

Vertical distribution and mortality of overwintering *Calanus*

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Abstract

Overwintering *Calanus* spp. were studied in four Norwegian fjords with different predator regimes and ranging in depth from 380 to 1300 m. Three fjords held both the planktivorous mesopelagic fish *Maurolicus muelleri* and *Benthosema glaciale* and invertebrate predators, whereas one lacked mesopelagic fish but had especially high abundance of several invertebrate predators. Co-occurrence of *C. finmarchicus*, *C. helgolandicus*, and *C. glacialis* rendered distinction between effects of environmental conditions and inherent species properties in choice of depth difficult. The highest daily per capita mortality rate for *Calanus* was estimated at 0.024–0.027 d⁻¹ (95% CI) in a fjord with high fish abundance and with the clearest water. Predation by *M. muelleri* and *B. glaciale* alone could explain the estimated winter mortality. The fjord devoid of mesopelagic fish but particularly rich in invertebrate predators gave the lowest estimated mortality rate; 0.008–0.009 d⁻¹ (95% CI). Our results indicate that mesopelagic fish pose a stronger predatory threat than invertebrates to overwintering *Calanus*. This concurs with *Calanus* selection of oceanic winter habitats below depths where planktivorous fish can forage efficiently by sight.

The life cycles of *Calanus* spp. in the North Atlantic include periods of dormancy in deep waters. Preadult stages descend for “overwintering” in summer or autumn and spend winter in an inactive, nonfeeding mode (Gran 1902; Sømme 1934; Marshall and Orr 1955; Østvedt 1955). The particular depth stratum occupied varies strongly geographically (Kaartvedt 1996), spanning from 600 to 2,000 m in the Norwegian Sea (Østvedt 1955; Heath 1999; Heath and Jónasdóttir 1999) to above 500 m in the Greenland Sea (Hirche 1999; Richter 1995).

Dormancy in deep, cold water may be metabolically motivated to reduce respiration costs (e.g., Hirche 1991) or driven so as to minimize mortality risk (cf. Aksnes and Giske 1990; Kaartvedt 1996). The predatory threat from visually hunting fish is lower in dark waters (Aksnes and Giske 1993; Aksnes and Utne 1997), whereas the state of inactivity may reduce the probability of *Calanus* being perceived by tactile invertebrate predators (cf. Gerritsen and Strickler 1977; Greene 1986). Kaartvedt (1996) suggested that mesopelagic fish represent a strong predatory threat to overwintering *Calanus*, but the relative importance of fish versus invertebrate predators to *Calanus* choice of overwintering depth or mortality is not known.

Winter mortality rates are an important factor in deciding the size of the *Calanus* spring spawning stock. Nisbet and Wood (1996) stressed the importance of field-based estimates of mortality rates, given that predation cannot be adequately measured in the laboratory. Still, such estimates are rare, and advection in open systems renders realistic estimation of mortality rates are difficult (Aksnes and Ohman 1996; Nisbet and Wood 1996).

Fjords are characterized by deep basins and shallow outer sills and hold populations of overwintering *Calanus*, as well as many of the same predators found in oceanic habitats (cf. Østvedt 1955; Matthews et al. 1990; Baliño and Aksnes 1993; Dalpadado et al. 1998; Dale et al. 1999). In winter, advection is primarily restricted to waters above sill depth, whereas the basin-water inhabited by *Calanus* is normally resident for prolonged periods (Gade and Edwards 1980; Farmer and Freeland 1983). Fjord basins may therefore be used to study *Calanus* overwintering.

This investigation focuses on the vertical distribution and mortality rates of *Calanus* overwintering in different predator regimes. To assess the relative impact of fish and invertebrates on overwintering *Calanus*, we addressed the entire pelagic community in a series of fjords. Our approach was to study fjords with and without mesopelagic fish and with different abundances of invertebrate predators. Differing bottom depths provided *Calanus* varying opportunities for avoiding predators.

Materials and methods

Data were collected on cruises with R/V *Håkon Mosby* to Sognefjorden, Masfjorden, Lurefjorden, and Sørfjorden during 19–25 October 1995, 4–10 January 1996, and 10–15 February 1996. Additional sampling of *Calanus* was made in Lurefjorden 11–12 December 1995. All fjords are located in western Norway between latitudes 60°00′–61°30′N (Fig.

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Acknowledgments

This investigation was supported by grants from the Research Council of Norway (project no. 108082/122) and TASC (Trans Atlantic Study of *Calanus finmarchicus*, European Commission Contract No. MAS3-CT95-0039). We are indebted to Rita Amundsen, Trine Dale, Knut Hjelmseth, Mette Hordnes, Esben Moland Olsen, Monica Roland, Thomas Torgersen, and Helge Ullebust for technical assistance. We thank the captain and the crew of R/V *Håkon Mosby*, as well as the cruise participants assisting in the data collection. Egil Ona gave valuable comments on the manuscript.

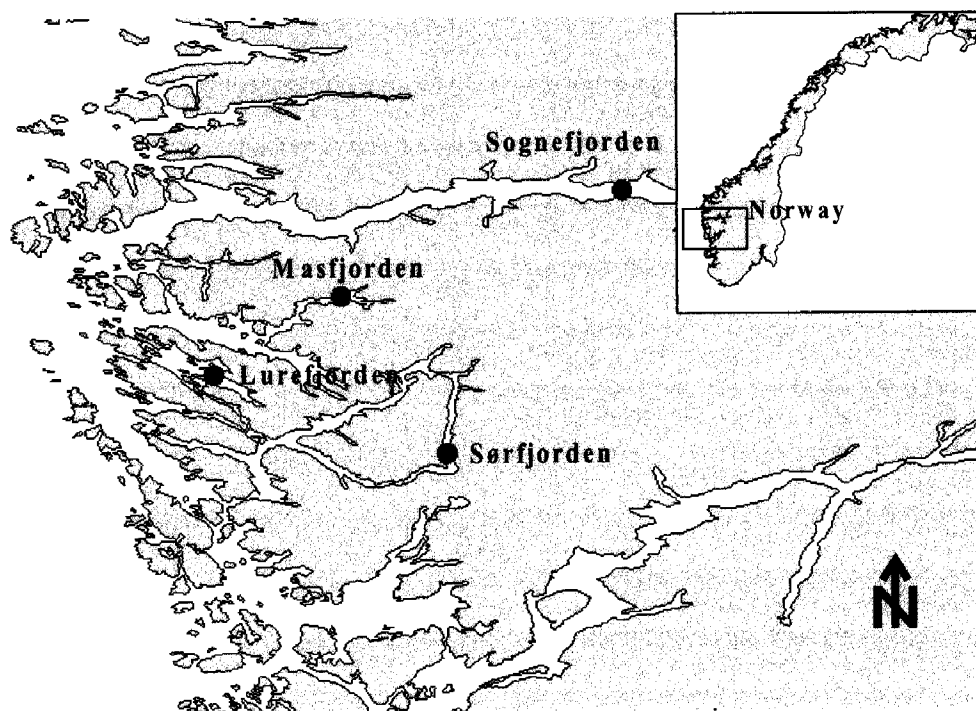


Fig. 1. The fjords with their respective sampling stations: Sognefjorden ($\sim 61^{\circ}07.80'N$, $06^{\circ}04.50'E$), Masfjorden ($\sim 60^{\circ}52.30'N$, $05^{\circ}24.70'E$), Lurefjorden ($\sim 60^{\circ}41.00'N$, $05^{\circ}10.50'E$), and Sørfjorden ($\sim 60^{\circ}30.00'N$, $05^{\circ}43.20'E$).

1). One sampling station was established in the deep basin of each fjord.

Sognefjorden is the deepest fjord in Norway (maximally $\sim 1,300$ m), and its deepest connection to adjacent waters is ~ 240 m. Masfjorden (maximally ~ 500 m deep) is separated from outer waters by an ~ 75 m deep sill (Kaartvedt et al. 1988; Giske et al. 1990). Sørfjorden (maximally ~ 380 m deep) is open in both ends, and its deepest connection to outer waters is ~ 90 m. These three fjords contain both mesopelagic fish and invertebrate predators (e.g., Kaartvedt et al. 1988; Fosså 1992; Salvenes et al. 1995a). Lurefjorden (maximally ~ 440 m deep) is practically landlocked, and its deepest connection to adjacent waters is only ~ 20 m (Fosså 1992). Mesopelagic fish are virtually absent in Lurefjorden, whereas several invertebrate predators are extraordinarily abundant (Fosså 1992; Eiane et al. 1999).

Environmental variables—Salinity, temperature, and density (σ) were measured by a Seabird CTD and water sampled by rosette-mounted Niskin water collectors. Oxygen content in the water column was analyzed by the modified Winkler titration method (results presented in Bagøien 1999). Light absorption at various wavelengths between 400 and 480 nm was measured in water collected from the basin waters during October and January (data in Eiane et al. 1999). Chlorophyll *a* concentrations were measured in water collected from 0, 5, 10, 20, 30, and 40 m (in February, also 50 m). One hundred milliliters of water were filtered on $0.45 \mu\text{m}$ Sartorius cellulose-nitrate filters (dim light), which were deep-frozen at -18°C for subsequent analysis of acetone ex-

tracted Chl *a* on a Turner Designs fluorometer (Strickland and Parsons 1972).

Sampling of Calanus and invertebrate predators—*Calanus* and small invertebrate predators were collected by a vertically hauled ($\sim 0.5 \text{ m s}^{-1}$) Kiel Multinet (0.25 m^2) equipped with five electronically operated nets (mesh size $180 \mu\text{m}$). Nine (eight) depth strata (standardized for each fjord) from near bottom to surface were sampled. Three parallel sampling series were made both day and night on each occasion. To sample the entire water column, each series was composed of two successive hauls. The catches were preserved with 4% borate buffered formaldehyde for later analysis. Because of problems with the flowmeters, the filtered volumes were estimated by multiplying the mouth area of the net with the range of each sampling interval under the assumption of 100% filtering efficiency. The vessel position was maintained by automatic satellite navigation in rough weather, and horizontal drift of the net was assumed to be negligible. Dense samples were split by a modified Lea-Wiborg divider (Wiborg 1951), and subsamples of at least 400 *Calanus* were counted (never constituting less than one tenth of the whole sample). *Calanus* copepodids were classified to developmental stage and adults to sex.

At the onset of the investigation, we assumed that *C. finmarchicus* was the only abundant *Calanus* species. However, molecular analyses of adult females revealed that *C. finmarchicus*, *C. helgolandicus*, and *C. glacialis* were present (Bucklin et al. 2000). *C. glacialis* was the most common species in the sample from Lurefjorden, but *C. finmarchicus*

and *C. helgolandicus* were also present (Bucklin et al. 2000). *C. glacialis* is reckoned as an arctic species (Conover 1988) and has, to our knowledge, not previously been reported to inhabit western Norwegian fjords. The samples from Sognefjorden and Masfjorden contained mixtures of *C. finmarchicus* and *C. helgolandicus* (Bucklin et al. 2000). Too few individuals from Sør fjorden were analyzed to evaluate its species composition. In presenting results on vertical distribution and mortality rates, all *Calanus* are treated as one entity.

Estimation of *Calanus* mortality rates—During periods with no recruitment to a population, daily per capita mortality rates (m) for *Calanus* spp. can be estimated by the relationship (e.g., Aksnes et al. 1997):

$$m = \frac{\ln[n(t_1)] - \ln[n(t_2)]}{t_2 - t_1},$$

where $n(t)$ is the total abundance of *Calanus* spp. at time t . The *Calanus* abundance estimates (depth-integrated, all stages) from each of the three day and three night sampling series were treated as six parallel values for each sampling occasion. Lines were fitted to *Calanus* abundance versus time on a semilog scale by simple linear regression. The slopes of the regression lines were interpreted as per capita mortality rates by assuming a closed local population and attributing all decrease in population size to mortality. The assumption of no recruitment seems to be valid, because only insignificant numbers of copepodites CI–CIII were observed. Percentage daily mortality is given by

$$(1 - e^{-m}) \times 100\%.$$

A surface mode of *Calanus* occurred in October, and possible advective loss of these individuals is accounted for in the estimation of mortality rates. The assumption of closed populations in the basin water below sill depth appeared to be met for Sognefjorden and Lurefjorden throughout the entire study period and for Masfjorden from October to January. Minor water intrusions below sill depth seemed to occur between October and January in Sør fjorden and between January and February in Masfjorden, but these did not appear to affect the mortality estimates seriously (see Discussion).

Invertebrate predators from the Multinet samples were counted and classified to varying taxonomic levels. Only depth-integrated numbers of size classes and taxa assumed to represent a threat to overwintering *Calanus* are presented in this paper. Their vertical distributions are given in Bagøien (1999). Highly mobile species like krill and shrimps may avoid the Multinet (Sameoto et al. 1993; Richter 1994). Hence, these catches were not used to evaluate abundance or distribution of such animals, but qualitative notes on their occurrence were made when trawling for fish (see below).

Fish abundance, distribution, and diet—Fish abundance and distribution were mapped acoustically by a SIMRAD EK500 38 kHz split-beam echo sounder. Samples for identification of acoustic targets, their size distributions, and analyses of fish stomachs were obtained by Harstad trawl

(Nedreaas and Smedstad 1987). Fifty-six tows were made in total.

Each catch was weighed, and a subsample was taken for assessment of the contribution of mesopelagic fish (*Benthosema glaciale* and *Maurollicus muelleri*). Standard lengths of 30 individuals of each species were measured when available. The mesopelagic fish were preserved in 10% formaldehyde for subsequent stomach analysis.

Acoustic data from the depth range 0–500 m were logged continuously and later analyzed by use of the BI 500 post-processing system (Knudsen 1990; Foote et al. 1991). To convert acoustic backscattering into numerical fish density, target strength (TS) distributions were established from in situ measurements in February, as described by Bagøien (1999) for *M. muelleri* and by Torgersen and Kaartvedt (2001) for *B. glaciale*.

In short, single individuals of *M. muelleri* could be resolved as they occasionally ascended above monospecific acoustic scattering layers (SL) composed of specimens within a limited size range. The peak of the TS frequency distribution was assigned all fish for a given SL in the conversion of integrated echo levels (S_A values) into number of fish.

For *B. glaciale*, we used target strength data obtained from vertically migrating individuals in the upper 20 m at night (Sør fjorden). A subsequent Harstad trawl tow in surface waters was dominated by *B. glaciale* with a modal length of 5.4 cm. Although the size of *B. glaciale* varied considerably between tows throughout the investigation, this size seemed to represent the *B. glaciale* populations reasonably well (cf. Table 3 below). We further assumed that nocturnal TS measurements in upper waters were representative for fish at their daytime depths and, for simplicity, applied the peak of the TS distribution (–58 dB) in all assessments of *B. glaciale* abundance.

Numerical fish abundance was obtained by use of the relation

$$\rho_v = \frac{S_A}{\langle \sigma \rangle},$$

where S_A is the area backscattering coefficient (m^2 nautical mile⁻²), or depth-integrated echo energy, and $\langle \sigma \rangle$ is the mean area backscattering cross section, derived from its relation to target strength:

$$\langle \text{TS} \rangle = 10 \log_{10}(\langle \sigma \rangle / 4\pi).$$

Young and adult *M. muelleri* were largely confined to separate scattering layers during day (see Results), as found in several previous investigations (e.g., Giske et al. 1990; Balaño and Aksnes 1993). These layers were most clearly separated from other targets in January and February, although distinctions between adult *M. muelleri* and the deeper-living *B. glaciale* were sometimes ambiguous. The integrated energy level of each layer was obtained separately and the total area backscattering coefficient S_A allocated to the respective targets. This exercise was not attempted for October. The BI 500 software integrated data every 8 min, and all daytime values obtained during trawling at 3–4 knots were averaged to reduce impact of small-scale patchiness.

B. glaciale co-occurred with various invertebrates and

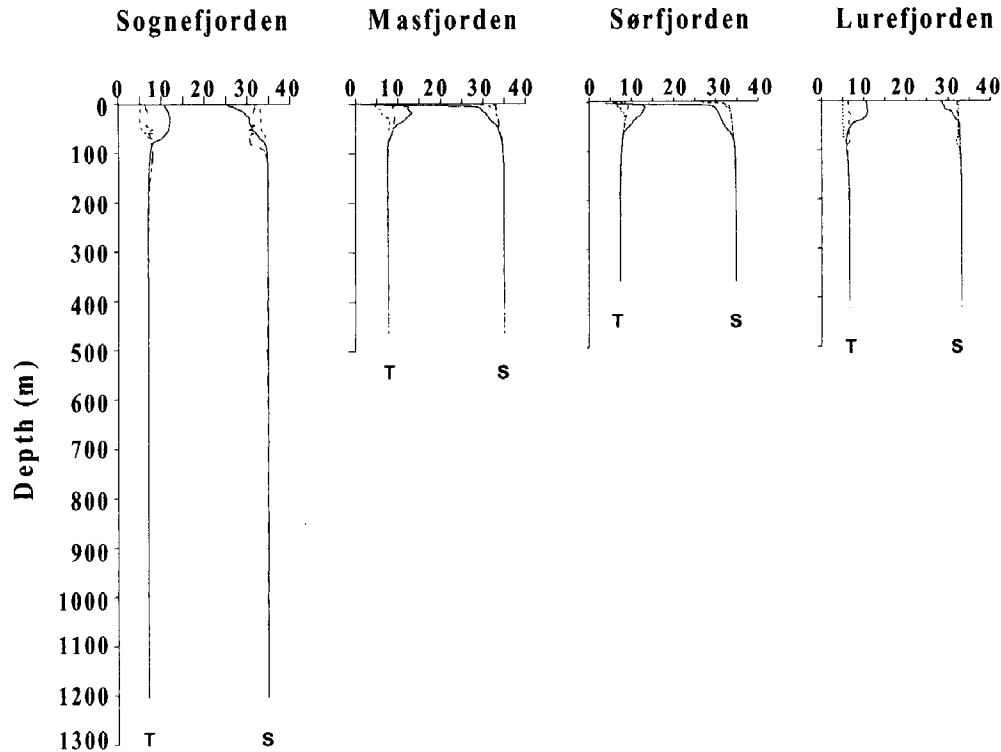


Fig. 2. Profiles of temperature ($^{\circ}\text{C}$, denoted T) and salinity (‰ , denoted S). Full line for October, broken line for January, and dotted line for February.

larger fish (piscivores). We neglected the echo contribution from invertebrates, which are very weak targets at 38 kHz when an S_v threshold of -82 dB is applied, as was done in this investigation (Bagøien 1999). To estimate the contribution from piscivores, the S_v threshold was increased during postprocessing until the diffuse echoes (ascribed to *B. glaciale*) disappeared, which occurred at about -64 ± 1 dB. Echoes from individual large fishes were then still visible. The remaining integrator values were subtracted from the total echo energy obtained when a -82 dB threshold was used, and the resulting values were ascribed to *B. glaciale*. This implies a slight underestimation of the echoes from large fishes, whose level to some extent becomes reduced by this procedure. Underestimating this contribution implies a corresponding overestimation of the echo contribution from *B. glaciale*. Also, any deep-living (more than ~ 200 m) *M. muelleri* would have been included in the acoustic estimate for *B. glaciale*. On the other hand, threshold induced bias in the integration (Reynisson 1996) may lead to underestimation of abundance of small fish in deep water. We have not assessed the magnitude of this bias, which probably was largest in January. A 2-dB noise reduction was then by mistake applied during data acquisition, and this affected the echograms visually in Masfjorden.

Stomach contents of *M. muelleri* and *B. glaciale* from Masfjorden and Sørffjorden were examined, with 40 individuals of each species analyzed from each tow if available. When possible, prey was identified to genus. Stomach fullness was assessed on a scale from 1 to 5, where 1 denotes empty, 2 some prey, 3 half full, 4 more than half full, and 5 full (Fotland et al. 1995). State of digestion was assessed

on a scale from 1 to 4, where 1 denotes undigested, 2 digestion started, 3 partly digested but prey recognizable, and 4 unrecognizable prey (Fotland et al. 1995).

Results

Environmental factors—For all fjords, temperature and salinity below ~ 75 – 100 m were practically homogeneous with depth (Fig. 2). The basin-water profiles were almost constant from October to February, whereas upper waters became colder and more saline (Fig. 2). The basin water was coldest and least saline in Lurefjorden, with temperature and salinity of $\sim 6^{\circ}\text{C}$ and 33‰ , compared with 7 – 8°C and 34 – 35‰ in the other fjords. Density (σ_t) in the basin water of all fjords decreased during winter, with exception of increased density at ~ 200 – 250 m in Sørffjorden from October to January and at ~ 250 – 300 m in Masfjorden from January to February (Bagøien 1999).

Chl *a* levels were low in all fjords (Fig. 3), although there was a surface maximum of ~ 2 mg m^{-3} in Lurefjorden in October. Some buildup from the winter minimum was apparent in February, being least noteworthy in Lurefjorden.

Calanus vertical distribution—The vertical distribution of *Calanus* in Sognefjorden, Masfjorden and Sørffjorden was bimodal in October (Fig. 4). The upper modes had largely disappeared by January.

Calanus was most vertically dispersed in Sognefjorden, with the bulk of the overwintering population distributed between 200 and 700 m (~ 15 – 25 *Calanus* m^{-3} in October) (Fig. 4). Concentrations were very low below 700 m.

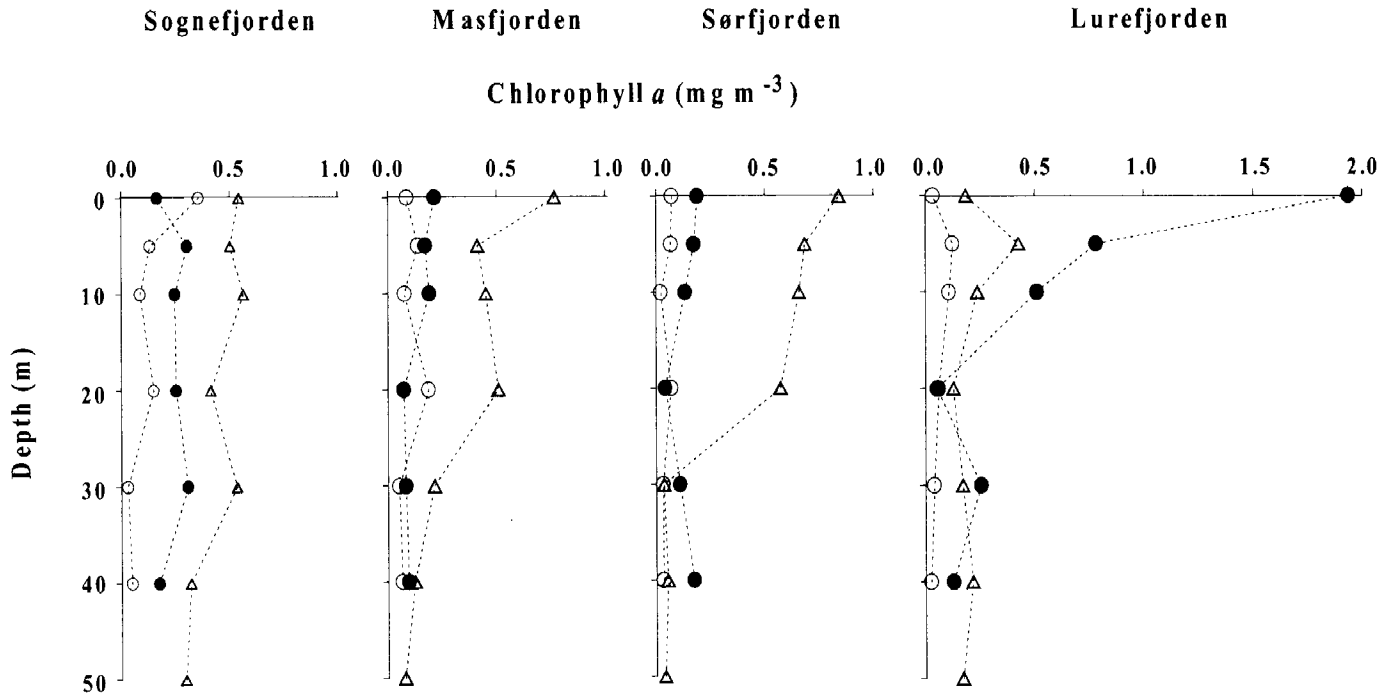


Fig. 3. Chl *a* concentrations. Filled circles for October, open circles for January, and triangles for February.

In Masfjorden, the bulk of the overwintering population was found between 150–250 m in early winter (~ 110 – 140 *Calanus* m^{-3} in October) (Fig. 4). A conspicuous minimum (~ 10 ind. m^{-3} in October) occurred between 50–150 m, and concentrations were fairly low (~ 40 – 60 ind. m^{-3} in October) below 250 m. In February, most of the small remaining population was found below 250 m.

Also in Lurefjorden, overwintering *Calanus* were most abundant at intermediate depths (Fig. 4). Here, the population bulk occurred between 100 and 250 m (~ 110 – 290 ind. m^{-3} in October), with its upper limit being shallower than in Masfjorden. Increased abundances in upper waters from January to February indicated that the spring ascent had begun, and the population in the upper 50–100 m then primarily consisted of females.

Concentrations of overwintering *Calanus* in Sørffjorden were higher at large than intermediate depths (maximally ~ 45 – 50 ind. m^{-3} in October) (Fig. 4). In January and February, *Calanus* was virtually absent above 150 and 200 m, respectively.

Calanus abundance and mortality rates—*Calanus* abundance (all stages) in October was highest in Lurefjorden ($48,400$ ind. m^{-2}) and lowest in Sørffjorden ($11,400$ ind. m^{-2}) (Fig. 5). Abundance decreased through winter in all fjords but at varying rates. Masfjorden and Lurefjorden represented the extremes (Fig. 5). From similar October abundances ($48,400$ ind. m^{-2} in Lurefjorden and $46,700$ ind. m^{-2} in Masfjorden), levels had dropped to $26,800$ ind. m^{-2} in Lurefjorden and $7,000$ ind. m^{-2} in Masfjorden by January.

The highest per capita mortality rate was estimated for Masfjorden at 0.024 – 0.027 d^{-1} (or 2.4% – 2.7% d^{-1}) (95% CI) for the period October–February (Table 1). Excluding

Calanus that inhabited waters above 50 m in October (see below) from the analysis reduced the estimated mortality rate to 0.018 – 0.021 d^{-1} (1.8% – 2.1% d^{-1}) (95% CI). This was done to obtain a minimum estimate in case all individuals at shallower depths were advected out of the fjord. Note that descent of individuals being advected into the fjord would lead to underestimation of mortality rates. Regardless of whether surface *Calanus* in October were excluded, the mortality rate estimated for Masfjorden during October–February was significantly higher than the corresponding rate for any other fjord (Table 1). The lowest per capita mortality rate as estimated for Lurefjorden was 0.008 – 0.009 d^{-1} (0.8% – 0.9% d^{-1}) (95% CI) during the same period.

Calanus stage proportions—Copepodid stage V (CV) dominated the overwintering populations in all fjords, with their relative proportions varying between 80% and 95% in January (Fig. 6). Practically none were present in Lurefjorden at any time. In the other fjords, CIV proportions (20%–35% in October) decreased during winter. Correspondingly, the CV proportions increased from October to January in all fjords except Lurefjorden. The proportions of adults increased in all fjords from January to February, most clearly in Lurefjorden (from $\sim 7\%$ to 65%).

Invertebrate predators—Numbers of chaetognaths (individuals >20 mm; mainly *Eukrohnia hamata*) were roughly an order of magnitude higher in Lurefjorden than in the other fjords (Table 2). The copepod *Euchaeta norvegica* was typically a factor of 5–10 times more abundant in Lurefjorden, and the mysid *Hemimysis abyssicola* practically only occurred in this fjord. Small jellyfish were most abundant in Sognefjorden and were very scarce in Lurefjorden (Table 2).

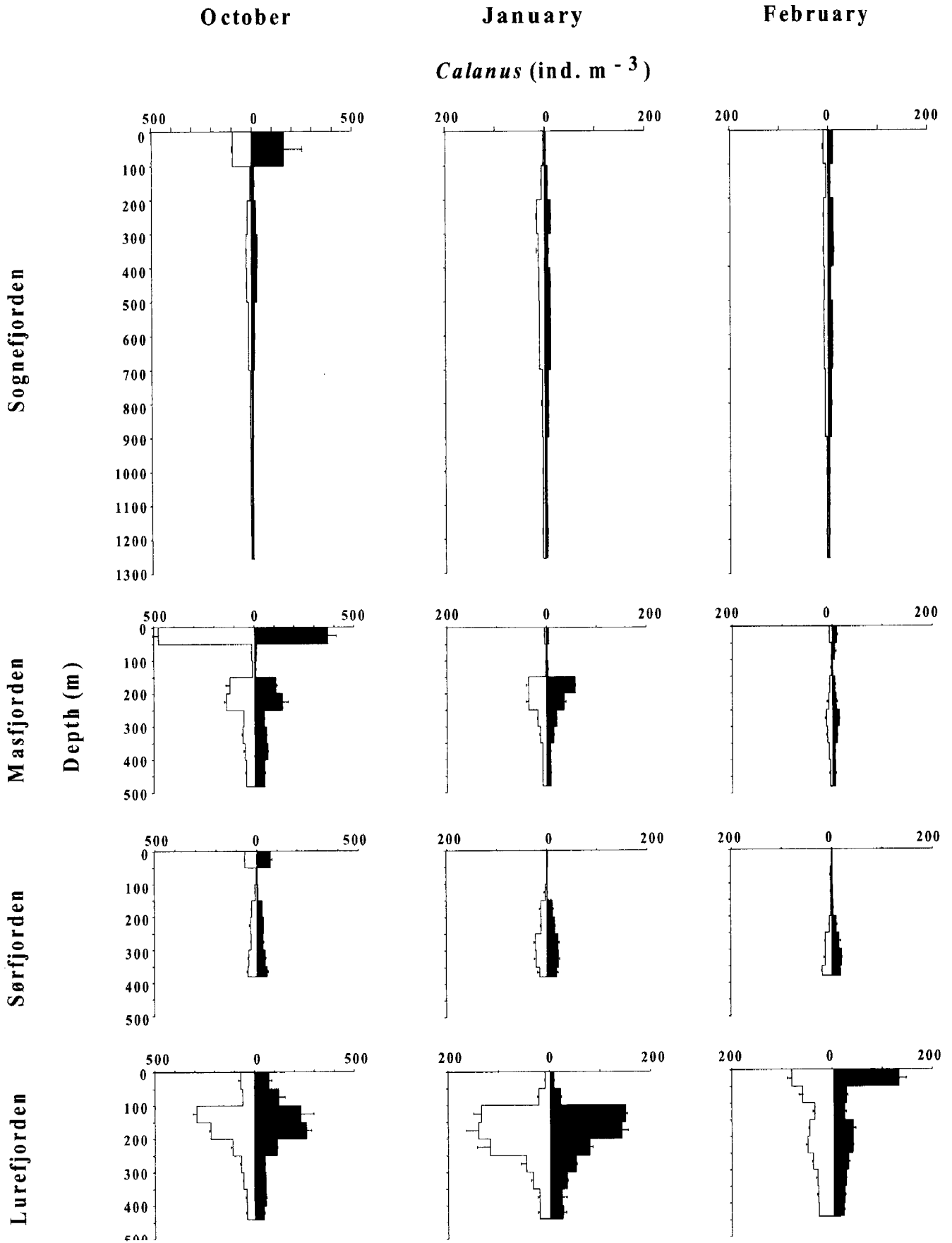


Fig. 4. Vertical distributions of *Calanus* spp. (all stages) (day in white and night in black). Averages of three samples with standard errors. Note the change in scale of x-axes from October to January.

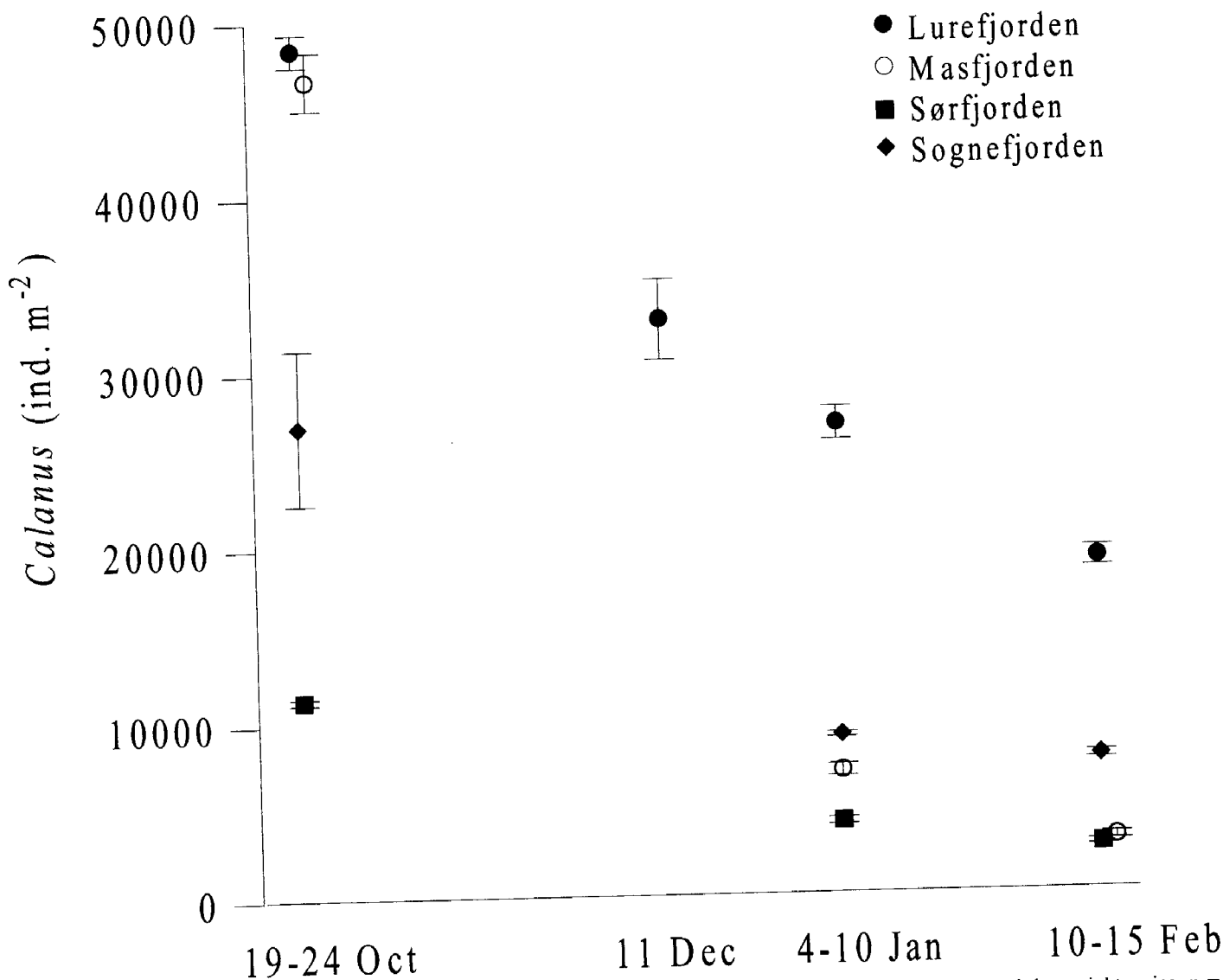


Fig. 5. *Calanus* spp. (all stages) abundance. Averages and standard errors of six sampling series (three day and three night series, $n = 6$). The deepest hauls were extrapolated to cover nonsampled meters closest to the bottom.

The copepod *Chiridius armatus* and the polychaet *Tomopteris* sp. occurred in much lower numbers than the other predators, being particularly scarce (or lacking) in Lurefjorden (Table 2).

Fish distribution—Trawl catches of the dominant species *M. muelleri* and *B. glaciale* were highest in Masfjorden and Sørfjorden, were intermediate in Sognefjorden, and none were caught in Lurefjorden (Table 3). Correspondingly, echo levels and estimated abundances of *M. muelleri* and *B. glaciale* were consistently highest in Masfjorden and Sørfjorden, whereas echo levels were extremely low in Lurefjorden (Fig. 7; Tables 4 and 5). In January and February, young *M. muelleri* (1 group) were caught in tows aimed at SL located at ~100 m during daytime (Fig. 7). Note that sampling was done at times of day when this SL was located shallower in the water column. Adult *M. muelleri* (mainly individuals >40 mm) lived deeper and were dominant in tows aimed at scattering layers

with daytime distribution near 100 m in October and 150 m in January and February (Table 3, Fig. 7). Also, deeper catches were made. *M. muelleri* performed a dusk ascent to the surface, followed by "midnight sinking," with a subsequent dawn rise to the surface before returning to the daytime depth (exemplified by results from Masfjorden in February; Fig. 8).

B. glaciale lived deeper than *M. muelleri* by day (below 150–200 m) but was typically captured in the shallowest night tows (Table 3). Although deep-living targets ascended to a varying extent, nocturnal backscattering below 100 m was still high.

Fish feeding—*M. muelleri* stomachs held the highest numbers of *Calanus* in October (Fig. 9). Fish captured at night occasionally had comparable stomach fullness with those captured during the day, but the food was then well digested (Fig. 9). In January in Masfjorden, the highest numbers of *Calanus* per stomach were for juveniles sampled dur-

Table 1. Estimated daily per capita mortality rates of *Calanus* spp.

	Data included in analysis	Mortality rate (d ⁻¹)	Lower	Upper	R ²
			limit 95% CI	limit 95% CI	
Sognefjorden	Oct, Jan, Feb	0.0114	0.009	0.014	0.85
	Oct, Jan, Feb*	0.0060	0.005	0.007	0.95
	Oct, Jan	0.0140	0.010	0.018	0.84
	Oct, Jan*	0.0064	0.005	0.008	0.94
Masfjorden	Jan, Feb	0.0046	0.003	0.006	0.78
	Oct, Jan, Feb	0.0245	0.024	0.027	0.99
	Oct, Jan, Feb†	0.0195	0.018	0.021	0.97
	Oct, Jan	0.0260	0.024	0.028	0.99
Sørfjorden	Oct, Jan†	0.0178	0.016	0.020	0.97
	Jan, Feb	0.0239	0.018	0.030	0.89
	Oct, Jan, Feb	0.0133	0.012	0.014	0.98
	Oct, Jan, Feb†	0.0102	0.009	0.011	0.95
Lurefjorden	Oct, Jan	0.0136	0.012	0.015	0.98
	Oct, Jan†	0.0092	0.008	0.011	0.94
	Jan, Feb	0.0125	0.008	0.017	0.82
	Oct, Jan, Feb	0.0083	0.008	0.009	0.97
	Oct, Jan	0.0078	0.007	0.009	0.96
	Jan, Feb	0.0096	0.007	0.013	0.85

Daily per capita mortality rates estimated by simple linear regression of depth-integrated abundance versus time on semilog scale. All developmental stages included in the analyses. For each sampling occasion, six parallels (three day and three night series) were used in the regressions.

* *Calanus* from the upper 100 m in October excluded from analysis.

† *Calanus* from the upper 50 m in October excluded from analysis.

ing descent in the morning (maximum of 11; tow number 24). However, even *M. muelleri* from the deepest tow, taken in the afternoon (tow number 28 at 280 m; Table 3) had an average stomach content of 0.8 *Calanus*, reflecting daytime feeding in deep water.

B. glaciale had little well-digested food in their stomachs at all times of day, and there was no diel pattern in stomach

fullness or degree of digestion (Fig. 10). *Calanus* were found in the stomachs of fish caught at all depths, but in Masfjorden identifiable *Calanus* were most commonly recorded for the most shallow-living individuals (~200 m) both in January and February (not apparent from Fig. 10).

Discussion

Vertical distribution—The presence of three *Calanus* species, having apparently differing relative proportions in the different fjords, rendered distinction between effects of environmental factors and inherent species properties on choice of overwintering depth difficult. Still, we can conclude that temperature, salinity, and oxygen level could not explain the vertical distributions. Below sill depth, the hydrography was almost homogeneous in all fjords, whereas the *Calanus* distributions varied. Oxygen concentrations were always above (3 ml O₂ L⁻¹; Bagøien 1999), which is well above the levels various *Calanus* species are able to tolerate (Vinogradov et al. 1992; Osgood and Checkley 1997; Bagøien et al. 2000).

Overwintering *Calanus* were largely found below the daytime depth of *M. muelleri* in Sørfjorden and particularly in the deep Sognefjorden, which provided most space for vertical dispersion of *Calanus*, thereby being the most “ocean-like” environment. However, *M. muelleri* appeared to be distributed at larger depths during winter than autumn. In Masfjorden, this resulted in an increasing overlap with the bulk (midwater peak) of the overwintering *Calanus*. Baliño and Aksnes (1993) showed that acoustic scattering layers of *M. muelleri* instantaneously adjusted their depth in response to varying cloud cover. Thus, as weather conditions or, at longer timescales, water clarity change, their vertical distribution will respond accordingly. The vertical positioning of dormant *Calanus* may not be equally dynamic. Hence, *M. muelleri* could harvest *Calanus* from increasing depths during the overwintering period, possibly imprinting depth-specific mortality on their vertical profiles.

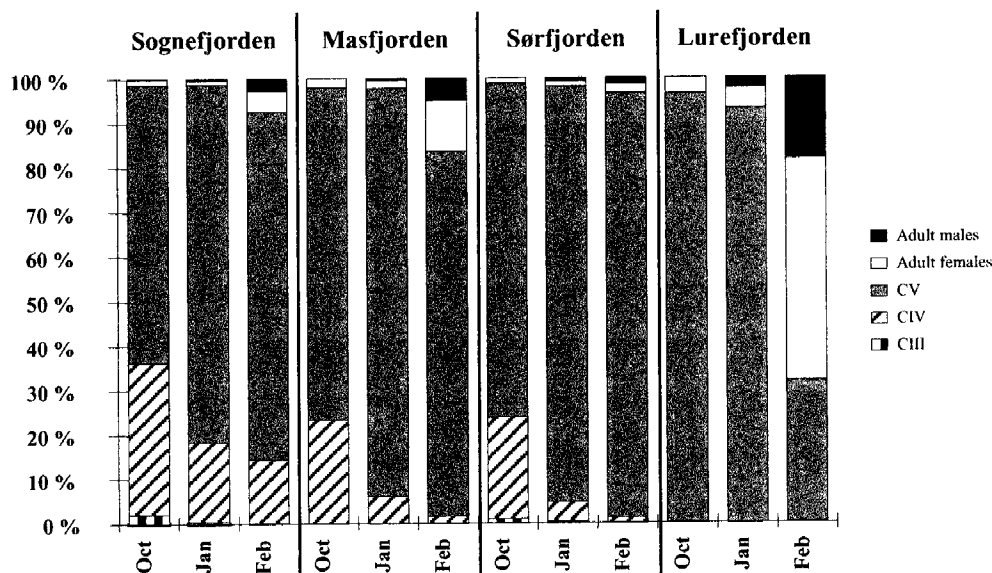


Fig. 6. Relative proportions of *Calanus* spp. developmental stages.

Table 2. Invertebrate predator abundance (ind. m⁻²), with standard error in brackets.

	Chaetognaths (>20 mm)	<i>Euchaeta</i> (CV + adult females)	<i>Chiridius</i> (adult females)	Jellyfish (less than ~20 mm)	<i>Hemimysis</i>	<i>Tomopteris</i>
Sognefj						
Oct	107 (12)	81 (6)	29 (4)	605 (85)	—	28 (5)
Jan	67 (6)	82 (8)	23 (4)	438 (32)	—	9 (3)
Feb	57 (8)	73 (7)	23 (5)	291 (23)	—	5 (1)
Masfj						
Oct	92 (19)	97 (23)	75 (8)	327 (58)	—	14 (5)
Jan	50 (7)	24 (6)	49 (8)	200 (42)	—	18 (3)
Feb	71 (9)	13 (1)	36 (4)	107 (19)	—	20 (4)
Sørfj						
Oct	17 (6)	56 (6)	11 (2)	179 (3)	—	—
Jan	46 (8)	60 (9)	21 (9)	91 (22)	—	5 (2)
Feb	44 (7)	36 (5)	9 (2)	123 (34)	—	6 (1)
Lurefj						
Oct	702 (76)	462 (47)	6 (2)	4 (3)	145 (8)	—
Jan	476 (60)	335 (21)	4 (2)	8 (2)	95 (9)	—
Feb	681 (45)	326 (36)	4 (3)	8 (3)	15 (8)	—

The vertical distribution of *B. glaciale* by and large overlapped with that of *Calanus* (except for the “fishless” Lurefjorden). The distributions of most invertebrate predators also generally overlapped with those of *Calanus* (Bagøien 1999), except for the population peak of *Calanus* in Lurefjorden, which occurred shallower than the highest concentrations of large chaetognaths, whose numbers increased toward the bottom.

Mortality rates—Basin-water renewals may wash overwintering *Calanus* out of fjords (cf. Lindahl and Hernroth 1998; Bagøien et al. 2000) and result in overestimation of mortality rates. This did not apply to Sognefjorden and Lurefjorden, given that in these fjords σ_t decreased during winter (Bagøien 1999), which is characteristic of “stagnant” basin waters as even low levels of turbulence mix near-surface water downward (Gade and Edwards 1980; Farmer and Freeland 1983). Deep-water replacements occur when the density of outer water masses at or above sill depth exceeds that within the basin (Gade and Edwards 1980; Farmer and Freeland 1983). Slight intrusions of new water were suggested for Sørfjorden between October and January and for Masfjorden between January and February. This was indicated by very subtle changes in the density profiles at ~200–300 m (Bagøien 1999), by increases of oxygen concentration at these depths (Bagøien 1999), and by a change in the optical properties of the basin-water in Sørfjorden from October to January (Eiane et al. 1999; optical properties were not examined in February). Nevertheless, the estimated *Calanus* mortality rates were much lower for Sørfjorden than Masfjorden, even for the period October to January, despite water replacement only being indicated in the first fjord. The estimated mortality rates for Masfjorden were similar for the two periods October–January and January–February (Table 1), although water replacement was only suggested during the last period. Evidently, the large differences in mortality rates between the fjords cannot be explained by basin-water renewals.

The lowest mortality rate was estimated for Lurefjorden (0.8%–0.9% d⁻¹, 95% CI), which lacked mesopelagic fish but contained the largest populations of several invertebrate predators (Table 2). This mortality is interpreted to be caused by invertebrate predators alone. Both chaetognaths and *Euchaeta* commonly co-occur with overwintering *Calanus* in oceanic environments (Dale et al. 1999), and various species of these taxa have been assumed to exert significant mortality on *Calanus* and other overwintering copepods (Bathmann et al. 1990; Øresland 1995; Ohman and Wood 1996). Combining depth-integrated abundance and daily mortality of *Calanus* and abundance of chaetognaths >20 mm implies a maximum feeding rate of ~0.55 *Calanus* chaetognath⁻¹ d⁻¹ for October and 0.45 *Calanus* chaetognath⁻¹ d⁻¹ for January if we assume that all mortality of *Calanus* in Lurefjorden was due to chaetognaths. A corresponding calculation that assumed that all *Calanus* mortality was due to *Euchaeta* would suggest a maximum predation rate of 0.85 *Calanus* *Euchaeta*⁻¹ d⁻¹ in October and 0.65 *Calanus* *Euchaeta*⁻¹ d⁻¹ in January. The estimates for chaetognaths and *Euchaeta* are mutually exclusive, and, furthermore, both are obviously overestimates, because other invertebrate predators were present. Especially, in addition to the taxa presented in Table 2, acoustic estimates suggested abundances of 40–80 individuals of the krill *Meganyctiphanes norvegica* m⁻² (Bagøien 1999), and Lurefjorden is also characterized by a high biomass of the large jellyfish *Periphylla periphylla* (Fosså 1992).

Extrapolating these nonadditive maximum predation rates to the standing stocks in Masfjorden suggests that chaetognaths there would probably have accounted for <4% of the *Calanus* mortality in October and <12% in January. Similarly, *Euchaeta* would probably have accounted for <7% in October and <8% in January. The comparatively low impact of the invertebrate predators in Masfjorden is consistent with the findings that the high *Calanus* mortality there could largely be explained by predation by mesopelagic fish (see below). We acknowledge, however, that these evaluations are

Table 3. Harstad trawl catches of mesopelagic fish (kg nautical mile⁻¹). Time is given as European standard time (GMT + 1 h), and refers to when fishing depth was reached. Tows normally lasted about 30 min. "D" and "N" give reference to day and night sampling, respectively. Depth denotes upper end of trawl. Mean lengths (mm) of mesopelagic fish are given in brackets.

	Trawl No.	Time	Fishing depth (m)	<i>Maurolicus muelleri</i>	<i>Benthosema glaciale</i>
Sognefj					
Oct	1	08:00 D	20	—	—
	2	12:26 D	175	4.1	0.1
	3	15:57 D	400–440	(47.5)*	(52.5)*
	4	18:15 N	30–40	3.8 (44.8)	0.3 (48.2)
Jan	16	09:20 D	5–10	—	—
	17	10:31 D	35	0.9 (26.9)	—
	18	12:35 D	200–230	1.6 (41.2)	(39.2)†
	19	14:50 D	300	0.8 (40.3)	2.6 (50.5)
	20	23:20 N	5–10	C	—
	21	22:15 N	60–65	0.7	—
	22	20:51 N	190–205	0.1	0.1
	23	19:10 N	290–310	0.1	1.4 (51.0)
Masfj					
Oct	5	14:55 D	45–60	—	—
	6	16:17 D	65–75	29.3 (44.3)‡	—
	7	16:12 D	80–90	*	—
	8	24:00 N	?	—	5.6 (48.3)‡
Jan	24	09:45 D	60	1.6 (21.1)‡	†
	25	14:20 D	135–145	31.2 (43.3)‡	—
	26	11:50 D	165–170	24.7 (43.6)	—
	27	13:20 D	200–210	4.8 (38.5)‡	1.8 (44.0)‡
	28	14:50 D	280	10.9 (46.5)‡	28.2 (64.4)‡
	29	18:42 N	20	1.7 (27.9)‡	1.3 (54.2)‡
	30	20:06 N	130–140	4.8 (49.9)‡	3.3 (58.6)‡
	31	17:25 N	170	7.7 (41.4)‡	8.8 (52.6)‡
	32	23:15 N	170–185	1.6 (42.1)‡	16.3 (58.5)‡
	33	21:37 N	205–215	2.5 (42.0)‡	11.3 (56.2)‡
Feb	45	09:00 D	80–105	1.6 (25.5)‡	—
	46	10:45 D	200	18.5 (41.0)‡	4.7 (48.5)‡
	47	00:33 N	0–20	—	0.9 (39.6)‡
	48	02:03 N	60	1.4 (33.8)‡	17.8 (58.9)‡
	49	03:37 N	170	6.1 (43.1)‡	14.4 (61.2)‡
Sørfj					
Oct	9	07:50 D	25	—	0.2 (58.3)§
	10	09:05 D	70–80	18.5 (39.5)‡	—
	11	10:35 D	170	6.8 (41.3)‡	30.5 (52.1)‡
	12	13:16 D	260–270	—	27.8 (56.7)‡
	13	21:45 N	20	1.1 (43.4)‡	25.9 (50.4)‡
	14	00:43 N	55	4.2 (41.3)‡	11.7 (51.0)‡
	15	02:10 N	240–270	—	17.6 (57.7)‡
Jan	34	09:20 D	30	(17.7)†	—
	35	14:10 D	125	44.7 (40.7)‡	—
	36	10:41 D	195–200	0.1 (40.3)	0.4 (54.6)‡
	37	12:15 D	265–270	(39.9)*‡	(55.3)*‡
	38	17:10 N	20	1.1 (27.5)	4.4 (57.9)‡
	39	18:27 N	100–110	4.3 (37.4)‡	7.5 (54.9)‡
	40	21:15 N	160–175	—	63.5 (55.6)
	41	19:50 N	195–200	1.4 (38.8)‡	14.1 (53.1)‡
Feb	50	09:10 D	75–110	18.8 (36.5)‡	—
	51	10:55 D	205	2.5 (40.0)*	16.1 (52.5)‡
	52	12:45 D	300	1.5 (38.2)	34.5 (56.4)‡
	53	22:50 N	0	—	6.5 (54.9)‡
	54	00:20 N	50		(56.1)*‡
	55	01:40 N	110	2.9 (40.0)‡	18.9 (55.3)‡
	56	03:10 N	250	—	50.0 (56.3)‡

Table 3. Continued.

	Trawl No.	Time	Fishing depth (m)	<i>Maurolicus muelleri</i>	<i>Benthosema glaciale</i>
Lurefj					
Jan	42	13:30 D	30	—	—
	43	14:16 D	70	—	—
	44	17:15 N	30	—	—

* Present but weight not available; (—) No catch.

† Present in negligible quantities.

‡ Fish used for stomach analysis.

§ Present but could be remains from preceding tow or caught in shallower strata.

|| No data.

insufficient because of several factors, including lack of quantitative data on krill and shrimps, which both occurred in Masfjorden (Bagøien 1999; see also Kaartvedt et al. 1988).

Mesopelagic fish seemed to represent a stronger predatory threat than invertebrates to the overwintering *Calanus*. Estimated mortality rates for Masfjorden during October–February (2.4%–2.7% d⁻¹, 95% CI) were markedly higher than for the other fjords. Masfjorden was rich in mesopelagic fish (Table 5), and their depth distribution overlapped significantly with that of the bulk of the overwintering *Calanus*. In addition, Masfjorden contained comparatively few invertebrate predators (Table 2). The estimated mortality suggests a daily loss of ~200 *Calanus* m⁻² in January. A crude estimate suggests that the total of 30 individual mesopelagic fish m⁻² (Table 5) alone could have caused this mortality with an average feeding rate of ~7 *Calanus* fish⁻¹ d⁻¹. This is within their feeding potential, evident from the stomach content in Masfjorden in January (maximal observations of 11 *Calanus* in juvenile and 8 for adult *M. muelleri* and 14 *Calanus* for *B. glaciale*).

These feeding rates seem realistic for the juvenile *M. muelleri* on basis of average stomach content (see below), but, for adult *M. muelleri* and particularly *B. glaciale*, the discrepancies between stomach contents and the required feeding rate of 7 *Calanus* per fish per day were large. However, to assess feeding rates, average stomach content should be multiplied by an appropriate factor to account for turnover, but it remains unclear how long single copepods remain recognizable in a fish stomach designed to handle much larger meal sizes (cf. Salvanes et al. 1995b).

Fish had a particularly strong impact on the shallow-living part of the *Calanus* population, and the copepods inhabiting upper layers evidently took higher risks than those staying at depth. *M. muelleri* does not appear to forage significantly in the darkness of night (Giske et al. 1990; Giske and Aksnes 1992), but vertically migrating *M. muelleri* exploited the near-surface *Calanus* during short periods at dusk and dawn, which provide sufficient light for visual predation on plankton but acceptable darkness for protection against visually hunting piscivores (so-called antipredation windows; Clark and Levy 1988; Rosland and Giske 1994, 1997). In January, juvenile *M. muelleri* in Masfjorden, that recently had taken advantage of this antipredation window on average held 2.5 *Calanus* when captured during descent after dawn. Under

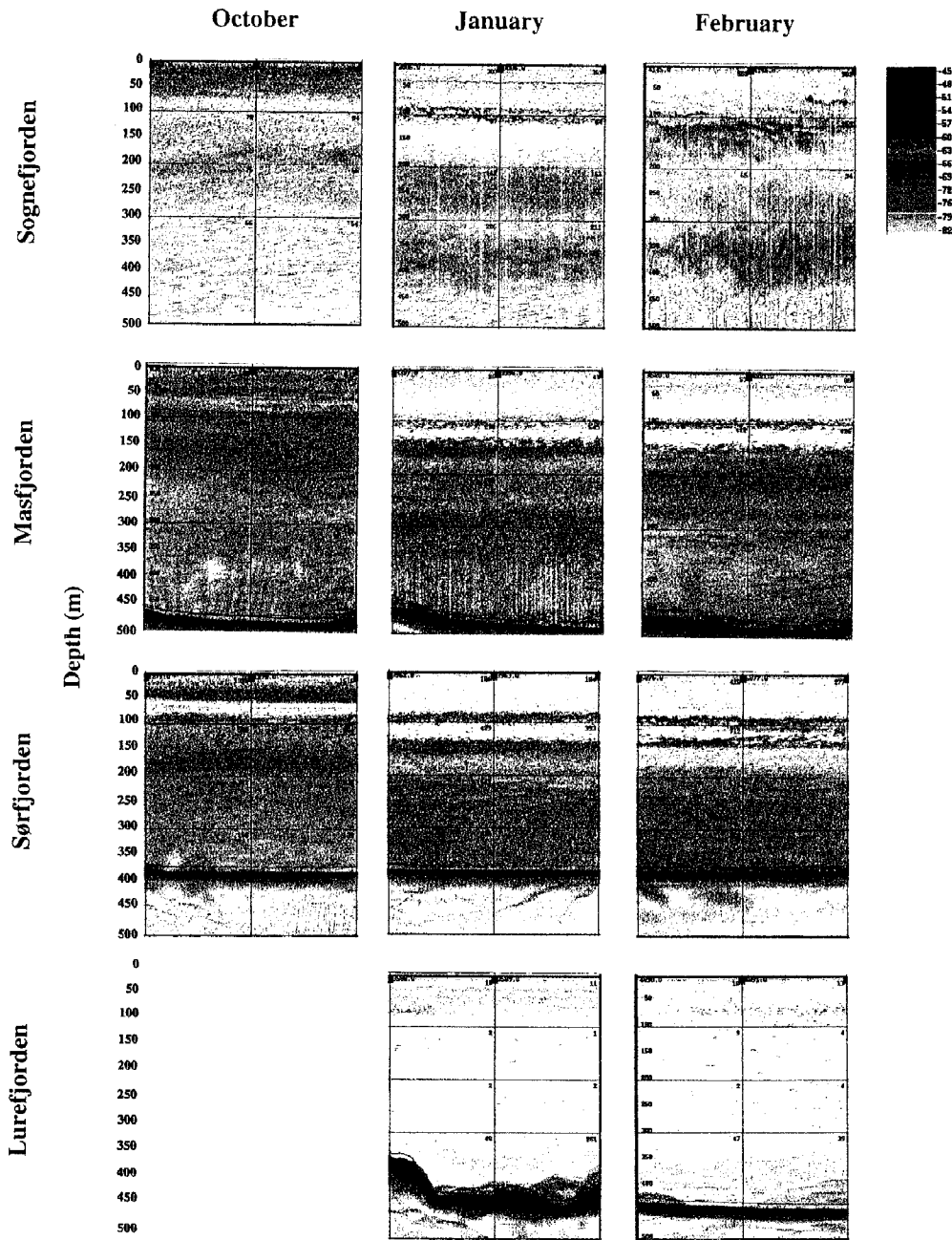


Fig. 7. Selected daytime echograms at 38 kHz (from BI500 program) obtained in Sognefjorden, Masfjorden, Sørfjorden, and Lurefjorden during 19–25 October 1995, 4–10 January and 10–15 February 1996 (records are missing for Lurefjorden in October). The bottom is displayed as a thick, red line (except for Sognefjorden). Color scale refers to volume backscattering strength (dB).

Table 4. Total integrated backscattering levels (S_A , 38 kHz, threshold of -82 dB) for the entire water column (upper 500 m for Sognefjorden) at day (D) and night (N) during the different surveys. SE is given in brackets. No daytime analysis for Lurefjorden in October.

	Sognefjorden		Masfjorden		Sørfjorden		Lurefjorden	
	D	N	D	N	D	N	D	N
Oct	550 (14)	459 (10)	2052 (38)	2031 (79)	2985 (174)	2007 (61)		21 (1)
Jan	658 (31)	620 (21)	1944 (75)	1863 (74)	1496 (60)	1449 (25)	21 (0)	30 (8)
Feb	1179 (212)	835 (4)	1552 (33)	1495 (42)	1493 (60)	1274 (30)	25 (1)	25 (3)

Table 5. Acoustic estimates of mesopelagic fish abundance (ind. m^{-2}). In converting the total echo level (S_A) assigned to the respective targets into number of fish, a TS of -63 was applied for small *Maurolicus muelleri* in Sognefjorden and Masfjorden, while a TS of -64 was applied for small individuals in Sørffjorden. All large *M. muelleri* were assigned a TS of -59.3 and all *Benthosema glaciale* a TS of -58 . SE is given in brackets, and n denotes number of nautical miles from which the average S_A is calculated.

	<i>M. muelleri</i> (small)			<i>M. muelleri</i> (large)			<i>Benthosema glaciale</i>		
	Ind m^{-2}	S_A	n	Ind. m^{-2}	S_A	n	Ind. m^{-2}	S_A	n
Sognefj									
Jan	3	60 (9)	15	1	53 (4)	15	6	375 (10)	9
Feb	1	31 (8)	10	3	149 (24)	10	5	323 (25)	8
Masfj									
Jan	8	167 (21)	24	6	337 (17)	24	16	1059 (26)	19
Feb	10	213 (13)	63	4	204 (9)	63	13	889 (23)	37
Sørffj									
Jan	12	200 (7)	33	5	278 (15)	33	12	850 (12)	28
Feb	15	265 (16)	48	3	182 (13)	43	11	718 (20)	29
Lurefj									
Jan	0	0		0	0		0	0	
Feb	0	0		0	0		0	0	

the assumption of equal predatory efficiency at dusk (Rosland and Giske 1994), one can suggest that each fish in January ate 5 individuals d^{-1} during these short periods combined. We then combine this estimated predation rate with number of juvenile fish in Masfjorden at that time ($8 m^{-2}$; Table 5) and the abundance of *Calanus* in the upper 50 m ($\sim 200 m^{-2}$). This suggests that the juvenile *Maurolicus*

alone could crop $\sim 20\%$ of the surface mode of *Calanus* daily during their stays in upper layer at dusk and dawn. By comparison, the estimated average daily *Calanus* mortality rate for the integrated water column was $\sim 2.5\% d^{-1}$.

Estimated mortality rates were lower in Sørffjorden ($1.2\% - 1.4\% d^{-1}$, 95% CI), despite a similar abundance of mesopelagic fish (Table 5). However, the bulk of *Calanus* was

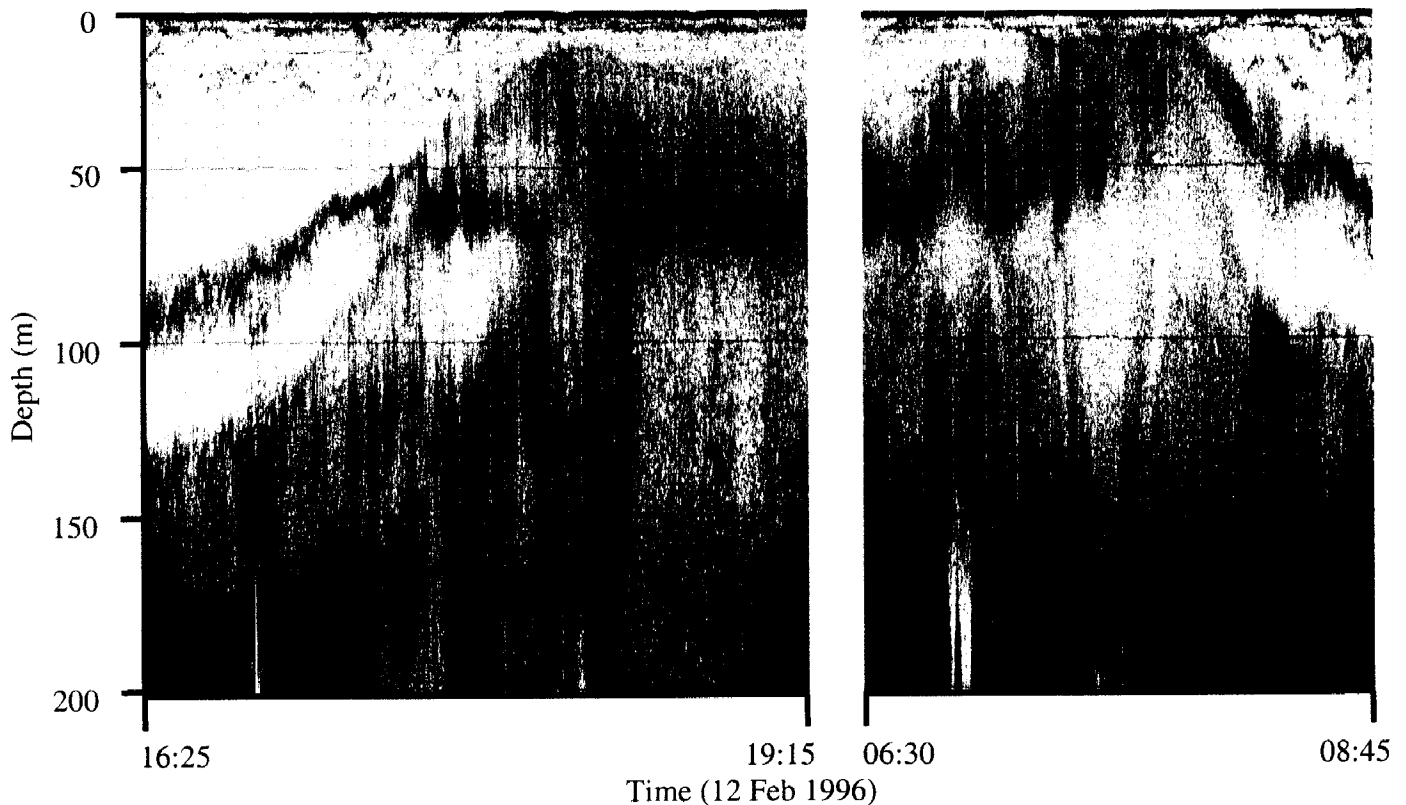


Fig. 8. Echograms at 38 kHz (from paper prints; Sv threshold -75 dB) near dusk (left) and dawn (right) for the upper 200 m of Masfjorden, 12 February 1996.

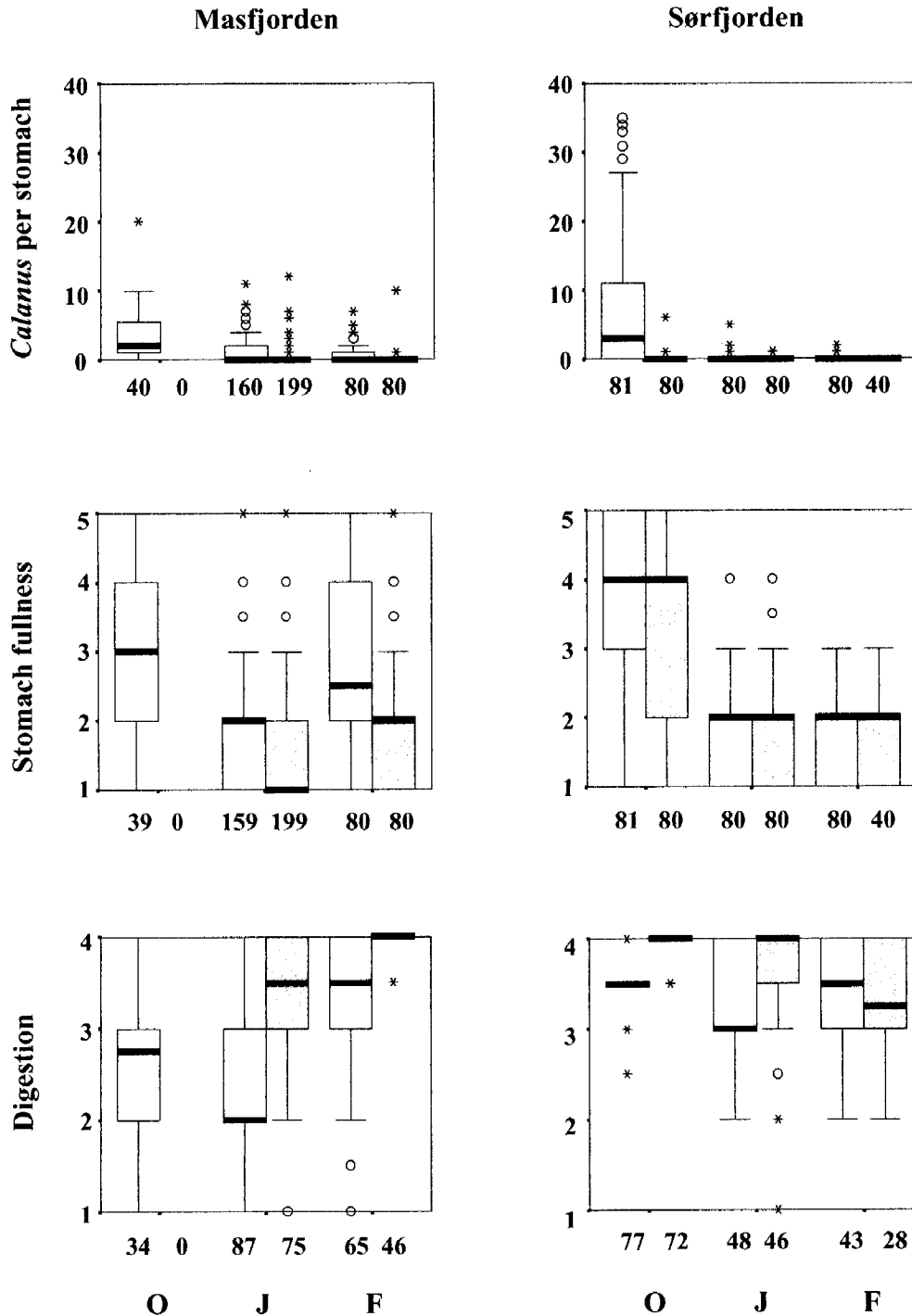


Fig. 9. Stomach content of *M. muelleri*. Results from daytime tows and nighttime tows (respectively) are pooled for each fjord and each cruise in the figure. Fully displayed boxes (day: left and open; night: right and shaded) encompass the 25–75 percentile of observations, with the median marked by a crossing line. Whiskers denote values within 1.5 box lengths from the upper or lower edge of the box. Circles denotes outliers (values between 1.5 and 3 box lengths from the upper or lower edge of the box) and asterisks extreme values (more than 3 box lengths from the upper or lower edge of the box). Note that each marked outlier and asterisk may represent more than one registration. In the scale for stomach fullness, 1 denotes empty and 5 denotes full (Fotland et al. 1995), and the in scale for digestion, 1 denotes undigested and 4 denotes prey unrecognizable (Fotland et al. 1995). The numbers below the plots denote number of observations (fish).

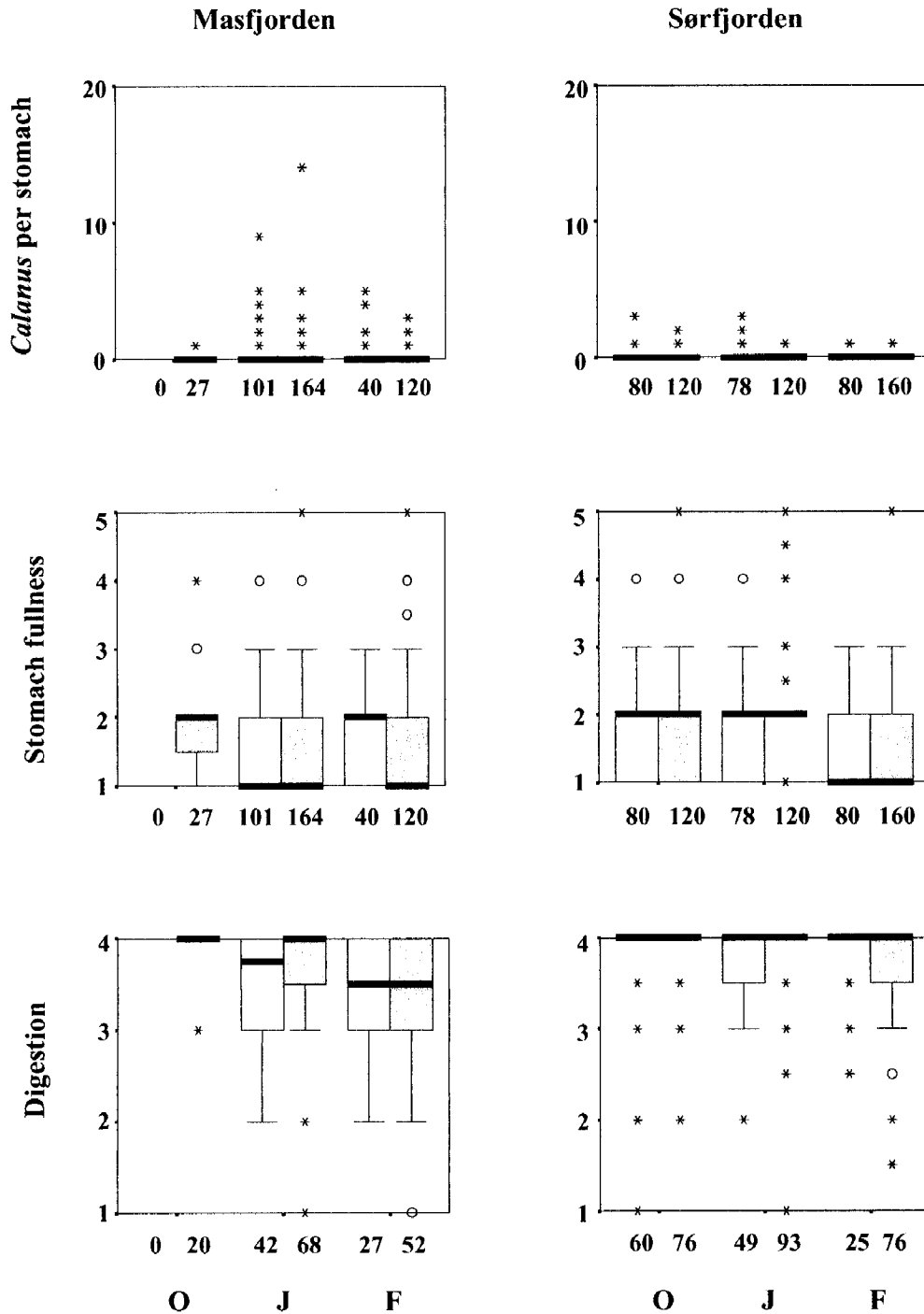


Fig. 10. Stomach content of *B. glaciale*. Results from daytime tows and nighttime tows (respectively) are pooled for each fjord and each cruise in the figure. Fully displayed boxes (day: left and open; night: right and shaded) encompass the 25–75 percentile of observations, with the median marked by a crossing line. Whiskers denote values within 1.5 box lengths from the upper or lower edge of the box. Circles denote outliers (values between 1.5 and 3 box lengths from the upper or lower edge of the box) and asterisks extreme values (more than 3 box lengths from the upper or lower edge of the box). Note that each marked outlier and asterisk may represent more than one registration. In the scale for stomach fullness, 1 denotes empty and 5 denotes full (Fotland et al. 1995), and in the scale for digestion, 1 denotes undigested and 4 denotes prey unrecognizable (Fotland et al. 1995). The numbers below the plots denote number of observations (fish).

Table 6. Comparison of mortality rates (percentage of the population per day).

Locality	Period	Mortality rate (% day ⁻¹)	95% CI	R ²	Study
Norwegian Sea	Nov (1948)–May (1949)	0.7	[0.2, 1.2]	0.43	Østvedt (1955)
Norwegian Sea	Sep–Dec (1949)	1.3	[–0.2, 2.8]	0.72	Østvedt (1955)
Lindåspollene	Summer–rest of year 1979	<1.0	—	—	Aksnes and Magnesen (1983)
Sognefjorden	Oct 1995–Feb 1996	1.1 (0.6)	[0.9, 1.4]	0.85	Present study
Masfjorden	Oct 1995–Feb 1996	2.5 (1.9)	[2.4, 2.7]	0.99	Present study
Sørfjorden	Oct 1995–Feb 1996	1.3 (1.0)	[1.2, 1.4]	0.98	Present study
Lurefjorden	Oct 1995–Feb 1996	0.8	[0.8, 0.9]	0.97	Present study

The estimation of mortality rates based on the data of Østvedt (1955) assumed negligible advective influence (i.e., no immigration/emigration). For the estimates in the present study, the rates in brackets account for possible advective losses in upper waters in October.

found at larger depths in Sørfjorden, mostly below the depth range of *M. muelleri*. In addition, the water clarity was lower (Eiane et al. 1999), rendering visual predation by *B. glacialis* less efficient. The low mortality rate in Sognefjorden (0.9%–1.4% d⁻¹, 95% CI) could be explained by the low fish abundance, as well as by *Calanus* being dispersed over a large depth range.

The mortality rates were estimated for the *Calanus* spp. assemblage. Justification for pooling species requires species size and activity level being similar, given that both are key factors in predator-prey relationships, affecting encounter rates and vulnerability (escape reactions) to predators (cf. Gerritsen and Strickler 1977; Greene 1986). This assumption was to some extent violated, because *Calanus* in Lurefjorden were slightly larger (Eiane et al. 1999) and had a different life cycle (which implies a higher swimming activity at the end of the winter) than *Calanus* in the other fjords. In Lurefjorden, the lack of CIVs in October was conspicuous, considering their proportions in the other fjords. Furthermore, this was the only site where significant parts of the population had ascended from overwintering by February. Adult females then constituted ~50% of all *Calanus*, with the corresponding proportions being <10% elsewhere. The environmental variables (including surface Chl *a* levels) offered no explanation for the earlier ascent in Lurefjorden, which may instead be due to differences in the life cycle of *C. glacialis* (dominant in Lurefjorden) versus those of the other *Calanus* spp., which prevailed in the other fjords.

Abundance and mortality rates of Calanus in fjords versus oceanic environments—Concentrations of overwintering *Calanus* in the Norwegian Sea appear to be lower than those observed in the fjords during the present study because of increased vertical dispersion, although depth-integrated abundances may be higher. The data of Østvedt (1955) give maximum concentrations of ~80 ind. m⁻³ between 600 and 1,000 m and ~70 ind. m⁻³ between 1,000 and 2,000 m during autumn (the maximum abundance was ~100,000 ind. m⁻²). The results of Hirche (1991), Richter (1994), and Dale et al. (1999) show similar, although often lower, concentrations of overwintering *Calanus* in the Greenland and Norwegian Seas. Concentrations of invertebrate predators such as chaetognaths and carnivorous copepods at *Calanus* overwintering depths in the Greenland and Norwegian Seas ap-

pear to be lower (Østvedt 1955) or similar (Richter 1994; Dale et al. 1999) to those in Lurefjorden.

Calanus winter mortality rates estimated in the present paper, in Aksnes and Magnesen (1983), and based on the data of Østvedt (1955) are compared in Table 6. The estimated rate for Masfjorden stands out as extraordinarily high. Aksnes and Magnesen studied Lindåpollene, a landlocked fjord in Western Norway without mesopelagic fish. *Calanus* in Østvedt's study mainly overwintered deeper than 600 m and would thus have been below mesopelagic fish layers associated with upper Atlantic Water masses (cf. Dale et al. 1999). Hence, the high mortality rate in Masfjorden is probably not representative for oceanic stocks. Nevertheless, it suggests that exposure to such fish in waters with sufficient light for efficient visual hunting is more risky than exposure to even high concentrations of various invertebrate predators (as in Lurefjorden).

The vertical range for visual foraging should increase in clear oceanic waters, and oceanic *Calanus* aiming to avoid depths where mesopelagic fish can hunt efficiently by sight would need to descend several hundred meters. This concurs with *Calanus* selection of deep oceanic winter habitats. Different copepod species hibernate in deep water in other oceans (e.g., Spiridonov and Kosobokova 1997; Peterson 1998). We hypothesize that one major ecological reason for the occupation of deep habitats among dormant copepods in the world oceans may be the need to escape predation by mesopelagic fishes.

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Received: 5 July 2000

Amended: 6 April 2001

Accepted: 7 May 2001