Bagøien et al. 2001). Although this difference in mortality rate does not seem large, these daily rates operate for several months (October–February) and the cumulative effect is quite dramatic. The proportion of *Calanus* surviving overwintering (as estimated by the abundance of CV copepodids present in early February 1996) in Lurefjorden is approxi-
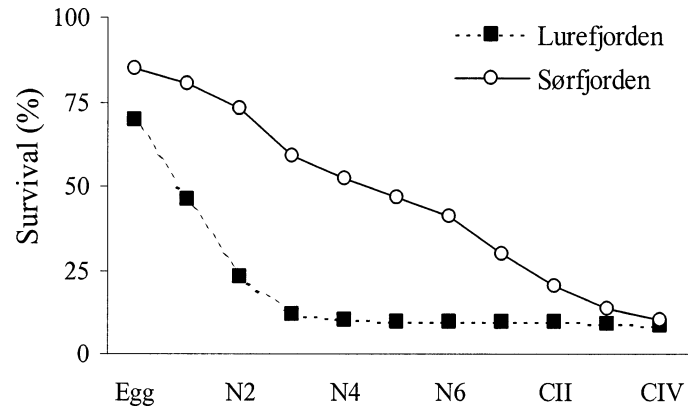


Fig. 6. Comparative survivorship curves of *Calanus* spp. from Sørfjorden and Lurefjorden from February–March through June.

mately 6.7 times higher than in Sørfjorden (Bagøien et al. 2001). Integrating the abundance of *Calanus* in the two fjords from early March to early June (upper panels in Fig. 3) results in a similar ratio ($\sim$6.3). Furthermore, estimates of mortality during the productive season do not indicate substantial differences in cumulative losses from eggs to the end of copepodid stage CIV (Fig. 6). Losses experienced by the population during the dormant season may thus prove to be a mechanism of decisive effect on the production of zooplankton in the subsequent spring period. This has been suggested previously by Colebrook (1985) and Ohman (1986).

High loss rates in early life (nauplii stages) and subsequent lower rates as animals age have been reported for several copepod populations (Mullin and Brooks 1970; Landry 1978; Ohman 1986; Aksnes and Magnesen 1988). It may therefore be common for cohorts of copepods to show a concave survivorship curve with age. However, the different loss rates from the *Calanus* spp. communities in the two fjords studied here suggest that this pattern may vary considerably over short geographic distances. The different loss rates of the two fjords also indicate that mortality rates may be decisive for the energy flow in the systems. The averaged mortality rates for the sampling season indicate that, in Sørfjorden, two thirds of a cohort would reach N3 and start feeding, whereas in Lurefjorden, about only one fourth of the cohort would do so (Fig. 6). This points to the importance of knowing the predator community when addressing populations in the field and their interactions with the environment. It also illustrates the limited usefulness of uniform mortality rates over the life span of zooplankton in ecological models. The two patterns of loss rates over the ontogeny of *Calanus* spp. found in this study may be close to the extremes of what will be characteristic of oceanic populations. Future work will have to address this question. Nevertheless, we conclude that top-down control of population loss rates can be a significant mechanism governing the dynamics of natural zooplankton populations.

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