
Effect of freshwater discharge, intrusions of coastal water, and bathymetry on zooplankton distribution in a Norwegian fjord system

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Abstract. Freshwater discharge from a hydroelectric power plant had a strong impact on plankton transport and distribution within the fjord system. Most zooplankters submerged beneath the outgoing brackish current, and subsequent advection by the compensation current caused high concentrations near the power plant outlet. Currents driven by wind-induced changes in the density field in the adjacent coastal waters dominated transport between the fjord system and outer regions. Normal plankton advection rates appeared to be on the same order of magnitude as local zooplankton growth within the fairly enclosed system. However, during strong, short-term intrusions of coastal water, plankton composition and distribution changed markedly in the course of a few days. The bathymetry seemed to be decisive for the distribution of *Acartia*, which was recurrently found in highest numbers at the shallowest sampling location.

Introduction

Fjords deviate from most estuaries by their much larger depth and major oceanic influence. While the water column often spans several hundred meters, the freshwater impact is restricted to a shallow, upper layer. Volume transport driven by wind-induced changes in the density field in the adjacent coastal water usually exceeds that by currents generated from local run-off, and currents related to coastal processes may flush fjord waters above sill depth on time scales of days to weeks (Svendsen and Thompson, 1978; Sætre *et al.*, 1988; Aksnes *et al.*, 1989; Kaartvedt and Svendsen, 1990a; Aure and Rey, 1992). Still, freshwater discharge may be important for the distribution and standing stock of zooplankton, even in fjords with deep basins. Primary production is confined to shallow waters, and so is seasonally a major portion of the zooplankton.

Copepods of coastal or oceanic origin, like *Calanus finmarchicus* and *Pseudocalanus* spp., are common in many fjords (Fosshagen, 1980; Matthews and Heimdal, 1980; Smetacek, 1986; Norrbin *et al.*, 1990). These species generally inhabit deep water during winter. Overwintering may take place in the fjord basins (Tande, 1982; Hirche, 1983; Hopkins *et al.*, 1984; Baliño and Aksnes, 1993), or in outer oceanic water (e.g. Østvedt, 1955), with a subsequent supply of individuals to the fjords during spring (Aksnes and Magnesen, 1983; Lindahl and Hernroth, 1988).

In shallow estuaries, the genus *Acartia* tends to be the dominant copepod (Smetacek, 1986). *Acartia* spp. maintain persistence during the non-growth

season by means of benthic eggs (Grice and Marcus, 1981; Uye, 1985) and other typical estuarine zooplankton are also known to have benthic resting stages (Smetacek, 1986). Shallow estuaries may be rapidly flushed and this selects for behavioral traits which ensure maintenance of the plankton population. Smetacek (1986) suggested that water depth per se, rather than salinity tolerance, is the decisive factor selecting which copepod assemblages may be found in fjords and estuaries.

In the present paper, we report results from two adjacent fjords. One (the Sandsfjord system) is heavily influenced by freshwater run-off, including discharge from the largest hydroelectric power plant in Norway. In the other (Jøsenfjorden), the local freshwater input has been removed due to this hydroelectric scheme. By comparing the plankton distribution in the fjords, as well as with the power plant turned on and off, we evaluated how the freshwater discharge influences plankton transport and distribution. Freshwater-driven transport was compared to the importance of other current systems. In the fjord devoid of freshwater input, we analyzed the plankton distribution along a gradient of shallowing bottom, but relatively constant salinity. We thus evaluated whether the species composition becomes more 'estuarine' at shallow depth, as indexed by the presence of *Acartia*.

Study area

The investigation was carried out in the Sandsfjord system and Jøsenfjorden as part of a project to evaluate effects of the man-made alterations in freshwater discharge. The Sandsfjord system consists of the branches Sandsfjorden, Hylsfjorden and Saudafjorden, which have a common, narrow connection with outer water (Figure 1). The sill depth is 110 m, and the maximum depths are 420 m (Sandsfjorden), 510 m (Hylsfjorden), and 380 m (Saudafjorden). A sketch of the bottom topography along the deepest sections, depicting depths at the main sampling stations, is given in Figure 2. These fjord branches are strongly influenced by freshwater run-off, both from natural sources and Hylen hydroelectric power plant. Establishment of the power plant has introduced an artificial river at the head of Hylsfjorden. Prior to the regulation, local freshwater input to this fjord branch was negligible.

The sill depth (a bottom plateau) of Jøsenfjorden is 90 m and the maximum depth is 670 m. Bottom depths at the sampling stations vary from 670 to 60 m (Figure 2), with the shallowest locations found towards the head of the fjord. Before the hydroelectric development, Jøsenfjorden received relatively high freshwater input from two rivers near the head. After the river regulation, these sources were shut off and there is now only occasional local freshening of the surface layer.

Freshwater discharge

During winter and early spring, the power plant is the main freshwater source. Electricity demand is high and natural run-off is low, with precipitation stored as snow in the mountainous watersheds. Through the months prior to our first

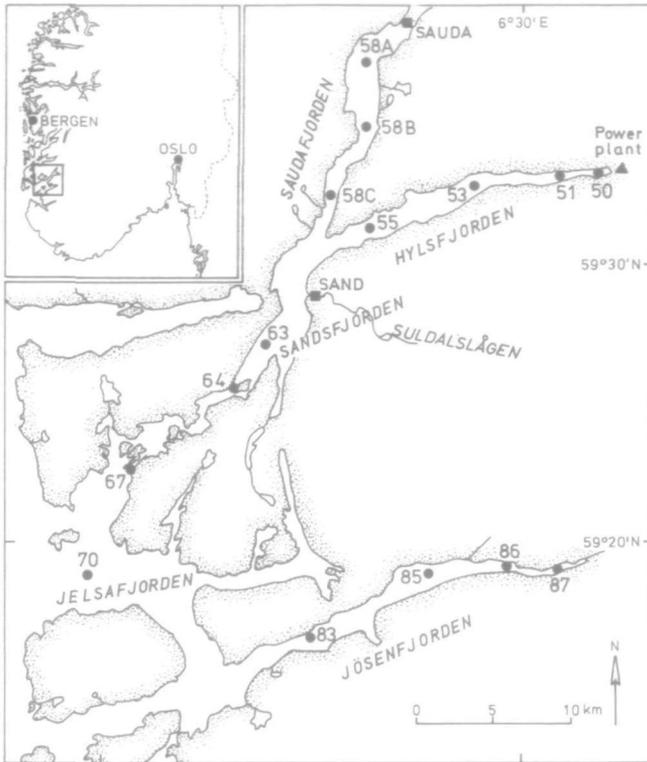


Fig. 1. Map of the study area with sampling stations.

survey (carried out 26 April–7 May 1989), the discharge from the power plant was on average $220 \text{ m}^3 \text{ s}^{-1}$. This made up $\sim 95\%$ of the freshwater input to Hylsfjorden and 75% of the total input to the entire Sandsfjord system (data from the Norwegian State Power Board). Just at the start of our survey, discharge was reduced due to lower demand for electricity, and was kept at $80\text{--}130 \text{ m}^3 \text{ s}^{-1}$ during most of the cruise.

The plant was not operated during the last 4 weeks prior to our second survey (carried out 25 July–6 August 1989), which was scheduled to study impacts of its restart. During July, the Suldalslågen river was the main freshwater source ($\sim 150\text{--}200 \text{ m}^3 \text{ s}^{-1}$). The power plant started operating on 29 July. Coincident heavy rain and associated snow melt in the mountains caused a strong increase in run-off from other sources (Kaartvedt *et al.*, 1991), giving a total freshwater pulse of $\sim 1000 \text{ m}^3 \text{ s}^{-1}$ to the Sandsfjord system. At the Hylsen power plant, water was taken through a bypass tunnel to prevent hazardous flow conditions in Suldalslågen river. Freshwater discharge at the head of Hylsfjorden exceeded $500 \text{ m}^3 \text{ s}^{-1}$ for a 12 h period and was thereafter kept at $\sim 300 \text{ m}^3 \text{ s}^{-1}$ until 3 August, when the flow was reduced to $100\text{--}200 \text{ m}^3 \text{ s}^{-1}$.

The freshwater supply to Jøsefjorden has virtually been turned off as a consequence of the hydroelectric scheme. However, at the end of July 1989, the

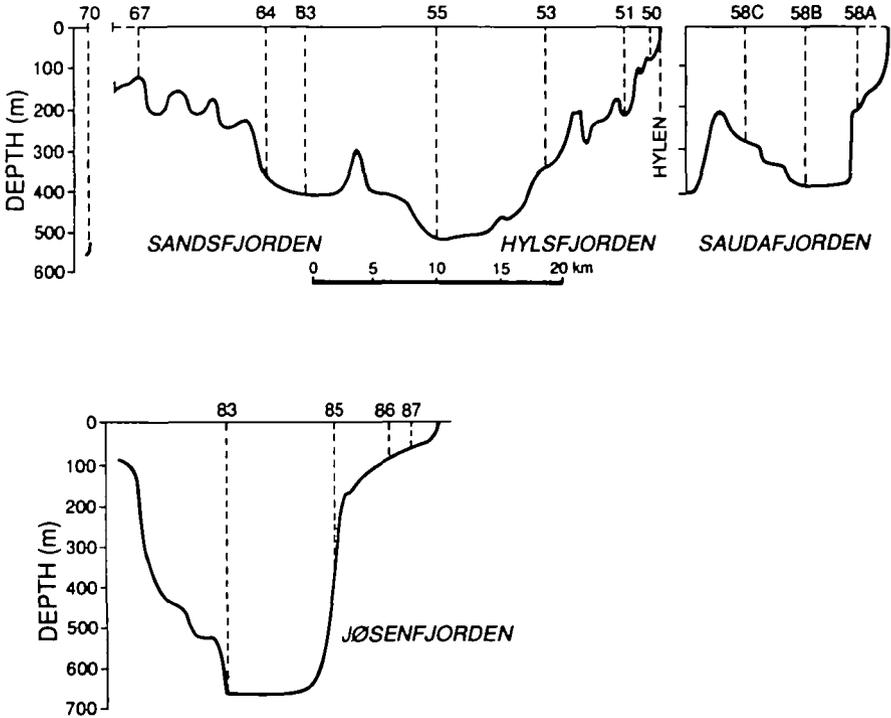


Fig. 2. Bottom topography with sampling stations depicted [modified after Fosshagen (1979) and Nordby (1992)].

main storage magazine was eventually loaded after years of filling. Water flowed over the magazine, and was fed back into the original river paths to Jøsenfjorden.

Method

Water exchange between Sandsfjorden and outer water was monitored from 25 January to 5 August 1989 by a mooring equipped with 11 Aanderaa current meters (Station 64). The original mooring was replaced by an equivalent rig at about the same position on 28 April. During the surveys, additional moorings with Aanderaa or Gytte current meters were located in outer Saudafjorden (Station 58C), and in outer (Station 55) and inner (Station 51) Hylsfjorden. Effects of tides were removed by using a 40 h moving average filter of hourly values.

Vertical profiles of salinity and temperature were obtained by CTD transects. Additional profiles were obtained from a mini-CTD, attached to the hose of a plankton pump during sampling.

Plankton were sampled by a vertically towed 180 µm double Juday net and by pump. The Juday net was used in three depth strata: from the bottom to 110 m (the sill depth of the Sandsfjord system), from 110 to 50 m (the lower range of

the plankton pump) and from 50 to 0 m. Pump sampling for fine-scale vertical resolution was occasionally performed down to 50 m, but in most cases was confined to the upper 15 or 20 m. Pump samples were generally obtained for each meter down to 6 m depth, thereafter in 2 m (to 10 m), 5 m (to 20 m) and 10 m intervals down to 50 m. The pump capacity was $\sim 0.8 \text{ m}^3 \text{ min}^{-1}$ and each sample represented a volume of $\sim 4 \text{ m}^3$. The samples were brought to the deck through a hose and filtered on a $180 \mu\text{m}$ plankton gauze kept in a water bath.

Samples from one of the Juday nets were frozen for biomass determination and one was preserved in 4% formalin for species analysis (species composition was only analyzed in the upper 50 m). Dry weights were determined by drying in an oven at 60°C and ash content by burning for 2 h at 480°C . For species analysis, further subsampling was carried out with a Lea–Wiborg plankton divider, except for some July samples where a modified Folsom splitter was used due to clogging of the Lea–Wiborg divider. A minimum of 1000 individuals were counted from each sample.

Pump samples were split into two parts by a modified Folsom splitter; one half was used to estimate biomass and subsamples of the other half for species identification.

Results

Water exchange between Sandsfjorden and coastal waters

Currents (Station 64) were strongest in the upper 25 m throughout the registration period, with velocities generally varying between 20 and 30 cm s^{-1} (Figure 3). Such velocities correspond to a daily transport of 5–8% of the volume in a matching depth interval inside Station 64 [using topographic data from Nordby (1992)]. From January to late April (the period prior to our first cruise), there was a prevailing outflow at 5 and 10 m. Below, and at 1 m, directions varied frequently.

From late April, surface currents became predominantly downfjord, and upfjord water transport was only recorded on 6 days until our registrations ended in August. Frequent reversals of direction were recorded below. From late May, directions in deeper layers were often mirror images of those in the upper 25 m (disregarding the surface current).

The fastest currents occurred during pulses of inflowing water in upper layers (but mainly below the surface current), when velocities reached $\sim 75 \text{ cm s}^{-1}$ (Figure 3). Three major intrusions (in May, June and July) were observed during the half-year registration period. One such event took place during the first days of our July/August cruise (Figure 3). A concurrent pulse of inflowing water was recorded in outer Saudafjorden and outer Hylsfjorden, but was barely detectable in inner Hylsfjorden [see Kaartvedt *et al.* (1991) and Svendsen *et al.* (1992) for details]. By assuming an average current velocity of 40 cm s^{-1} in the upper 15 m, 50–60% of the fjord water (inside Station 64) in this depth stratum was renewed in the course of this 4–5 day event (disregarding any recycling).

Thereafter, currents reversed once more, with outflow at all registration depths of the upper 25 m and inflow below. This reversal of currents coincided

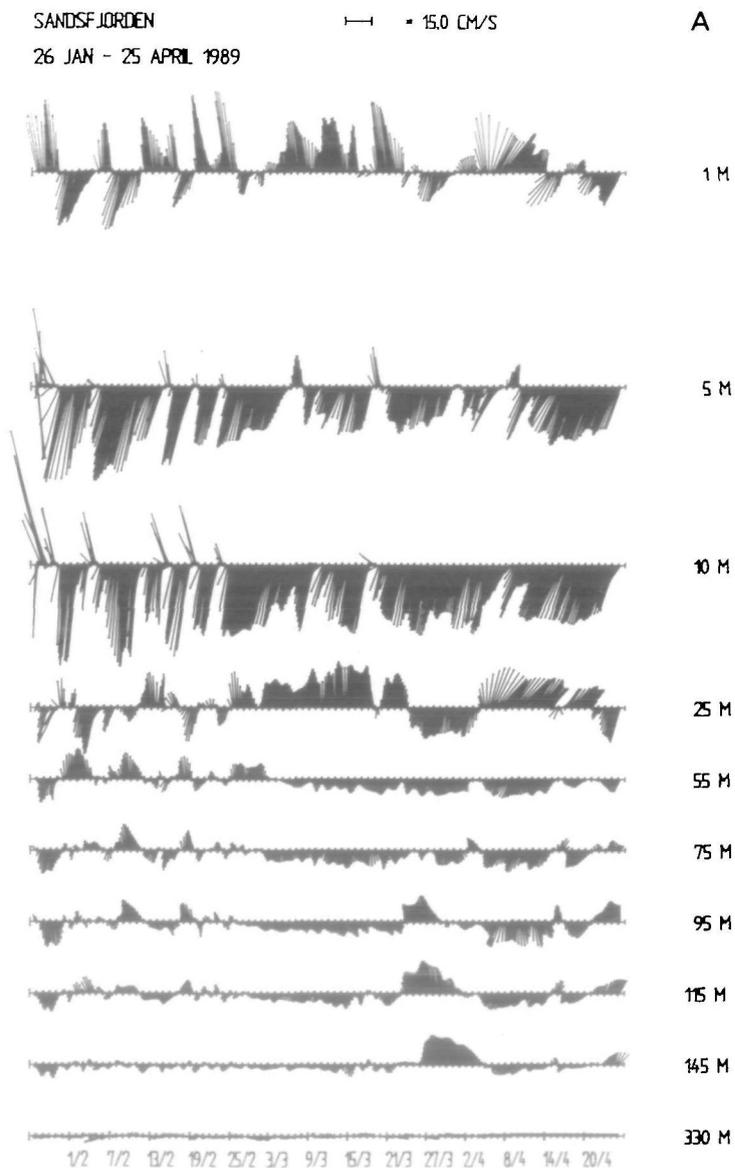


Fig. 3A. Current measurements at Station 64 in January–April 1989. The horizontal axis shows dates. Downward lines represent outgoing currents; upward lines represent incoming currents.

with the large pulse of freshwater to the fjord system, as well as with an ongoing upwelling of denser water offshore (Figure 4).

Freshwater-driven currents in Hylsfjorden

Only weak evidence of an estuarine circulation was detected in Hylsfjorden

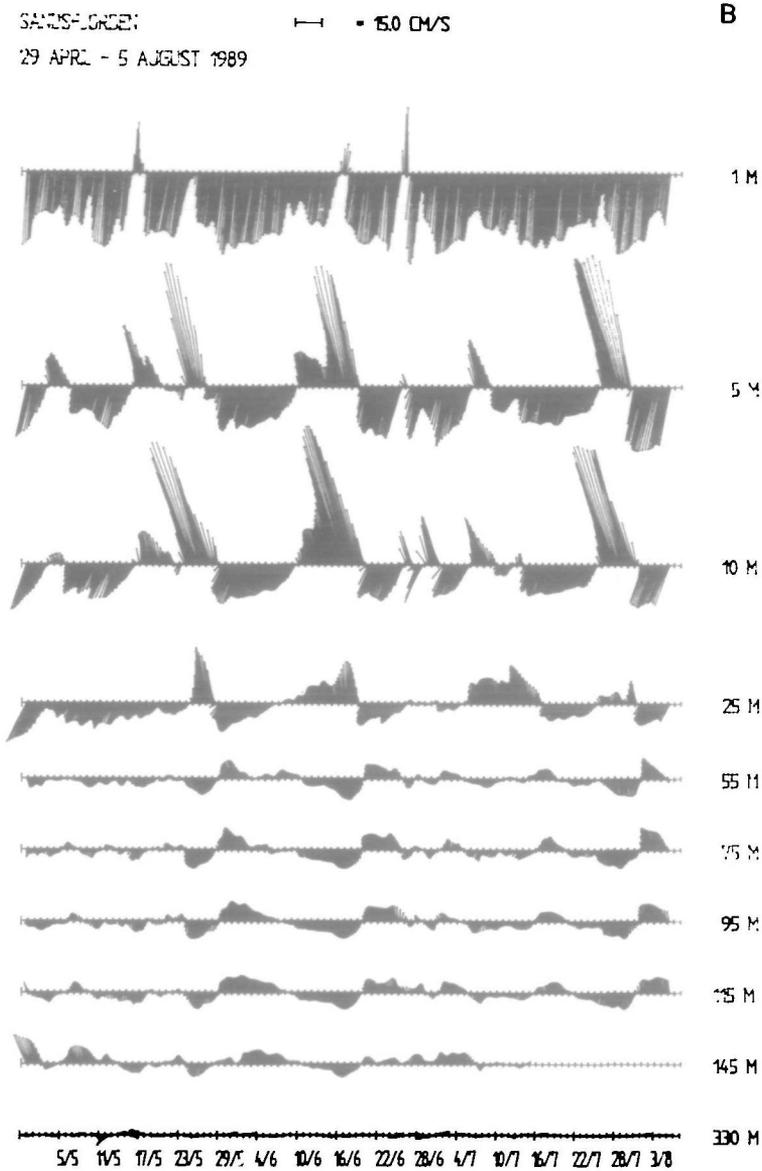


Fig. 3B. Current measurements at Station 64 in April–August 1989. The horizontal axis shows dates. Downward lines represent outgoing currents; upward lines represent incoming currents

during the spring cruise. A downfjord brackish surface current attained velocities of $10\text{--}20\text{ cm s}^{-1}$ (Station 51), while incoming currents beneath 6 m depth reached a few centimeters per second (not shown).

In July, the restart of the power plant generated strong currents in Hylsfjorden. Velocities were low prior to discharge (a few centimeters per second in the inner part), while the outflowing brackish current caused by the

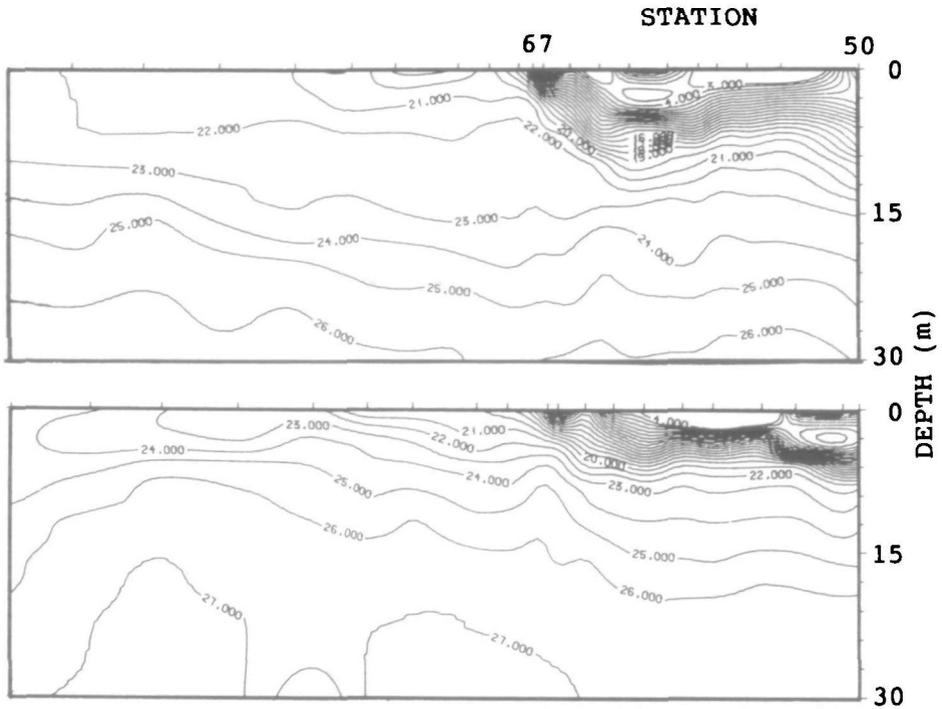


Fig. 4. Isolines of Sigma- t as determined during CTD transects through the Sandsfjord system and coastal water on 30 July (upper) and 4–5 August 1989 (lower).

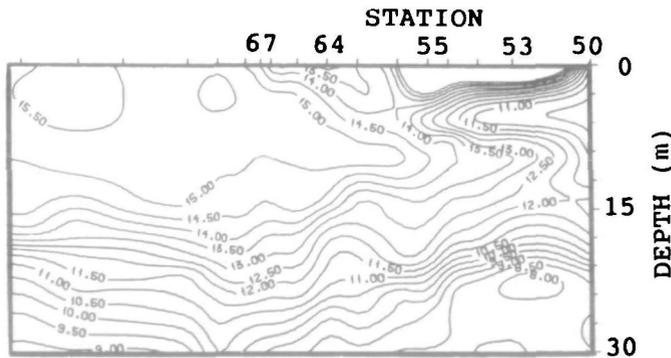


Fig. 5. Temperature isopleth for Hylsfjorden (right), Sandsfjorden and outside the fjord system on 30 July 1989 (day after start of power plant).

discharge nearly attained 80 cm s^{-1} in inner Hylsfjorden (Station 51) and 40 cm s^{-1} near the outlet (Station 55) [for further details, see Kaartvedt *et al.* (1991) and Svendsen *et al.* (1992)]. Strong mixing at the power plant outlet made the discharge water mass denser than the existing surface water of the fjord. It accordingly proceeded outward at subsurface depths, easily identifiable by the low temperature implanted by the contributing freshwater (Figure 5). The

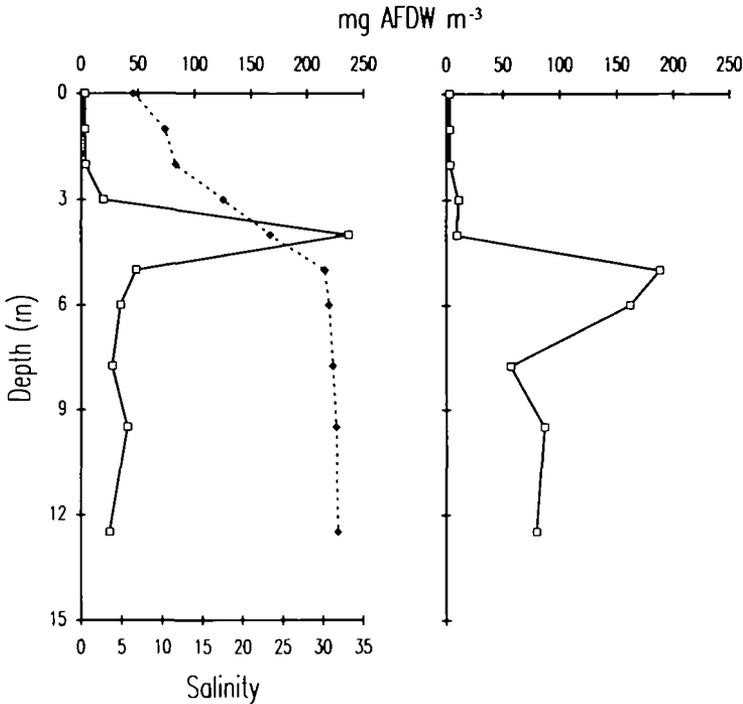


Fig. 6. Vertical biomass distributions (ash-free dry weight) in April/May 1989. (**Left**) Sandsfjorden (inside Station 63) at night and (**right**) Hylsfjorden (Station 53) during the day (results from Hylsfjorden are averages of three pump profiles). The superimposed salinity profile (stippled) was taken concurrently to the zooplankton sampling by a mini-CTD attached to the hose intake of the plankton pump. Data points depict sampling depths in the upper 6 m and mean depths of sampling intervals below.

Table 1. Estimated daily biomass transport at Station 64 during intrusions of coastal water in the upper layer 3–5 May 1989. Biomass data (ash-free dry weight; AFDW) are from pump samples on 3 May, current velocities are taken from Figure 3, and these results are combined with topographic data from Nordby (1992) to calculate transport rates. – Represents out-transport; + represents in-transport

Depth (m)	Biomass (mg AFDW m ⁻³)	Currents (cm s ⁻¹)	Daily transport (tonne AFDW)
0–2	4.5	30	–0.1
3–5	340	15	+4.6
6–10	140	7	+1.5
Net			+6.0

compensation current was not properly mapped due to the vertical positioning of the current meters [but see Kaartvedt and Aksnes (1992)].

Plankton distribution and transport during spring

In April/May, 61% of the biomass was found in waters above sill depth (110 m),

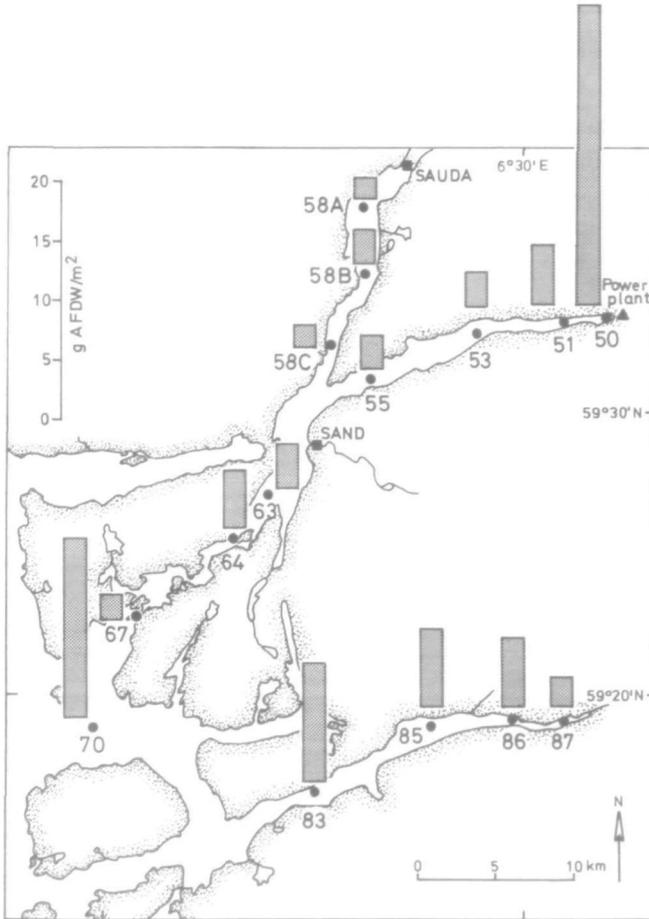


Fig. 7. Distribution of biomass (ash-free dry weight) through the Sandsfjord system and Jøsenfjorden in April/May, 1989, as determined from vertically towed nets (110–0 m).

of which 90% was caught in the upper 50 m (all stations combined). Fine-scale sampling revealed main concentrations in the upper 10 m, although most plankters avoided the brackish surface water of the Sandsfjord system (Figure 6, Table I). On 3 May, we estimated a net daily import to Sandsfjorden of 6 t ash-free dry weight (AFDW) in the upper 10 m during a modest inflow of water (Table I). This roughly represented 4% of the biomass in the upper 10 m within the fjord system or 2.7% of the biomass above sill depth. The sampling on 3 May incidentally took place during a short reversal of the water transport, which otherwise was mainly outwardly directed in upper layers (cf. Figure 3).

A conspicuous biomass maximum occurred at the head of Hylsfjorden, close to the power plant (Figure 7). In contrast, the surface integrated biomass apparently declined towards the head of Jøsenfjorden. *Calanus finmarchicus* (Figure 8) was the main contributor to the biomass peak at the head of

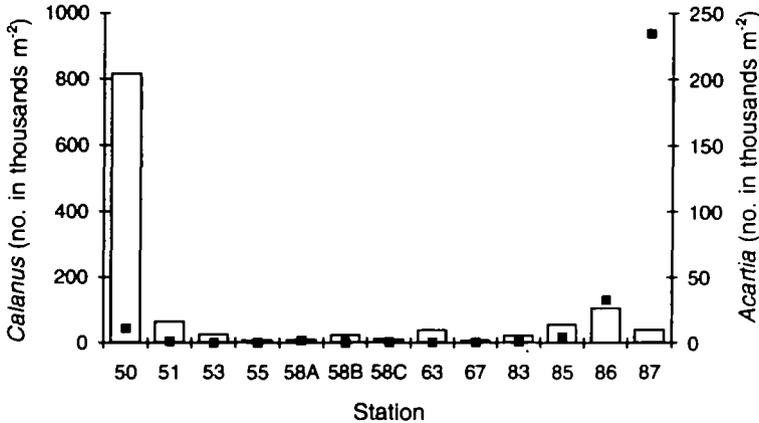


Fig. 8. Distribution of *C. finmarchicus* (open bars) and *Acartia* (black squares) from the Sandsfjorden system (Stations 50–67) and Jøsenfjorden (Stations 83–87) in April/May 1989 as determined from vertically towed nets (50–0 m). Station 50 (left) is at the head of Hylsfjorden, near the power plant outlet, and Station 87 (right) is at the head of Jøsenfjorden

Table II. Taxonomic composition (no. individuals m^{-3} ; Juday net; 50–0 m) at the central part (Stations 53 and 85) and head (Stations 50 and 87) of Hylsfjorden and Jøsenfjorden, April/May 1989

Taxon	Hylsfjorden stations		Jøsenfjorden stations	
	53	50	85	87
<i>Calanus finmarchicus</i>	485	24 496	1118	784
<i>Pseudocalanus elongatus</i>	16	513	112	38
<i>Paracalanus parvus</i>	8	176	6	22
<i>Pseudocalanus/Paracalanus</i> juveniles	80	641	195	128
<i>Temora longicornis</i>	99	7564	42	618
<i>Oithona</i>	1170	3782	634	672
Cyphonates larvae	2	1026	13	128
<i>Acartia</i>	0	224	91	4701

Hylsfjorden, but all common species increased abruptly in numbers towards the power plant outlet (Table II). The abundance of *Acartia* (predominantly *A. clausi*), however, deviated from the distribution of biomass. *Acartia* was almost absent from most parts of the fjord system, but increased strongly in numbers at the shallowest station in inner Jøsenfjorden (Figure 8).

Plankton distribution and transport during summer

Patterns at the end of July. The zooplankton were distributed somewhat deeper during summer. At this time, 34% of the total catch (biomass) was taken above sill depth, and 68% of this in the upper 50 m. As during spring, biomass was low in the brackish surface layer (see Kaartvedt and Aksnes, 1992).

Most species were more common in Jøsenfjorden and Sandsfjorden than in the inner branches Saudafjorden and Hylsfjorden (Table III). Furthermore,

Table III. Taxonomic composition (Juday net; 50–0 m) in different parts of the fjord system. July/August 1989. For Hylsfjorden (Stations 50, 51, 53, 55), Saudafjorden (Stations 58A, 58B, 58C) and Sandsfjorden (Stations 63, 64, 67), upper digits show catches for 26–27 July, lower digits show catches for 5 August (averages for each fjord branch). Samples in Jøsenfjorden (Stations 85, 86, 87) were collected on 3 July and in Jelsafjorden (Station 70) on 5 August

Taxon	Hylsfjorden		Saudafjorden		Sandsfjorden		Jelsafjorden		Jøsenfjorden	
	No. m ⁻³	P	No. m ⁻³	P	No. m ⁻³	P	No. m ⁻³	P	No. m ⁻³	(No. m ⁻³)
<i>Calanus finmarchicus</i>	40		61		261					374
<i>Acartia</i>	74		148		106				54	1342
	14		36		166				78	
<i>Pseudocalanus elongatus</i>	122	°	257		72				205	309
	18		18		408					
<i>Temora longicornis</i>	146	°	193	°	125	°				138
	41		15		207				35	
<i>Oithona</i>	126		138	°	128					808
	243		334		1592				91	
<i>Microcalanus</i>	542		517		304			°		4
	17		18		4				0	140
<i>Centropages</i>	1	°	8		1					
	1		0		42				46	25
<i>Podon</i>	47	° °	227	***	84				2	37
	29		24		43					
<i>Evadne nordmanni</i>	15		16		5*				2	
	18		34		77				2	
<i>Bivalve larvae</i>	69		31		26					
	14		11		581					
	101	°	209	**	169				139	250

Significance: ° <0.05, ** <0.01, *** <0.001 from one-way ANOVA comparing log-transformed data in a fjord branch for the two sampling periods.

numbers could increase by a factor of 10–100 from inner to outer Sandsfjorden (Stations 63, 64 and 67). Examples of this trend comprised *Centropages*, for which the subsequent outward increase in Sandsfjorden was 0, 31 and 95 individuals m^{-3} , *Pseudocalanus* (67, 297, 860) and bivalve larvae (37, 255, 1451). *Microcalanus* deviated from this general pattern. On 26–27 July, it was more common in the inner fjord branches, and numbers in Sandsfjorden decreased from inner to outer stations (8, 5 and 0 individuals m^{-3}).

Plankton distribution in Hylsfjorden had changed notably since spring. The major discrepancy in the horizontal biomass distribution between April/May and July was a minimum at the head of Hylsfjorden now that the power plant was turned off (Figure 9). *Calanus finmarchicus* was rare in catches from the inner part of this fjord branch (Figure 10). *Acartia* (predominantly *A. clausi*) was still most abundant in inner Jøsenfjorden (Figure 10).

Changes in the course of the summer cruise. The abundance and distribution of several species changed markedly between 26/27 July and 5 August (Table III). In Sandsfjorden, there was a non-significant doubling in the numbers of *Centropages* from the first to the second sampling series. A decrease was indicated in most other species, although it was significant only for *Oithona* and *Podon* (in part due to large within-fjord variance).

The numbers of *Centropages*, *Pseudocalanus* and bivalve larvae increased by about an order of magnitude (or even more) in the inner fjord branches Saudafjorden and Hylsfjorden. *Microcalanus*, on the other hand, had virtually disappeared from the sampling stations in Hylsfjorden on 5 August (Table III).

Discussion

Exchange between Sandsfjorden and coastal water

The excess of freshwater flows out of Sandsfjorden in upper layers. Strong mixing at the power plant outlet, however, creates a denser water mass than at other freshwater sources (Kartvedt and Svendsen, 1990b; present study). When ordinary river run-off is relatively small, currents of the subsequent thin surface layer become subject to local winds (Svendsen, 1981). Direction will vary accordingly, as observed during winter and early spring. Water from the power plant probably left the fjord as part of the prevailing subsurface outflow (Figure 3). Snow melt in the mountainous watersheds causes increased run-off from natural sources during summer (Lie *et al.*, 1992), and the resulting barotropic surface current explains the predominantly outflow measured at 1 m depth from May to August.

In spite of substantial freshwater input, exchange between Sandsfjorden and outer water was mainly driven by coastal processes (e.g. upwelling and downwelling). Periodic inflow at subsurface depth was coupled to deeper, outflowing currents rather than downfjord transport of brackish water. **Even during summer, there was no consistent countercurrent below the outflowing surface current.** The two-layered structure observed during the major freshwater discharge at the end of July (Figure 3) was partly related to coincident upwelling

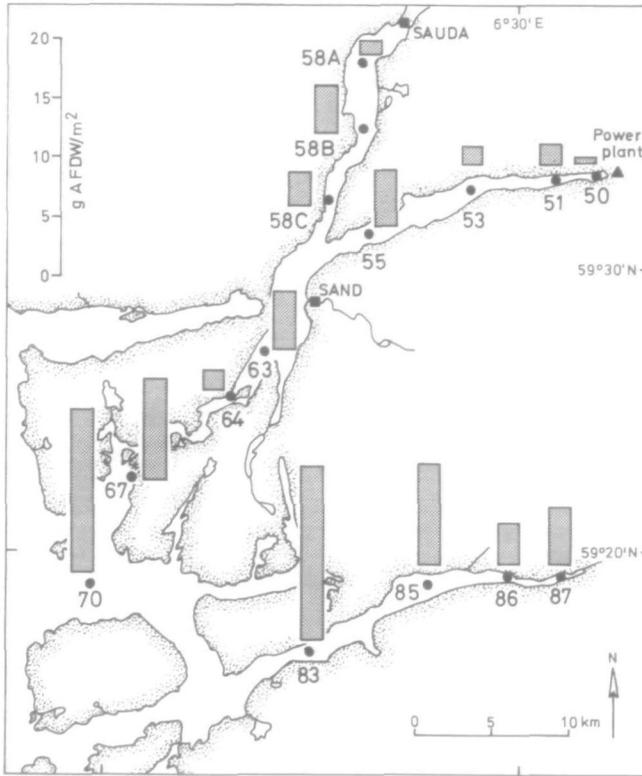


Fig. 9. Distribution of biomass (ash-free dry weight) through the Sandsfjord system and Jøsenfjorden in July 1989, as determined from vertically towed nets (110–0 m)

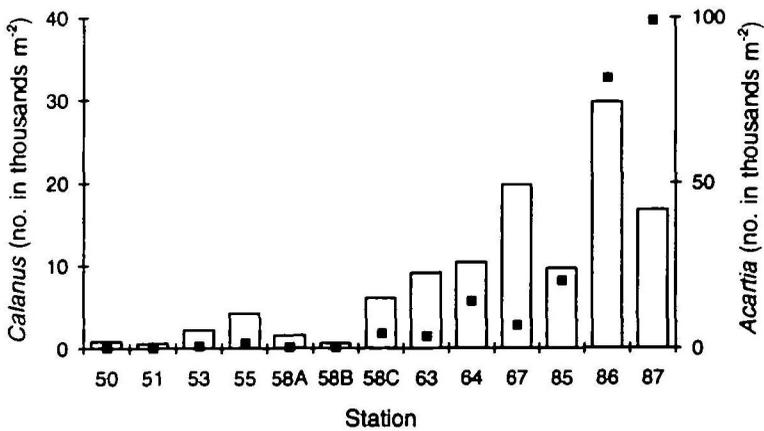


Fig. 10. Distribution of *C. finmarchicus* (open bars) and *Acartia* (black squares) in the Sandsfjord system (Stations 50–67) and Jøsenfjorden (Stations 85–87) in July 1989, as determined from vertically towed nets (50–0 m). Station 50 (left) is at the head of Hylsfjorden, near the power plant outlet, and Station 87 (right) is at the head of Jøsenfjorden.

at the coast (Figure 4). The resulting horizontal pressure field apparently caused the offshore water to pour in above the sill, where it displaced the lower part of the intermediate water in the fjord. This was compensated for by outflow above (i.e. augmenting the freshwater-driven flow).

The opposite circulation pattern, with inflow in upper layers and outflow below, develops during periods of downwelling (Svendsen and Thompson, 1978; Aure and Sætre, 1981; Sætre *et al.*, 1988). Extensive exchange between fjords and outer water thus represents a principal stochastic element of the fjord ecology, with the frequency and magnitude of inflow and outflow at different depths depending on weather conditions.

The cross-sectional area at the entrance of a fjord is a primary boundary property, and the ratio between this area and the total fjord volume indicates the importance of advection versus internal biological processes (Aksnes *et al.*, 1989; Kaartvedt, 1991). The Sandsfjord system is fairly enclosed, with a large body of water commuting with outer regions through a relatively narrow constriction. Nevertheless, exchange with coastal water clearly influenced plankton abundance and distribution. The estimated advection rates during spring were on the same order of magnitude as zooplankton growth rates (Aksnes *et al.*, 1989). The impact of advection was, furthermore, evidenced by considerable changes in plankton distribution associated with physical oceanographic events during the July/August survey (Table III). The decimation of *Podon* in Sandsfjorden following the pulse of freshwater was apparently caused by freshwater-driven flushing, as *Podon* mainly inhabited the brackish layer (unpublished results from pump sampling; see also Kaartvedt and Nordby, 1992). Intrusion of coastal waters (Figure 3) apparently supplied *Centropages*, *Pseudocalanus* and bivalve larvae. These groups were initially more common in outer parts of the fjord system, and became augmented in the inner fjord branches Saudafjorden and Hylsfjorden following the inflow. The dynamic environment related to the large freshwater discharge presumably contributed in redistributing plankton between the fjord branches.

Advection of plankton in Hylsfjorden

Currents driven by local freshwater discharge prevail in Hylsfjorden. The conspicuous biomass accumulation at the head during operation of the power plant in April/May (Figure 7) was obviously due to supply by the compensation current, as animals submerging beneath the brackish water (Figure 6) became exposed to the inward flow. Although only a weak estuarine circulation was recorded when we were in the fjord system, currents were probably stronger preceding the survey, when the power plant was operated at full capacity. We have reported elsewhere strong estuarine circulation (with inflow below ~5 m) in Hylsfjorden during periods of optimum discharge (Kaartvedt and Svendsen, 1990b).

In July, the restart of the power plant (including overflow through the bypass tunnel) caused pronounced plankton transport in Hylsfjorden. For the period of maximum discharge, Kaartvedt and Aksnes (1992) estimated the daily import of

plankton by the freshwater-driven compensation current at 26% of the total standing stock in the upper 50 m of the fjord branch. Such upfjord advection caused the apparent elimination of *Microcalanus*. Since *Microcalanus* was scarce in the outer source waters (Table III), no outer population could replace the individuals that had been transported towards the head. By using an outboard and sampling closer to the power plant than the research vessel could go, high numbers of *Microcalanus* (as well as other species) were found by Kaartvedt and Aksnes (1992) after the freshwater discharge (3 August). This was due to physical accumulation, as none were caught in this location prior to discharge.

The establishment of an artificial river at the head has altered the plankton dynamics of Hylsfjorden. Prior to the regulation, this fjord branch almost invariably contained low numbers of *C. finmarchicus* (Fosshagen, 1979), which is a species characteristic for outer, more oceanic conditions. Inner Hylsfjorden is only slightly affected by intrusions of coastal water, although Fosshagen (1979) occasionally found changes in fauna composition related to such events. Thus, increased freshwater input has paradoxically made the fauna more marine, a trend sometimes strengthened by removal of the shallow-living brackish water fauna by flushing (Kaartvedt and Nordby, 1992).

A continuous supply of plankton, however, is apparently necessary to maintain high abundance, as indicated by the impoverished fauna at the end of July after the power plant had been shut down for less than a month. This leads to the question what is the fate of this plankton? Our observations suggest that inner Hylsfjorden may be a dead end, literally speaking. We have seen abundance of fish, probably foraging on advected prey. Plankton may also be killed by osmotic stress in the mixing zone between freshwater and seawater at the power plant outlet (Kaartvedt and Aksnes, 1992).

Jøsenfjorden

In April, *Acartia* increased strongly in numbers at the shallowest station in inner Jøsenfjorden (Figure 8), where it was also most numerous in July (Figure 10). Furthermore, population maxima of *Acartia* at the head were observed on other surveys (as well as before removal of the local freshwater supply; Fosshagen, 1979). In November 1987, concentrations in the upper 50 m increased from 9 m⁻³ at Station 85 to 1320 m⁻³ at Station 87, and in October 1988 from 438 m⁻³ at Station 85 to 9584 m⁻³ at Station 87.

This distribution cannot be explained by estuarine circulation, since there is virtually no freshwater run-off to Jøsenfjorden after the river regulation. Wind-driven advection sometimes causes plankton accumulation at the head (Kaartvedt, 1991), but the taxon-specific pattern and the temporal persistence of the maxima suggest that the aggregation of *Acartia* is not caused by transport processes.

The more estuarine characteristics of the plankton composition at the head of Jøsenfjorden (as indexed by the abundance of *Acartia*) apparently are not related to salinity. There were no essential salinity gradients along the fjord in

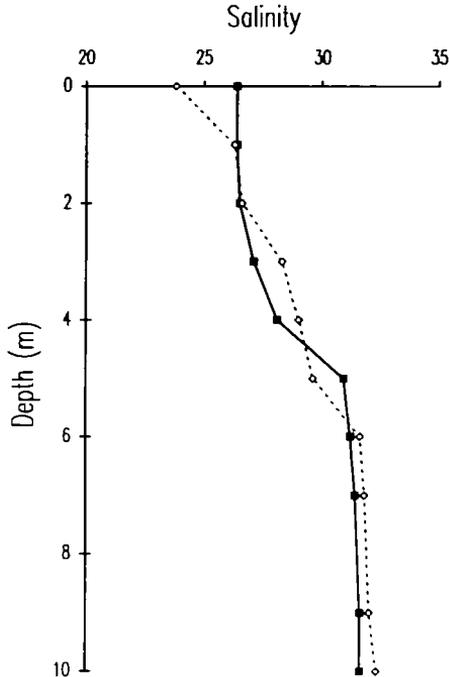


Fig. 11. Vertical salinity profiles in outer (Station 83; solid line) and inner (Station 87; stippled line) Jøsenfjorden in April 1989.

April (Figure 11), nor in November 1987 (not measured inside Station 86) and October 1988. Water at the head was, however, strongly diluted in July 1989 (salinities of 6 at 2 m), but this was a unique event, related to the flow over at the main storage magazine (see the previous section on freshwater discharge). *Acartia* was not numerous in the freshwater-influenced Sandsfjord system (Figures 8 and 10).

We relate the increasing numbers of *Acartia* towards the head of Jøsenfjorden to shallowing depths. Some invertebrate predators are excluded above shallow topography [see, for example, Kaartvedt (1993)], which may reduce the mortality of small copepods. More specific for *Acartia*, however, the production of benthic resting eggs in this genus represents an obvious link to the bottom, suggesting higher recruitment in relatively shallow habitats. Moreover, if maintenance of horizontal distribution above shallow bottom contributes to reproductive success [discussed further in Kaartvedt (1993)], this may select for copepod behavior enhancing retention in such favorable locations (e.g. Kimmerer and McKinnon, 1987; Sinclair, 1988; Kaartvedt and Nordby, 1992).

Conclusion

The major findings in this investigation were the high concentration of

zooplankton in inner Hylsfjorden in April/May, the changes in plankton abundance and distribution in the course of the July/August cruise, and the high abundance of *Acartia* in inner Jøsenfjorden. We ascribe the two first observations to transport processes, while we relate the abundance of *Acartia* to a favorable habitat.

The establishment of an artificial river at the head of Hylsfjorden has pronouncedly altered the plankton transport in this fjord branch. Freshwater-driven currents generally cause inward advection of marine mesoplankton in Hylsfjorden. The well-developed halocline acts as an upper barrier for marine species, which accordingly become entrained by the compensation current.

Exchange between Sandsfjorden and outer water is apparently mainly driven by coastal processes. Estimated exchange rates are on the same order of magnitude as zooplankton growth rates, suggesting a fairly similar importance of local growth and advection on the mesoplankton standing stock in the Sandsfjord system. However, pulsed intrusions of coastal water represent a major stochastic element, and can change the plankton composition and distribution in the fjord system on time scales of days.

In Jøsenfjorden, the abundance of *Acartia* increased at shallow depths along a transect of unaltered salinity, advocating the importance of bottom topography for estuarine species composition.

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