

Vertical distribution of fish and krill beneath water of varying optical properties

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ABSTRACT: The distribution of acoustical scattering layers of fish and krill changed markedly in concert with fluctuating fluorescence (chlorophyll *a*) in upper waters, possibly due to a varying 'shadow effect'. Beneath clear waters on the outer Norwegian shelf (about 300 m depth), mesopelagic fish (*Maurolicus muelleri*) were located at approximately 150 to 200 m by day. Krill (mainly *Thysanoessa inermis*) was primarily found below the mesopelagic fish and above planktivorous demersal fish (Norway pout *Trisopterus esmarkii*). The vertical distributions changed abruptly across a front into water with less light penetration associated with increased fluorescence (chlorophyll *a*). Mesopelagic fish ascended by about 100 m accompanied by a rise of krill. Demersal fish left the benthic boundary zone, with ascending Norway pout foraging in the lower part of the krill layer. We suggest that the intermediate light conditions inside the front provided an 'antipredation window' (sensu Clark & Levy 1988: Am Nat 131:271–290) and thereby favorable feeding conditions for the planktivore. These results indicate that properties of upper layers may impact plankton and fish distributions and their predator-prey interactions throughout the water column on continental shelves.

KEY WORDS: Shading · Visual predation · Plankton behavior

INTRODUCTION

Fish generally depend on vision for efficient foraging (e.g. Zaret & Suffern 1976, Gliwicz 1986, Thetmeyer & Kils 1995). The light level and optical properties of the environment, therefore, are key elements for predator-prey relationships of fish and plankton with piscivores and planktivores (Clark & Levy 1988, Aksnes & Giske 1993, Giske et al. 1994, Rosland & Giske 1994, Fiksen & Giske 1995).

The vertical distribution of plankton and fish may reflect a trade-off between food intake and mortality risks (Johnsen & Jakobsen 1987, Clark & Levy 1988, Rosland & Giske 1994). Plankton often seem to optimize this trade-off by inhabiting upper, food rich layers in the shelter of darkness by night, and hiding at depth by day. Piscivores may constrain foraging behavior of planktivores so that the ratio of planktivore feeding rate to mortality risks reaches a maximum at intermediate levels of light intensity (Clark & Levy 1988).

Over continental shelves sufficient light may reach the bottom for visual predators to detect their prey throughout the water column. Predation on plankton by demersal fish is prominent on shallow banks (Isaacs & Schwartzlose 1965, Hobson & Chess 1986, Genin et al. 1988, 1994, Hobson 1989). Here, fish forage on vertically migrating individuals that, after having been carried by surface currents onto the shelf-bank at night, are trapped by the relatively shallow bottom during their morning descent. Apparently, plankton from oceanic populations are especially vulnerable to predators in this setting, which is very different from their normal daytime habitat (Hobson 1989).

Banks and continental shelves are also inhabited by more or less resident plankton populations (e.g. Hobson & Chess 1986, Barange & Pillar 1992, Kaartvedt 1993). Shelf species are adapted to their relatively shallow habitat, and probably possess behavioral traits to counteract the threat of both pelagic fish from above and bottom associated fish from below. Recent studies of freshwater and marine zooplankton have shown that occurrence of pelagic fish may stim-

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ulate downward plankton swimming by day (Bollens & Frost 1989, 1991, Bollens et al. 1992a, b, Dawidowicz & Loose 1992, Frost & Bollens 1992, Neill 1992, Huang et al. 1993). Studies on plankton behavioral responses to the presence of demersal predators appear to be lacking.

In this paper, we address the distribution of mesopelagic planktivorous fish (*Maurollicus muelleri*), krill (*Thysanoessa inermis*), and bottom associated planktivorous fish (Norway pout *Trisopterus esmarkii*) along a cross-shelf transect from oceanic waters and through a front on the shelf. We suggest that shading of light transmission by phytoplankton may be essential in governing the distribution of fish and krill and their predator-prey relationships, and we report on possible krill behavior that may reduce interactions with their demersal fish predators.

MATERIAL AND METHODS

The study was carried out off northern Norway in April 1993 (Fig. 1). A cross-shelf transect was first covered by RV 'Johan Hjort' and, about 5 h later, by RV 'G.O. Sars'. The distributions of macroplankton and fish were continuously recorded acoustically by ship-mounted SIMRAD EK 500, 38 kHz and 120 kHz split-

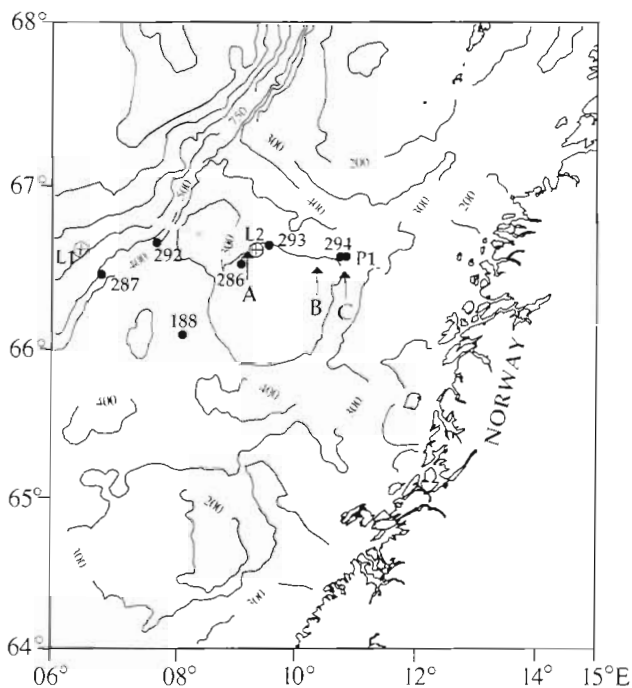


Fig. 1 Map of study area with bottom contours. Track of acoustical transect is indicated by dotted line. Points A, B, and C depict locations studied and referred to in other figures. Locations of trawling stations (see Table 1), and stations for light measurements (Stns L1 and L2) are given

beam echo sounders. Concurrent continuous measurements of salinity, temperature and fluorescence were made in water from the ship's sea water pump (taken at 5 m), using a Meerestechnik 1500 mini-CTD (conductivity, temperature, depth profiler) and a Turner design fluorometer. Water samples for chlorophyll *a* (chl *a*) analyses were taken at 10 m with Niskin bottles, and 260 ml subsamples were filtered through Whatman GF/C filters and analyzed by standard methods. A linear relationship was found between these chl *a* values at selected stations and corresponding data from the continuous measurements of fluorescence along the transect ($\text{Chl } a = 11.5 \text{ Fluorescence} - 5.3$; $r^2 = 0.88$, $n = 9$). This relationship was used to convert the continuous fluorescence measurements into chl *a* values.

Vertical profiles of salinity, temperature, fluorescence and light extinction were measured at selected stations. We used Neil Brown CTDs (apparently giving salinity values about 0.1‰ higher than the mini-CTD), and a Seatech fluorometer that was attached to the CTD of RV 'G.O. Sars'. Downwelling irradiance was measured with a Biospherical light meter, which measured light on separate wavelengths and was also equipped with a CTD and a fluorometer.

For identification of acoustical targets, sound-scattering layers (SSLs) were sampled by various midwater trawls [Harstad trawl (Nedreaas & Smedstad 1987); Method Isaacs-Kidd midwater trawl (MIK; Munk 1988) and Åkra trawl (Valdemarsen & Misund 1995)]. Sampling depths were monitored by a Scanmar trawl eye or Scanmar depth sensor. Details are given in Table 1.

Feeding of Norway pout was investigated from analysis of stomach content of fish caught in the Harstad trawl. Stomachs were dissected out, injected with 10% formalin and stored in separate jars with 10% formalin.

RESULTS

Acoustical recordings

Off the shelf, and on the outer part of the shelf, recordings at 38 kHz revealed a narrow SSL situated at about 150 to 200 m by day (e.g. to the left in Fig. 2). A more diffuse layer of weaker targets was observed below, extending almost down to the bottom on the outer shelf, where they sometimes occurred in relatively dense aggregations (i.e. denser than appears to the left in Fig. 2). Fairly strong targets (fish) dominated in the benthic boundary zone.

The mesopelagic fish Müller's pearlside *Maurollicus muelleri* prevailed in catches from trawling aimed at

Table 1. Trawl catches in acoustical structures designated by their relative vertical distribution during daytime. Locations of stations are depicted in Fig. 1. Time refers to start of tow and is given as European standard time (GMT + 1 h). ÅT: Åkra trawl; HT: Harstad trawl; MIK: Method Isaacs-Kidd midwater trawl

Acoustical structure	Stn	Gear	Date (1993)	Time (h)	Fishing depth (m)	Catches (kg per nautical mile)
Upper layer	292	ÅT	22 April	04:10	145–100	<i>Maurolicus muelleri</i> (2.1), <i>Periphylla periphylla</i> (0.7), <i>Clupea harengus</i> (0.6), <i>Pollachius virens</i> (0.5)
	188	HT	18 April	14:50	220–180	<i>M. muelleri</i> (0.8), unidentified krill (0.2)
	286	HT	19 April	18:00	70–50	<i>M. muelleri</i> (0.8), <i>Thysanoessa inermis</i> (0.7), <i>Meganyctiphanes norvegica</i> (0.07)
Intermediate layer	287	ÅT	20 April	13:35	230–200	<i>M. muelleri</i> (6.7)
	293	HT	22 April	13:00	170–140	<i>T. inermis</i> (6.0), <i>M. muelleri</i> (0.4), <i>M. norvegica</i> (0.2), <i>Nyctiphanes megalops</i> (0.06), <i>Trisopterus esmarkii</i> (0.05), <i>Argentinus silus</i> (0.05)
Intermediate/ bottom associated layer	P1	MIK	23 April	21:30	70–50	<i>T. inermis</i> (0.7), <i>Thysanoessa longicaudata</i> (0.001)
	294	HT	22 April	20:25	220–170	<i>T. inermis</i> (6.5), <i>M. norvegica</i> (2.9), <i>T. esmarkii</i> (0.7), <i>M. muelleri</i> (0.01), <i>A. silus</i> (0.01)

the upper SSL (Table 1). Samples from the intermediate, diffuse layer consisted mainly of the krill *Thysanoessa inermis* (Table 1). The benthic boundary zone was not sampled.

During the cross-shelf transect, the vertical distribution of all targets changed abruptly after about 70 km of mapping. The upper layer (interpreted as mesopelagic fish; see 'Discussion') ascended by approximately 100 m. There was a coinciding ascent of the diffuse targets (interpreted as krill). Demersal fish left the benthic boundary zone. This could be better visualized by expanding the bottom 10 m of the acoustic records (Fig. 2). These were not temporal effects, as similar patterns were observed by the 2 research vessels making their records almost 5 h apart.

Landward of this sudden rise, ascending 'demersal' fish were observed in the lower 50 to 100 m of the water column during the subsequent ~50 km of acoustical recordings in daylight. Their distribution partly extended into the lower component of the krill layer, on several occasions apparently accompanied by a concurrent ascent of krill. The most prominent example of concurrent rise by fish and krill is presented in Fig. 3. Outside a patch of fish, the krill layer extended almost down to the sea floor. With increased numbers of fish rising from the benthic boundary zone, the distribution of krill became shallower, and a

more compact SSL was formed about 100 m above bottom. Parallel to the ascent, the values of fish backscattering (a measure of fish biomass) increased by an order of magnitude (Fig. 3), and peaked in the region of shallowest krill distribution. Thereafter integrated fish values decreased and both fish and krill descended. The total backscattering of krill was fairly constant along this section (Fig. 3).

Trawl catches in the ascending layer consisted mainly of krill and Norway pout *Trisopterus esmarkii* (Table 1). *Thysanoessa inermis* was the only identifiable prey item in the stomachs of Norway pout (Table 2).

Table 2. Stomach content of a subsample of 9 Norway pout *Trisopterus esmarkii* from a midwater trawl catch at Stn 294 on 22 April 1993 (20:25 h European standard time: GMT + 1 h). Bottom depth 295 m, sampling depth 170 to 220 m. Scale for stomach fullness is from 1 (empty) to 5 (full and distended). Scale for state of digestion is from 1 (fresh) to 5 (mushy)

Fish length (cm)	Stomach content (g)	Dominant prey item, n	Stomach fullness	State of digestion
11	Empty	–	–	–
11	0.334	<i>Thysanoessa inermis</i> (17–20 mm), 5	4	1, 3
14	0.100	<i>T. inermis</i> (19 mm), 5	3	2–3
14	0.085	Unidentified krill, 2	3	3
14	Empty	–	1	–
15	0.466	<i>T. inermis</i> (20, 21 mm), 2	4	–
15	0.471	<i>T. inermis</i> (17–20 mm), 5	4	2
16	0.169	Unidentified krill, 2	3	3
17	1.128	Unidentified krill	4	3

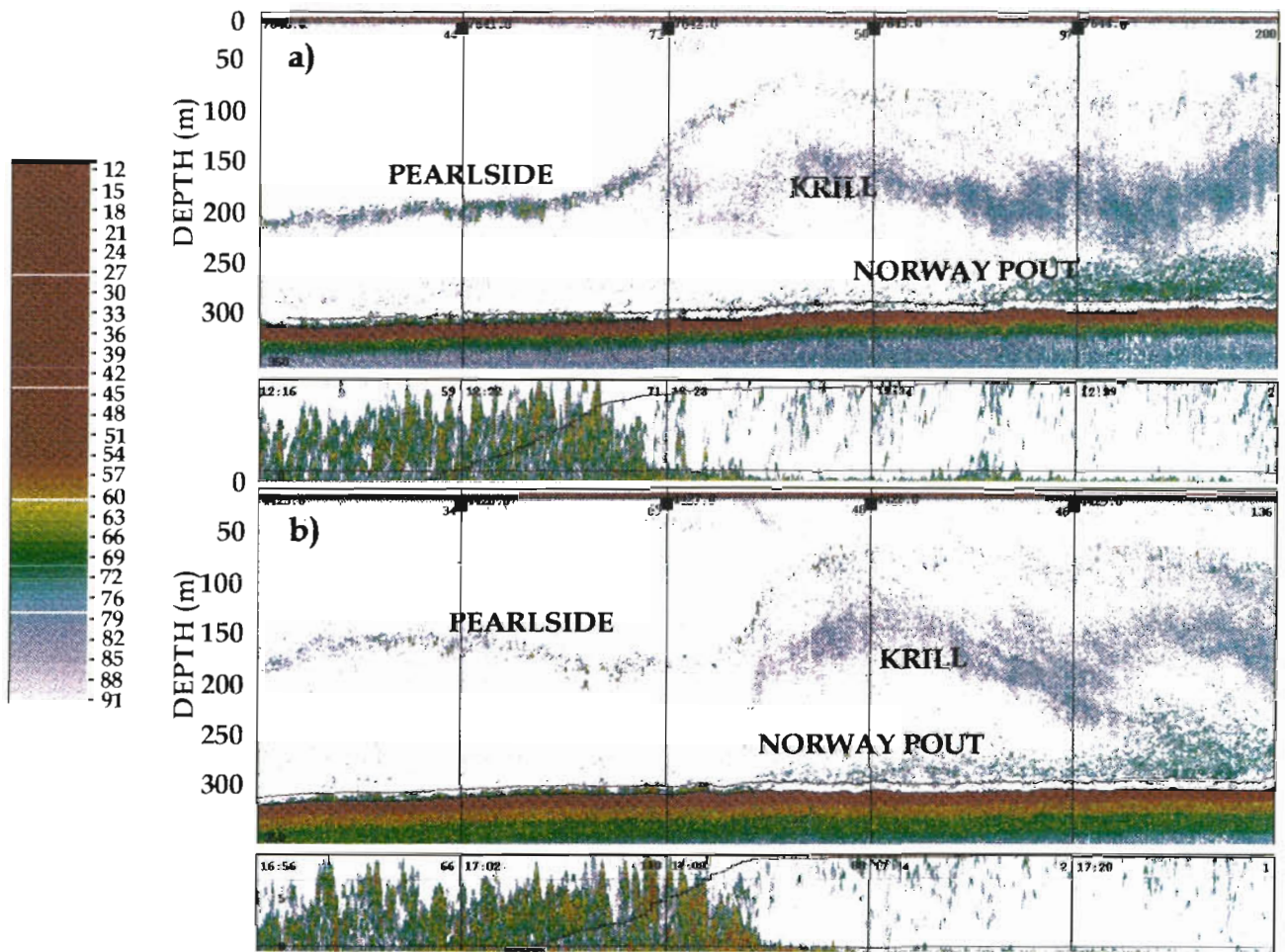


Fig. 2. Echograms (38 kHz) from (a) RV 'Johan Hjort' at 13:16–13:45 h European standard time (GMT + 1 h) and (b) RV 'G.O. Sars' at 17:56–18:25 h on 22 April 1993. Location of the abrupt changes in vertical distributions corresponds to Point A of Fig. 1. Color code refers to volume backscattering strength (db). Vertical lines delineate nautical miles. Lower, narrow panels show vertical expansions of the lowermost 10 m above the sea floor. Build-up lines of integrated backscattering for these bottom windows are superimposed. Identities of acoustical layers are suggested

Environmental characteristics

The abrupt changes in vertical distributions depicted in Fig. 2 were associated with a front, as demonstrated by concurrent drops in surface (5 m) salinity and temperature, and increased chl *a* (fluorescence) values (Fig. 4; point A). There was no apparent change in the hydrography at depth. Changes in surface salinity and temperature were relatively small, while fluorescence and light extinction inside the front were much higher than in oceanic water (Figs. 4 to 6; vertical profiles of light extinction not available from just outside the front).

The ascent of demersal fish and krill further landward, portrayed in Fig. 3, took place beneath a surface lens of slightly saltier, warmer water with intermediate

concentrations of chl *a* (Fig. 4; between points B and C). There was no apparent change in the hydrography at depth (Fig. 6).

DISCUSSION

Identification of SSLs

The use of acoustics provides unsurpassed temporal and spatial coverage and also offers the advantage of mapping fish and larger zooplankton simultaneously. Identifications of targets may, however, represent a problem and must partly rely on supplementary methods. Based on the net catches, acoustic characteristics, and previous investigations, we feel confident that the

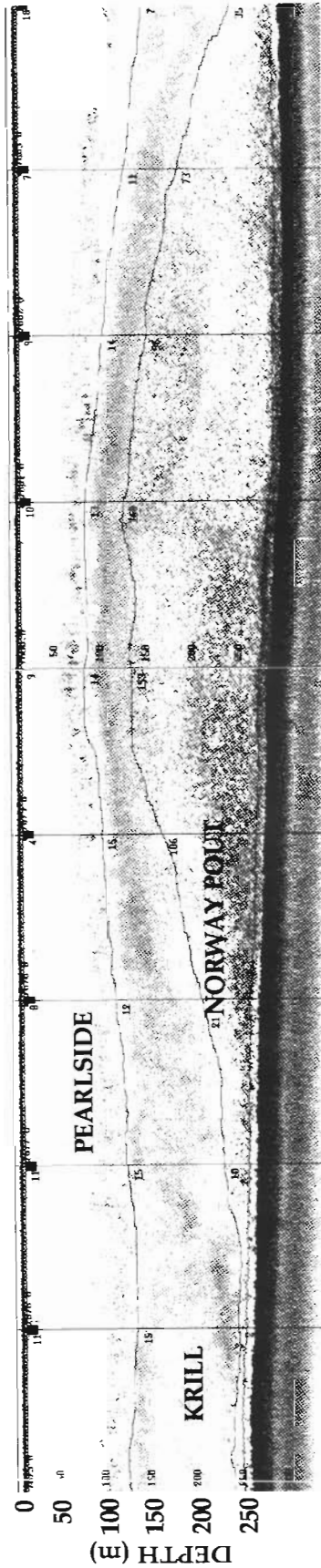


Fig. 3. Echogram (38 kHz) from RV 'Johan Hjort' at 18:37–19:55 h European standard time on 22 April 1993. Left and right of the figure correspond to Points B and C of Fig. 1. Vertical lines delineate nautical miles. Interpreted pearlside, krill and Norway pout distributions are delineated. Digits in upper right corners give integrated echo level for the outlined 'blocks', as calculated by the Bergen Echo Integrator system (Foote et al. 1991)

3 groups of targets addressed in this investigation are correctly identified.

Maurolicus muelleri prevailed in samples from trawling aimed at the upper mesopelagic SSL, though catches were small (Table 1). This corresponds to other offshore sampling in this type of acoustical structure (Bergstad 1990, Melle et al. 1993). In Norwegian fjords, both video recordings and trawling have clearly revealed that *M. muelleri* is the main target in this kind of layer, characterized by narrow vertical extension and considerable horizontal patchiness (Giske et al. 1990, Skjoldal et al. 1993, Rasmussen & Giske 1994, Bjelland 1995, authors' unpubl. results).

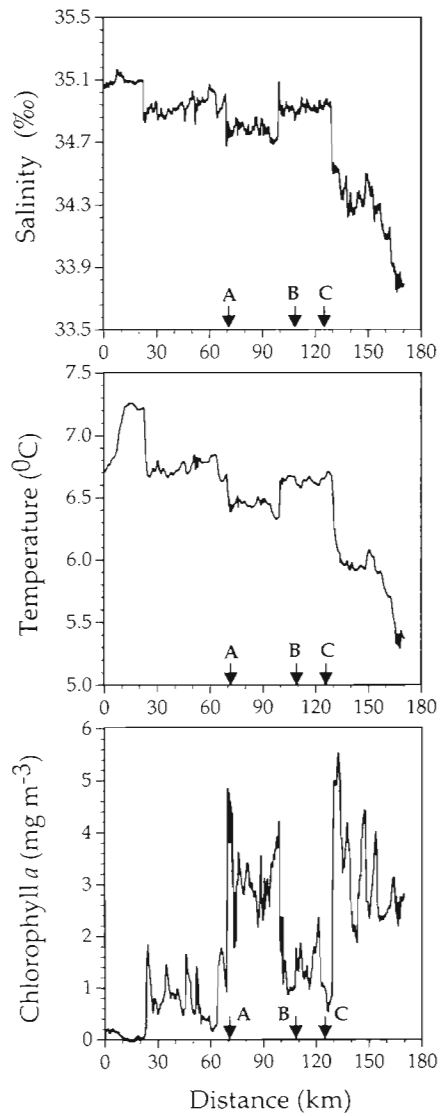


Fig. 4. Continuous measurements of salinity, temperature and chlorophyll *a* (as estimated by the regression $Chl\ a = 11.5\ Fluorescence - 5.3$; $r^2 = 0.88$, $n = 9$) at 5 m depth during the cross-shelf transect from oceanic (left) to coastal water (right). Points A, B, and C denote locations referred to in Fig. 1

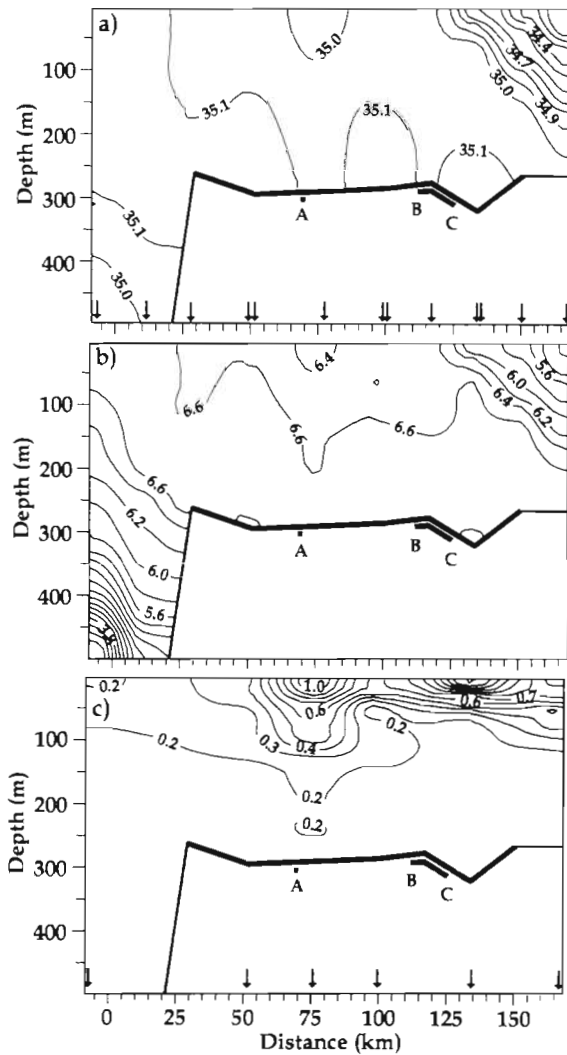


Fig. 5. Isolines of (a) salinity, (b) temperature and (c) fluorescence across the continental shelf from oceanic (left) to coastal water (right) on 22 April 1993. Bottom contour is processed from acoustical data obtained during the transect. CTD profiles from RV 'Johan Hjort' and RV 'G.O. Sars' are combined while fluorescence results are from 'G.O. Sars'. Arrows depict sampling stations. Points A, B, and C depict locations referred to in Fig. 1. The less haline and colder water shoreward of Point C represents the Norwegian coastal current

Catches in the diffuse SSL were dominated by krill (predominantly *Thysanoessa inermis* and some *Meganyctiphanes norvegica*; Table 1). Also the acoustical signature and comparison between the 2 frequencies suggested that this SSL was composed of many relatively small organisms. While ascending into the upper 100 m at night, i.e. within the range of the 120 kHz sounder, these targets were more distinctly revealed by the higher frequency (not shown). Krill is at the lower end of the detectable size range at 38 kHz, and

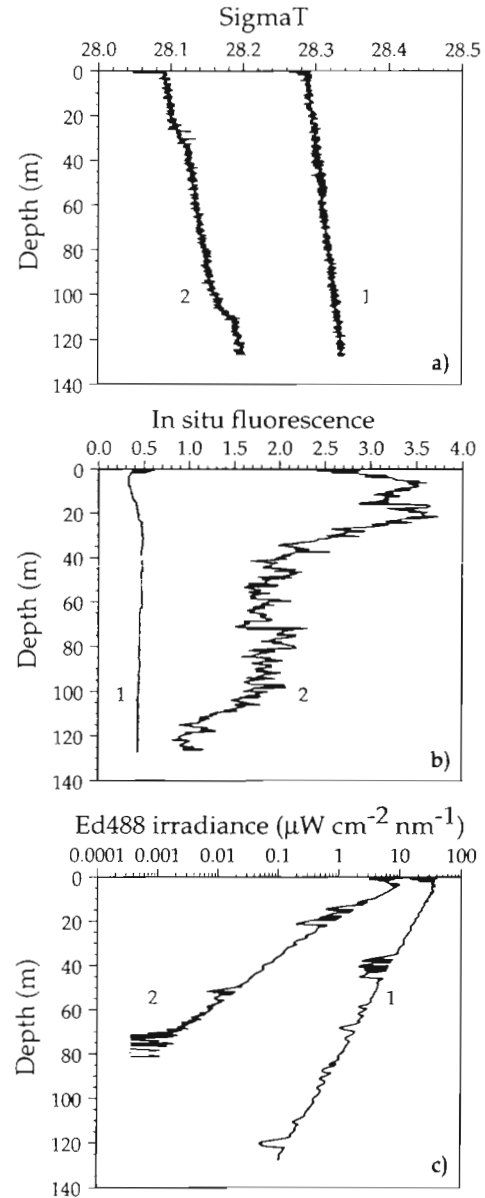


Fig. 6. Vertical profiles of (a) sigma T, (b) fluorescence, and (c) transmission of blue light in (1) waters outside the shelf break (Stn L1) and (2) just inside Point A (Stn L2)

will be better displayed at 120 kHz (Everson et al. 1990, Foote et al. 1990, Greene et al. 1991).

We did not carry out bottom trawling during the survey, but have 1 trawl catch identifying the ascending fish as Norway pout. On other cruises, bottom trawling on the shelf has yielded catches dominated by Norway pout in similar acoustical structures (Torgersen 1995, unpubl. data from the Institute of Marine Research, Bergen). The color code of single fish echoes indicates that the prevailing demersal targets were relatively small fish.

Factors governing vertical distributions

Distribution of scattering layers across fronts has elsewhere been found to follow water types (Sameoto 1982). Our results, however, were apparently not explainable by preference for a particular water mass, as temperature and salinity in deeper waters were fairly homogeneously distributed along the transect. We suggest that the 'shadow effect' caused by algal growth in waters inside the front played an instrumental part in shaping vertical distributions.

Light levels appeared to be roughly corresponding in the layer of *Maurolicus muelleri* outside and inside the front. Light intensity at the top of the pearlside layer just inside the front (taken as 80 m) was 0.0002 and 0.0005 $\mu\text{W cm}^{-2} \text{nm}^{-1}$ for blue (488 nm) and green (520 nm) light respectively. By extrapolating the light extinction curves for water outside the shelf break (Stn L1), corresponding values were found at 230 m (blue) and 170 m (green). The pearlside layer in this specific location was recorded between 180 and 210 m. Previous studies have shown that the pearlside is very sensitive to fluctuating light, for example rapidly adjusting its vertical distribution in response to variable cloudiness (Giske et al. 1990, Baliño & Aksnes 1993, Rasmussen & Giske 1994)

Also, Norway pout and euphausiids are sensitive to the ambient light (e.g. Gordon 1977, Sameoto 1980, Kulka et al. 1982, Albert 1993) and may have responded to the 'dusk' inside the front. Besides, the algae represent a food source for the krill. In the example portrayed in Fig. 3, however, the vertical distribution of krill apparently shallowed in concordance with increased predation pressure from below. This was evidenced by enhanced fish abundance (an order of magnitude), their vertical extension into the krill layer and fish stomach content (Table 2). Alternatively to a causal relationship with krill adjusting their vertical distribution when exposed to the ascending predators, the upward displacement may have had a physical cause, such as internal waves (e.g. Haury et al. 1979). The incident took place fairly late in the afternoon (~0.5 to 1.5 h prior to sunset), but the shallow distribution apparently did not reflect an initiation of diel vertical migration as the ascent was followed by a subsequent descent. The intermediate fluorescence of upper layers (Fig. 4) implies higher transparency than elsewhere on the inner shelf, but lower than in outer shelf waters.

Trophic interactions

Distribution of demersal Norway pout and krill was mainly vertically disjunct outside the front, while the

pout ascended into the lower part of the krill layer inside the front, foraging on *Thysanoessa inermis*. Small fish, like Norway pout (e.g. Table 2), are themselves potential prey of visually hunting fish, and possibly become more vulnerable to predation when foraging in the water column (see for example Donnelly & Dill 1984, Lima & Dill 1990). Piscivores need more light than planktivores to hunt efficiently since the numerical density of fish prey is much lower than zooplankton (Clark & Levy 1988). Thus, the ratio of mortality risk to feeding rate for the planktivore reaches a minimum at intermediate levels of light intensity, a so-called 'antipredation window'. In the original model by Clark & Levy (1988), 'antipredation windows' for planktivores occur for brief intervals at dawn and dusk. We suggest that the model may as well apply along horizontal transects in, or below, waters of different optical properties. This would be in accordance with laboratory studies ascribing increased planktivorous feeding in waters of intermediate turbidity to reduced potential risk to predators (Gregory & Northcote 1993).

Acknowledgements. We thank Egil Sakshaug and Runar Dal-løkken for access to light data, and Karsten Hansen, Thomas Torgersen and Tom Viken for technical assistance. This is a contribution from the research program *Mare Cognitum*.

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