RESEARCH ARTICLE

Variable predator–prey relations in zooplankton overwintering in Subarctic fjords

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Abstract

Zooplankton predator–prey relations in northern Norwegian fjords are highly variable in time and space, and the mechanisms driving this variability are still poorly understood. Replicate Juday net sampling in October and February from 1983 to 2005, which included five repeated tows from bottom to surface, was conducted in Saltfjord and Mistfjord, northern Norway. The time-series provided evidence of in situ variability in species abundance, as well as seasonal and interannual changes in standing stock abundance. The shallow sill of one fjord caused accumulation of coastal water in the fjord's basin, while the other fjord's deeper sill selected denser water of Atlantic origin from the same open shelf habitat. The selective advection caused differences in the immigration of species recruiting to the fjords' specific overwintering communities of zooplankton. Statistical analyses of the cumulated replicate data indicated significant in situ variability in the spatial density of species. Cases with an abundance of carnivores relating positively to other species probably resulted from the carnivores' attraction to patches with concentrations of prey. Interspecific negative density relations likely indicated either predator avoidance or substantial trophic activity during the sampling. During years of high abundance, some wintering stocks of carnivores evidently reduced the local stocks of overwintering prey. We conclude that predator–prey interactions and stock variability in Subarctic fjords result from complex bio-geophysical interactions that occur on the scales of local habitats and basin-scale population systems.

To access the supplementary material, please visit the article landing page

Introduction

The Subarctic fjords of northern Norway provide wintering habitats for the zooplankton biota of mixed boreal and Arctic species. Many species establish local stocks by immigrating from extensive population systems in the Arctic Mediterranean (Tchernia 1980), where the ecosystem has been evolving since the first glaciation of the Pleistocene period (Dunbar 1968). The relative abundance of wintering stocks in fjords changes with the hemispheric climate by its effects on large-scale thermohaline circulation within the Arctic Mediterranean ecosystem, which eventually influences the local shelf-to-fjord advection of both oceanic NAC water and shelf water of lower salinity (Skreslet et al. 2015; Espinasse et al. 2018). Temporal changes in a fjord's abundance of wintering zooplankton

are a balance between local mortality and the exchange of water with outside habitats. While some mortality results from predation by a wide range of benthonic and nektonic planktivores in fjords, some is due to predator–prey relations on different spatial scales within defined zooplankton communities. Studies of interspecific trophic relations on zooplankton community levels are rare and not easily achieved; in this study, we applied an approach that to our knowledge is new to plankton science.

Saltfjord and Mistfjord are two fjords situated just above the Arctic Circle in northern Norway and are separated by the Bodø peninsula (Fig. 1). Both fjords lock mesopelagic basin water behind the sills at their entrances, but their differing sill depths permit the selective import of water and zooplankton species from the outside shelf habitat. This causes their basin water quality, as well as

the biodiversity and species abundance of the accumulated zooplankton, to correlate differently with hemispheric climate variability recorded as North Atlantic Oscillation, Arctic Oscillation and Atlantic Multidecadal Oscillation (Skreslet et al. 2015).

Saltfjord receives a significant amount of Norwegian Sea zooplankton during September and October (Heath et al. 2000; Skreslet et al. 2000), when the north-running NCC shifts its transversal surface vector of coastal water from seaward to landward (Helland-Hansen & Nansen 1909; Haakstad 1979). This shift is a result of the decreased stratification of the NCC caused by reduced freshwater discharge after summer and increased turbulence forced by winds during autumn (Haakstad 1977), while prevailing south-western winds in September and October accelerates the surface advection of NCC water towards the Norwegian coast and fjords in general (Aure et al. 2007). However, Espinasse et al. (2018) observed that the inflow frequency and residence time of the water qualities in Saltfjord and Mistfjord differ according to local winds that change on short temporal scales.

The 220 m sill depth of Saltfjord allows a deep inflow of NAC water (≥34.5 psu) into its 382 m deep basin several times per year (Skreslet et al. 2000). The 34 m sill depth of Mistfjord selects shelf water (<34.5 psu) to enter its 297 m deep basin from an intermediate layer of the same stratified shelf sea habitat (Skreslet et al. 2015). The sampling location in Saltfjord is subject to mixing by a tidal jet that, on average, advects about 3×10^8 m³ of surface water from the more inshore fjord on every falling tide (Eliassen et al. 2001). This generates extensive turbulent thermohaline diffusion, which is generally (Aure et al. 2007) understood to reduce the density of resident basin water and facilitate frequent deep inflows of new NAC water into the basin. In Mistfjord, major replacements of new coastal water to its basin occur only at decadal intervals, facilitated by slow turbulent diffusion mostly forced by internal tidal waves, which are normal in sill fjord basins (Fjeldstad 1964; Skreslet & Schei 1976; Skreslet & Loeng 1977; Skreslet et al. 2015).

In general, immigration of zooplankton from deep shelf habitats to sill fjords during winter is related to capacities for vertical migration and facilitated by upwelling caused by local katabatic winds (Skreslet & Loeng 1977) or by regional coastal upwelling that results from Ekman transport (Aure et al. 2007; Espinasse et al. 2018). Both processes lift dense shelf water residing outside the sill, which may lead to overflow into the fjord basin. Deep inflows of NAC water to Saltfjord favour the immigration of species that prefer ambient water with salinity >34.5 psu. The Mistfjord basin receives only coastal water, which reduces the import of zooplankton that predominate at >34.5 psu. Thus, specific life history adaptations,

shelf sea stratification, sill topography and seasonal climate variability are among the factors that explain observed differences in biodiversity between the two fjord communities of wintering zooplankton (Skreslet et al. 2015). This likely also applies to the meroplanktonic life stages of various species that establish fjord stocks of benthic predators of holoplankton. Differences in sill depth between fjords also structure the recruitment of fish to local fjord stocks in this region and lead to a greater abundance of planktivorous species in Saltfjord than in Mistfjord (Skreslet 1994). Accordingly, the food webs of fjord basin communities tend to be fjord-specific and complex, as well as variable in time and space.

Studies of predator–prey relations in zooplankton are frequently arranged in dishes and aquaria. Mesocosm enclosures submerged in the sea are scientific arrangements that are closer approximations to trophic activities in real patches of zooplankton (Sullivan et al. 1994). Here, we use empirical field data and statistical methods to investigate the interannual variability and seasonal change of interspecific trophic relations in zooplankton biota that overwinter in the mesopelagic basins of two Subarctic fjords. Since the annual import of species varies in response to combinations of local topography and the hemispheric climate, we hypothesize that interannual variability in the import of carnivorous plankton shifts the biodiversity and predator–prey relations in ways that are specific for each fjord. We test this hypothesis on materials obtained from a multiannual time series based on replicate sampling. This method allows for the interspecific testing of the fjord basin's stock abundance relationships as well as relationships on smaller spatial scales that might result from the trophic activity at the time of the sampling.

Ecological rationale

In relative terms, zooplankton are normally sparse in parts of the water space, occurring mostly in denser aggregations characterized by varying vertical and horizontal dimensions. Physical factors, such as discontinuity layers and turbulence, influence zooplankton distribution but are frequently insufficient to explain spatial patterns. There is a biological rationale for zooplankton aggregation, which reduces the risk of predation, both collectively and individually. However, predators that locate aggregations of prey may rearrange the spatial distribution of that prey. Swarms are formations of single species that result from intraspecific behaviour, while patches occur when several taxa aggregate (Folt & Burns 1999). Turbulence may disperse patches and reorganize motile species to form new patches. Small animals with low motility can

only form patches during physical tranquillity, while they disintegrate when turbulence increases (Ledbetter 1979; Skreslet 1989).

Zooplankton tend to perform DVM, which is typically a result of photo-tactic behaviour that causes them to migrate closer to the surface in decreasing daylight and to greater depths when daylight increases. The depth range and seasonality of DVM depend on the size and motility of the organisms and on their trophic position in food webs. Herbivorous zooplankton that grow throughout their early ontogenetic stages stay mainly in the euphotic zone during phytoplankton production seasons. However, the depth and depth range of epipelagic DVM tend to increase with ontogenetic development and size (Osgood & Frost 1994; Dale & Kaartvedt 2000).

Calanus spp. (Copepoda) in Norwegian fjords enter diapause after ecdysis into their last adolescent copepodid stage, CV (Tarrant et al. 2008). Then DVM ceases and the copepodids occupy mesopelagic habitats where they remain inactive for a period. Those that enter diapause after summer in Norwegian shelf waters occupy overwintering habitats in troughs and basins, where their biomass is fed into food webs that support a variety of carnivorous zooplankton. Some predators of *Calanus* spp., such as *Themisto abyssorum* and juvenile *Paraeuchaeta norvegica*, may feed and perform DVM throughout the year, while adult *P. norvegica*, *Aglantha digitale* and chaetognaths remain at depths occupied by diapausing *Calanus* spp. (Baliño & Aksnes 1993; Tønnesson et al. 2006; Johnson et al. 2008; Kraft et al. 2013).

The biodiversity of patch structures established at depth during daytime changes when some species perform positive phototaxis at dusk, while their negative phototaxis at dawn re-establishes communion with species that do not perform DVM, such as diapausing *Calanus* spp. (Onsrud & Kaartvedt 1998). Four copepods of this genus (*C. finmarchicus*, *C. glacialis*, *C. helgolandicus* and *C. hyperboreus*) are major secondary producers at low trophic levels in food webs of the Northeast Atlantic. *Calanus finmarchicus* predominates in the Norwegian Sea, while *C. helgolandicus* predominates in the North Sea. *Calanus glacialis* is circumpolar in Arctic shelf seas, while *C. hyperboreus* is an oceanic species with pan-Arctic distribution, reproducing mainly in the Greenland Sea (Hirche 2004); however, both species have been observed to co-occur with *C. finmarchicus* and *C. helgolandicus* in northern Norwegian fjords (Olsen 2002; Choquet et al. 2017).

Calanus spp. that occur in Norwegian fjords drift with the currents between the fjords and open continental shelf habitats (Bucklin et al. 2000). After summer, fractions of their populations accumulate and overwinter in deep basins of northern Norwegian fjords (Sømme 1934; Heath et al. 2000; Skreslet et al. 2000; Olsen 2002) in company with carnivorous zooplankton, transported by advection under atmospheric forcing (Skreslet et al. 2015). The species remain in the fjords from the peak of their immigration from September or October until February to March, when adult copepods ascend from mesopelagic overwintering to reproduce in epipelagic habitats while being advected offshore by surface currents (Sømme 1934; Skreslet et al. 2000; Espinasse et al. 2016).

Recent genomic research (Choquet et al. 2017; Choquet et al. 2020) has redirected taxonomic and ecological research on *Calanus* spp. It raises many new questions about the interspecific relations between *C. finmarchicus* and *C. glacialis*, not least in Saltfjord and Mistfjord, where both are abundant. *Calanus glacialis* dominates over *C. finmarchicus* in Mistfjord and reproduces there, which has not been investigated in Saltfjord.

Methods

Logistical approach and geophysical background

Our field material was sampled at one station in each fjord on a regular basis in February and October from 1983 to 2005. Sampling dates varied from early to late in these months and were occasionally performed as early as two days before the beginning and as late as 22 days after the end of the intended month (Supplementary Table S1). All monthly sampling occurred at noon and on dates that differed between the fjords.

Initially, we made temperature, salinity and oxygen observations at standard depths established by the International Council for the Exploration of the Sea using Nansen bottles with calibrated reversing thermometers, laboratory salinometers and Norwegian Standard Winkler titration, respectively. In 1992, these methods were replaced by conductivity–temperature–depth instruments (SBE25 from SeaBird Electronics and various models from Sensordata, Norway) calibrated against water samples and laboratory procedures involving International Standard Seawater.

The surface salinity of Saltfjord and Mistfjord in October and February varied between 30 and 34 psu, and the epipelagic water column was stratified and subject to seasonal and interannual variability (Skreslet et al. 2015). The mesopelagic basin water was rather well-mixed in both fjords; however, their basins were, in terms of average temperature, salinity and oxygen concentration, distinctly different habitats for wintering zooplankton (Supplementary Table S2). The Saltfjord basin contained NAC water (salinity ≥34.5 psu) during every sampling, and both temperature and oxygen concentrations were

higher and less variable than in Mistfjord (Fig. 2). Mistfjord was colder and contained coastal water (salinity <34.5 psu) during every sampling; however, both salinity and temperature increased after 1993. Marked increases of salinity resulted from deep inflows of shelf water from 1992 to 1994 and from February to October in 2005. The basins were never anoxic; the lowest oxygen concentration was 1.77 ml L^{-1} at a depth of 290 m in Mistfjord during February 2000.

Zooplankton sampling

Plankton sampling made at each station and on each date comprised five replicate vertical tows with a Juday zooplankton net (0.1 m^2 opening and 180 μm mesh size) from about 10 m above the bottom to the surface at the deepest part of each fjord (Fig. 1). Every vertical net cast took at least 20 minutes while the ship drifted according to wind and tides, which caused the sampling of each replicate to occur at a random distance from the previous one. Considering that tidal currents in intermediate and deep layers may move in directions other than the surface advection, we are confident that each replicate represented a random sample from gradients between maxima and minima in zooplankton density projected on a 0.1 m^2 sea surface. The procedure enabled us to observe both intraspecific and interspecific differences in zooplankton abundance between replicates sampled

around noon at the same date and station. Accordingly, the material reflected the habitats' patchiness in terms of the horizontal distribution of zooplankton during the day of the sampling.

We deliberately selected carnivorous zooplankton species that normally occur in Juday net plankton samples from one or both fjords. These are *A. digitale* and *Dimophyes arctica* (Cnidaria), *P. norvegica* (Copepoda), *T. abyssorum* (Amphipoda), *Tomopteris helgolandica* (Polychaeta), and *Parasagitta elegans* and *Eukrohnia hamata* (Chaetognatha). *Parasagitta elegans* were 15–25 mm long, while the lengths of *E. hamata* were <5–30 mm. After we counted the non-crustacean carnivores in Mistfjord from 1993 onwards (Table 1, Supplementary Table S3), we recorded the abundance of small (<15 mm) *E. hamata* separately from the larger specimens by subsampling the smaller specimens and counting the larger specimens directly.

We are aware that the species included in this study have different swimming habits and escape reactions, and that our abundance estimates from a small net only represent approximations of the densities of the species in situ. However, we considered bias by escape to be random for each species, and we appreciated the advantage offered by using a small sampling net. It reduced laboratory subsampling that would have introduced methodological stochasticity and a lack of precision in the abundance estimates. Species that occurred in low numbers were quantified by direct counts from each
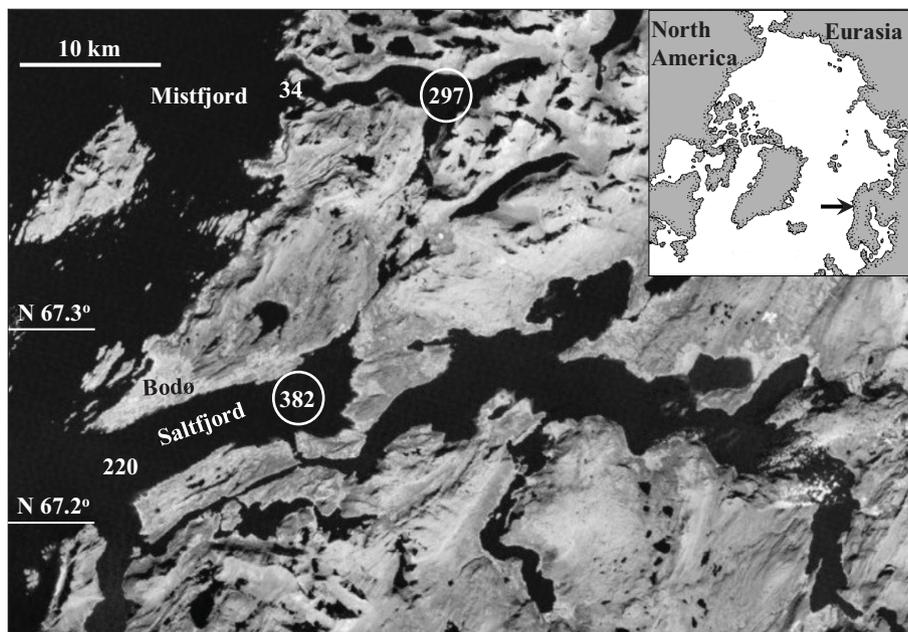
Fig. 1 Investigation area north of the Arctic Circle in northern Norway. The sampling stations in Saltfjord and Mistfjord are at the centre of the encircled maximum basin depths (m). The numbers at the entrance of both fjords indicate the depth and position of the sill. Geographical position is indicated by an arrow in the polar projection inset in the larger image.
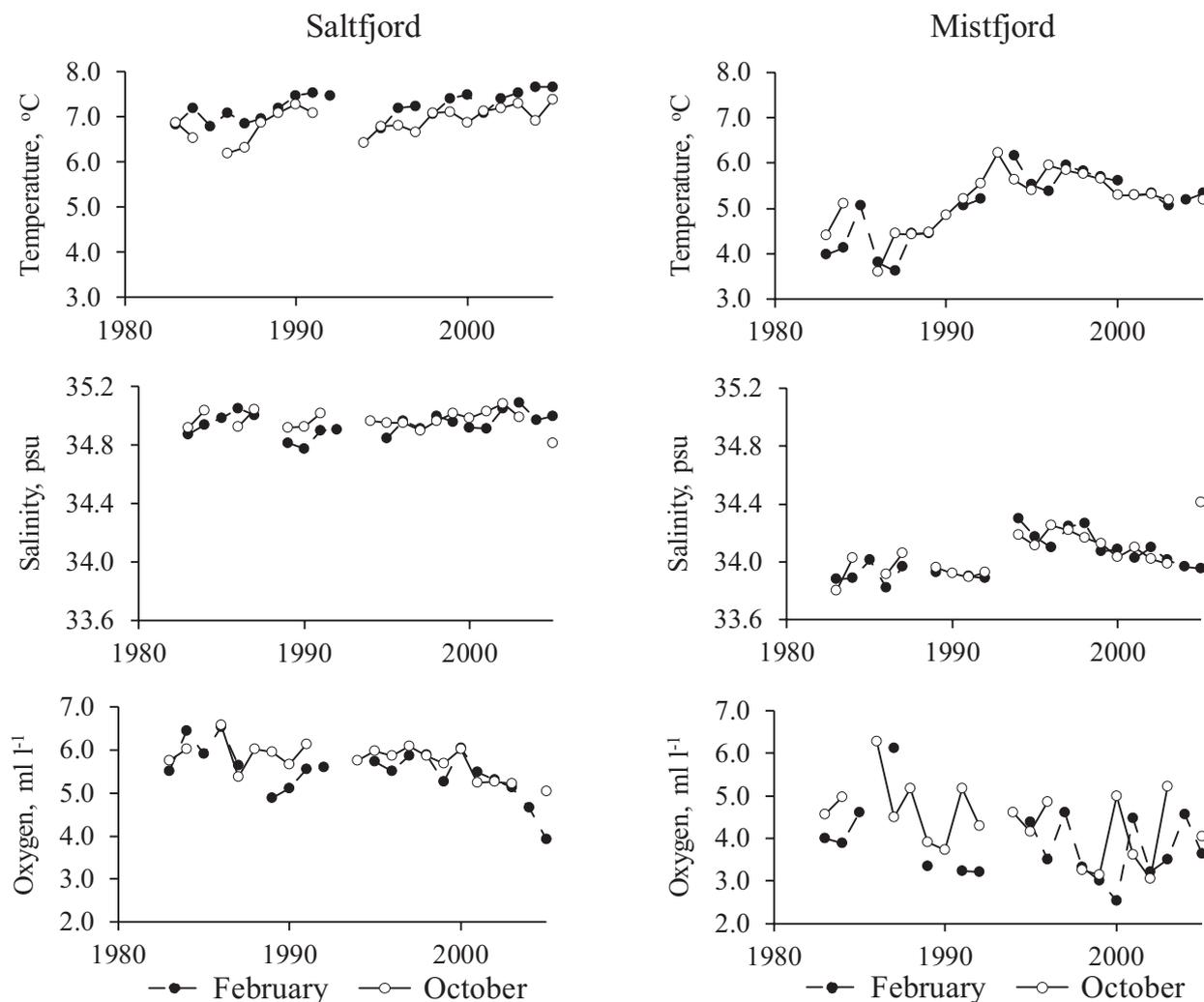
Fig. 2 Average temperature, salinity and oxygen concentration at the 200–290 m depth range in Mistfjord and the 250–370 m depth range in Saltfjord, 1983–2005.

replicate. We subsampled particularly abundant species using a Wiborg-Lea plankton splitter or a Folsom plankton divider.

We routinely subsampled *Calanus* spp. that were originally identified as *C. finmarchicus* but proved to be a species complex. A particular investigation with frequent sampling in Saltfjord during 1997 and 1998 (Skreslet et al. 2000; Olsen 2002) revealed that fractions of *C. glacialis* and *C. helgolandicus* corrupted counts of *C. finmarchicus*. Recent genomic investigations by Choquet et al. (2017) established that influence is even more significant than previously assumed. This is why we present three *Calanus* spp. here as a species complex of *C. finmarchicus* + *C. glacialis* + *C. helgolandicus*, not including *C. hyperboreus*. On average, in both fjords and months, 70–80% of copepodids in the *Calanus* spp. complex were in stage CV, <20% were in stage CIV and the remaining were mostly adult CVI,

amounting to <10% in February. The prosome length of the CV in both fjords was 2.0–3.0 mm, with very few outside of this range. *Calanus hyperboreus* was clearly distinguished from other *Calanus* spp. by its larger size and was never subsampled (Hirche et al. 1994). To avoid confusion here, *Calanus* spp. refer to all four species, while we refer to the complex of three species as the *Calanus* spp. complex.

Distinction between replicate abundance and stock abundance

The "replicate abundance" of a species refers to the counts of specimens in each replicate, while the average abundance of species calculated from ≤5 replicates at the same location represents the fjord's "stock abundance" at each date. We observed the influence of the number

Table 1 Average stock abundance per m² of sea surface area (ind m⁻²) of zooplankton species, calculated from all replicates sampled at noon on all dates and ranked according to October from 1983 to 2005 and 1993 to 2005 (asterisks).

	October	Stock status in February (%)		
	ind m⁻²	Average[a]	Maximum[b]	Minimum[b]
Saltfjord				
Calanus spp. complex[c]	47503.3	22.68	71.66	5.86
Calanus hyperboreus	1416.5	62.82	224.57	21.72
Eukrohnia hamata	813.1	218.13	678.76	40.87
Dimophyes arctica	381.5	55.46	428.57	6.05
Parasagitta elegans	369.2	75.70	327.66	6.34
Paraeuchaeta norvegica	120.7	65.46	607.14	25.35
Themisto abyssorum	86.1	93.30	483.33	22.46
Tomopteris helgolandica	37.6	73.55	1640.00	10.00
Aglantha digitale	28.3	64.61	1200.00	13.51
Mistfjord				
Calanus spp. complex[c]	32851.4	46.20	100.11	22.16
C. hyperboreus	3285.1	61.24	107.89	30.90
*P. elegans**	196.0	56.00	102.99	11.58
P. norvegica	75.8	186.45	585.71	62.22
*E. hamata**	55.2	118.39	322.22	22.73
T. abyssorum	40.3	90.80	400.00	14.29
*D. arctica**	6.2	I.d.[d]	I.d.[d]	I.d.[d]
*A. digitale**	5.5	I.d.[d]	I.d.[d]	I.d.[d]
*T. helgolandica**	4.8	I.d.[d]	I.d.[d]	I.d.[d]

[a]Average stock status in February is given as the percentage of average stock abundance in October. [b]Maximum and minimum stock abundances in February calculated from ≤5 replicates represent the time series extremes in the percentage of stock abundance during the previous October. [c]*C. finmarchicus*, *C. glacialis* and *C. helgolandicus*. [d]Inadequate data.

of replicates on our estimation of stock abundance by varying the number of replicates from one to four, comparing the estimates with the mean of five replicates. We selected three calanoid copepod species that differed by approximately one and two orders of magnitude (*Calanus* spp. complex ca. 25 000 ind m⁻²; *C. hyperboreus* ca. 2000 ind m⁻²; *P. norvegica* ca. 100 ind m⁻²). All stations containing five replicates were included in the analysis regardless of year, season and fjord, amounting to 82 stations and 410 replicate samples. We calculated a DI using replicates from every station in the following formula:

$$\mathrm{DI}_n = \frac{\sqrt{(x_n - X)^2}}{X},$$

where n is the number of replicates, x_n is the stock assessment computed from one, two, three and four randomly selected replicates and X is the true stock value estimated from the five replicates (Supplementary Table S3).

Using only one replicate to estimate seasonal stock abundance was clearly different from using five replicates, and the median DI decreased gradually with the number of replicates (Fig. 3). Stock estimate indices of the *Calanus* spp. complex and *C. hyperboreus* were similar even though their abundance, on average, differed by about one order of magnitude. *Paraeuchaeta norvegica* was less abundant, and its deviation indices differed more from the true stock abundance calculated by the five replicates.

Statistical analyses

Except for two occasional cases in Saltfjord (Supplementary Table S1), our stock abundance estimates were based on full sets of five replicates. To identify cases of inter-annual variability regarding interspecific zooplankton stock relations, we paired the stock abundance estimates in 2 × 2 contingency tables based on the class intervals of abundance < median and ≥ median. Direct and inverse proportionality between the abundance of two species appeared from the tables, and we tested the hypothesis of independence through Fisher's exact probability test using a calculator offered by http://vassarstats.net/tab2x2.html.
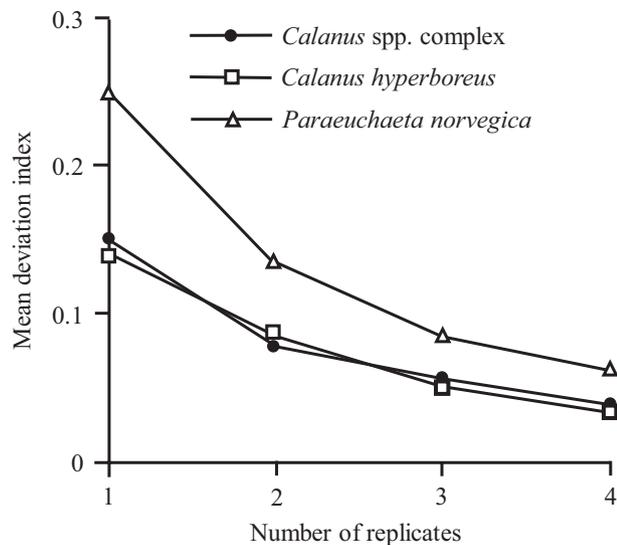
Fig. 3 Median deviations from the calculated stock abundance of three copepod species (mean of five replicates) calculated with one to four random replicates from each sampling date at a total of 82 stations visited in Saltfjord and Mistfjord during February and October from 1983 to 2005. The *Calanus* spp. complex refers to the three species *C. finmarchicus*, *C. glacialis* and *C. helgolandicus*.

We also used 2 × 2 contingency tables and Fisher's exact test to test the hypothesis of independence between the densities of the species in situ. We then cumulated all replicate abundance estimates given as the original ind per 0.1 m² sea surface area for each locality and month. Fisher's exact test is feasible for small data sets and tolerates deviations from normality. It is less sensitive than other methods that we could not use because our interspecific comparisons of abundance were not linear and rarely normally distributed, even after log transformation. We therefore tested the correlations between abundance of species in replicate samples using the non-parametric Kendall's tau test (Kendall 1970; Banjamini & Hochberg 1995). Positive and negative statistical correlations as given by Kendall's test were not equal to the significant direct and inverse proportionality observed from the 2 × 2 contingency tables and Fisher's exact test. To avoid confusion, we refer to the interrelations of abundances as negatively or positively related.

Fisher's exact test tolerates replicate outliers because they do not carry more weight than less extreme values within the same class interval. Our Kendall's tau correlations are based on every single replicate abundance and are sensitive to outliers. Acknowledging and accepting the differences in sensitivity, we maintain trust in the significant results from both tests with the cumulated replicate data.

Results

Range and variability in zooplankton stock abundance

Stock abundance of the *Calanus* spp. complex in both fjords in October from 1983 to 2005 was, on average, higher than for other species (Table 1). The decrease in average stock abundance from October to February was the greatest in Saltfjord; here, the seasonal decrease varied from 28 to 94%. The decrease in Mistfjord varied less, from negligible to about 77%, which, on average, made *Calanus* spp. complex more abundant than in Saltfjord in February.

Calanus hyperboreus was, on average, more abundant in Mistfjord than in Saltfjord during October. The average stock status percentage during February was about the same; however, there was less seasonal variability in Mistfjord. There, it varied interannually from an increase of about 7% to a decrease of about 69%, while the stock abundance in Saltfjord varied from a 124% increase to a 78% decrease.

The prosome length of the stage CV copepodids of the *Calanus* spp. complex was roughly half the size of the *C. hyperboreus* CV, and the biomass was nearly an order of magnitude lower (Hirche et al. 1994). Thus, the average biomass of all *Calanus* spp. in October from 1983 to 2005 did not deviate much between the fjords because the greater abundance of *C. hyperboreus* in Mistfjord than in Saltfjord compensated for the greater abundance of the *Calanus* spp. complex in Saltfjord.

Calanus hyperboreus reproduces in both fjord systems and proximate shelf waters mainly in January and February, producing a regional spring generation (Sømme 1934; Olsen 2002; Choquet et al. 2020). In Saltfjord in 1997, *C. hyperboreus* remained a diapausing CV until July (Olsen 2002) when the spring generation was probably lost to the shelf together with other *Calanus* spp. CV during maximum vernal freshwater discharge, which culminated in July (Skreslet et al. 2000). In Mistfjord, the landscape's small catchment area causes only weak estuarine circulation and low vertical turbulent diffusion during the summer, which probably reduces the frequency of basin water replacement (cf. Skreslet & Loeng 1977). The shallow sill depth retained the fjord's aging basin water for years between the two major inflows of new basin water, one between 1992 and 1994 and the other in 2005 (Skreslet et al. 2015). Accordingly, in normal years, some locally produced *C. hyperboreus* CV possibly diapaused in Mistfjord until October, when the immigration of newcomers joined the resident standing stock of CV. This may explain why *C. hyperboreus* in October was, on average, more abundant in Mistfjord than in Saltfjord.

Eukrohnia hamata in Saltfjord was, on average, the most abundant carnivore during October from 1983 to 2005 and increased before February by 118% (Table 1). By counting smaller (<15 mm) and larger specimens separately from 1993 to 2005, we observed that a seasonal increase of small animals varied from a minimum of 382 ind m^{-2} in 1995 to a maximum of 5424 ind m^{-2} in 1999, usually compensating for a seasonal decrease of larger specimens. On average, 346 ind m^{-2} of large specimens in October declined by 45% in February, while 413 ind m^{-2} small specimens increased by 294%. In Mistfjord, 40 ind m^{-2} of large specimens in October had decreased by 17% in February, whereas 16 ind m^{-2} of small specimens increased by 24%. Accordingly, the higher abundance of *E. hamata* in Saltfjord was mainly due to increased stocks of juveniles (Fig. 4).

In Saltfjord, the average abundance of *P. norvegica* decreased from October to February, which is different from the seasonal increase in Mistfjord (Table 1). We have no demographic data that explain this difference.

Tomopteris helgolandica was, on average, the least abundant species in Mistfjord during October and was, together with *D. arctica* and *A. digitale*, absent in many replicates. This is why we did not calculate their stock status in February (Table 1).

All seven carnivores were subject to considerable seasonal variability in Saltfjord, where *T. helgolandica* during February deviated more from the long-term average in October than other species. Its stock abundance in October usually varied between 0 and 64 ind m^{-2}, except in 2001 when it was 170 ind m^{-2} and decreased to 62 ind m^{-2} in February 2002. In contrast, it increased from 15 ind m^{-2} in October 1987 to 164 ind m^{-2} in February 1988.

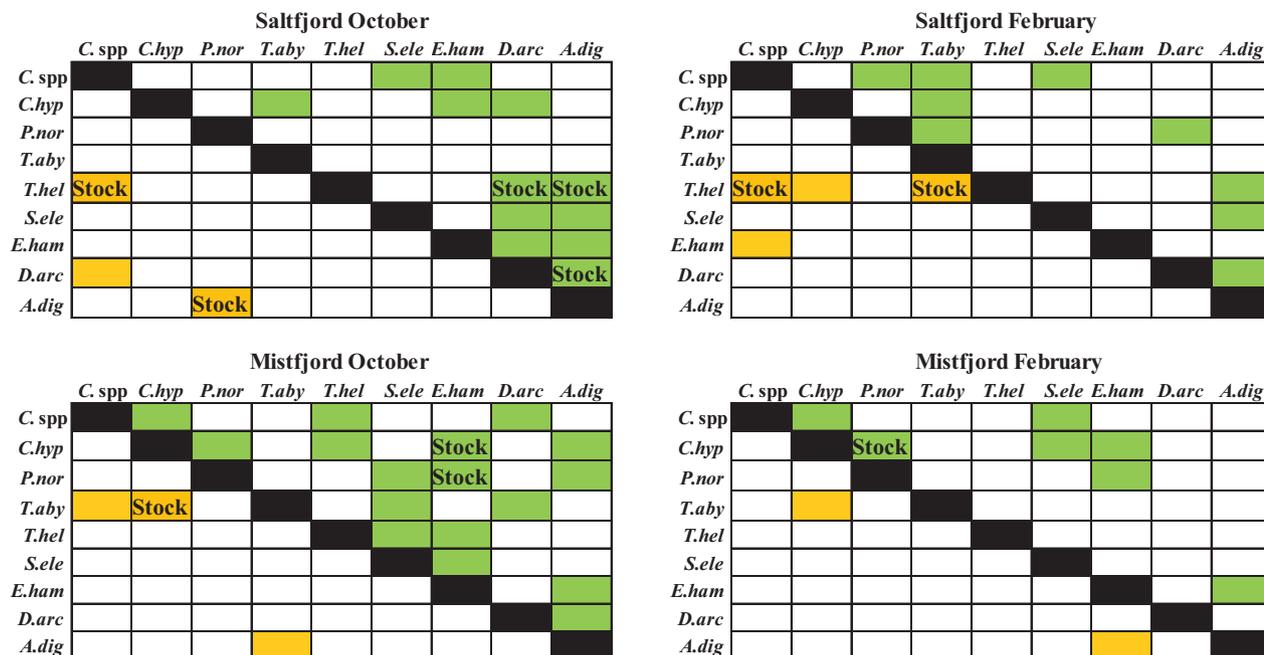### Matrices of interspecific relations

The number of significant relations between the abundance of two species varied between locality and month (Fig. 5). Every one of the 11 cases of significant positive or negative stock abundance relations matched 11 out of 57 cases testing significant with replicate abundance. The number of significant cases with replicates was higher in Mistfjord than in Saltfjord during October and lower in Mistfjord during February.

Interspecific standing stock abundance relations

The stock abundance of *T. helgolandica* in Saltfjord was negatively related to the *Calanus* spp. complex in both October and February and to *T. abyssorum* in February (Table 2, Fig. 5). In Mistfjord, *T. abyssorum* was negatively related to
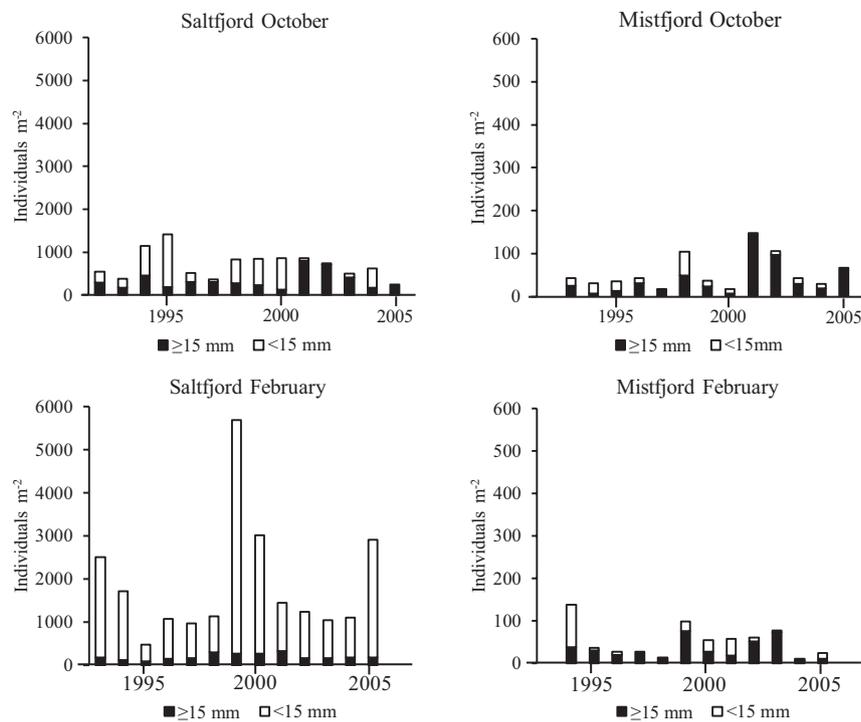
Fig. 4 Histograms for the abundance of *Eukrohnia hamata* with body lengths <15 mm and ≥15 mm. Note the differences in scale in terms of abundance between the fjords.

Fig. 5 Matrices for the interspecific relations in the abundance of zooplankton in Saltfjord and Mistfjord according to the statistics in Tables 2 and 3. White: not significant; green: positive in situ relation; yellow: negative in situ relation; stock: significant stock relationship included. Abbreviated taxa: *C.* spp: the *Calanus* spp. complex (*C. finmarchicus*, *C. glacialis* and *C. helgolandicus*); *C. hyp*: *Calanus hyperboreus*; *P. nor*: *Paraeuchaeta norvegica*; *T. aby*: *Themisto abyssorum*; *T. hel*: *Tomopteris helgolandica*; *P. ele*: *Parasagitta elegans*; *E. ham*: *Eukrohnia hamata*; *D. arc*: *Dimophyes arctica*; *A. dig*: *Aglantha digitale*.

C. hyperboreus during October (Table 3, Fig. 5). Stock abundance relations between *T. helgolandica* and the *Calanus* spp. complex in Saltfjord, and between *T. abyssorum* and *C. hyperboreus* in Mistfjord were not linear and were rather hyperbolic (Table 4, Fig. 6). The only other negative stock abundance relation was between *P. norvegica* and *A. digitale* in Saltfjord during October (Tables 2, 4, Fig. 5).

Positive stock abundance relations in Saltfjord occurred only in October; *T. helgolandica* was related to both *D. arctica* and *A. digitale*, and the two coelenterates were related to each other (Table 2, Fig. 5). In Mistfjord, both *C. hyperboreus* and *P. norvegica* related positively to *E. hamata* during October, and the two copepods related positively during February (Table 3, Fig. 5).

Interspecific in situ relations observed in cumulated replicates

In Saltfjord during February, both Fisher's exact test and Kendall's tau test (Table 2, Fig. 5) indicated that the replicate abundance of the *Calanus* spp. complex was related negatively with *T. helgolandica* and *E. hamata*, while *T. abyssorum* was related negatively with *T. helgolandica*. In other negative cases, either Fisher's or Kendall's test established a significant relationship (*C. hyperboreus* with *T. helgolandica* in February, the *Calanus* spp. complex with

T. helgolandica and *D. arctica* in October and *P. norvegica* with *A. digitale* in October).

In Mistfjord (Table 3, Fig. 5), both tests established that *T. abyssorum* was negatively related to the *Calanus* spp. complex in October and to *C. hyperboreus* in February. Kendall's test made *T. abyssorum* relate negatively to *C. hyperboreus* and *A. digitale* in October. *E. hamata* tested negatively with *A. digitale* in February, according to Fisher's exact test.

Replicate abundances of the *Calanus* spp. complex and *C. hyperboreus* were not related in Saltfjord during October and February but were related positively in Mistfjord during both months (Fig. 5). They related neither negatively nor positively to *A. digitale* in any fjord and month, while their relation to other carnivores did not repeat itself according to fjord or month. In October, *T. helgolandica*, *P. elegans* and *E. hamata* were positively related with *D. arctica* and *A. digitale* in Saltfjord, and in Mistfjord, several carnivores were positively related to more than one and up to three other carnivores. In February, few carnivores related positively to more than one other carnivore.

Interspecific shifts in trophic relations between major species

The stock of *T. helgolandica* in Saltfjord was negatively related with the *Calanus* spp. complex both in October

Table 2 Significant interspecific relations in the abundance of zooplankton sampled from Saltfjord between 1983 and 2005 and calculated using Fisher's exact probability test and Kendall's tau correlation test. Stock results refer to tests with an average abundance calculated from five replicates sampled at noon on the same date. Replicate results refer to tests with every original replicate count (individuals per 0.1 m² of sea surface). Significant results calculated using Fisher's exact test refer to two-tailed probability. The significant results in bold italics indicate negative relationships, while positive relationships are indicated otherwise.

| | | Stock abundance | | Replicate abundance | | | | |
| | | Fisher | | Fisher | | Kendall | | |
		p^{a}	N^{b}	p^{a}	N^{b}	T^{c}	p^{a}	df^{d}
Saltfjord October								
Crustacea								
Calanus spp. complex[e]	*T. helgolandica*	***0.009***	22			***−0.23***	***0.001***	105
	P. elegans					0.16	0.018	105
	E. hamata			0.002	107	0.16	0.016	105
	D. arctica			***0.021***	107			
C. hyperboreus	*T. abyssorum*					0.16	0.015	105
	E. hamata			0.034	107	0.18	0.006	105
	D. arctica					0.18	0.006	105
P. norvegica	*A. digitale*	***0.043***	22	***0.021***	107			
Polychaeta								
T. helgolandica	*D. arctica*	0.009	22	0.004	107	0.32	<0.001	105
	A. digitale	0.030	22			0.19	0.009	105
Chaetognatha								
P. elegans	*D. arctica*					0.24	<0.001	105
	A. digitale			0.034	107	0.38	<0.001	105
E. hamata	*D. arctica*					0.20	0.002	105
	A. digitale			0.007	107	0.18	0.012	105
Coelenterata								
D. arctica	*A. digitale*	0.002	22	<0.001	107	0.33	<0.001	105
Saltfjord February								
Crustacea								
Calanus spp. complex[e]	*P. norvegica*			0.012	108	0.32	<0.001	106
	T. abyssorum			<0.001	108	0.45	<0.001	106
	T. helgolandica	***0.030***	22	***0.034***	108	***−0.30***	***<0.001***	106
	P. elegans					0.17	0.008	106
	E. hamata			***0.038***	108	***−0.21***	***0.002***	106
C. hyperboreus	*T. abyssorum*					0.20	0.003	106
	T. helgolandica					***−0.20***	***0.005***	106
P. norvegica	*T. abyssorum*			<0.001	108	0.42	<0.001	106
	D. arctica			0.002	108			
T. abyssorum	*T. helgolandica*	***0.043***	22	***<0.001***	108	***−0.30***	***<0.001***	106
Polychaeta								
T. helgolandica	*A. digitale*			0.027	108	0.19	0.007	106
Chaetognatha								
Paraagitta elegans	*A. digitale*			0.017	108			
Coelenterata								
D. arctica	*A. digitale*			0.009	108	0.26	<0.001	106

[a]Probability (significance level). [b]Number of observations. [c]Kendall's tau correlation coefficient. [d]Degrees of freedom (*N*-2). [e]*C. finmarchicus*, *C. glacialis* and *C. helgolandicus*.

and February and with *T. abyssorum* in October. A negative in situ relationship occurred between the polychaete and *C. hyperboreus* only during February (Fig. 7). In Mistfjord, we observed no relation between stock abundances of the polychaete and the *Calanus* spp. complex in any month, whereas the stocks of *T. abyssorum* and *C. hyperboreus* were negatively related in October and the relation was reduced to an in situ relationship in February.

Table 3 Significant interspecific relations in the abundance of zooplankton sampled from Mistfjord between 1983 and 2005 and 1993 and 2005 (see Table 1) and calculated using Fisher's exact probability test and Kendall's tau correlation test. Stock results refer to tests with an average abundance calculated from five replicates sampled at noon on the same date. Replicate results refer to tests with every original replicate count (individuals per 0.1 m² of sea surface). Significant results calculated using Fisher's exact test refer to two-tailed probability. The significant results in bold-italics indicate negative relationships, while positive relationships are indicated otherwise.

| | | Stock abundance | | Replicate abundance | | | | |
| | | Fisher | | Fisher | | Kendall | | |
		p^a	N^b	p^a	N^b	T^c	p^a	df^d
Mistfjord October								
Crustacea								
Calanus spp. complex[e]	*C. hyperboreus*			<0.001	105	0.32	<0.001	103
	T. abyssorum			***<0.001***	105	***−0.24***	***0.001***	103
	T. helgolandica			0.029	65			
	D. arctica			0.025	65	0.32	0.001	63
C. hyperboreus	*P. norvegica*					0.21	0.002	103
	T. abyssorum	***0.030***	21			***−0.25***	***<0.001***	103
	T. helgolandica					0.29	0.001	63
	E. hamata	0.030	13	0.025	65			
	A. digitale					0.21	0.013	63
P. norvegica	*P. elegans*			0.046	65			
	E. hamata	0.030	13	0.005	65			
	A. digitale					0.26	0.004	63
T. abyssorum	*P. elegans*					0.26	0.017	63
	A. digitale					***−0.24***	***0.012***	63
	D. arctica			0.041	65			
Polychaeta								
T. helgolandica	*P. elegans*					0.29	0.006	63
	E. hamata					0.25	0.015	63
Chaetognatha								
P. elegans	*E. hamata*					0.38	0.001	63
E. hamata	*A. digitale*			0.029	65			
Coelenterata								
D. arctica	*A. digitale*			0.009	65			
Mistfjord February								
Crustacea								
Calanus spp. complex[e]	*C. hyperboreus*					0.21	0.002	98
	P. elegans			0.038	60	0.26	0.005	58
C. hyperboreus	*P. norvegica*	0.023	20	<0.001	60	0.39	<0.001	98
	T. abyssorum			***0.015***	100	***−0.32***	***<0.001***	98
	P. elegans			0.007	60	0.25	0.005	58
	E. hamata					0.25	0.006	58
P. norvegica	*E. hamata*					0.27	0.004	58
Chaetognatha								
E. hamata	*A. digitale*			***0.048***	60			

[a]Probability (significance level). [b]Number of observations. [c]Kendall's tau correlation coefficient. [d]Degrees of freedom (*N*-2). [e]*C. finmarchicus*, *C. glacialis* and *C. helgolandicus*.

Discussion

### *Evidence of stock decline of Calanus spp. as a result of predation*

Zooplankton imported by advection to Saltfjord and Mistfjord merge with two biota that differ in terms of local predators. Saltfjord hosts a richer fauna of planktivorous fish than Mistfjord (Table 6), and this difference probably changes the composition of zooplankton imported from the same shelf habitat of the Norwegian Sea. For instance, we could not exclude the possibility that the higher

Table 4 Logarithmic least squares regression models ($y = e^a x^b$) for the stock abundance of assumed prey as negatively related to the stock abundance of predators in two Subarctic fjords in northern Norway. The significance of the relations is calculated by Fisher's exact test and presented in Tables 2 and 3.

Locality	Month	Predator	Prey	a[a]	b[b]
Saltfjord	October	*T. helgolandica*	*Calanus* spp. complex[c,d]	11.518	−0.778
		A. digitale	*P. norvegica*	5.169	−0.180
	February	*T. helgolandica*	*Calanus* spp. complex[c,d]	10.048	−0.322
			T. abyssorum[c]	5.166	−0.588
Mistfjord	October	*T. abyssorum*	*C. hyperboreus*[c]	10.803	−0.986

[a]Intercept. [b]Slope. [c]Also significant in situ (see Table 5). [d]*C. finmarchicus*, *C. glacialis* and *C. helgolandicus*.
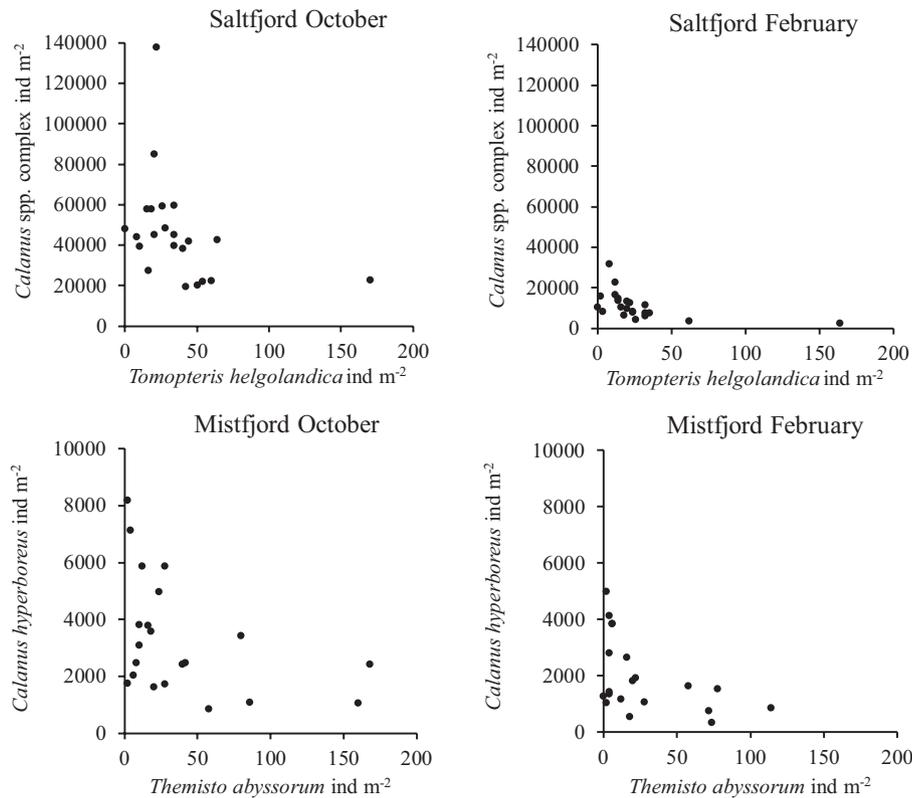
**Fig. 6** Stock abundance per m² of sea surface area calculated from ≤5 replicate samples of *Calanus* spp. complex (*C. finmarchicus, C. glacialis* and *C. helgolandicus*) in Saltfjord and *C. hyperboreus* in Mistfjord as functions of *T. helgolandica* and *T. abyssorum* abundance, respectively, from 1983 to 2005. Relations proved to be significant at *P* < 0.001 using Kendall's tau test on ≥100 estimates of replicate abundance (see Tables 2, 3).

average stock abundance of *C. hyperboreus* in Mistfjord during both October and February (Table 1) resulted from lower mortality by predation from fish than in Saltfjord. Planktivory by fish may also explain the stronger seasonal stock decline of the *Calanus* spp. complex in Saltfjord than in Mistfjord. However, *T. helgolandica* seemed to compete efficiently with fish when the polychaete was abundant in Saltfjord, which established negative standing stock relations with the *Calanus* spp. complex both at the beginning and at the end of the wintering season (Figs. 5–7).

We note that the stock abundance of *T. helgolandica* was negatively related to *T. abyssorum* in Saltfjord during February but not during October (Fig. 5). We speculate that the greater abundance of *Calanus* spp. in October led to *T. helgolandica* neglecting *T. abyssorum*. The polychaete may have included predation on the amphipod in years with a shortage of preferred prey at the end of winter, especially if the *Calanus* spp. complex scarcity coincided with the immigration of *T. helgolandica* after October. In Mistfjord, *T. helgolandica* was rare and left *T. abyssorum*

free to prey on copepods, probably preferring *C. hyperboreus* over the *Calanus* spp. complex (Fig. 7) due to its
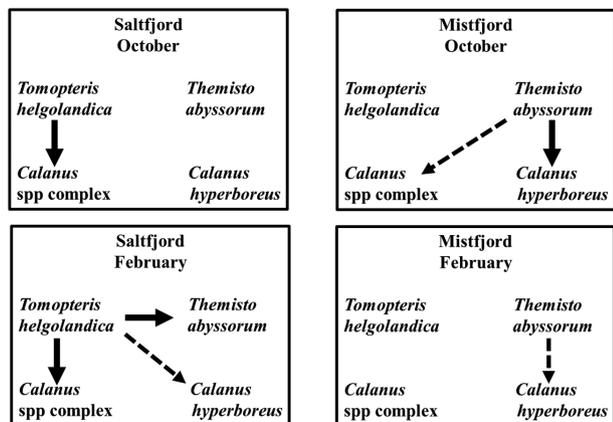
Fig. 7 Differences in significant negative predator–prey relations observed in two Subarctic fjords from 1983 to 2005. All arrows indicate a negative Kendall's tau correlation resulting from in situ relations observed by cumulated replicate abundance at the time of the sampling. Fisher's exact probability test distinguishes solid arrows from stippled arrows. Solid arrows: predation resulting in reduction of the prey's stock abundance. Stippled arrows: no evidence of stock abundance reduction of the prey.

larger body size and nutritional value in terms of energy invested in the chase.

Themisto abyssorum has a one-year life cycle and practices brood protection (Dalpadado 2002), which means that its local wintering stocks may produce resident generations. *Calanus hyperboreus* remaining in the Mistfjord basin over summer, as argued earlier, may then have become subject to continuous predation by local *T. abyssorum*. However, increased immigration of the amphipod during some winters (Table 1) probably increased the mortality of *C. hyperboreus* in Mistfjord.

In general, the carnivores sampled by us probably fell prey to planktivores that normally forage on higher trophic levels in fjords (Bagøien et al. 2001; Eiane et al. 2002), which explains the seasonal declines in their stock abundance (Table 1). *T. helgolandica* is a voracious and omnivorous carnivore (Fauchald & Jumars 1979) but was itself probably subject to predation in Saltfjord, which, for example, reduced the maximum stock abundance of 170 ind m^{-2} in October 2001 to 36.4% in February 2002. However, cases of increased stock abundance in February indicated immigration after October, which was noticeable when the stock increased from 15 ind m^{-2} in October 1987 to 164 ind m^{-2} in February 1988. The negative effect of this predator on the stock abundance of the *Calanus* spp. complex and *T. abyssorum* at the end of winter was therefore

Table 5 Kendall's tau correlation coefficients with 95% bootstrapped confidence intervals indicating negative in situ relations between the cumulated replicate abundances of predators and assumed prey in two Subarctic fjords in northern Norway (see Tables 2, 3 for significance).

Locality	Month	Predator	Prey	T[a]	95% CI[b]
Saltfjord	October	*T. helgolandica*	*Calanus* spp. complex[c,d]	−0.23	−0.36, −0.10
	February		*Calanus* spp. complex[c,d]	−0.30	−0.43, −0.16
			C. hyperboreus	−0.20	−0.34, −0.05
			T. abyssorum[c]	−0.30	−0.42, −0.18
		E. hamata	*Calanus* spp. complex[d]	−0.21	−0.34, −0.08
Mistfjord	October	*T. abyssorum*	*Calanus* spp. complex[d]	−0.24	−038, −0.10
			C. hyperboreus[c]	−0.25	−0.39, −0.10
			A. digitale	−0.24	−0.43, −0.02
	February		*C. hyperboreus*	−0.32	−0.43, −0.21

[a]Kendall's tau correlation test. [b]Confidence intervals. [c]Also significant in terms of stock level (see Table 4). [d]*C. finmarchicus*, *C. glacialis* and *C. helgolandicus*.

Table 6 Average abundance per trawling hour of planktivorous fish caught using a demersal prawn trawl at the stations for zooplankton sampling in Saltfjord between 1982 and 1993 and Mistfjord between 1981 and 1993. Data were taken from Skreslet (1994).

Species	Saltfjord (28 samples)		Mistfjord (22 samples)	
	Abundance	CV (%)[a]	Abundance	CV (%)[a]
Argentina silus	53.25	127	0.27	258
Benthosema glaciale	29.82	124	3.41	181
Trisopterus esmarkii	4.71	460	7.68	283
Micromesistius poutassou	83.57	70	0.14	343
Gadiculus argenteus thori	54.75	242	0.41	326

[a]Coefficient of variation, that is, % ratio of the standard deviation to the mean.

probably a function of both the time of *T. helgolandica*'s immigration to Saltfjord and its survival rate there (Fig. 7).

Aglantha digitale is a substantial cnidarian predator on copepods (Pagès et al. 1996), which was not evident in its stock relations with the *Calanus* spp. complex and *C. hyperboreus* (Fig. 5). However, *A. digitale*'s trophic relationship with copepods may explain the negative stock abundance relation between *P. norvegica* and *A. digitale* in Saltfjord during October. The coelenterate may preferably have preyed upon nauplii or small copepodids of *P. norvegica* in offshore habitats during summer, reducing the standing stock of its prey before advection into the fjord. This may explain why *P. norvegica* did not influence the stock abundances of *Calanus* spp. and *C. hyperboreus* even though its predation capacity is 10–100 times greater than that of chaetognaths during autumn and spring (Tønnesson et al. 2006).

Although *E. hamata* and *P. elegans* were quite abundant in both fjords, we observed no negative relationships indicating their capacity to reduce copepod stock abundance (Fig. 5). This may result from their low competitiveness compared with other predators.

Interpretation of positive stock relations

The positive and negative zooplankton stock relations observed in Saltfjord and Mistfjord during October (Fig. 5) likely depended on the prehistory of abiotic and biotic interactions that had occurred before the annual import in September and October (Haakstad 1977, 1979; Heath et al. 2000; Skreslet et al. 2000; Olsen 2002; Skreslet et al. 2015).

Positive stock relations within a cluster of *T. helgolandica*, *D. arctica* and *A. digitale* in Saltfjord during October suggest joint association with mesopelagic NAC water advected into the basin from the shelf. *Aglantha digitale* and *D. arctica* are cosmopolitan species with a wide distribution, while *T. helgolandica* is neritic in the North Atlantic and mainly distributed to the north of southern UK (Read & Fauchald 2018). We consider that dominant species in the *Calanus* spp. complex were part of the same cluster, and that the negative stock relation with *T. helgolandica* discussed earlier expresses a predator–prey relation established in their common Norwegian Sea habitat. Accordingly, and from recent genomic research, *C. finmarchicus* would be the dominant *Calanus* spp. in the cluster of these immigrants (Choquet et al. 2017).

In Mistfjord, positive stock relations that associate *C. hyperboreus* and *P. norvegica* with *E. hamata* during October, possibly resulted from joint occurrence in epipelagic coastal water advected from the shelf. However, we speculate that some *C. hyperboreus* were produced locally during the spring and remained in its basin over summer.

Thus, the stock's high average abundance in Mistfjord during October and its negative relation with *T. abyssorum* may, to some extent, have resulted from a local trophic relationship during previous months.

Trophic behaviour, replicate deviation and stock abundance precision

We observed that the average abundance of three calanoids, as calculated from a reduced number of replicates in both months and fjords from 1983 to 2005, deviated from the stock abundance estimated from a full set of five replicates (Fig. 3). Deviation indices were similar for the *Calanus* spp. complex and *C. hyperboreus*, although the former was an order of magnitude more abundant than the latter. Considering that our materials of *Calanus* spp. were mainly stage CV copepodids in diapause, we suppose that the similar response of the DI to the number of replicates in the *Calanus* spp. complex and *C. hyperboreus* did not result from active locomotion related to swarming. Rather, it may have resulted from statistical randomness in combination with dispersal or concentrations by turbulence and the effects of predation. We speculate that the higher deviation indices of *P. norvegica* resulted from predatory behaviour, causing the species to accumulate in aggregations of prey and contributing to the structure of multispecies patches as defined by Folt & Burns (1999).

The *P. norvegica* and other carnivores that were sampled by us may have shifted between stalking within density gradients of potential prey and their own evasion of higher-order predators foraging in patches of prey. The dynamic nature of zooplankton patchiness stresses the importance of sampling several replicates when estimating stock abundance from vertical tows with plankton nets. Two replicates might be a good trade-off between effort spent and precision in the stock assessment of non-motile species, while inclusion of motile species requires more replicates. Our sampling method for the calculation of stock abundance from a small sampling net is obviously not applicable for species that are very motile and dispersed or occur in very dense and discretely distributed swarms, as such species require other sampling strategies (Wiebe 1971).

In situ spatial variability of predator–prey interactions

Each replicate abundance estimate is an in situ function of local standing stock abundance and interspecific trophic and spatial relations at the time of the sampling. This is evident in cases where both stock abundance and replicate abundance relationships were significantly positive or negative (Fig. 5). However, many cases proved

significant only with replicate material, indicating that their interspecific relationship was not an effect of prolonged trophic activity inside the fjords or in source habitats outside. We rather think they originated from evolution in past and present ecosystems and were in our fjords expressed by in situ activities resulting from behaviour related to intrinsic roles as predator or prey. We support the views of Dunbar (1968) that the Arctic Mediterranean ecosystem is still young, resulting from continuous evolution during the Pleistocene period into our time. The evolution of the ecosystem has since shifted to the current Anthropocene age, in which global climate change restructures autecological as well as synecological relations and premises for interspecific co-evolution in Arctic marine regions. Though our material represents a two-decade time capsule with ecological conditions that probably differ from previous and future decades, our observations enhance our general understanding of predator–prey relations among wintering zooplankton.

Diapausing Calanus spp. are supposedly unable to swarm and perform DVM, accumulating at depth by gravitation. However, the replicate abundance of the *Calanus* spp. complex related positively to *C. hyperboreus* in Mistfjord in both October and February (Fig. 5). It would probably not occur by random horizontal distribution and may have resulted from in situ predation on *Calanus* spp. by predators aggregating in patches. The replicate abundance of both the *Calanus* spp. complex and *C. hyperboreus* related negatively with *T. abyssorum* abundance in October and predation by the amphipod seemed even able to suppress the stock abundance of *C. hyperboreus*. *Themisto abyssorum* may have been a dominant predator that caused non-random spatial distribution of the *Calanus* spp., and swarming behaviour by the predator may have generated in situ minima in the spatial distribution of the prey. Predation by *T. helgolandica* on the *Calanus* spp. complex, *C. hyperboreus* and *T. abyssorum* in Saltfjord could produce the same kind of patchiness. The polychaete's preference for the *Calanus* spp. complex and *T. abyssorum* in Saltfjord, as well as its very low stock abundance in Mistfjord, probably caused the predator–prey relations between the amphipod and the copepods to differ between the fjords (Fig. 7).

A swarm of predators that depletes its source of prey may benefit from DVM by ascending at dusk and descending at dawn, re-establishing new foraging opportunities that are relatively unaffected by the trophic activities of the previous day. Accordingly, the relative abundance of species in each replicate resulted from predator–prey activities during the morning before our in situ sampling at noon. In general, carnivores may stalk swarms of prey or patches of both prey and competitors through sensory detection. They may be guided by visual stimuli in prey density gradients (Skreslet 1989) or by pressure waves from locomotion if not by the attractive scent of damaged prey (Valdés et al. 2015). Such abilities may explain 39 cases of positive relations in our material of replicate abundance (Fig. 5), which possibly resulted from trophic activity during our in situ sampling, while carnivores were chasing either herbivores or subordinate carnivores in the temporarily established food chains. On the other hand, scent from predators' faeces or from injury or remains of conspecifics may lead to predator evasion (Dale et al. 1999; Mathuru et al. 2012), causing antagonistic evasion in patches where carnivores feed. This may explain two in situ negative relationships in Mistfjord, where *A. digitale* was related with *T. abyssorum* in October and *E. hamata* in February. However, we could not identify the prey in each case because we had no information on size distribution and food preference, which change with age.

In Saltfjord during February, both Fisher's exact and Kendall's tau tests support that in situ abundance of the *Calanus* spp. complex and *T. abyssorum* was reduced in patches with a relatively high presence of *T. helgolandica* (Fig. 5). In years with a high stock abundance of *T. helgolandica*, its predation was strong enough to significantly reduce the abundance of both crustacean stocks. This contrasts with the trophic effect of *E. hamata*, the most abundant predator in Saltfjord. This chaetognath is known to stay at depth together with *Calanus* spp. (Baliño & Aksnes 1993). We observed a negative in situ relation with the *Calanus* spp. complex during February, but its predation did not reduce the prey's stock abundance. The stock of *E. hamata* in February consisted mostly of juveniles <15 mm in length (Fig. 4) and probably did not compete significantly when *T. helgolandica* established strong wintering stocks.

In Mistfjord, *P. elegans* was on average the most abundant predator present in October. Its stock declined more than other species before February and indicates that itself was subject to predation. However, its positive in situ relation with both the *Calanus* spp. complex and *C. hyperboreus* in February (Fig. 5) may indicate attraction to prey.

Conclusion

Our dual approach that tested the interspecific relations in replicate and stock abundance of wintering zooplankton helped us to understand that the effects of predator–prey relations are highly variable in time and space. Fjord sill topography structures the geophysical selection of immigrants from basin-scale population systems. Above-normal local accumulation of voracious planktonic predators may significantly reduce the wintering stocks of appropriate prey and modify overwintering zooplankton communities in ecological patterns that are specific to the individual

fjord. Patch structures likely vary in situ because of specific differences in DVM, predator avoidance and mortality by predation. Seasonal and interannual changes in stock abundance result from the dynamic imbalance between rates of mortality and immigration due to the local advection of water from external shelf habitats.

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Disclosure statement

The authors report no conflict of interest.

Data archiving

Tables containing the original hydrographic data and the counts, subsamples and abundance estimates of zooplankton are stored on Excel files at the marine science database of the Faculty for Biosciences and Aquaculture at Nord University. The Norwegian Marine Data Centre at www.imr.no stores the materials' metadata.

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