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NE Atlantic zooplankton wintering in fjord habitats responds to hemispheric climate

Stig Skreslet, Ketil Olsen, Marina Chelak, and Ketil Eiane

Faculty for Bioscience and Aquaculture

University of Nordland

PO Box 1490, NO-8049 Bodø, Norway

e-mail: stig.skreslet@uin.no

Phone.: +47 75129742

Cellphone: +47 99459010

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Abstract

The study addresses how local abiotic variability links zooplankton stocks to climate systems. Four zooplankton species and abiotic environmental data were sampled annually during October and February 1983-2005 in two northern Norwegian fjord basins. Inter-decadal change in abundance occurred in both fjords but differed between the two communities, presumably resulting from combinations of topography, specific life history strategies and preference for ambient water qualities before advective migration into the habitats. The shallow Mistfjord sill led to accumulation of coastal water in the fjord basin, while the deeper Saltfjord sill allowed frequent seasonal

exchange of Atlantic basin water. Changes in basin water temperature and salinity were decadal in the Mistfjord basin, and inter-annual in the Saltfjord basin. Several biotic and abiotic variables co-varied with climate indices, which indicates causal relationships between hemispheric climate variability and abundance of wintering zooplankton, but the processes involved are not fully understood. North Atlantic Oscillation apparently forced vernal freshwater discharge from Norway, summer reproduction in neritic waters and geographic distribution of basin-scale population systems. Stratospheric forcing as indicated by Arctic Oscillation seems to be involved in geophysical relationships which influence dynamic processes in zooplankton population systems within the Arctic Mediterranean.

Introduction

Climate regulates trophodynamic activity in the NE Atlantic, which is evident in the Norwegian and Barents Seas (Skjoldal and Sætre, 2004; Drinkwater et al., 2011). Sea surface temperature (SST) measured in different parts of the North Atlantic has been used as a proxy for complex geophysical air-sea interactions in studies related to variability in fisheries resources (i.a. Izhevskii, 1964).

Atlantic SST is highly variable on short seasonal scales but averages calculated over longer time scales referred to as the Atlantic Multidecadal Oscillation (AMO) are now widely used in studies on how climate interacts with oceanographic relationships. However, Drinkwater et al. (2014) discussed mechanisms responsible for the AMO and concluded that the primary forcing factor is still under debate, with no firm conclusions made.

North Atlantic Oscillation (NAO) which represents the variability in barometric difference at sea level between the Azores and Iceland, is recognized as a major forcing factor in temperate and

arctic regions of the Atlantic sector. NAO above the long-term average (positive NAO) generates southwesterly winds towards Scandinavia (Hurrell, 1995) which discharges latent heat and precipitation over Norwegian coastal landscapes while NAO below average (negative NAO) is associated with dryer climate. Seasonal accumulation of snow and vernal meltwater runoff causes large river discharge in May-July (Tollan, 1976) which generates pronounced geophysical changes in coastal recipients (Sætre, 2007). Several authors have discussed how natural freshwater discharge and lowered salinity during summer may influence neritic biological production (Helland-Hansen and Nansen, 1909; Izhevskii, 1964; Skreslet, 1976, 1997; Skardhamar et al., 2007; Gislason et al., 2009). Large-scale hydroelectric production of energy regulates the vernal freshwater discharge to Norwegian coastal waters (Asvall, 1976) which may influence geophysical processes (Sætre, 2007) and biological productivity during summer (Skreslet et al., 1976; Skreslet, 1986, 2003). However, so far only Aksnes et al. (2009), have presented data that indicate ecologically significant effects of regulated freshwater discharge.

Heath et al. (2000) observed that *Calanus finmarchicus* (Copepoda, Calanoida) accumulating during autumn in Saltfjord, northern Norway, probably originated from a population system inhabiting the Norwegian Sea. Skreslet and Borja (2003) reported that the fjord's wintering stock was subject to inter-annual changes that were positively correlated with NAO in March-July and Arctic Oscillation (AO) in July-September. While NAO is a tropospheric relationship in the North Atlantic, AO covers more of the Arctic and can be interpreted as the surface signal of modulations in the strength of a circumpolar stratospheric air jet known as the polar vortex (Thompson and Wallace, 1998). Baldwin and Dunkerton (2012) argue that periodic AO anomalies first appear in the stratosphere and propagate downward into the weather system of the troposphere in a few weeks. Such atmospheric transfer of kinetic energy possibly generate air-sea interactions that are presently not resolved.

Here we study how climate indices are related to overwintering zooplankton stocks of three copepods (*C. finmarchicus*, *Calanus hyperboreus*, *Paraeuchaeta norvegica*) and an amphipod (*Themisto abyssorum*) in two fjords in northern Norway.

Population ecology of study species

Calanus finmarchicus and *Calanus hyperboreus* are herbivorous copepods of large importance to transfer of biogenic energy from planktonic primary producers to higher trophic levels. Both have established large population systems being subject to geographic dispersal by the thermo-haline circulation system of the Arctic Mediterranean which includes all regional seas between the Eurasian and North American continents (Tchernia, 1980; Aagaard et al., 1985).

C. finmarchicus has a trans-Atlantic boreal distribution (Melle et al., 2014) but is subject to genetic differentiation which is probably due to retention in three oceanographic gyres in the North Atlantic (Bucklin et al., 2000). The population system of the Norwegian Sea Gyre (Heath et al., 2000; Melle et al., 2004; Broms et al., 2009) includes the East Iceland Current (Astthorsson and Gislason, 2003), the Greenland Sea (Hirche, 2003; Torgersen and Huse, 2005), and extends into all Arctic Mediterranean waters influenced by advected Atlantic water (Backhaus et al., 1994; Harms et al., 2000; Kosobokova and Hirche, 2009; Hirche and Kosobokova, 2011; Dalpadado et al., 2012).

During winter, *C. finmarchicus* diapauses in an advanced ontogenetic stage (CV) in cold Arctic Intermediate Water habitats close to the Norwegian and Scottish continental slopes (Ruud, 1929; Heath and Jónasdóttir, 1999; Halvorsen et al., 2003). Wintering copepodids of *C. finmarchicus* also accumulate in deep northern Norwegian fjord basins until their reproduction in March-April (Sømme, 1934; Wiborg, 1954; Skreslet and Rød, 1986; Falkenhaus et al., 1997; Heath et al., 2000). *C. finmarchicus* females and CV offspring relocate from fjords during summer due to advection

associated with terrestrial runoff (Skreslet et al., 2000) which causes plumes of plankton-rich fjord water to accumulate in convergence structures and eddies on the Norwegian continental shelf (Skardhamar et al., 2007). *C. finmarchicus* reproduces in a convergence system on the inner mid-Norwegian shelf during June-August, the abundance of nauplii being negatively correlated with surface salinity (Skreslet et al., 2005). Similarly, Gislason et al. (2009) found that biological productivity and production of zooplankton in southwestern Icelandic coastal waters was governed by freshwater discharge.

Hirche (2003) proposed that the western part of the Greenland Sea Gyre (GSG) constitutes the Arctic Mediterranean population center of *C. hyperboreus*, which is the source for emigration northwards into the high-Arctic oceanic basins of the Polar Sea as well as southwards into the sub-Arctic basins of the Norwegian Sea. Considering that *C. hyperboreus* has a multiannual life cycle (Hirche, 2003; Melle et al., 2004) and is common in Beaufort Sea slope waters (Walkusz et al., 2010) it is possible that the species maintains a single pan-Arctic population system. *C. hyperboreus* wintering in northern Norwegian fjord basins becomes sexually mature and ascends to reproduce in the upper mixed layer during late winter, becoming subject to predominant wind-driven seaward transport of surface water into more open shelf waters where reproduction proceeds (Sømme, 1934).

The calanoid copepod *Paraeuchaeta norvegica*, and the hyperiid amphipod *Themisto abyssorum* are carnivorous species that prey *i.a.* on calanoid copepods in epi- and mesopelagic habitats (Yen, 1987; Tønnesson et al., 2006; Laakmann et al., 2009). Both are associated with Atlantic water in the Norwegian Sea. *P. norvegica* occurs in the upper 2000m depth range (Østvedt, 1955) with peak abundance of adults and juveniles at 400-500m and 100-300m, respectively (Fleddum et al., 2001). Its occurrence in Norwegian coastal waters (Eiane et al., 2002; Skarra and Kaartvedt, 2003) is

associated with advection of Atlantic water (Willis et al., 2008). *T. abyssorum* is a boreal species widely distributed in the Norwegian Sea and southwestern Barents Sea where its distribution is partly driven by advection of Atlantic water masses (Dalpadado et al., 2001). It feeds actively during wintertime (Kraft et al., 2013), probably completing a full life cycle within one year in the Norwegian Sea (Melle et al., 2004).

Relations between northern Norwegian zooplankton and neritic geophysical forcing

Fjord plumes from Norway merge into the northward flowing Norwegian Coastal Current (NCC), its salinity, volume, seaward extension and velocities being proportional to seasonal variation in freshwater runoff (Sætre, 2007). Leaving the North Sea coast at 62°N the NCC flows onto the inner parts of the mid-Norwegian continental shelf, on top of denser Atlantic water covering sea bottom deeper than 100-150m depth (Sætre and Aure, 2007). The wide shelf retains the upper layer of shelf water in large eddies of intermediate salinity which separates the fresher NCC from direct contact with the more haline surface water of the Norwegian Atlantic Current (NAC) that flows northwards along the shelf break.

Zooplankton generations produced in Norwegian fjords and shelf waters are subject to general northward advection by the NCC, but the transport may become delayed by seasonal cross-shelf migration between fjords, shelf, and slope habitats (Slagstad and Tande, 1996; Skreslet, 1997; Pedersen et al., 2000; Halvorsen et al., 2003). Termination of the meltwater discharge season in August weakens the vertical density gradient of the NCC and contributes to increasing its mixed layer depth. This causes the NCC surface water to shift its lateral velocity vector from seaward during summer to landward during autumn (Haakstad, 1977). The shift may explain that import of zooplankton in general and *C. finmarchicus* in particular seems to accumulate in northern

Norwegian fjords during September-November (Skreslet and Rød, 1986; Skreslet et al., 2000; Heath et al. 2000).

Migration of epipelagic zooplankton into fjords may occur due to horizontal advection of water across sills from external habitats due to southwesterly winds and Ekman transport, storm surges caused by low barometric pressure, tidal exchange, and estuarine compensation currents (Aure et al., 2007). However, denser and deeper water masses outside the sill is subject to upwelling when northeasterly winds along the coast causes off-shore Ekman transport. During such events, upwelling water may spill over the sill and fill the fjord basin inside, provided previous turbulent mixing and dilution of the basin water has reduced its density (Skreslet and Loeng, 1977). Such renewal of basin water possibly recruits bathypelagic plankton such as diapausing *Calanus* spp., and *P. norvegica* and *T. abyssorum* associated with Atlantic shelf water.

Objective

Here we aim to test the hypothesis that abiotic basin water variables carry evidence of causal relationships between the northern hemisphere climate and local abundance of zooplankton stocks wintering in northern Norwegian fjords. However, we recognize that different zooplankton species have evolved unique life history strategies and specific preferences to ambient physical qualities. Thus, we sub-hypothesize that different wintering stocks may display specific responses to climate variability due to a) particular adaptations to their ambient environment and b) effects of fjord topography that regulates advection of water from stratified external habitats.

Material and methods

This investigation is limited to four zooplankton species sampled from two wintering habitats near Bodø in northern Norway, just north of the Arctic Circle (Fig. 1). The wintering stocks of each species supposedly belong to larger Arctic Mediterranean population systems.

Zooplankton was collected in February and October from 1983 to 2005 by five replicate vertical tows with a Juday zooplankton net (0.1m² aperture and 180µm mesh size) from about 10m above bottom to surface on one station in the deepest parts of the Saltfjord and Mistfjord basins. Sampling dates varied from early to late in the months and were occasionally performed as early as two days before and as late as 22 days after the intended month. The time series are not complete for technical or logistic reasons. All samples are stored at the Marine Research Station of the University of Nordland in Bodø, Norway.

Sampled *C. finmarchicus* occurred in large numbers and were subsampled by a Wiborg-Lea plankton splitter in an early period and later by a Folsom plankton divider. Skreslet et al. (2000) reported that low numbers of *Calanus helgolandicus* occurred together with *C. finmarchicus* in material from weekly sampling in Saltfjord during 1997-98. Some samples could also contain occasional *Calanus glacialis* (Olsen, unpublished) that according to Gabrielsen et al. (2012) may be misidentified as *C. finmarchicus*. Because our long-term standard routine did not distinguish *C. helgolandicus* and *C. glacialis* our abundance estimates of *C. finmarchicus* are randomly inflated. According to Olsen (unpublished) the error was <2% in October 1997 and <5% in February 1998.

Observations of temperature, salinity, and oxygen in standard depths established by the International Council for the Exploration of the Sea (ICES) were initially made by Nansen bottles with calibrated reversing thermometers, laboratory salinometers and Winkler titration, respectively.

These methods were replaced with electronic CTD instruments (SBE25 from SeaBird Electronics and various models from Sensordata, Norway) calibrated against water samples and laboratory procedures involving international standard seawater. Because this paper addresses inter-annual relationships with tele-connected forcing, we have avoided statistical analysis based on data from 0-50m depth in Mistfjord and 0-75m depth in Saltfjord, because short-period local factors introduce large unwanted stochastic variance in the upper depth range. We have also not used oxygen concentration in statistical tests for correlation, because the variable is not conservative, being subject to rapid changes caused by photosynthesis and respiration of organisms.

Monthly averages of atmospheric indices for North Atlantic Oscillation (NAO) and Arctic Oscillation (AO), and Atlantic Multidecadal Oscillation (AMO) were downloaded from the US National Oceanographic and Atmospheric Administration (NOAA) from respectively:

http://www.norm_nao_monthly_b5001_current_ascii_table.mht,

http://www.monthly_ao_index_b50_current_ascii_table.mht”, and

<http://www.esrl.noaa.gov/psd/data/correlation/amon.us.long.data>.

Statistical calculations of Pearson correlation coefficients were made in Microsoft Office Excel 2007. Tests with plankton were made on averages calculated from replicate counts.

We also applied Fisher’s exact test for independence according to <http://research.microsoft.com/en-us/um/redmond/projects/mscompbio/> on data organized in 2x2 contingency tables. Tests with plankton abundance were made on parameters from every replicate count.

To observe statistical distances between biological samples collected in 1983-1993 and 1994-2005 we applied Principal Component Analysis (PCA) Canoco version 5.0 (ter Braak and Smilauer, 2012).

Results

The Mistfjord basin was in all years characterized by coastal water with salinity below 34.5psu, while the Saltfjord basin was always dominated by Atlantic water with higher salinity (Fig. 2). The haline stratification makes us define a mixed deep layer with rather homogenous salinity in 200-290m depth in Mistfjord and 250-370m in Saltfjord. We also define the 75-150m depth range in Mistfjord and 100-200m in Saltfjord as an intermediate discontinuity layer situated below sill depth in the former location and above sill in the latter.

In both fjords, the average oxygen concentration of the mixed bottom layer was lower in February than in October. The median value in Mistfjord during February was 3.58ml l⁻¹ (max=6.11; min=2.53) and 5.54ml l⁻¹ in Saltfjord (max=6.54; min=3.91). There were no indications of long-term decline that could indicate stagnating basin water.

Average temperature and salinity at 200-290m depth in Mistfjord were positively correlated both in October ($r=0.579$, $p=0.01$, degrees of freedom (df) =17) and February ($r=0.791$, $p=0.01$, df=20). Parameters of both variables were significantly lower in 1983-1993 than in 1994-2005, both in October and February (Figs. 3 and 4). Notable increases in salinity occurred from October 1992 to February 1994 and from February to October in 2005. There was a gradual salinity decrease between these events both in October 1994-2003 ($r=-0.799$, $p=0.01$, df=8) and February 1994-2005 ($r=-0.840$, $p=0.01$, df=10).

Temperature at 250-370m depth in Saltfjord during February differed significantly from 1983-1992 to 1995-2005 (Fig. 3). The salinity in February decreased substantially from 1987 to 1989 (Fig. 4)

before it gradually increased ($r=0.880$, $p=0.01$, $df=12$) in following years. The trend was not related with NAO in March-July, according to neither Fisher's test for independence nor a Pearson correlation test.

Average AMO for 1983-1994 was negative (-0.13°C) and positive (0.15°C) in 1995-2005. Seasonal AMO in March-July that was strongly correlated with annual AMO ($r=0.986$, $p=0.01$, $df=21$) was mainly negative in 1983-1994 and positive in most of the next 11 years (Fig. 5). NAO in March-July was mainly in a positive phase until 1995 when the average anomaly index for 1983-1994 changed from $\text{NAO}^+=0.33$ to $\text{NAO}^-=-0.10$ in 1995-2005. AO for July-September was subject to considerable inter-annual variability before 1995 (Fig. 5) until 1995-2005 when the anomalies were more frequently negative and closer to the long-term average. The average anomaly index changed from positive ($\text{AO}^+=0.06$) in 1983-1994 to negative ($\text{AO}^-=-0.03$) in 1995-2005.

In 1983-2005, seasonal averages of NAO and AMO in March-July were negatively correlated ($r=-0.509$, $p=0.02$, $df=21$) while no correlation existed between AO and AMO in July-September ($p>0.1$). NAO correlated positively ($p=0.01$, $df=21$) with AO in the same seasons of March-September, March-July and July-September ($r=0.684$, 0.660 and 0.548 , respectively). NAO in March-July and AO in July-September were not correlated ($p>0.1$).

Average salinity at 200-290m depth in Mistfjord during October correlated negatively with NAO in March-July, and positively with AMO in March-July and March-September (Table I). Average salinity at 250-370m depth in Saltfjord during February was negatively correlated with AO in July-September (Table I).

Basin water temperature did not correlate with NAO in March-July and AO in July-September in any of the two fjords. AMO correlated positively with average temperature in both 75-150m and

200-290m depth in Mistfjord during February, and in 250-370m depth in Saltfjord during both October and February (Table I).

C. finmarchicus was the most abundant among the four species during October, with *C. hyperboreus* ranking second and *T. abyssorum* last (Table II). Species abundance was mostly higher in October than in February, with minor exceptions for *P. norvegica* and *T. abyssorum*. During February, both *Calanus* spp. were more abundant in Mistfjord than in Saltfjord.

By organizing all replicates in 2x2 contingency tables with class intervals for abundance higher and lower than median, we observed significant decadal change in abundance from 1983-1993 to 1994-2005 in three species, according to Fisher's exact test (Table II). The abundance of *C. finmarchicus* in Saltfjord and *T. abyssorum* in Mistfjord decreased from the first to the next decade, which was notable in both months but both species showed an increase in the other fjord, according to data from October only. The abundance of *C. hyperboreus* increased during both months in Mistfjord, but only during February in Saltfjord.

During October, the abundance of *C. finmarchicus* in Saltfjord was positively correlated with seasonal NAO and AO (Table III, Fig. 6). The correlation with NAO in March-July was stronger than with NAO in the longer season of March-September, while the correlation with AO in March-September was stronger than that of AO in the shorter season of July-September. Saltfjord abundance in February was only positively correlated with AO in July-September. In Mistfjord during October and February, the abundance of *C. finmarchicus* was positively correlated with AO in the previous March-September.

The abundance of *C. hyperboreus* in Mistfjord was negatively correlated with seasonal NAO and AO (Table III, Fig. 6), being more strongly correlated with NAO in March-September than NAO in the shorter season of March-July.

In Saltfjord during October, the abundance of *P. norvegica* was positively correlated with AO in July-September while the abundance of *T. abyssorum* was positively correlated with AMO in March-July (Table III). Abundances of *C. finmarchicus*, *C. hyperboreus* and *P. norvegica* were not correlated with any seasonal AMO.

The interspecific numerical relationship between the four species changed from one decade to the next in Mistfjord while no difference appeared in Saltfjord (Fig. 7).

No average estimate of species abundance in Saltfjord correlated with the fjord's basin water salinity. In Mistfjord, the abundance of *P. norvegica* and *T. abyssorum* was negatively correlated with salinity at 200-290m depth during October and the abundance of *T. abyssorum* was still negatively correlated with salinity in February (Table IV). The abundance of *C. hyperboreus* correlated positively with salinity during February.

Discussion

Our results indicate that effects of climate on planktonic wintering habitat systems in northern Norwegian fjords are variable and nontrivial. Decadal change in the PCA clustering of the four studied species in Mistfjord possibly indicated a community response to changes in local ecological conditions, which did not occur in Saltfjord (Fig. 7). On the other hand, the species displayed independent decadal differences in abundance in both study localities (Table II). In part, this

ambiguity likely resulted from complex relationships between local ecological factors, but may also have originated from abiotic and biotic factors that acted on different spatial and temporal scales within the larger Arctic Mediterranean ecosystem. In addition, specific life history strategies probably combined with local topography and advection which regulated the accumulation of species to wintering habitats in fjords. Our discussion attempts to resolve some of these complexes and evaluate possible causal relationships by addressing temporal shifts in local variables (Table II, Figs. 3, 4 and 7) and hemispheric climate indices (Fig. 5).

We have cross-correlated local variables and tested their correlations with seasonal NAO and AO that are specific for the troposphere and stratosphere, respectively. They are necessarily coupled by vertical atmospheric interaction but their positive correlation during 1983-2005 became weaker when the seasonal index for March-September was subdivided into March-July and July-September. It makes us consider that on short time scales some of our marine variables were mainly forced by either tropospheric forcing in the Atlantic sector or by circumpolar stratospheric forcing.

Geophysical coupling of fjord and proximal shelf habitats

The basin water salinity of Mistfjord in October and Saltfjord in February was negatively correlated with NAO in the previous seasons of March-July and AO in July-September, respectively (Table I). Both cases were probably related to freshening of seawater in the eastern Norwegian Sea, but we attribute the distinction with different climate indices to effects of local sill depth (Fig. 1) on exchange of basin water. The shallow sill in Mistfjord caused its basin to store only coastal water (Fig. 2) imported from the NCC where the salinity probably varied in response to NAO in March-July and vernal freshwater discharge in May-July (Hurrell, 1995; Tollan, 1976). The deeper sill of Saltfjord allowed inflow and storage of water with an Atlantic signature (Fig. 2) advected from a

deeper layer resting on the mid-Norwegian shelf (Aure and Sætre, 2007). A period of low basin water salinity in Saltfjord during February 1989-95 (Fig. 4) possibly resulted from a positive NAO mode in 1986-94 (Fig. 5), which may have increased the transfer of freshwater from the NCC to the NAC. Taking into consideration that AO was strongly correlated with NAO in March-September, it may have enforced the turbulent mixing that diluted the NAC, or interacted with the advection of diluted Atlantic water in ways that explains correlation of Saltfjord basin salinity with AO (Table I).

Both fjord basins had well oxygenated water at the bottom and we did not observe multiannual trends or modes in O₂ concentrations which could indicate periods of stagnation and oxygen deficiency by inadequate advection from outside. Skreslet et al. (2000) observed Atlantic water inflow to the Saltfjord basin on three occasions during the summer of 1997. These events probably resulted from periodic local estuarine circulation which may in general induce turbulent diffusion and density reduction of resident basin water in fjords (Skreslet and Loeng, 1977). In contrast, the smaller catchment areas and weaker estuarine circulation in Mistfjord make us consider the possibly larger relative importance of advected low-salinity coastal water into the 75-150m depth range and subsequent thinning of the mixed layer at 200-290m depth due to turbulent diffusion (Fig. 4).

In Mistfjord, negative correlation between NAO in March-July and salinity in 200-290m depth (Table I) may largely depend on the number of years with positive NAO during the first decade (Fig. 5). Larger than normal freshwater outflow to the NCC (Hurrell, 1995) probably maintained low basin water salinity in Mistfjord (Fig. 4) by persistent tidal advection of coastal water with relatively low salinity. NAO did not co-vary with the salinity of coastal water at 100-200 m depth in Saltfjord. This we attribute to a strong tidal jet generated by a narrow and shallow channel that connects Saltfjord with an extensive fjord system farther inshore (Fig. 1), causing strong local turbulence (Eliassen et al., 2001) which possibly weakened or erased an original NAO signal.

We observed positive correlation ($p=0.01$) between temperature and salinity in Mistfjord in October and even stronger correlation in February, which possibly means that coastal water advected by tides into the fjord became colder after summers with large freshwater outflow and density decrease. Increased stratification makes the coastal water thinner and increases its seaward extension farther into the Norwegian Sea (Haakstad, 1977; Sætre, 2007). Thus, we reason that net radiation of heat from a thinner than normal mixed layer during autumn and winter at these latitudes may cause more pronounced cooling than when the mixed layer is thicker after summers with less stratified water (Albretsen et al., 2011).

In Mistfjord the basin water salinity increased markedly from October 1992 to October 1994 and then declined gradually until it again increased rapidly from February to October in 2005 (Fig. 4). The two episodes of saline coastal water inflow occurred after the salinity of the resident basin had declined to well below 34psu. Thus, the inflows may be attributed to negative NAO in March-July 1993 and 2005, respectively (Fig. 5) because low vernal freshwater discharge from Norwegian landscapes would generate denser than normal coastal water with increased potential for cascading into the Mistfjord basin. A pronounced negative NAO in 1998 did not cause subsequent cascading, probably because the resident basin water was still too dense.

After 1994 there was a significant salinity decline in the Mistfjord basin observed both in October and February (Fig. 4) which indicate more modest annual inflows and cumulative storage of coastal water over the period of years when NAO was close to normal and even negative in 1999-2004 (Fig. 5). Thus, the abiotic changes in Mistfjord were clearly decadal, which deviated from the more inter-annual changes in Saltfjord where only temperature in February differed significantly between the two decades (Fig. 3).

Decadal shifts in the two basins' salinity and temperature and in three seasonal climate variables about 1994 (Figs. 3, 4 and 5), coincided with the shift from an era of cold AMO in 1965-94 to a warm era in the following years (Sutton and Hodson, 2005). However, we noticed that the decadal shift in AMO during March-July lagged several years after temperature increases observed in both Mistfjord and Saltfjord. Taking into consideration Drinkwater et al. (2014) who conclude that the primary forcing of AMO is still under debate, we refrain from speculating how basin water temperature at 200-290m depth in Mistfjord and 250-370m depth in Saltfjord was correlated with only AMO in periods prior to sampling, and not with NAO and AO (Table I).

Interspecific differences in decadal abundance of planktonic stocks in fjords

Both fjords exchanged water masses and plankton with a common external habitat (Fig. 1), yet the interspecific composition of the Mistfjord community displayed inter-decadal change which the Saltfjord community did not (Fig. 7). Perhaps most striking was how the October abundance of *C. finmarchicus* in Saltfjord correlated positively with NAO in March-July and AO in July-September while *C. hyperboreus* correlated negatively in Mistfjord (Table III, Fig. 6). Another major difference was the decadal change in zooplankton abundance (Table II) that was more clearly related to decadal differences in abiotic variables in Mistfjord than in Saltfjord (Figs. 3 and 4, Table IV). We think this was largely related to differences in the exchange of water between the surrounding shelf and fjord basins brought about by the fjords' different sill depths (e.g. Eiane et al. 1998) which manifested basin specific differences in hydrography (Fig. 2). We observed that decadal changes in abundance were species specific as well as specific for the two fjords (Table II) which probably indicates that differences in life history strategies and autecological preferences contributed to the observed spatial and temporal differences in community composition (Fig. 7).

Decadal increase in the abundance of *C. hyperboreus* in Mistfjord during both months and of *C. finmarchicus* in October (Table II) was possibly associated with the change from high to low frequency of positive NAO in March-July about 1995 (Fig. 5) which assumedly decreased the annual vernal freshwater discharge to the NCC in succeeding years (Hurrell, 1995). It may have resulted in less stratified coastal water during the second decade which possibly facilitated upwelling and inflow of saline coastal water (Fig. 4) from mesopelagic depths outside the sill where potential immigrants of *Calanus* spp likely resided. This may explain how NAO correlated negatively with salinity at 200-290m depth (Table I) and abundance of *C. hyperboreus* (Table III, Fig. 6) during October, as well as how salinity at 200-290m depth correlated positively with abundance of *C. hyperboreus* in February (Table IV). The abundance of *C. hyperboreus* in Mistfjord correlated more strongly with NAO in March-September than with NAO averaged over the shorter season of March-July (Table III) which seems to strengthen that a dry spring, summer and autumn season facilitated upwelling and inflow of dense coastal water.

We attribute the decadal decrease in abundance of *C. finmarchicus* in Saltfjord during October (Table II) and its positive relationship with NAO in the previous spring (Table III, Fig. 6) to predominantly positive NAO in the first decade (Fig. 5). This probably led to larger than normal vernal freshwater discharge which possibly stimulated biological productivity and, accordingly, the copepod's reproduction in coastal waters during summer (Skreslet et al., 2005; Skardhamar et al., 2007; Gislason et al., 2009). The correlation between abundance of *C. finmarchicus* in Saltfjord was stronger with NAO in March-July than with NAO extended to March-September (Table III) which may indicate that freshwater discharge during August-September did not contribute much to the annual seasonal reproduction.

The abundance of *C. finmarchicus* and basin water salinity in Saltfjord did not co-vary, possibly because most of the wintering stock in this fjord resided in mesopelagic Atlantic basin water (Skreslet et al., 2000), being disconnected from less saline coastal water typical of their epipelagic reproduction and growth habitats off-shore (Pedersen et al., 2000; Melle et al., 2004; Skreslet et al., 2005, Skardhamar et al., 2007). Copepodids present in Saltfjord during October were probably accumulated from different neritic and oceanic habitats of the Norwegian Sea (Heath et al., 2000) some emerging by advection of coastal water during weeks before. The immigrants were probably about to initiate their diapause and most had maybe completed their descent into the Atlantic basin water of Saltfjord (Skreslet et al., 2000), thereby becoming decoupled from the intermediate layer of coastal water (Fig. 2) that originally may have contained the NAO signal observed in Mistfjord basin salinity (Table I).

We have no information on how AO correlated differently with zooplankton abundance in the two fjords (Table III, Fig. 6). AO in July-September was very variable before 1995 (Fig. 5) which makes us suppose that significant correlations with abundance depended mostly on inter-annual variability in AO during the first decade. NAO was then in a positive mode which probably influenced the stability of surface water in the eastern Norwegian Sea (Hurrell, 1995) and possibly prepared conditions for variable cross-shelf advection forced by AO.

The abundance of *C. finmarchicus* in Mistfjord was correlated neither with salinity nor with NAO, as was also the case with *C. hyperboreus* in Saltfjord. We assume that declines in their abundance from October to February (Table II) resulted from predation by macro-zooplankton and planktivorous fish which may have weakened climate signals in abundance of *Calanus* spp. The meso-planktonic *P. norvegica* and *T. abyssorum* are known to prey on small copepods (Bagoien et

al., 2001, Kraft et al., 2013) but were themselves probably subject to predation, so their contribution to the over-all predation on the two herbivores may have been subordinate.

Although not correlated with NAO, the abundance of *P. norvegica* and *T. abyssorum* in Mistfjord did correlate negatively with salinity at 200-290m depth (Table IV), and the abundance of *T. abyssorum* declined from the first to the next decade (Table II). We suggest that predominant positive NAO and increased freshwater influence (Fig. 4) during the first decade (Fig. 5) increased the coastal production of planktonic herbivores like *C. finmarchicus* which favored reproduction of the two predators.

Our statistical results that relate NAO to winter habitat salinity and zooplankton abundance is probably influenced by effects of extensive Norwegian hydroelectric production on marine biological productivity. The industry decreases regional vernal freshwater discharge to coastal habitats (Asvall, 1976) which may have blurred effects of natural hydrological cycling on marine biological processes and weakened results from our statistical tests.

Arctic Mediterranean ecosystem perspectives

Summing up discussion above, the indirect effects of freshwater discharge on biological productivity and zooplankton reproduction in marine recipients possibly explains the decadal decrease in abundance of *C. finmarchicus* in Saltfjord and its positive correlation with seasonal NAO, which also applies to the decrease in abundance of *T. abyssorum* in Mistfjord and the negative correlations of *P. norvegica* and *T. abyssorum* with salinity in Mistfjords (Table II, III and IV). It does not apply to the increased abundance of *C. hyperboreus* in Mistfjord, its negative correlation with NAO and its positive correlation with salinity. These relationships seems rather related to geophysical variability, either directly in shelf habitat systems or due to indirect

telecommunication from distant processes in the Arctic Mediterranean. Several positive and negative correlations with seasonal AO adds to our understanding that we face a range of processes that couples the geographic distribution of zooplankton populations and their transportation to hydrological effects of climate variability.

Vernal freshwater discharge causes seaward extension of Norwegian coastal water during summer (Haakstad, 1977; Sætre, 2007) which forces juvenile *C. finmarchicus* from shelf habitats into the central Norwegian Sea (Skreslet and Rød, 1986). Direct effects of NAO on advection in the Norwegian Sea (Blindheim, 2004) possibly influence the distribution and production of *C. finmarchicus* in the population's oceanic core habitat. Several geophysical processes are probably involved in the exchange of advanced copepodids from the Norwegian Sea and into Norwegian fjords by on-shelf currents (Melle et al., 2004). Thus, the decline in abundance from 1983-1993 to 1994-2005 in Saltfjord (Table II), possibly tells that the total population of *C. finmarchicus* in the north-east Atlantic part of the Arctic Mediterranean (Bucklin et al., 2000) was larger in the first decade due to a predominance of positive NAO in March-July (Fig. 5).

The accumulation of *C. finmarchicus* in Saltfjord possibly includes copepodids from the southern Norwegian Sea (Heath et al., 2000). However, the NAC takes a year to advect water from the northern border of the North Sea at 62°N to our latitude (Mork and Blindheim, 2003), while advection by the NCC frontal jet and the Norwegian shelf break jet is more than 10 times faster (Poulin et al., 1996). The northward transportation of *C. finmarchicus* by these jets may add to copepodids produced in mid-Norwegian shelf waters and the central Norwegian Sea. Southwesterly winds during periods of positive NAO may accelerate the northward advection of surface seawater (Dickson et al., 2000) and force phytoplankton production (Rey, 2004) that probably stimulates reproduction and growth of zooplankton. Thus, the positive correlation between NAO in March-

July and the abundance of *C. finmarchicus* in Saltfjord (Fig. 6) may have resulted from an inter-annual combination of increased reproduction per unit sea surface area and transportation from an extended area. Thus, the decadal shift from on average positive to negative NAO (Fig. 5) probably explains the decadal decline of this species in Saltfjord (Table II).

The population systems of the four species probably responded to inter-annual and decadal variability in basin-scale geophysical processes according to their life history evolution which may be why we observed specific relationships with NAO, AO and AMO (Table II and III). For instance do *C. finmarchicus* and *T. abyssorum* have generation times that do not exceed one year in the Norwegian Sea, so the annual production of their population systems may be expected to display inter-annual changes in response to climate. The populations of *C. hyperboreus* and *P. norvegica* have multiannual life-cycles and remain more stable between years which may be expected to weaken relations with climate on inter-annual scales. On the other hand, we expect the geographical distribution of each population system to vary with effects of climate on thermohaline circulation in the Arctic Mediterranean ecosystem.

Decadal modes of NAO have been associated with changes in transport of polar sea ice from the Fram Strait and into the Greenland Sea (Dickson et al., 2000), and eastward advection of polar seawater across the Norwegian Sea and narrowing of the warmer NAC (Blindheim, 2004). Albretsen et al. (2011) link decadal variability in temperature and salinity in Norwegian waters to circulation in the North Atlantic Subpolar Gyre (SPG) and the Subtropical Gyre (STG). Thus, our observations on effects of climate on planktonic fjord habitat systems may be due to air-sea interactions occurring in the Atlantic sector of the northern hemisphere.

Sundby and Drinkwater (2007) considered several events of Great Salt Anomalies (GSA) that circulate anti-clockwise in the northern North Atlantic and concluded that they do not result from advective propagation of water masses. The authors rather suggested that the salinity signal was caused by changes in position of fronts and gradients along the circulation system. They contended a strong link between the inflow to the Arctic by the Norwegian Atlantic Current and outflow from the Arctic through the Fram Strait or through the Canadian Archipelago. They speculated that NAO variability was involved but found little support for that.

Déry and Wood (2004) observed that river discharge to Hudson Bay was negatively correlated with AO, which possibly explains that the eastern part of the Atlantic SPG was subject to freshening through the 1980s and into the 1990s, subsequently followed by a period of increasing salinity (IPCC, 2007). Salinity anomalies in the northern Northwest and Northeast Atlantic tend to vary in opposite phase, being negative on one side when positive on the other (Sundby and Drinkwater, 2007). These relationships possibly contributes to explain our negative correlation between AO in July-September and salinity of Atlantic water accumulated at 250-370m depth in the Saltfjord basin during February next year (Table I). Thus, the theory that GSAs are not due to advection but to shifts in position of fronts and gradients (Sundby and Drinkwater, 2007), may suggest that the decline in salinity of the Saltfjord basin water during February in 1989-1995 (Fig. 4) resulted from a passing GSA. However, the drop was not noticeable in October which indicates that Atlantic GSA water was probably kept at a distance from the coast before the start of winter, and implies that cross-shelf advection and exchange of basin water was subject to strong seasonal variability in AO. However, we maintain that a positive mode in NAO (Fig. 5) probably contributed to the decline in salinity (Fig. 4) as previously discussed.

In October, the abundance of *C. hyperboreus* in Mistfjord correlated negatively with NAO in March-July and AO in July-September while both indices correlated positively with *C. finmarchicus* in Saltfjord (Table III, Fig. 6). AO extended to March-September improved the correlation with *C. finmarchicus* abundance in Saltfjord and revealed positive correlations in Mistfjord during both October and February. Similarly, NAO extended to March-September improved the correlation with *C. hyperboreus* abundance in Mistfjord during October. The observation makes us consider that NAO and AO acting on an extended seasonal time scale possibly forced geophysical processes on larger spatial scales in the Norwegian Sea. We also consider that the decadal increase in *C. hyperboreus* abundance and the decadal decrease in *C. finmarchicus* abundance (Table II) may be associated with large-scale processes on their population levels.

Fromentin and Planque (1996) observed negative correlation between NAO and abundance of *C. finmarchicus* in the North Sea, later attributed to geographical shifts in the population system (Beaugrand et al., 2002). This could be the result of decadal patterns in southwesterly winds into the Norwegian Sea (Dickson et al., 2000) which possibly brought the population center closer to our sampling localities. However, it does not contradict that inter-annual variation in NAO in March-July may influence reproduction of *C. finmarchicus* and *T. abyssorum* in the eastern Norwegian Sea. Rather, we reason that decadal variability in vernal freshwater discharge from Norway may cause multiannual cumulative variation in geophysical processes that forces planktonic productivity in the Nordic Seas.

A modeling experiment based on 1959-2004 data from the Continuous Plankton Recorder (CPR) survey by Chust et al. (2014) suggested that *C. finmarchicus* displayed a consistent poleward shift triggered by sea warming, and that *C. hyperboreus* was shifted southward in the NW Atlantic. Our

data were sampled farther north than the CPR domain, and cannot be easily explained by results from the survey. However, the decadal increase of *C. hyperboreus* (Table II) and its negative correlation with AO in July-September (Table III, Fig. 6) may support southward expansion of its population system.

We cannot fully comprehend how NAO and AO were both involved in the development of Arctic Mediterranean zooplankton populations being represented by local stocks in fjord habitats during winter. However, NAO appears to be mostly associated with hydrological cycling within the North Atlantic sector's troposphere (Hurrell, 1995) which may influence biological productivity in the eastern Norwegian Sea. AO is associated with the circumpolar vortex of the stratosphere (Thompson and Wallace, 1998) which displays anomalies that can propagate to the troposphere within a few weeks (Baldwin and Dunkerton, 2012). Thus, we speculate that air-sea effects of seasonal variability in AO may generate on-shelf advection and upwelling of shelf water that spills over the sills of the two fjords and affects their basins. Differences in sill depth selected unequal water qualities to the Saltfjord and Mistfjord basins (Fig. 2) and imported plankton from different depths outside the sills. Local zooplankton community differences (Fig. 7) probably depended on how specific life history strategies and autecological requirements combined with synecological relationships in the particular basin water habitat system.

Conclusion

Although seasonal AMO correlated with basin water temperature in both fjord basins and salinity in one, the influence of Atlantic SST on our investigated zooplankton wintering stocks was nearly absent. However, we have presented evidence that the abundance of species and their abiotic

environment varied on inter-annual and decadal scales in response to seasonal NAO and AO. NAO forcing of seasonal freshwater discharge from Norwegian drainage basins probably regulated annual biological productivity and its trophic effects on zooplankton reproduction in marine recipients. We suggest that multiannual modes in NAO caused cumulative change in zooplankton biomass over years which explains observed decadal differences in stock abundance. Variability in NAO and AO possibly caused changes in advection of seawater in the eastern Norwegian Sea and thus, cross-shelf recruitment of immigrants to wintering stocks of zooplankton in fjord basins. Telecommuted effects of freshwater discharge from Hudson Bay drainage basins forced by AO possibly influenced North Atlantic SPG salinity and generated GSA variability, influencing neritic advection in northern Norway and recruitment of zooplankton to the investigated fjord basins. Sampled time series differed between the two fjord basins, probably resulting from unequal sill depths which selected different abiotic and biotic qualities from the external shelf habitat. The material at hand represents two decades with modal shifts in climate indices which probably makes the results quite unique and not representative for other periods of time. Trophic interaction between animal populations in the Arctic Mediterranean Ecosystem and their specific relations with basin-scale geophysical processes are complex and vary on longer time scales. Adding a range of anthropogenic influence, causal relationships between climate indices, hydrography and zooplankton overwintering in fjord basins can't be fully understood from our limited investigation.

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Data Archiving

Metadata on original data used in this publication are archived at the Norwegian Marine Data Center in Bergen, Norway. Hard copies of original counts of zooplankton as well as hydrographic data recorded on ICES Hydro Master Cards have been scanned and are permanently stored together with electronic CTD data on a server operated by the University of Nordland, Bodø, Norway.

References

Aagaard, K., Swift, J. H. and Carmack, A. C. (1985) Thermohaline circulation in the Arctic Mediterranean Seas. *J. Geophys. Res.* **90**, 4833-4846.

Aksnes, D. L., Dupont, N., Staby, A., Fiksen, Ø. and Kaartvedt, S. (2009) Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. *Mar. Ecol.: Prog. Ser.* **387**, 39-49.

Albretsen, J., Aure, J., Sætre, R. and Didriksen, D. S. (2011) Climatic variability in the Skagerrak and coastal waters of Norway. *ICES J. Mar. Sci.* **69**, 758-763.

Astthorsson, O. S. and Gislason, A. (2003) Seasonal variations in abundance, development and vertical distribution of *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis* in the East Icelandic Current. *J. Plankton Res.* **25**, 843-854.

Asvall, R. P. (1976) Effects of regulation on freshwater runoff. In Skreslet, S., Leinebø, R., Matthews, J. L. B. and Sakshaug, E. (eds) *Fresh Water on the Sea*. The Association of Norwegian Oceanographers, Oslo, pp 15-20.

Aure, J., Asplin, L. and Sætre, R. (2007) Coast/fjord water exchange. In Sætre, R. (ed.) *The Norwegian Coastal Current – Oceanography and Climate*. Tapir Academic Press, Trondheim, pp. 115-124.

Backhaus, J. O., Harms, I. H., Krause, M. and Heath, M. R. (1994) An hypothesis regarding the space-time succession of *Calanus finmarchicus* in the northern North Sea. *ICES J. Mar. Sci.* **51**, 169-180.

Bagøien, E., Kaartvedt, S., Aksnes, D. L. and Eiane, K. (2001) Vertical distribution and mortality of overwintering *Calanus*. *Limnol. Oceanogr.* **46**, 1494-1510.

Baldwin, M. P. and Dunkerton, T. J. (2012) Propagation of the Arctic Oscillation from the stratosphere to the troposphere. *J. Geophys. Res.: Atmos.* **104**, 30937-30946.

Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A. and Edwards, M. (2002) Reorganization of North Atlantic marine copepod diversity and climate. *Science* **296**, 1692-1694.

- Blindheim, J. (2004) Oceanography and climate. In Skjoldal, H. R. (ed.), *The Norwegian Sea Ecosystem*. Tapir Academic Publishers, Trondheim, pp. 65-96.
- Broms, C. T. Å., Melle, W. and Kaartvedt, S. (2009) Oceanic distribution and life cycle of *Calanus* species in the Norwegian Sea and adjacent waters. *Deep-Sea Res., Pt II* **56**, 1910-1921.
- Bucklin, A., Astthorson, O. S., Gislason, A., Allen, L. D., Smolanack, S. B. and Wiebe P. H. (2000) Population genetic variation of *Calanus finmarchicus* in Icelandic waters; preliminary evidence of genetic differences between Atlantic and Arctic populations. *ICES J. Mar. Sci.* **57**, 1592-1604.
- Chust, G., Castellani, C., Licandro, P., Ibaibarriaga, L., Sagarminaga, Y., and Irigoien, X. (2014) Are *Calanus* spp. shifting poleward in the North Atlantic? A habitat modelling approach. *ICES J. Mar. Sci.* **71**, 241-253.
- Dalpadado, P., Borkner, N., Bogstad, B. and Mehl, S. (2001) Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. *ICES J. Mar. Sci.* **58**, 876-895.
- Dalpadado, P., Ingvaldsen, R. B., Stige, L. C., Bogstad, B., Knutsen, T., Ottersen, G. and Ellertsen, B. (2012) Climate effects on Barents Sea ecosystem dynamics. *ICES J. Mar. Sci.* **69**, 1303-1316.
- Déry, S. J. and E. F. Wood (2004) Teleconnection between Arctic Oscillation and Hudson Bay river discharge. *Geophys. Res. Lett.* **31**, L18205, doi:10.1029/2004GL020729.
- Dickson, R. R., Osborne, T. J., Hurrell, J. W., Meincke, J., Blindheim, J., Ådlandsvik, B., Vinje, T., Alekseev, G. and Maslowski, W. (2000) The Arctic Ocean response to the North Atlantic Oscillation. *J. Clim.* **13**, 2671-2696.

Drinkwater, K., Loeng, H., Titov, O. V., and Boitsov, V. D. (2011) Global warming and climate change. In Jakobsen, T. and Ozhigin, V. K. (eds). *The Barents Sea. Ecosystem, Resources, Management*. Tapir Academic Publishers, Trondheim, pp 777-807.

Drinkwater K. F., Miles M., Medhaug, I., Otterå, O. H., Kristiansen, T., S. and Gao, Y. (2014) The Atlantic Multidecadal Oscillation: Its manifestations and impacts with special emphasis on the Atlantic region north of 60°N. *J. Mar. Syst.* **133**, 117-130.

Eiane, K., Aksnes, D. L. and Ohman, M. D. (1998). Advection and zooplankton fitness. *Sarsia* **83**, 87-93.

Eiane, K., Aksnes, D. L., Ohman, M. D., Wood, S. and Martinussen, M. B. (2002) Stage-specific mortality of *Calanus* spp. under different predation regimes. *Limnol. Oceanogr.* **47**, 636-645.

Eliassen, E. K., Heggelund, Y. and Haakstad, M. (2001) A numerical study of the circulation in Saltfjorden, Saltstraumen and Skjerstadfjorden. *Cont. Shelf Res.* **21**, 1669-1689.

Falkenhaus, T., Tande, K. S. and Semenova, T. (1997) Diel, seasonal and ontogenetic variations in the vertical distribution of four copepods. *Mar. Ecol.: Prog. Ser.* **149**, 105-119.

Fleddum, A., Kaartvedt, S. and Ellersten, B. (2001) Distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica* in habitats of shallow prey assemblages and midnight sun. *Mar. Biol.* **139**, 719-726.

Fromentin, J. M. and Planque, B. (1996) *Calanus* and environment in the Eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol.: Prog. Ser.* **134**, 111-118.

Gabrielsen, T. M., Merkel, B., Søreide, J. E., Johansson-Karlsson, E., Bailey, A., Vogedes, D., Nygård, H., Varpe, Ø. and Berge, J. (2012) Potential misidentification of two climate indicator species of the marine arctic ecosystem: *Calanus glacialis* and *C. finmarchicus*. *Polar Biol.* **35**, 1621-1628.

Gislason, A., Petursdottir, H., Astthorsson, O. S., Gudmundsson, K. and Valdimarsson, H. (2009) Inter-annual variability in abundance and community structure of zooplankton south and north of Iceland in relation to environmental conditions in spring 1990-2007. *J. Plankton Res.* **31**, 541-551.

Haakstad, M. (1977) The lateral movement of the coastal water and its relation to vertical diffusion. *Tellus* **29**, 144-150.

Halvorsen E., Tande, K. S., Edvardsen, A., Slagstad, D. and Pedersen, O.P. (2003) Habitat selection of wintering *Calanus finmarchicus* in the NE Norwegian Sea and shelf waters off northern Norway in 2000-02. *Fish. Oceanogr.* **12**, 339-351.

Harms, I. A., Heath, M. R., Bryant, A. D., Backhaus, J. O. and Hainbucher, D. A. (2000) Modeling the Northeast Atlantic Circulation: implications for spring invasion of shelf regions by *Calanus finmarchicus*. *ICES J. Mar. Sci.* **57**, 1694-1707.

Heath, M. R. and Jónasdóttir, S. H. (1999) Distribution and abundance of overwintering *Calanus finmarchicus* in the Faroe-Shetland Channel. *Fish. Oceanogr.* **8**, 40-60.

Heath, M. R., Astthorsson, O. S., Dunn, J., Ellertsen, B., Gislason, A., Gaard, E., Gurney, W. S. C., Hind, A. T., Irigoien, X., Melle, W., Niehoff, B., Olsen, K., Skreslet, S. and Tande K. S. (2000) Comparative analysis of *Calanus finmarchicus* demography at locations around the northeast Atlantic. *ICES J. Mar. Sci.* **57**, 1562-1580.

Helland-Hansen, B. and Nansen, F. (1909) The Norwegian Sea. Its physical oceanography based on the Norwegian researches 1900-1904. *Report on Norwegian Fishery and Marine-Investigations*, **11** (2), <http://web.gfi.uib.no/The%20Norwegian%20Sea/TNS-001.htm>.

Hirche, H. J. (2003) Zooplankton habitats of the Greenland Sea: An experimental laboratory for studies of pelagic ecology. In Skreslet, S. (ed.), *Jan Mayen Island in Scientific Focus*. Kluwer Academic Publishers, Dordrecht, pp. 123-133.

Hirche, H. J. and Kosobokova, K. N. (2011) Winter studies on zooplankton in Arctic seas: the Storfjord (Svalbard) and adjacent ice-covered Barents Sea. *Mar. Biol.* **158**, 2359-2376.

Hurrell, J. W. (1995) Decadal trends in the North Atlantic Oscillation: Regional temperature and precipitation. *Science* **269**, 676-679.

IPCC (2007) North Atlantic Subpolar Gyre, Labrador Sea and Nordic Seas. IPCC Fourth Assessment Report, Working Group I: Climate Change 2007.

http://www.ipcc.ch/publications_and_data/ar4/wg1/en/ch5s5-3-2-1.html.

Izhevskii, G. K. (1964) *Forecasting of Oceanological Conditions and the Reproduction of Commercial Fish*. Translation from Russian by Israel Programme for Scientific Translations, Jerusalem (1966).

Kosobokova, K. N. and Hirche H. J. (2009) Biomass of zooplankton in the eastern Arctic Ocean - A base line study. *Prog. Oceanogr.* **82**, 265-280.

Kraft, A., Berge, J., Varpe, Ø. and Falk-Petersen, S. (2013) Feeding in Arctic darkness: Mid-winter diet of the pelagic amphipods *Themisto abyssorum* and *T. libellula*. *Mar. Biol.* **160**, 241-248.

Laakmann, S., Kochzius, M. and Auel, H. (2009) Ecological niches of Arctic deep-sea copepods: Vertical partitioning, dietary preferences and different trophic levels minimize interspecific competition. *Deep Sea Res., Part I* **56**, 741-756.

Melle, W., Ellertsen, B. and Skjoldal, H. R. (2004) Zooplankton: The link to higher trophic levels. In Skjoldal, H. R. (ed.) *The Norwegian Sea Ecosystem*. Tapir Academic Publishers, Trondheim, pp 137-202.

Melle, W., Runge, J., Head, E., Plourde, S., Castellani, C., Licandro, P., Pierson, J., Jonasdottir, S., Johnson, C., Broms, C., Debes, H., Falkenhaus, T., Gaard, E., Gislason, A., Heath, M., Niehoff, B., Nielsen, T. G., Pepin, P., Stenevik, E. K., Chust, G. (2014) The North Atlantic Ocean as habitat for *Calanus finmarchicus*: Environmental factors and life history traits. *Prog. Oceanogr.* **129**, 244-284.

Mork, K. A. and Blindheim, J. (2003) Heat loss of the Norwegian Atlantic Current toward the Arctic. *ICES Mar. Sci. Symp.* **219**, 144-149.

Olsen, K. (unpublished) Sesongutskiftinger av *Calanus finmarchicus* (Gunnerus) i Saltfjorden (Norw.). MSc thesis, University of Tromsø 2002, pp 1-63. 253 pp.

Østvedt, O. J. (1955) Zooplankton investigations from weather ship M in the Norwegian Sea, 1948-1949. *Hvalradets Skr.* **40**, 1-93.

Pedersen, O. P., Tande, K. S., Timonin, A., and Semenova, T. (2000) A possible connection between hydrography and the distribution of *Calanus finmarchicus* on the Norwegian midshelf in 1997. *ICES J. Mar. Sci.* **57**, 1645-1655.

- Poulin, P. M., Warn-Varnas, A. and Niiler, P. P. (1996) Near surface circulation of the Nordic Seas as measured by Lagrangian drifters. *J. Geophys. Res.* **101**, 18237-18258.
- Rey, F. (2004) Phytoplankton: the grass of the sea. In Skjoldal, H. R. (ed.) *The Norwegian Sea Ecosystem*. Tapir Academic Publishers, Trondheim, pp 91-136.
- Ruud, J. T. (1929). On the biology of copepods off Møre 1925-1927. *Rapp. P.-V. Reun. - Cons. Int. Explor. Mer* **56** (8), 1-84.
- Sætre, R. (ed.) (2007) *The Norwegian Coastal Current – Oceanography and Climate*. Tapir Academic Press, Trondheim, pp. 99-114.
- Sætre, R., and Aure, J. (2007) Characteristic circulation features. In Sætre, R. (ed.) *The Norwegian Coastal Current – Oceanography and Climate*. Tapir Academic Press, Trondheim, pp. 99-114.
- Skardhamar, J., Slagstad, D. and Edvardsen, A. (2007) Plankton distributions related to hydrography and circulation dynamics on a narrow continental shelf off Northern Norway. *Estuarine, Coastal Shelf Sci.* **75**, 381-392.
- Skarra, H. and Kaartvedt, S. (2003) Vertical distribution and feeding in the carnivorous copepod *Paraeuchaeta norvegica*. *Mar. Ecol.: Prog. Ser.* **249**, 215-22.
- Skjoldal, H. R. and Sætre, R. 2004 Climate and ecosystem variability. In Skjoldal, H. R. *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim, pp 507-534.
- Skreslet, S. (1976) Influence of freshwater outflow from Norway on recruitment to the stock of Arcto-Norwegian cod (*Gadus morhua*). In Skreslet, S., Leinebø, R., Matthews, J. L. B., and

Sakshaug, E. (eds) *Fresh Water on the Sea*. The Association of Norwegian Oceanographers, Oslo, pp 233-237.

Skreslet, S. (ed.) (1986) *The Role of Freshwater Outflow in Coastal Marine Ecosystems*. Springer, Berlin. 453 pp.

Skreslet, S. (1997) A conceptual model of the trophodynamical response to river discharge in a large marine ecosystem. *J. Mar. Syst.* **12**, 187-198.

Skreslet, S. (2003) The interference of hydro-electric power production with natural effects of the North Atlantic hydrological cycle on a marine food web. *J. Rech. Oceanogr.* **28**, 123-126.

Skreslet, S., Leinebø, R., Matthews, J. L. B. and Sakshaug, E. (eds.) (1976) *Fresh Water on the Sea*. The Association of Norwegian Oceanographers, Oslo, pp 101-107.

Skreslet, S. and Loeng, H. (1977) Deep water renewal and associated processes in Skjomen, a fjord in north Norway. *Estuarine Coastal Mar. Sci.* **5**, 383-398.

Skreslet, S. and Rød, N. Å. (1986) Advection of *Calanus finmarchicus* between habitats in Norwegian coastal waters. In S. Skreslet (ed.), *The Role of Freshwater Outflow in Coastal Marine Ecosystems*. Springer-Verlag, Heidelberg, pp. 375-388.

Skreslet, S., Olsen, K., Mohus, Å. and Tande, K. S. (2000) Stage-specific habitats of *Calanus finmarchicus* and *Calanus helgolandicus* in a stratified north Norwegian fjord. *ICES J. Mar. Sci.* **57**, 1656-1663.

Skreslet, S., and Borja, A. (2003) Interannual correlation between hemispheric climate and northern Norwegian wintering stocks of two *Calanus* spp. *ICES Mar. Sci. Symp.* **219**, 390-392.

Skreslet, S., Borja, A., Bugliaro, L., Hansen, G., Meerkötter, R., Olsen, K. and Verdebout, J. (2005) Some effects of ultraviolet radiation and climate on the reproduction of *Calanus finmarchicus* (Copepoda) and year class formation in Arcto-Norwegian cod (*Gadus morhua*). *ICES J. Mar. Sci.* **62**, 1293-1300.

Slagstad, D. and Tande, K. S. (1996) The importance of seasonal vertical migration in across shelf transport of *Calanus finmarchicus*. *Ophelia* **44**, 189-205.

Sundby, S. and Drinkwater, K. (2007) On the mechanisms behind salinity anomaly signals of the northern North Atlantic. *Prog. Oceanogr.* **72**, 190-202.

Sutton, R. T. and Hodson D. R. L. (2005). Atlantic Ocean Forcing of North American and European summer climate. *Science* **309**, 115-118.

Sømme, J. D. (1934) Animal production of the Norwegian coast waters and the open sea I. Production of *Calanus finmarchicus* (Gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten area. *FiskDir. Skr. Ser. HavUnders.* **4**, 1-163.

ter Braak, C. J. F., and Smilauer, P. (2012) CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Ordination (Version 5.0), Centre for Biometry, Wageningen.

Tchernia, P. (1980) *Descriptive Regional Oceanography*. Pergamon Press, Oxford. 253 pp.

Thompson, D. W. J. and Wallace, J. W. (1998) The Arctic Oscillation Signature in the wintertime geopotential height and temperature fields. *Geophys. Res. Lett.* **25**, 1297-1300.

- Tollan, A. (1976) River runoff in Norway. In Skreslet, S., Leinebø, R., Matthews, J.L.B., and Sakshaug, E. (eds) *Fresh Water on the Sea*. The Association of Norwegian Oceanographers, Oslo, pp 11-13.
- Torgersen, T. and Huse, G. (2005) Variability in retention of *Calanus finmarchicus* in the Nordic Seas. *ICES J. Mar. Sci.* **62**, 1301-1309.
- Tønnesson, K., Nielsen, T. G. and Tiselius, P. (2006) Feeding and production of the carnivorous copepod *Pareuchaeta norvegica* in the Skagerrak. *Mar. Ecol.: Prog. Ser.* **314**, 213-225.
- Walkusz, W., Paulic, J. E., Kwasniewski, S., Williams, W. J., Wong, S. and Papst, M. H. (2010) Distribution, diversity and biomass of summer zooplankton from the coastal Canadian Beaufort Sea. *Polar Biol.* **33**, 321-335.
- Wiborg, K. F. (1954) Investigations on zooplankton in coastal and offshore waters of western and north-western Norway. *FiskDir. Skr. Ser. Havunders.* **11** (1), 1-246.
- Willis, K. J., Cottier, F. R. and Kwasniewski, S. (2008) The impact of warm water advection on the winter zooplankton community in an Arctic fjord. *Polar Biol.* **31**, 475-481.
- Yen, J. (1987) Predation by *Euchaeta norvegica* Boeck on eggs and larvae of the Atlantic cod *Gadus morhua* L. *J. Exp. Mar. Biol. Ecol.* **112**, 283-296.

Legends for Tables and Figures

Table I.

Correlations between seasonal climate indices and hydrography in 1983-2005. NAO: North Atlantic Oscillation. AO: Arctic Oscillation. AMO: Atlantic Multidecadal Oscillation. df: Degrees of freedom. *r*: Pearson correlation coefficient. *p*: Level of significance. *: Variable tested against seasonal indices from the previous calendar year.

Table II.

Seasonal and decadal change in abundance per square meter sea surface area (# m⁻²) of four zooplankton species in two locations from 1983-2005. N: Total number of replicate samples. Abundance: Estimated from number of specimens in a 0.1m² Juday net being multiplied by 10. *p* refers to significance of Fisher's exact test with 2x2 contingency tables. NS: No significance (*p*>0.1). Increase: Relative frequency of replicates with abundance above median increased from first (1983-1993) to second decade (1994-2005). Decrease: Relative frequency of replicates with abundance above median decreased from first to second decade.

Table III.

Correlations between climate indices and average abundance per square meter sea surface (# m⁻²) of zooplankton in 1983-2005 calculated from ≤5 replicates. NAO: North Atlantic Oscillation. AO: Arctic Oscillation. AMO: Atlantic Multidecadal Oscillation. df: Degrees of freedom. *r*: Pearson correlation coefficient. *p*: Level of significance. *: Abundance tested against seasonal index from the previous calendar year.

Table IV.

Correlations between salinity at 200-290m depth in Mistfjord 1983-2005 and average abundance of zooplankton per square meter sea surface ($\# \text{ m}^{-2}$) calculated from ≤ 5 replicates. df: Degrees of freedom. r : Pearson correlation coefficient. p : Level of significance.

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Investigation area north of the Arctic Circle in northern Norway. Sampling stations in Saltfjord (N67°16' E14°38') and Mistfjord (N67°27' E14°54') are at the center of the encircled maximum basin depths. Numbers at the entrance of both fjords indicate depth and position of sill.

Geographical position is indicated by arrow in the inserted Polar projection.

Figure 2.

Salinity in ICES standard depths 1983-2005. Vertical line at 34.5psu is chosen to distinguish typical Norwegian coastal water from oceanic water typical of the Norwegian Atlantic Current. Dashed line indicates approximate sill depth.

Figure 3.

Inter-annual differences in basin water temperature. *p* refers to Fisher's exact two-sided tests with data organized in 2x2 contingency tables with class intervals for periods 1983-1993 and 1994-2005 versus temperatures cut below the median. NS: Not significant ($p>0.05$).

Figure 4.

Inter-annual differences in basin water salinity (psu). *p* refers to Fisher's exact two-sided tests with data organized in 2x2 contingency tables with class intervals for periods 1983-1993 and 1994-2005 versus salinity cut below the median. NS: Not significant ($p>0.05$).

Figure 5.

Seasonal average anomalies of Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) indices, calculated from monthly data extracted from NOAA time series 1950-2009.

Figure 6.

Abundance of *Calanus finmarchicus* and *Calanus hyperboreus* per square meter sea surface in Saltfjord and Mistfjord plotted against seasonal NAO and AO. Each plot represents one out of ≤ 5 replicate tows sampled on the same depth and station from bottom to surface during October 1983-2005. See Table III for correlations between average abundance estimates and climate indices.

Figure 7.

Decadal PCA ordination plots of zooplankton abundance data collected in February and October in Saltfjord and Mistfjord during 1983-2005. Each circle represents a weighted average of the scores of samples collected in a year. The distance between the circles of each decade approximates the average dissimilarity of species abundances between years as measured by their Euclidean distance.

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Salinity, psu						
Locality	Month	Depth, m	Index	df	<i>r</i>	<i>p</i>
Mistfjord	October	200-290	NAO Mar-Jul	17	-0.555	0.02
			AMO Mar-Jul	17	0.483	0.05
			AMO Mar-Sep	17	0.498	0.05
Saltfjord	February*	250-370	AO Jul-Sept	17	-0.642	0.01

Temperature, °C						
Locality	Month	Depth, m	Index	df	<i>r</i>	<i>p</i>
Mistfjord	February*	75-150	AMO Mar-Jul	19	0.578	0.01
			AMO Mar-Jan	19	0.546	0.01
				19	0.427	0.05
Saltfjord	October	250-370	AMO Mar-Jul	18	0.499	0.05
			AMO Mar-Sep	18	0.545	0.02
	February*		AMO Mar-Jul	19	0.524	0.02
			AMO Mar-Jan	19	0.616	0.01

Table II. Seasonal and decadal change in abundance per square meter sea surface area (# m⁻²) of four zooplankton species in two locations from 1983-2005. N: Total number of replicate samples. Abundance: Estimated from number of specimens in a 0.1m⁻² Juday net being multiplied by 10. *p* refers to significance of Fisher's exact test with 2x2 contingency tables. NS: No significance (*p*>0.1). Increase: Relative frequency of replicates with abundance above median increased from first (1983-1993) to second decade (1994-2005). Decrease: Relative frequency of replicates with abundance above median decreased from first to second decade.

Species	Location	Month	N	Abundance, #m ⁻²			<i>p</i>	Change
				Max	Median	Min		
<i>Calanus finmarchicus</i>	Saltfjord	October	107	190 080	39 400	14 560	0.01	Decrease
		February	108	38 400	10 300	390	0.05	Decrease
	Mistfjord	October	105	136 960	23 360	5 840	0.05	Increase
		February	100	61 760	10 420	1 350	NS	
<i>Calanus hyperboreus</i>	Saltfjord	October	107	5 050	1 110	40	NS	
		February	108	2 670	610	50	0.05	Increase
	Mistfjord	October	105	9 760	2 800	540	0.001	Increase
		February	100	6 560	1 495	200	0.001	Increase
<i>Paraeuchaeta norvegica</i>	Saltfjord	October	107	360	120	0	NS	
		February	108	310	70	0	NS	
	Mistfjord	October	105	370	70	0	NS	
		February	100	350	100	10	NS	
<i>Themisto abyssorum</i>	Saltfjord	October	107	440	60	0	0.01	Increase
		February	108	300	70	0	NS	
	Mistfjord	October	105	250	20	0	0.001	Decrease
		February	100	140	10	0	0.001	Decrease

Table III. Correlations between climate indices and average abundance per square meter sea surface (# m⁻²) of zooplankton in 1983-2005 calculated from ≤5 replicates. NAO: North Atlantic Oscillation. AO: Arctic Oscillation. AMO: Atlantic Multidecadal Oscillation. df: Degrees of freedom. *r*: Pearson correlation coefficient. *p*: Level of significance. *: Abundance tested against seasonal index from the previous calendar year.

Species	Locality	Month	Index	df	<i>r</i>	<i>p</i>
<i>Calanus finmarchicus</i>	Saltfjord	October	NAO Mar-Jul	20	0.530	0.02
			NAO Mar-Sep	20	0.453	0.05
			AO Mar-Sep	20	0.649	0.01
			AO Jul-Sep	20	0.537	0.01
	Mistfjord	February*	AO Jul-Sep	20	0.464	0.05
			AO Mar-Sep	20	0.474	0.05
<i>Calanus hyperboreus</i>	Mistfjord	October	AO Mar-Sep	18	0.488	0.05
			NAO Mar-Jul	19	-0.552	0.01
	Mistfjord	October	NAO Mar-Sep	19	-0.614	0.01
			AO Jul-Sep	19	-0.493	0.05
			AO Jul-Sep	20	0.587	0.01
<i>Paraeuchaeta norvegica</i>	Saltfjord	October	AO Jul-Sep	20	0.587	0.01
<i>Themisto abyssorum</i>	Saltfjord	October	AMO Mar-Jul	20	0.424	0.05

Table IV. Correlations between salinity at 200-290m depth in Mistfjord 1983-2005 and average abundance per square meter sea surface ($\# \text{ m}^{-2}$) of zooplankton calculated from ≤ 5 replicates. df: Degrees of freedom. r : Pearson correlation coefficient. p : Level of significance.

Species	Month	df	r	p
<i>Paraeuchaeta norvegica</i>	October	19	-0.447	0.05
<i>Themisto abyssorum</i>			-0.526	0.02
	February	18	-0.593	0.01
<i>Calanus hyperboreus</i>			0.497	0.05

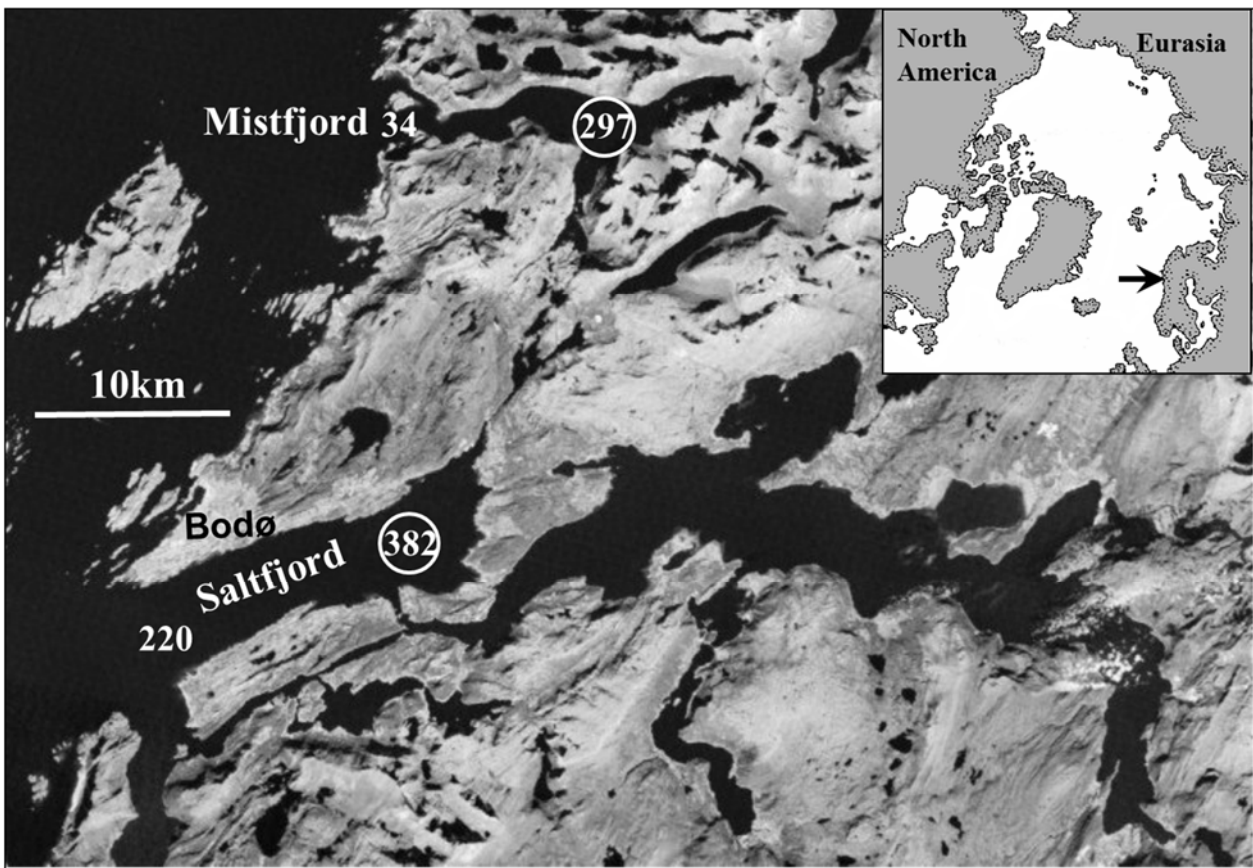


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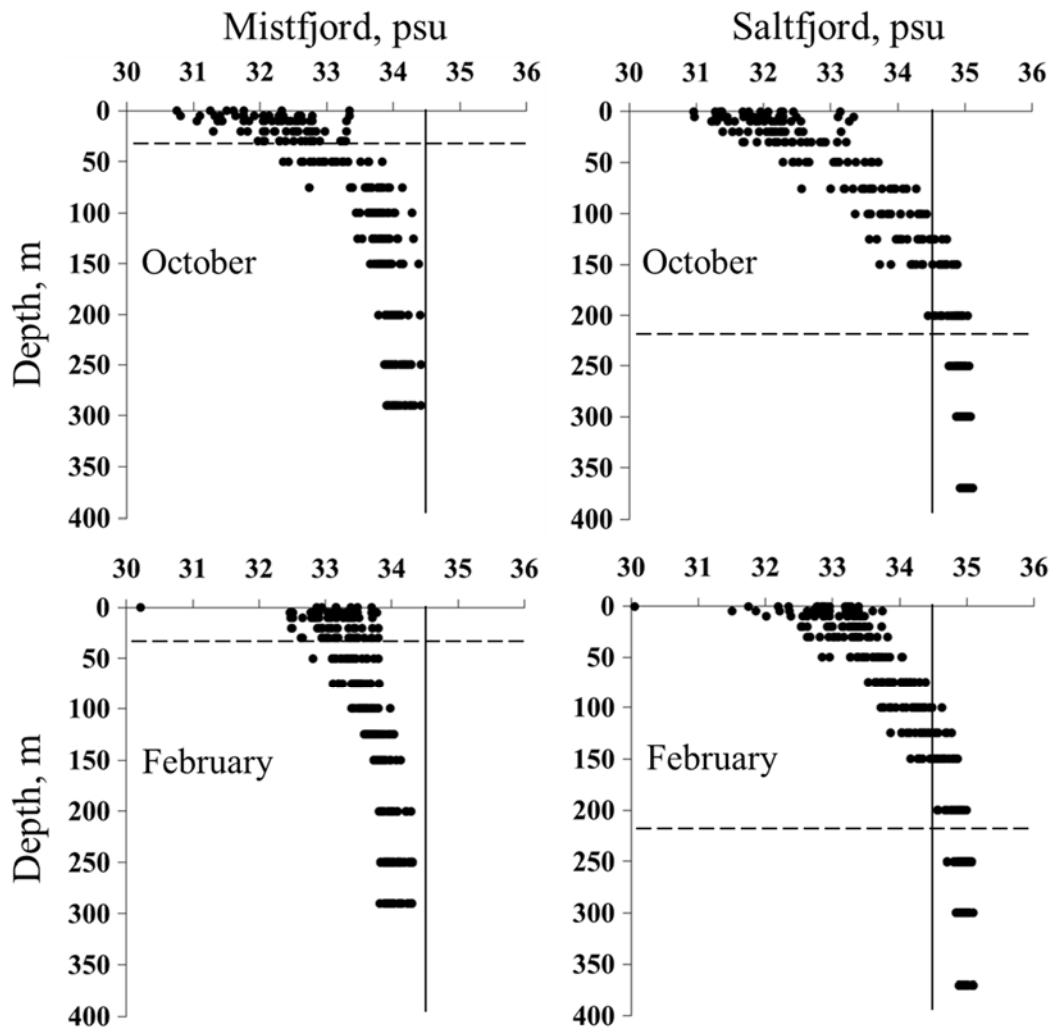


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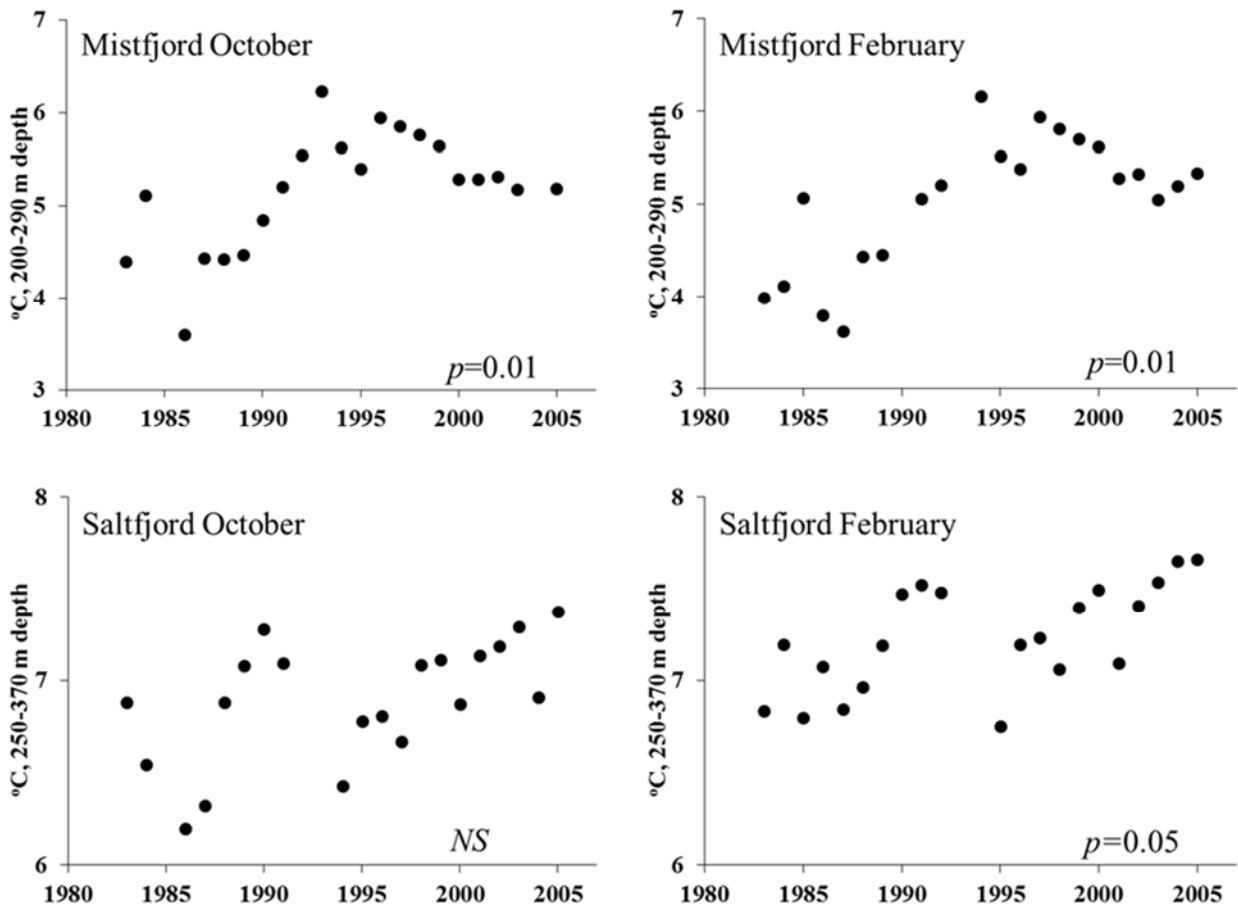


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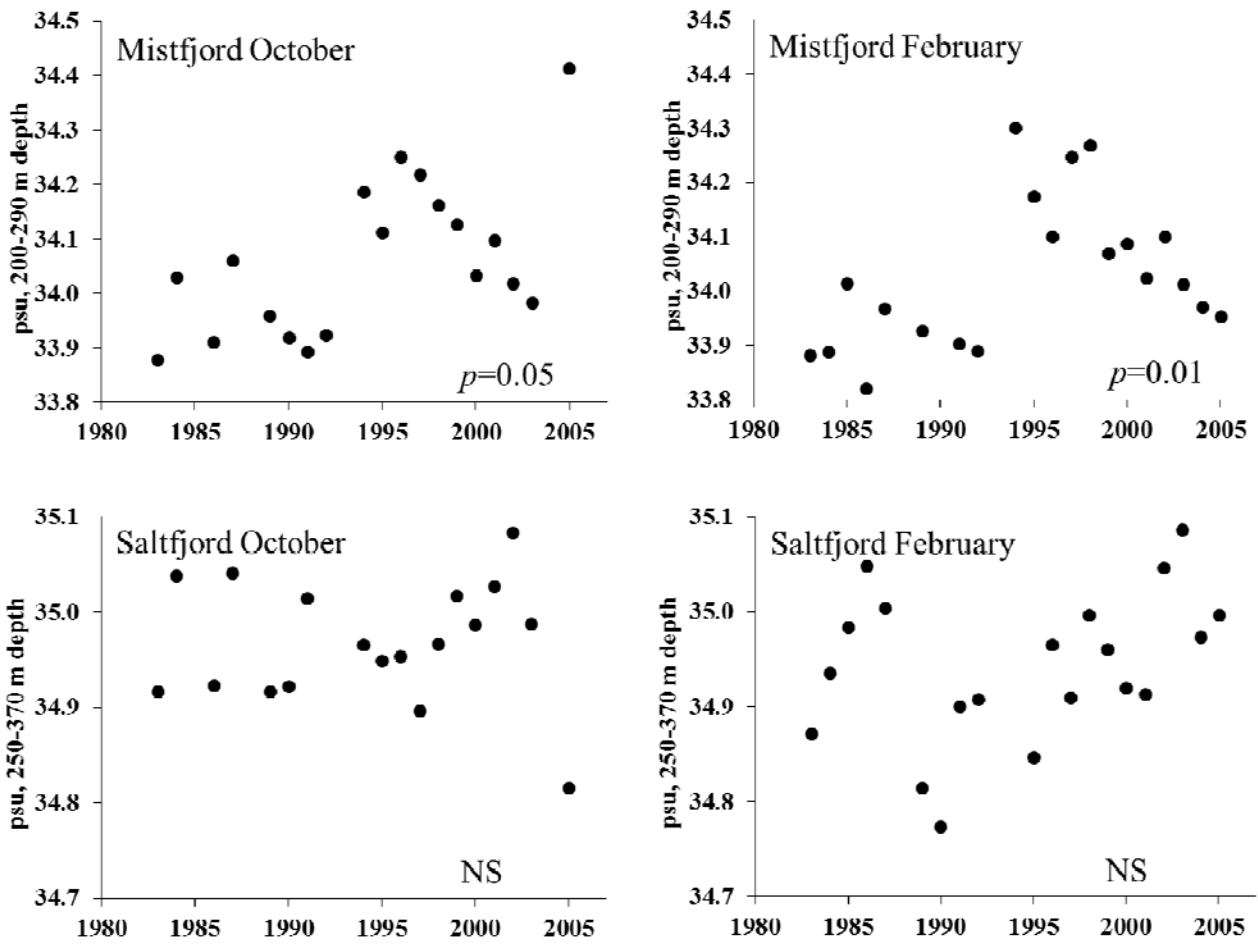


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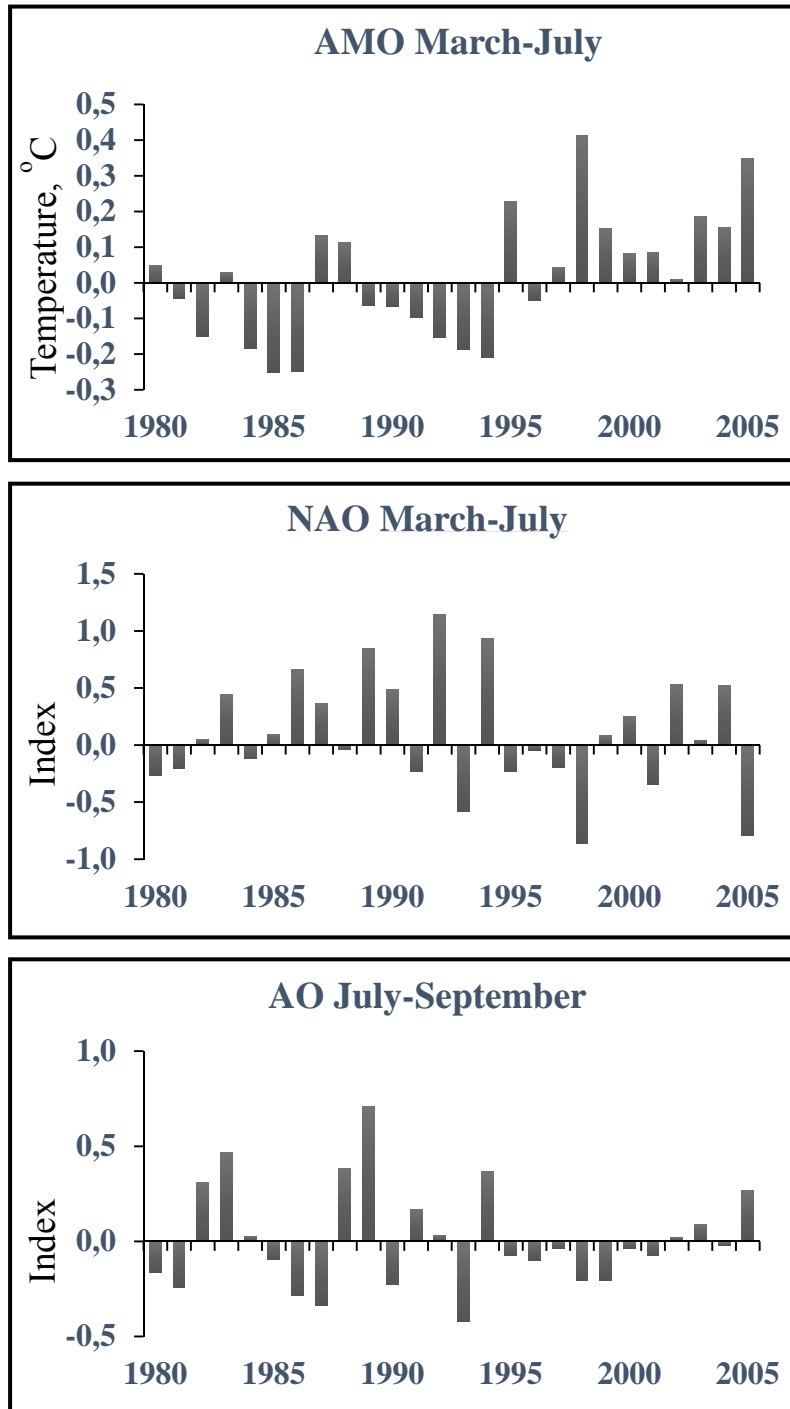


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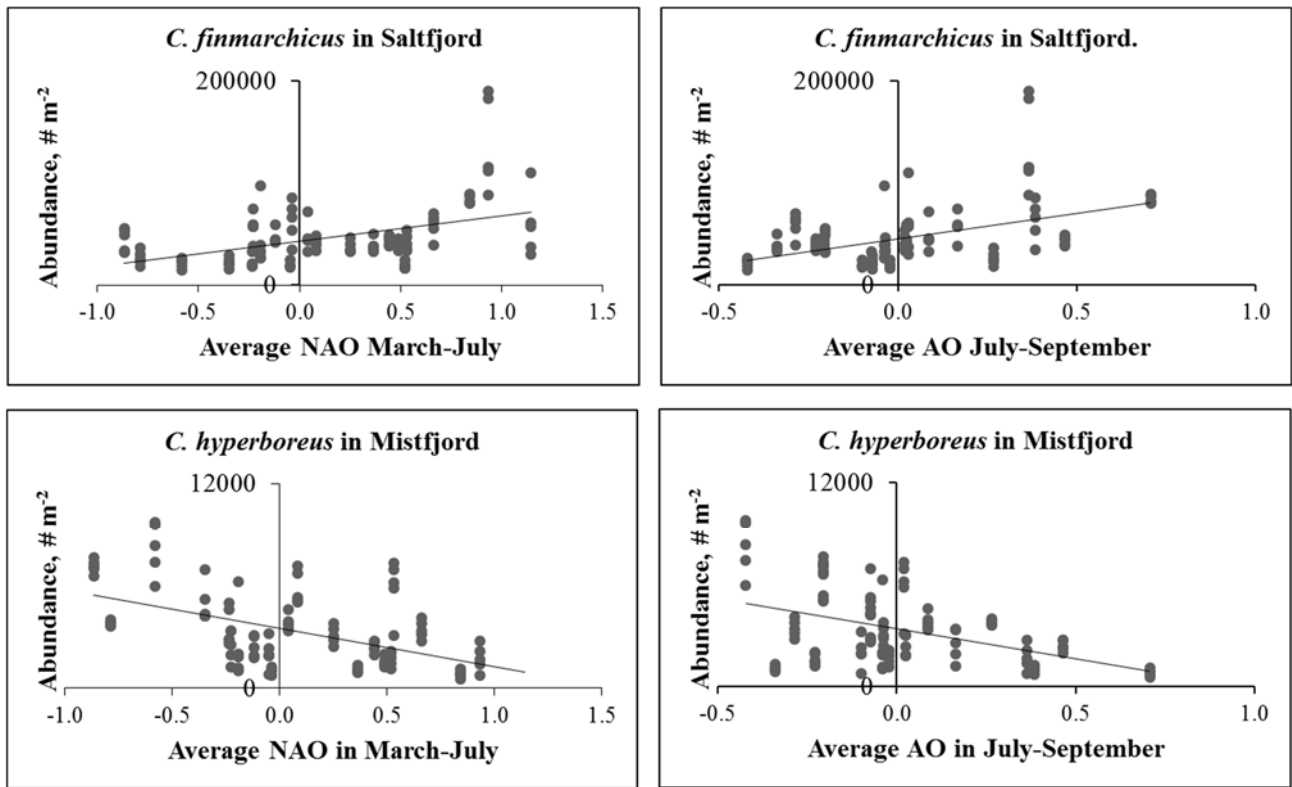


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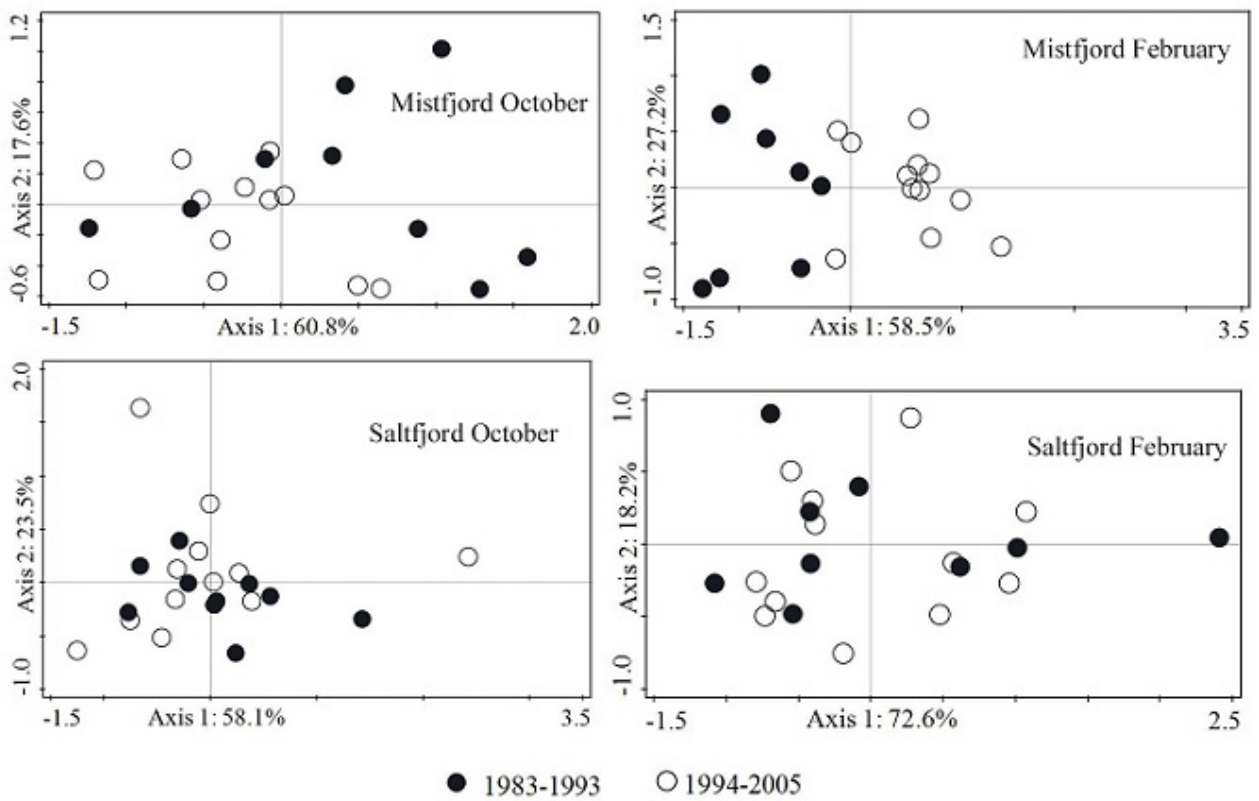


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