Stage-specific habitats of *Calanus finmarchicus* and *Calanus helgolandicus* in a stratified northern Norwegian fjord

S. Skreslet, K. Olsen, Å. Mohus, and K. S. Tande

During 12 months from April 1997, *Calanus* spp. copepodites were sampled in the 380-m deep Saltfjord by means of a 200-μm WP-2 net at four depth intervals. Nauplii were sampled with a 100-μm bongo net. Chlorophyll *a* and phytoplankton were sampled with a hose in the 0–40 m depth range. Environmental variables were recorded by CTD and an *in situ* fluorimeter. *C. helgolandicus* occurred in low numbers as adults and CV during most of the year. During the spring bloom in April, it avoided the upper cold 0–50 m depth range, where *C. finmarchicus* reproduced. In August–September, adults of the two species were equally numerous in the 0–50 m depth range. The adult *C. finmarchicus* had probably developed from the local spring generation, whereas *C. helgolandicus* had probably been imported from shelf waters. Nauplii present in August may be attributed to both species, but they did not grow into CI locally. Therefore, *C. finmarchicus* CV that accumulated in September–October were more likely imported from the shelf, probably by surface advection. Predators possibly reduced numbers up to January 1998, when both species again increased, probably because of deep inflow of shelf water.

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Introduction

Bucklin *et al*. (1995) used DNA base sequence analyses to discriminate between copepod species of the genus *Calanus*. They suggested that *Calanus helgolandicus* may be older and more distinct from *Calanus finmarchicus* than some of the other *Calanus* spp. in the North Atlantic. Fleminger and Hulsemann (1977) observed that the oceanic occurrence of *C. helgolandicus* was associated with the North Atlantic Drift, from the Atlantic coast of North America to the Fram Strait, where Atlantic surface flow submerges into the Arctic Ocean. *C. finmarchicus* overlaps the distribution of *C. helgolandicus*, but is also distributed into the colder parts of the North Atlantic.

There are some observations of *C. helgolandicus* from the fjords of the western coast of Scandinavia. Hirche (1983) observed it overwintering in the Gullmarfjord, Sweden, but he did not find it in the Korsfjord near Bergen, southern Norway, in August–November 1978.

However, in May 1997, Hygum *et al.* (2000) sampled low numbers of *C. helgolandicus* females from the 0–100 m depth range in the Raunefjord that exchanges water with the Korsfjord. In the Lurefjord close to Bergen, *C. helgolandicus* is more abundant than *C. finmarchicus* (P. Lindeque, pers. comm.). In the Oslofjord, Bucklin *et al.* (1999) observed a predominance of *C. helgolandicus* over two other *Calanus* spp., including *C. finmarchicus*.

Considering the fast advection of water along the Norwegian coast from the eastern North Sea (Poulin and Warn-Varnas, 1996; Sætre, 1999), *C. helgolandicus* could be expected in the fjords of northern Norway as well. Saltfjord is a typical, northern Norwegian overwintering and spring-spawning habitat for *C. finmarchicus* (Sømme, 1934; Skreslet and Rød, 1986). The present study was carried out there for a year to observe any presence of *C. helgolandicus*, its abundance relative to *C. finmarchicus*, and the distribution of the two species in relation to depth-dependent environmental factors.
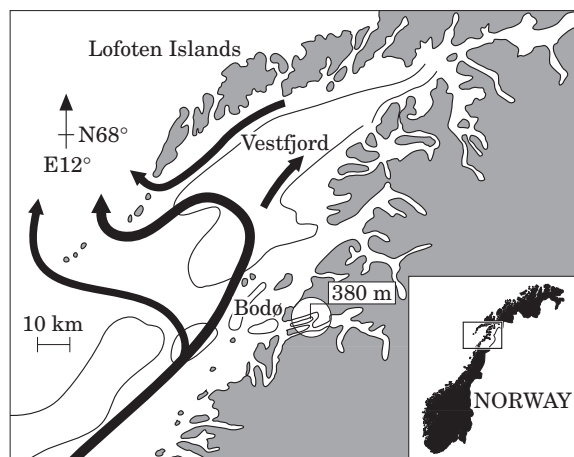
Figure 1. The Vestfjord region, with the 380-m-deep Saltfjord sampling location in the centre of the circle. The 250-m depth contour is drawn in the Saltfjord, the Vestfjord proper, and in shelf areas to the southwest, but not in several other deep fjords. Arrows indicate the main surface currents, according to Sundby (1978), Poulin and Warn-Varnas (1996), and Sætre (1999).

The Vestfjord is a large basin situated between the Lofoten Islands and the northern Norwegian mainland (Figure 1). The Norwegian Coastal Current enters the outer Vestfjord, where it subdivides into two branches that cross the fjord and run onto the shelf west of the Lofoten Islands. The inner branch feeds coastal water into the southeastern parts of the Vestfjord and compensates for the more brackish outflow on its northwestern side.

A 220 m sill depth at the tip of the Bodø Peninsula separates the 380 m deep Saltfjord basin from the Vestfjord basin and from trenches on the continental shelf. The inner part of the Saltfjord is connected by a tidal channel (Saltstraumen) 26 m deep and 255 m wide to a 260 km^2 fjord system that receives freshwater from several river systems, including the Junkerdal River. However, the tidal current forces considerable mixing in the sampling area during ebb tide and causes relatively high surface salinity in the Saltfjord.

Methods

The sampling programme (Table 1) was done on a single station situated at the 380-m maximum depth of the Saltfjord basin (Figure 1), allowing sampling to an intended depth of 370 m. Sampling of *Calanus* spp. copepodites was done using a 200-µm WP-2 net towed vertically in the four depth ranges 370–200, 200–100, 100–50, and 50–0 m. It was carried out during daylight at weekly or monthly intervals over a full year from winter 1997. In some cases, monthly average abundance

has been calculated when more than one sample was taken during a month.

Calculations of the relative abundance of *Calanus* spp. were based on random selection and identification of up to 100 specimens. *C. finmarchicus* and *C. helgolandicus* were distinguished from *Calanus glacialis* and *Calanus hyperboreus* by their length (Hirche *et al.*, 1994). According to Frost (1974) and Fleminger and Hulsemann (1977), *C. finmarchicus* and *C. helgolandicus* can be systematically separated only when they are in copepodite stages CV-VI. The method is based on the shape of the fifth pair of swimming legs (P5) that had to be dissected and inspected under a microscope at 200–400× magnification. In P5 of CV and female CVI, the two species differ in the curvature of the first basipod (BP1). This feature is equal in male CVI separated by differences in the morphology of the endo- and exopodites.

Samples containing more than 300 specimens of *Calanus* spp. were split by a Folsom divider. The abundance of each species was obtained by multiplying the total number by the relative abundance of each species.

To monitor the presence of *Calanus* spp. nauplii, monthly or bimonthly double oblique tows were made from the surface to 370 m using a 100-µm bongo net (20-cm diameter). A flowmeter in the net aperture was used to calculate the filtered volume.

In situ profiles of salinity and temperature were recorded with a SeaBird SBE25 Sealogger CTD and/or a Sensordata SD200 mini CTD in the depth range 0–370 m. On every SBE25 cast, options on the SBE32/33 Carousel were used to calibrate seawater temperatures against reversing thermometer readings at about 370 m depth. One water sample from the same depth was analysed on a Guildline laboratory salinometer to calibrate the recorded salinity. The SD200 was calibrated against the SBE25. The Norwegian Standard Winkler titration of seawater samples was applied to calibrate data from the SBE25's oxygen sensor.

In situ fluorescence profiles were recorded using a Dansk Havteknik Q300 fluorometer in the 0–60 m depth range. A glass-reinforced flexible plastic hose was utilized to sample seawater for estimates of chlorophyll *a* and phytoplankton average concentration in the 0–40 m depth range. Chlorophyll *a* was sampled and analysed according to the Norwegian Standard. Phytoplankton cells were counted under an inverted microscope in accordance with the standard Utermöhl method (Hasle, 1978).

Results

Freshwater run-off in the Junkerdal River, part of the drainage area of the Saltfjord, increased in May and culminated in June. It then decreased, but there were smaller maxima in July, September, November, and December (Figure 2).

Table 1. Sampling dates and gear and depths (m) sampled in the Saltfjord (67°13.95′N, 13°39′E), northern Norway. SD200 refers to the Sensordata SD200 mini CTD, SBE25 to the SeaBird Electronics SBE25 CTD, Q300 to the Dansk Havteknik Q300 Fluorometer, Hose to a 0.5 hose for water samples analysed for abundance of phytoplankton and standard photometric determination of chlorophyll *a*, B20 to a bongo plankton sampler with 100-μm net, oblique tows from surface to recorded depth and back, and WP-2 to a 180-μm closing net sampling in 370–200, 200–100, 100–50, and 50–0 m depth intervals.

| Date	SD200	SBE25	Q300	Hose	B20	WP-2
13 Feb 1997		0–370	0–63	0–40	0–370	
13 Mar 1997		0–370	0–60		0–360	
01 Apr 1997		0–265	0–60		0–360	0–370
11 Apr 1997				0–40		0–370
28 Apr 1997		0–360	0–60	0–40	0–360	0–370
06 May 1997				0–40		0–370
22 May 1997	0–380			0–40		0–370
28 May 1997	0–380			0–40		0–370
02 Jun 1997	0–360	0–360	0–62	0–40	0–370	0–370
12 Jun 1997	0–380			0–40		0–370
20 Jun 1997		0–370	0–60		0–372	0–370
24 Jun 1997	0–380			0–40		0–370
02 Jul 1997	0–380			0–40		0–370
09 Jul 1997	0–380			0–40		0–370
15 Jul 1997	0–380			0–40		0–370
22 Jul 1997		0–370	0–60	0–40	0–370	0–370
29 Jul 1997	0–380			0–40		0–370
25 Aug 1997		0–360	0–60	0–40	0–360	0–370
05 Sep 1997	0–380			0–40		0–370
10 Sep 1997	0–380			0–40		0–370
23 Sep 1997	0–360	0–360	0–60	0–40	0–360	0–370
01 Oct 1997	0–380			0–40		0–370
09 Oct 1997	0–380			0–40		0–370
27 Oct 1997		0–370	0–61		0–366	0–370
19 Nov 1997	0–367	0–367	0–60		0–368	0–370
18 Dec 1997	0–370					0–370
13 Jan 1998		0–370	0–60	0–40	0–360	0–370
09 Feb 1998		0–370	0–60	0–40	0–360	0–370
11 Mar 1998		0–370	0–60	0–40	0–360	0–370
20 Apr 1998		0–370	0–60	0–40	0–360	0–370
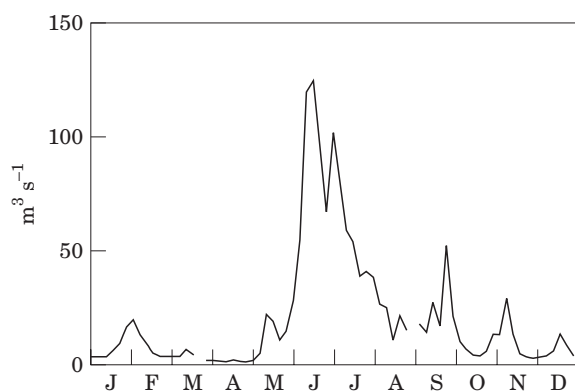
Figure 2. Five-day average run-off in the Junkerdal River recorded in 1997 at water gauge no. 163.5 (data from the Norwegian Water and Electricity Board).

Salinities were as low as 30.5–31, about 5 m deep in late June, July, and September. The upper part of the 0–50 m depth range was characterized by periods when the salinity was <32, in June–July and September–November 1997, and in February 1998 [Figure 3(a)]. At about 5 m depth the temperature was below 5°C from February to April in both years, while the maximum exceeded 11°C in September [Figure 3(b)]. The maximum salinity at 50 m was close to 34 in June. The seasonal salinity variations in the 50–100, 100–200, and 200–370 m depth ranges occurred within approximately 32.5–34.5, 33.5–34.5, and 34.5–35, respectively. The seasonal temperature variations in the 50–100, 100–200, and 200–370 m depth ranges were within approximately 5–11, 5–8, and 6–7°C, respectively.

The entire water column was well oxygenated throughout the year, with no observation <5.75 ml l^{-1}, a value recorded near the bottom in February 1997 [Figure 3(c)]. Pigment maxima recorded by *in situ* fluorescence occurred in three seasons: April, June–July, and September, the latter two being associated with low surface salinity [Figure 3(d)]. The average concentration of chlorophyll *a* in the 0–40 m depth range exceeded
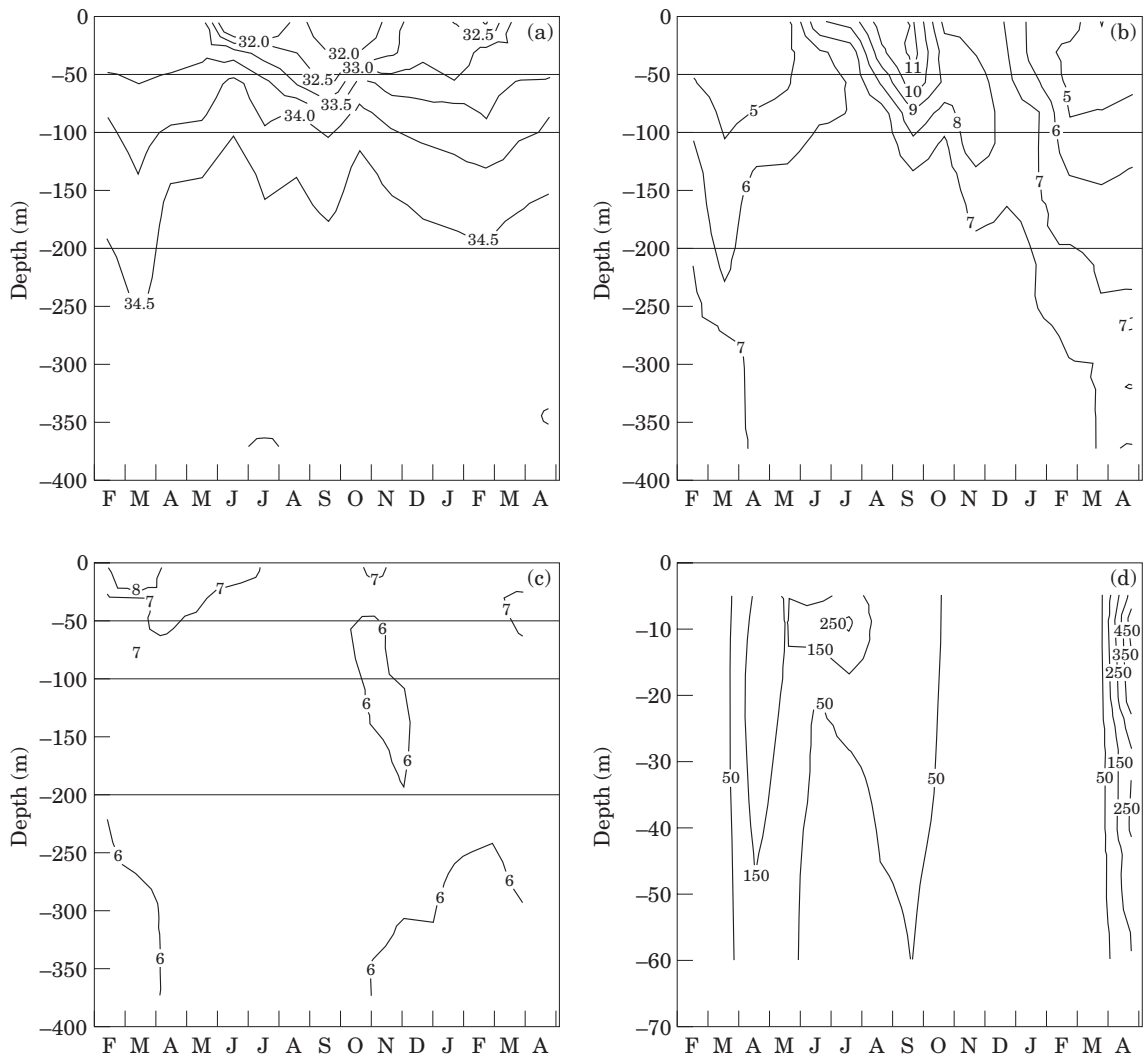
Figure 3. Depth vs. time contour diagram of (a) salinity, (b) temperature (°C), (c) oxygen concentration (ml l^{-1}), (d) fluorescence voltage in the Saltfjord, 1997–1998.

$1.0 \, \mu g \, l^{-1}$ in April–September, with maxima $>3.0 \, \mu g \, l^{-1}$ in April, early June, and late July (Figure 4). The abundance of diatoms declined in May, but then they started to bloom in early June and dominated by numbers in June and July (Figure 5). The flagellates, mainly $<10 \, \mu m$, were numerous from May to August but dropped to a minimum in early July. Dinoflagellates were found only occasionally in small numbers.

The abundance of *Calanus* nauplii was $>5000 \, m^{-2}$ in bongo samples from March to early July in 1997 and in March and April 1998 (Figure 6). From July to October, only one sample was obtained >4000 nauplii m^{-2} in August.

Calanus CI were present only in April and May 1997 and in April 1998 (Figure 7). Copepodites grouped as CI-III were numerous only in April and May 1997,
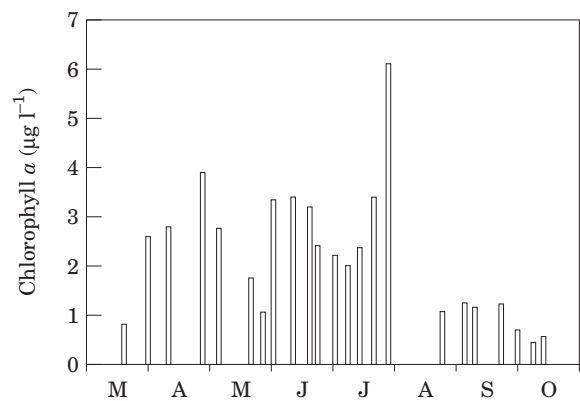

Figure 4. Average concentration of chlorophyll *a* in the 0–40 m depth range in the Saltfjord, March–October 1997.
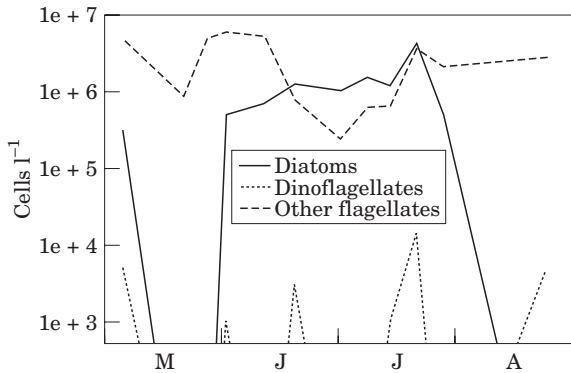
Figure 5. Average abundance of phytoplankton in the 0–40 m depth range in the Saltfjord, May–August 1997.
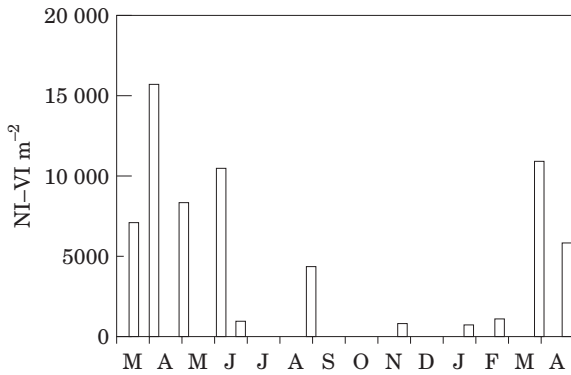

Figure 6. Abundance of *Calanus* spp. nauplii I–VI in double oblique bongo tows, Saltfjord, March 1997 to April 1998.
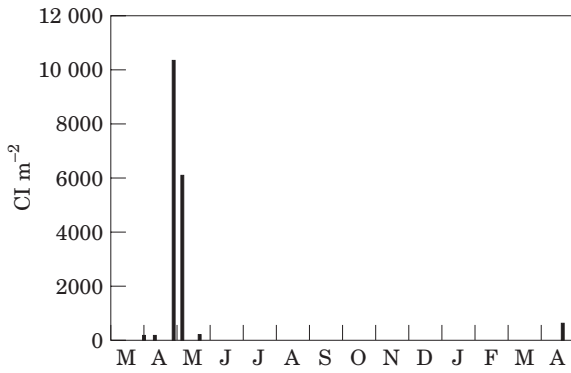

Figure 7. Abundance of *C. finmarchicus* and *C. helgolandicus* CI expressed as the sum of samples from vertical WP-2 tows in four different depth ranges between 370 m and the surface, Saltfjord, March 1997 to April 1998.
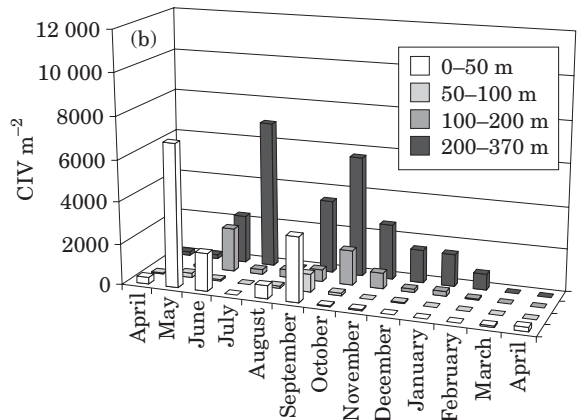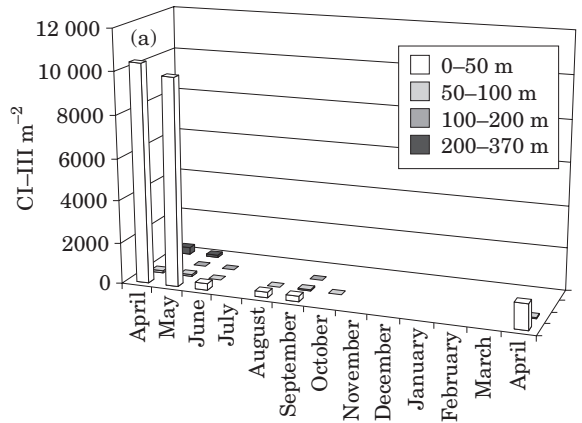

Figure 8. Abundance of *C. finmarchicus* and *C. helgolandicus* (a) CI–CIII, (b) CIV sampled by WP-2 net in four different depth ranges in the Saltfjord, April 1997 to April 1998.

but some were also present from August to October, predominantly in the 0–50 m depth range [Figure 8(a)]. *Calanus* CIV were abundant in two periods, in May–July and September–January, being noticeable at the surface at the beginning of each period, but primarily being found closer to the bottom [Figure 8(b)].

Abundance of *C. finmarchicus* CV changed with time, much like *Calanus* CIV, but they were more numerous in the 200–370 m depth range [Figure 9(a)]. That was also the case with the adults, but they were most numerous in February 1998 [Figure 9(b)], exceeding 3200 m^{-2}. *C. helgolandicus* CV occurred in most depths in September and October, but did not build up a stable wintering stock [Figure 10(a)]. With the exception of July, *C. helgolandicus* adults were always present in some of the depth ranges [Figure 10(b)].

In most cases during this investigation, standing stocks of *C. finmarchicus* CV-VI outnumbered *C. helgolandicus* CV-VI by more than an order of magnitude. Only in August and September 1997, and only in the case of adults in the 0–50 m depth range, was the abundance of the two species at the same order of magnitude [Figures 9(b), 10(b)].
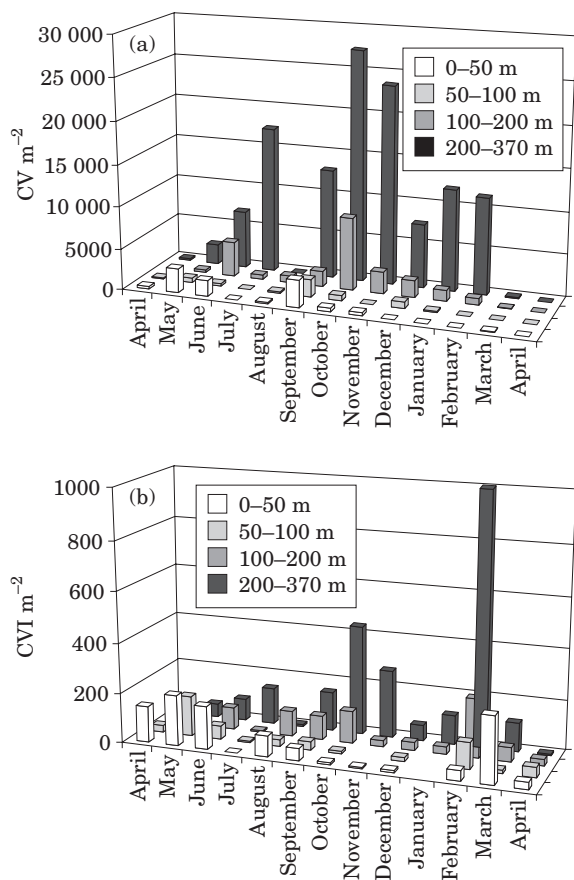
Figure 9. Abundance of *C. finmarchicus* (a) CV, (b) copepodite adults sampled by WP-2 net in four different depth ranges in the Saltfjord, April 1997 to April 1998. The column at 200–370 m depth in February in (b) is truncated (see text).
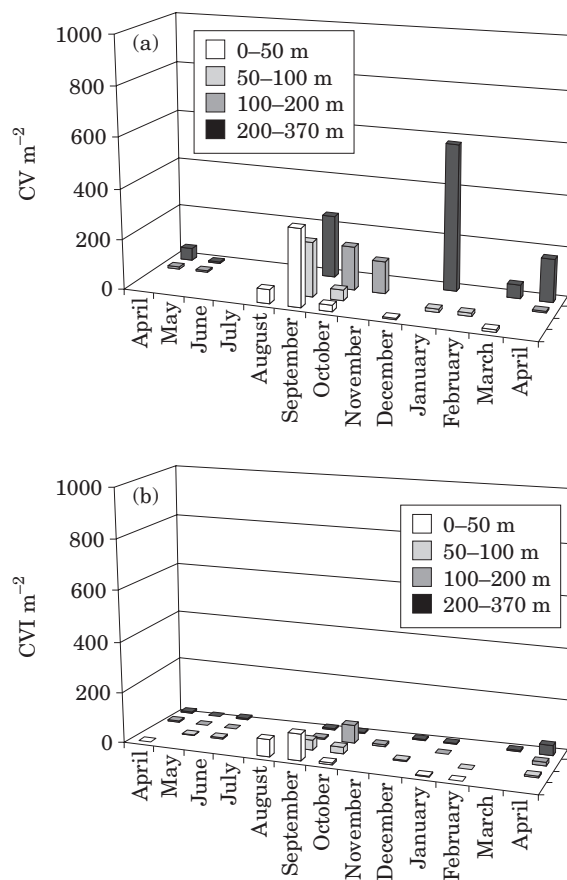
Figure 10. Abundance of *C. helgolandicus* (a) CV, (b) co-pepodite adults sampled by WP-2 net in four different depth ranges in the Saltfjord, April 1997 to April 1998.

Discussion

The seasonal variation in run-off data from the Junkerdal River was probably representative of the discharge from several of the major watercourses in the catchment area around the Saltfjord. In May–July 1997, the meltwater discharge caused a reduction in the surface salinity of the fjord and probably generated an estuarine circulation that influenced the exchange of plankton with the shelf. Estuarine circulation probably also resulted from the run-off in September that is typical of the pluvio-nival regime of the western Norwegian coast (Tollan, 1976), but the exchange of water and plankton was probably more complex. The high temperature recorded in the 0–50 m depth range in September probably resulted from the annual surface advection of shelf water into the fjord (Haakstad, 1979). This normal event causes importation of plankton as well as heat accumulated by shelf water during summer.

Intermediate inflow of coastal water that caused the salinity to increase in the 50–150 m layer in April–June and September–October could be forced by factors such as wind-induced upwelling, atmospheric pressure gradients, and the effects of estuarine circulation.

Freshwater run-off from Norway carries colloids of humus that dissolve in seawater (Aas, 1976). This yellow matter (gelbstoff) is fluorescent and has probably contributed to the fluorescence recorded in the Saltfjord. Therefore, the fluorescence voltage readings cannot be transformed to chlorophyll *a* without serious bias. However, the high concentrations of chlorophyll *a* in April and June–July are in fair agreement with the maxima in fluorescence, indicating two main periods of phytoplankton production that involved diatoms.

No phytoplankton counts were made in September–October when the concentration of chlorophyll *a* was rather low, but when there is usually a third autumn bloom. Fluorescent matter recorded to about 60 m depth in September possibly indicates the presence of viable phytoplankton to that depth, but yellow matter of

both terrestrial and marine origin may have contributed to the fluorescence (cf. Aas, 1976).

Very few adult *C. helgolandicus* were present in April–July 1997, indicating that the reproductive activity of *Calanus* in the Saltfjord during the first phytoplankton bloom in April was attributable to *C. finmarchicus*. The spring bloom that fed egg-producing female *C. finmarchicus* resulted in a substantial production of *Calanus* nauplii. The abundance of *Calanus* CI declined during May, and none were observed during the frequent sampling in June, although nauplii were still abundant in early June and present at the end of the month. Food was probably not a limiting factor for reproduction, because the fluorescence, chlorophyll *a* concentration and phytoplankton abundance indicated that a second phytoplankton bloom had started in early June and lasted until late July. The bloom was probably initiated by stratification that resulted from the increasing meltwater discharge and forced by turbulence associated with the estuarine circulation (cf. Sakshaug, 1976). The brackish outflow may have flushed nauplii produced during June onto shelf waters, where they would have developed into copepodites. However, those that had been produced at an earlier date and developed into stages more advanced than *Calanus* CI in May and June seem to have accumulated as *Calanus* CIV in the 200–370 m depth range from June to July.

A substantial number of the locally produced generation of *C. finmarchicus* developed into CV-VI between May and July. It is therefore likely that the adults 0–50 m deep in the Saltfjord in August and September had completed their life cycle locally. This was not the case with *C. helgolandicus* adults in the upper 0–50 m in August, because there was no local standing stock of CV in the period June–July. Both CV and adults of this species were probably advected from the shelf in August.

The appearance of adult *C. helgolandicus* and *C. finmarchicus* in August occurred after the maxima of chlorophyll *a* and fluorescence in June/July, and after the abundance of diatoms had declined. Therefore, the carrying capacity for reproductive activity was probably low, but some *Calanus* nauplii were still observed in August, indicating that one or both species did reproduce locally. However, the total absence of *Calanus* CI and the very few *Calanus* CI-III observed in August–October indicate that the high abundance of *Calanus* CIV, and the CV and adults of *C. finmarchicus* and *C. helgolandicus* observed in the same period, cannot be attributed to local reproduction. Even the CII-III may to some extent have been advected from the shelf, as happened during autumn in the Malangen, a fjord farther north in Norway (Falkenhaug *et al.*, 1997).

Wind-driven surface advection, the intermediate inflow of shelf water that compensates for freshwater outflow during autumn, and the annual surface inflow of shelf water to the Saltfjord in September (Haakstad, 1979) are probably the main physical processes that caused the CV of *C. finmarchicus* and *C. helgolandicus* to populate the Saltfjord between August and November. Deep inflow of Atlantic Water, which frequently crosses the sills and sinks into the fjord basins of northern Norway (Skreslet and Loeng, 1977), is an additional factor that starts in early autumn, and increases in relative importance during late autumn and winter. Such inflow was probably evident from December to January, when the abundance of *C. finmarchicus* and *C. helgolandicus* CV increased after a period of decrease that may have been caused by predation.

In general, before and during the spring bloom, adult *C. helgolandicus* were not associated with the 0–50 m depth range, possibly owing to low temperatures, in contrast to *C. finmarchicus* that reproduced there. In September, both species were at the surface and bottom, but most of the *C. finmarchicus* were 200–370 m deep, i.e. in water of Atlantic origin. Most *C. helgolandicus* were in the 0–100 m depth range, in coastal water characterized by higher temperature and lower salinity. According to Fleminger and Hulsemann (1977), *C. helgolandicus* are found in the eastern Norwegian Sea, so those that accumulated in the Saltfjord during autumn possibly originated from summer spawning on the Norwegian Shelf.

The stage-specific distribution of *C. finmarchicus* in different depth ranges seems to be related to stratification in the Saltfjord. Local reproduction occurred in the upper 0–50 m, in water characterized by large seasonal variation in salinity, temperature, and phytoplankton production. Both the CV that were produced locally in May/June, and those that were advected into the fjord after August, occupied the dysphotic and well-oxygenated fjord basin where the salinity and temperature did not change much over the year. Few individuals occupied the depth ranges in between, in particular the 50–100 m range, possibly because of predation risk or actual predation. Dale *et al.* (1999) observed that the presence of *C. finmarchicus* in the Norwegian Sea was negatively related to the acoustic backscattering from planktivorous mesopelagic fish and suggested predator avoidance by the former.

Previous investigations on *C. finmarchicus* in the Vestfjord region (e.g. Sømme, 1934; Wiborg, 1954; Skreslet and Rød, 1986) probably included *C. helgolandicus* in their abundance estimates. However, the results of the present investigation indicate that most previous findings presented as *C. finmarchicus* should still hold true because of the low abundance of *C. helgolandicus*. Therefore, for purposes of practical research in the region, the sum of the abundance of the two species is representative of stock changes in *C. finmarchicus*, but not in *C. helgolandicus*. However, care should be applied in near-surface studies that address *Calanus* CV and adults in early autumn.

Conclusions

C. finmarchicus and *C. helgolandicus* seem to have had different requirements in respect of the physical environment. In early spring, spawning *C. finmarchicus* occupied the cold 0–50 m depth range avoided by adult *C. helgolandicus*. In autumn, both were present as adults in the 0–50 m depth range, but a large fraction of *C. finmarchicus* CV and adults occupied the 200–370 m depth range, where only a minor fraction of *C. helgolandicus* CV and adults were present.

The distribution of *C. finmarchicus* and *C. helgolandicus* in different depth ranges may not be a simple response to a stratified physical environment. It may also be a function of food and predators that occupy specific strata that structure the vertical distribution of the copepods.

C. finmarchicus reproduced locally in the Saltfjord, in association with the spring bloom. That resulted in a new generation of CV that occupied the fjord's basin water, but they disappeared in August, probably as a result of sexual maturation and ontogenetic migration towards the surface.

For *C. helgolandicus*, present in low numbers during most of the year, the Saltfjord appears to be an accumulation habitat during autumn for CV and adults. They possibly originated from summer production over the Norwegian Shelf.

Both species may have produced the nauplii recorded in August, but irrespective of their origin, the offspring did not contribute to any noticeable accumulation of copepodites, possibly owing to predation or advective loss to the shelf. For practical purposes, though, the few *C. helgolandicus* present during most of the year represent very little contamination of samples generally attributed to *C. finmarchicus*.

Acknowledgements

References

Aas, E. 1976. The influence of freshwater on light conditions in fjords. *In* Fresh Water on the Sea, pp. 11–13. Ed. by S. Skreslet, R. Leinebø, J. B. L. Matthews, and E. Sakshaug. Association of Norwegian Oceanographers, Oslo. 246 pp.

Bucklin, A., Frost, B. W., and Kocher, T. D. 1995. Molecular systematics of six *Calanus* and three *Metridia* species (Calanoida: Copepoda). Marine Biology, 121: 655–664.

Bucklin, A., Guarnieri, M., Hill, R., Bentley, A., and Kaartvedt, S. 1999. Taxonomic and systematic assessment of planktonic copepods using mitochondrial COI sequence variation and competitive, species-specific PCR. Hydrobiologia, 401: 239–254.

Dale, T., Bagien, E., Melle, W., and Kaartvedt, S. 1999. Can predator avoidance explain varying overwintering depth of *Calanus* in different oceanic water masses? Marine Ecology Progress Series, 179: 113–121.

Falkenhaug, T., Tande, K., and Timonin, A. 1997. Spatio-temporal patterns in the copepod community in Malangen, northern Norway. Journal of Plankton Research, 19: 449–468.

Fleminger, A., and Hulsemann, K. 1977. Geographical range and taxonomic divergence in North Atlantic *Calanus* (*C. helgolandicus*, *C. finmarchicus* and *C. glacialis*). Marine Biology, 40: 23–48.

Frost, B. W. 1974. *Calanus marshallae*, a new species of calanoid copepod closely allied to the sibling species *C. finmarchicus* and *C. glacialis*. Marine Biology, 26: 77–99.

Haakstad, M. 1979. Exchange of water between the Norwegian coastal current and the fjords in autumn. Nordland College, Section of Natural Science, Report 4/79.

Hasle, G. R. 1978. Using the inverted microscope. *In* Phytoplankton manual, pp. 191–196. Ed. by A. Sournia. UNESCO, Paris. 337 pp.

Hirche, H-J. 1983. Overwintering of *Calanus finmarchicus* and *Calanus helgolandicus*. Marine Ecology Progress Series, 11: 281–290.

Hirche, H-J., Hagen, W., Mumm, N., and Richter, C. 1994. The northeast water polynia, Greenland Sea. 3. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during spring. Polar Biology, 14: 491–503.

Hygum, B. H., Rey, C., Hansen, B. W., and Tande, K. 2000. Importance of food quantity to structural growth and neutral lipid reserves accumulated in *Calanus finmarchicus*. Marine Biology, 136: 1057–1073.

Poulin, P. M., and Warn-Varnas, A. 1996. Near-surface circulation of the Nordic Seas as measured by Lagrangian drifters. Journal of Geophysical Research, 101: 18237–18258.

Sakshaug, E. 1976. Dynamics of phytoplankton blooms in Norwegian fjords and coastal waters. *In* Fresh Water on the Sea, pp. 139–143. Ed. by S. Skreslet, R. Leinebø, J. B. L. Matthews, and E. Sakshaug. Association of Norwegian Oceanographers, Oslo. 246 pp.

Skreslet, S., and Loeng, H. 1977. Deep water renewal and associated processes in Skjomen, a fjord in north Norway. Estuarine and Coastal Marine Science, 5: 383–398.

Skreslet, S., and Rød, N. Å 1986. Advection of *C. finmarchicus* between habitats in Norwegian coastal waters. NATO ASI Series G, 7: 375–387.

Sundby, S. 1978. In/out flow of coastal water in Vestfjorden. ICES CM 1978/C: 51, 17 pp.

Sætre, R. 1999. Features of central Norwegian shelf circulation. Continental Shelf Research, 19: 1809–1831.

Sømme, J. D. 1934. Animal plankton of the Norwegian coast waters and the open sea. 1. Production of *Calanus finmarchicus* (Gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten area. Fiskeridirektoratets Skrifter Serie Havundersøkelser, 4(9): 1–163.

Tollan, A. 1976. River runoff in Norway. *In* Fresh Water on the Sea, pp. 11–13. Ed. by S. Skreslet, R. Leinebø, J. B. L. Matthews, and E. Sakshaug. Association of Norwegian Oceanographers, Oslo. 246 pp.

Wiborg, K. F. 1954. Investigations on zooplankton in coastal and offshore waters of western and north-western Norway. Fiskeridirektoratets Skrifter Serie Havundersøkelser, 11: 1–246.