

LARGE SCALE DISTRIBUTION OF ACOUSTICAL SCATTERING LAYERS AT THE NORWEGIAN CONTINENTAL SHELF AND THE EASTERN NORWEGIAN SEA

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Vertical and horizontal distributions of fish and micronekton were mapped in a zigzag pattern from Lofoten, northern Norway to Stadt, southwestern Norway, in March 1992. Pearlsides (*Maurolicus muelleri*) were present whenever depth was sufficient for daytime requirements (i.e. > 150-200 m). They performed diel vertical migrations, characterized by ascent at dusk, followed by nocturnal descent, and a dawn ascent before downward migration to day depth. Nocturnal descent among pearlsides has previously been explained by preference for warm water to speed up digestion, but this could not explain the results in this study as relevant vertical temperature gradients were minor. A deep scattering layer consisting of mesopelagic fish, pelagic shrimps and other macroplankton was present outside the shelf. This layer was located beneath ca 300 m by day, while the tendency to carry out diel vertical migrations varied strongly between water masses. Blue whiting (*Micromesistius poutassou*) associated with the layer by day consistently swam into upper waters by night. Dense concentrations of blue whiting at the shelf break, however, remained near the bottom both day and night. Herring (*Clupea harengus*) were confined to the shelf, staying near the bottom by day and ascending into upper waters by night. Norway pout (*Trisopterus esmarkii*) lived near the bottom by day, while degree of diel vertical migration appeared to differ among locations.

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INTRODUCTION

One aim of the research program *Mare Cognitum* is to evaluate factors influencing fish distribution and behavior in the Norwegian sea as well as the impact exerted by fish on lower trophic levels (SKJOLDAL & al. 1993a). A first step to reach this goal may be to establish large scale distribution and behavior along environmental gradients, which may form the basis for more process oriented studies addressing causes behind patterns and variability.

Acoustical methods, in combination with visualization techniques, provide the opportunity of addressing large scale patterns. Planktivorous fishes are major fauna components and prevailing acoustical targets in Norwegian shelf waters and in the Norwegian Sea. Herring (*Clupea harengus*; during the spawning season) and Norway pout (*Trisopterus esmarkii*) are preva-

lent species on the shelf. Blue whiting (*Micromesistius poutassou*) is common both at the shelf break and in the open Norwegian Sea, while the mesopelagic fishes pearlsides (*Maurolicus muelleri*) and northern lanternfish (*Benthosema glaciale*) are major components of the fauna in deep oceanic locations (MELLE & al. 1993). These species are mainly visual predators, exploiting, and possibly structuring meso- and macroplankton assemblages.

In this paper, we study acoustical scattering layers along the Norwegian shelf and the adjacent Norwegian Sea during spring. We address patterns of vertical and horizontal distributions, and when applicable, discuss results with respect to environmental variables. By visualizing large scale trends in the distribution of planktivores, we also to some extent formulate the patchy predatory regime encountered by zooplankton.

MATERIAL & METHODS

The survey was carried out with R/V *G.O. Sars* from 13 March to 29 March 1992. It started off Lofoten, northern Norway, and ended off Stadt, southwestern Norway, following a zigzag cruise pattern across the shelf into oceanic water (Figure 1). An additional 24 h station was carried out at a fixed location (Figure 1). The distributions of scattering layers were continuously recorded by a hull mounted SIMRADEK 500 38 kHz echo sounder. Data for the upper 500 m were stored by means of Bergen Echo Integrator system (KNUDSEN 1990, FOOTE & al. 1991), and later compressed and plotted using UNIRAS. The volume backscattering threshold (S_v) was - 84 dB. During post-processing, acoustic area backscattering (S_A) were assigned to 12 m depth channels for each nautical mile (nm), and the presented plots are based on interpolation. The area backscattering S_A is expressed as backscattering m^2/nm^2 for a given depth interval (KNUDSEN 1990, FOOTE & al. 1991) and relates to S_v by the formula

$$S_A = 4\pi 1852^2 \int_{z_1}^{z_2} S_v dz$$

where z_1 and z_2 are the layer limits.

Bottom depth for each nautical mile was defined as the greatest depth in that mile. In regions of varying bottom topography, this occasionally has caused demersal targets to seem to be off the bottom. Due to much noise and few animals, the shallowest channel (5-17 m) was excluded in the plots. Here we only present the compressed plots, though we partly rely on more high resolution ping-based prints in identification of organisms that caused the acoustical structures. Further details are given by TORGENSEN (1995).

For further identification of acoustical targets, sound scattering layers were sampled by a pelagic Harstad trawl (NEDREAAS & SMEDSTAD 1987), and on one occasion by bottom trawl. Details are given in Table 1.

Vertical profiles of salinity and temperature were measured at selected stations, using a Neil Brown CTD. Water samples from attached Niskin bottles were used to measure chlorophyll *a* (chl*a*). Zooplankton were sampled by MOCNESS, but these data are only briefly referred to in the 'Discussion'.

As the survey spanned two weeks and extensive latitudinal and longitudinal gradients, local timing of sunset and sunrise was estimated with a precision of 1 minute by a model provided by Institute for Theoretical Astrophysics, University of Oslo.

RESULTS

Hydrography and chl*a*

Temperature profiles from the northernmost and southernmost transects are given in Fig. 1. A wedge of relatively cold water with reduced salinity was present at the shelf. Surface temperatures and salinities were

lowest nearshore (ca 4.5-6 °C and 34) and increased westward (attaining about 8 °C and 35 on outer shelf regions). Outside the shelf, saline and warm water extended down to about 400 m close to the shelf, but only down to about 200 m further offshore in southern parts of the survey area, where transects extended relatively far into oceanic water. Temperatures were here near 0 °C in the deepest registrations.

Chl*a* values were low throughout the sampling area, never exceeding 1 mg m⁻³.

Acoustics and trawl catches

A layer identified as pearlside from trawl catches (Table 1) and acoustical characteristics (see Discussion) was distributed throughout the survey area, except for the shallow shelf in southern areas (Fig. 1). The vertical distribution by day varied between 120-230 m, with a vertical extension of about 20-50 m. There was considerable small scale (100 m) and large scale (several km) horizontal patchiness in acoustical backscattering.

The pearlside performed diel vertical migrations. They ascended towards the surface around sunset, followed by a nocturnal descent. In northern areas, the layer was often found deeper than 100 m by night, but distribution sometimes varied locally with an amplitude of more than 100 m. The vertical extension by night usually was about 50-100 m. The nocturnal distribution in southern waters appeared to be confined to the upper 100 m, though presence of other targets occasionally inhibited interpretations on pearlside distribution.

A dawn ascent was seemingly initiated 38-88 minutes (mean 61 min.) prior to sunrise, with no systematic difference in timing observed between locations. This was followed by a descent towards day-depth which was initiated 0-13 min. (mean 5 min.) prior to sunrise in transects 1-7 (mainly above the shelf). The descent started somewhat earlier (30-64, mean 43 min.) off the shelf in southern regions (transects 13-15).

Outside the shelf, a diffuse scattering layer was located deeper than 300 m by day (Fig. 1; transects 1-2, 12-15). Trawl catches (Table 1) consisted of fish (blue whiting, northern lightfish, pearlside) and larger plankton or micronekton (krill, *Meganyctiphanes norvegica*; shrimps, *Sergestes arcticus* and *Pasiphaea multidentata*; a few large jellyfish, *Periphylla periphylla*).

The nocturnal distribution varied between locations. In transects 1-2, 12-13 and the fixed 24 h station (Fig. 1), the layer mainly remained deeper than 250-300 m at night, although some fish in the upper part ascended toward the surface (revealed by the high resolution prints; not shown). Trawl catches suggest that the ver-

tically migrating fish were blue whiting. In transects 14 and 15 (further off the shelf), the entire deep layer performed a conspicuous diel vertical migration (Fig. 1).

Demersal layers were often pronounced at the shelf break, particularly in transects 1-8. No trawling was carried out in these registrations. These targets remained near the bottom both day and night.

Even denser schools prevailed further inward on the shelf in southern transects. One trawl in this structure (tow # 147, transect 8) gave almost exclusively herring (Table 1). The schools resided near the bottom by day,

irrespective of bottom depth, and ascended by night. Some herring were caught by nocturnal trawling in the near-surface registrations (tows # 148 and 149, transect 9; Table 1).

Additional demersal registrations of loose aggregations of relatively small fish (as apparent from the color code of the echogram; not shown) were made throughout the shelf regions. One bottom trawl was taken in this type of registration, and yielded almost exclusively Norway pout (tow # 140, transect 5; Table 1). These targets partly left the bottom by night in

Table 1. Composition of trawl catches. All sampling was by pelagic Harstad trawl, except for tow # 140 which represents demersal trawling. Time depicts start of tows, which generally lasted for about 20 min. Digits give number of individuals when not otherwise stated.

		depth (m)	date	time	station number	pearlside	norway pout	northern lanternfish	blue whiting	herring	other fish species	krill	shrimp	<i>Periphylla periphylla</i>	
S H A L O W	D A Y	0	19	13:35	136	-	-	-	-	-	-	55g	-	-	
		90-100	21	05:59	142	53	-	-	-	-	-	-	-	-	
		125-150	16	15:33	135	4750	-	-	-	-	-	-	-	-	
		140-160	28	14:15	155	12	-	-	-	-	-	-	-	-	
		165-170	20	17:24	140	-	19162	-	-	-	177	-	-	-	
		160-200	26	14:55	153	1128	-	-	-	-	-	-	-	-	
		180-200	19	14:25	137	150	-	-	-	-	-	-	-	2	
		200	29	07:50	161	20	-	-	-	-	1	-	1	-	
		0	20	04:19	139	750	-	-	-	-	-	-	150g	-	-
		0	21	05:12	141	-	-	-	-	-	-	-	-	-	-
W	N I G H T	25	22	21:35	148	68	169	-	-	29	-	2213g	-	-	
		25-50	23	01:40	149	21	1kg	-	-	98	-	500g	-	-	
		50-70	22	03:05	145	17	8	-	-	-	-	300g	-	-	
		50-100	22	05:23	146	1354	-	-	-	-	1	-	-	-	
		60-115	28	20:40	157	98	-	-	15	3	-	1086g	-	1	
		100-130	24	17:41	151	10979	10	-	3	-	7	-	-	-	
		120	19	22:05	138	308	1	-	-	-	1	666g	-	-	
		125-150	29	02:35	159	125	-	-	19	-	-	2155g	-	-	
		250-275	22	14:05	147	100g	-	-	-	1297	-	-	-	-	
		250-300	24	14:00	150	179	31	-	2	-	10	2025g	-	-	
D E E P	D A Y	280-320	21	13:25	144	12	1	-	125	147	14	-	-	-	
		400-450	26	15:49	154	14	-	118	-	-	-	744g	-	2	
		390-470	28	15:16	156	-	-	191	4	-	-	-	1	-	
		400-500	29	08:50	162	141	-	108	-	-	3	1341g	12g	6	
		565-570	21	07:15	143	16	-	114	10	-	78	-	-	3	
		200-240	24	18:32	152	32	-	15	12	1	4	944g	-	3	
		400	29	03:29	160	67	-	40	4	-	2	1284g	47g	1	
		400	28	21:35	158	-	-	140	8	1	-	1462g	209g	4.3kg	

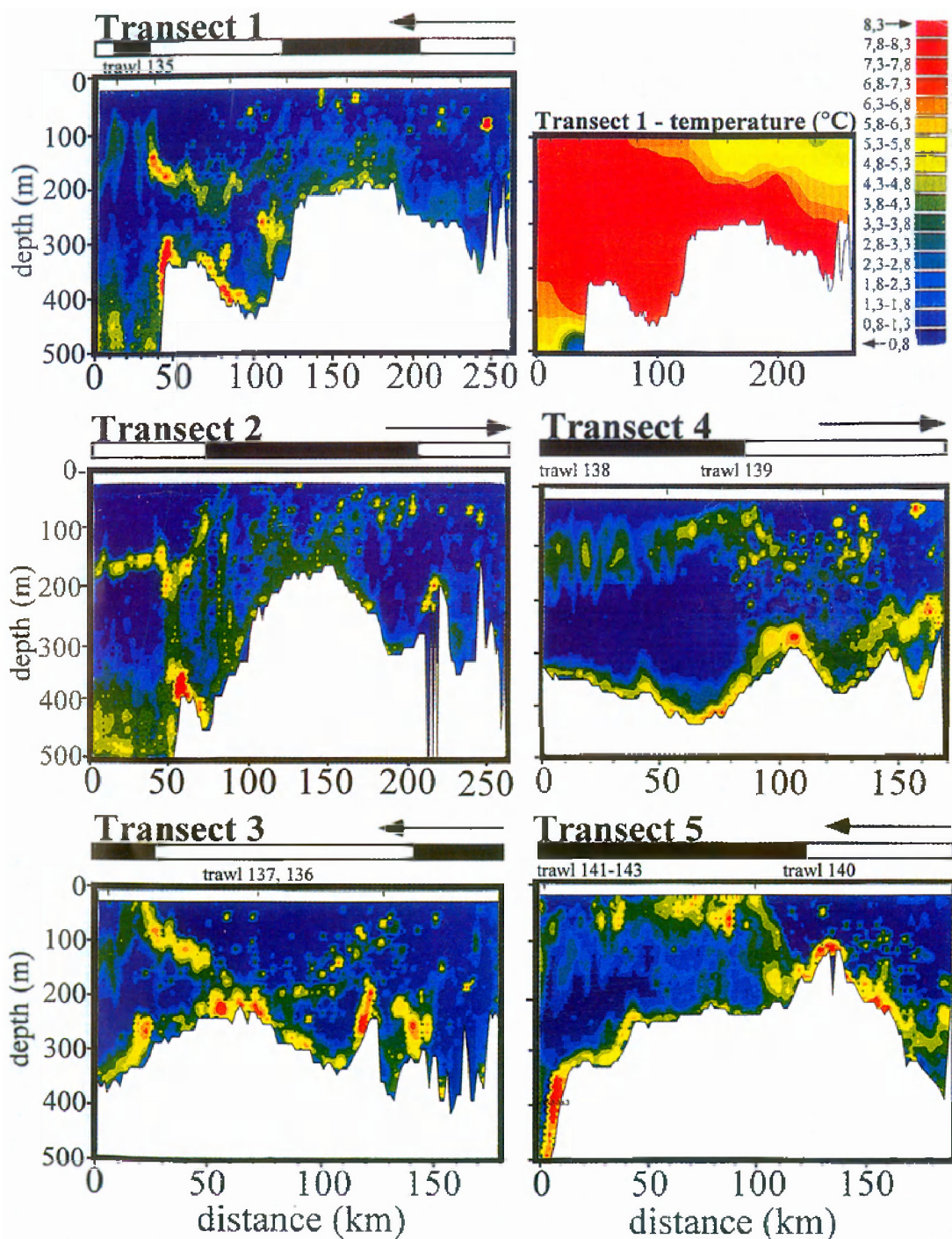


Figure 1. Acoustical area backscattering (m^2nm^{-2}) versus depth along the Norwegian shelf and eastern Norwegian Sea. Color scale refers to level of area backscattering (S_A , KNUDSEN 1990, FOOTE & al. 1991). Cruise lines and location of the 24 h station are depicted on maps, where outlined sections correspond to transect number displayed in the figures.

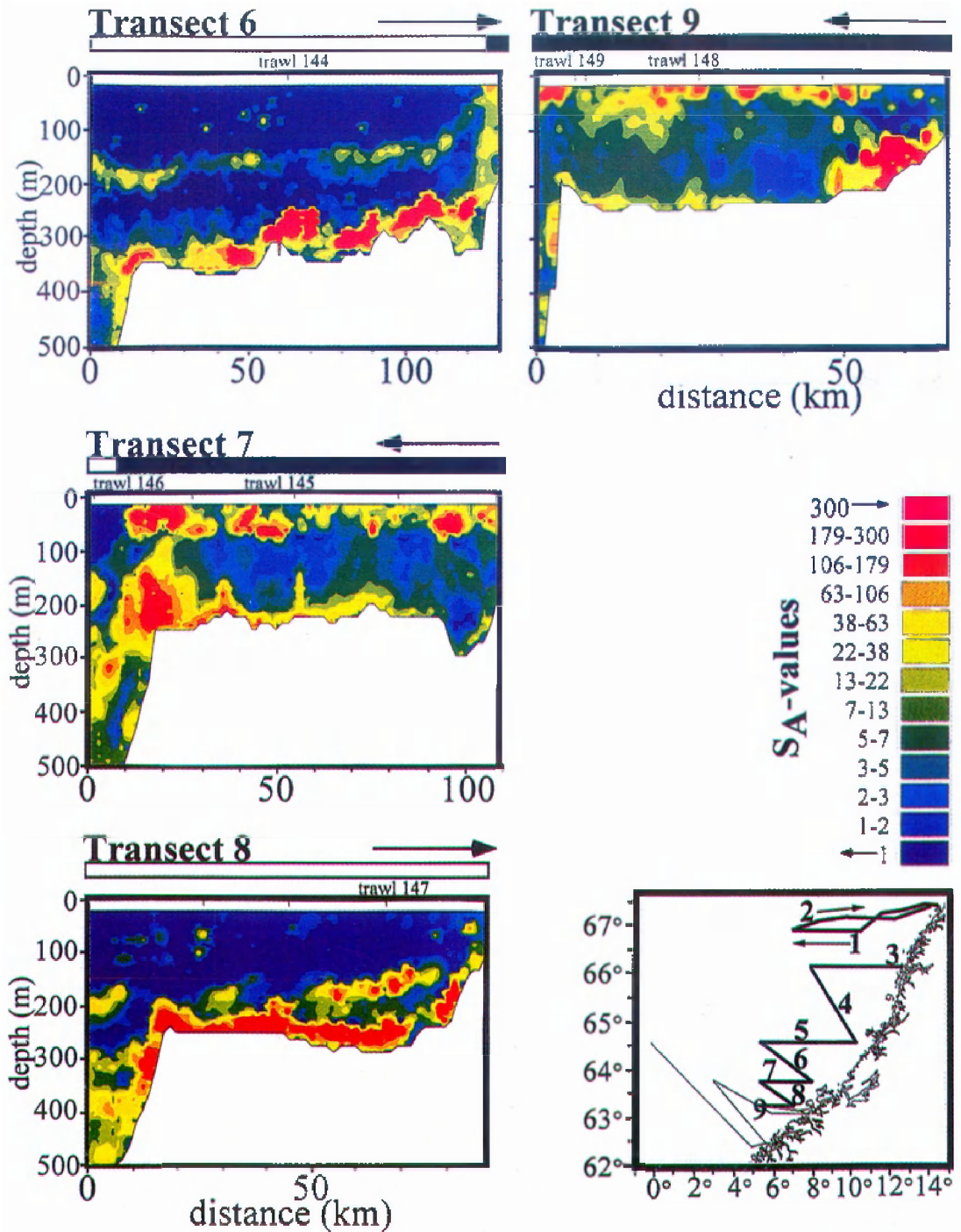


Figure 1 continued. Arrows depict direction of cruise track. Locations (times for the 24 h stations) of trawling are indicated. Bottom topography is generated from the acoustic registrations (deepest point for each mile). Time interval between sunset and sunrise is denoted by a dark bar. Temperatures for the northernmost and southernmost transect are given.

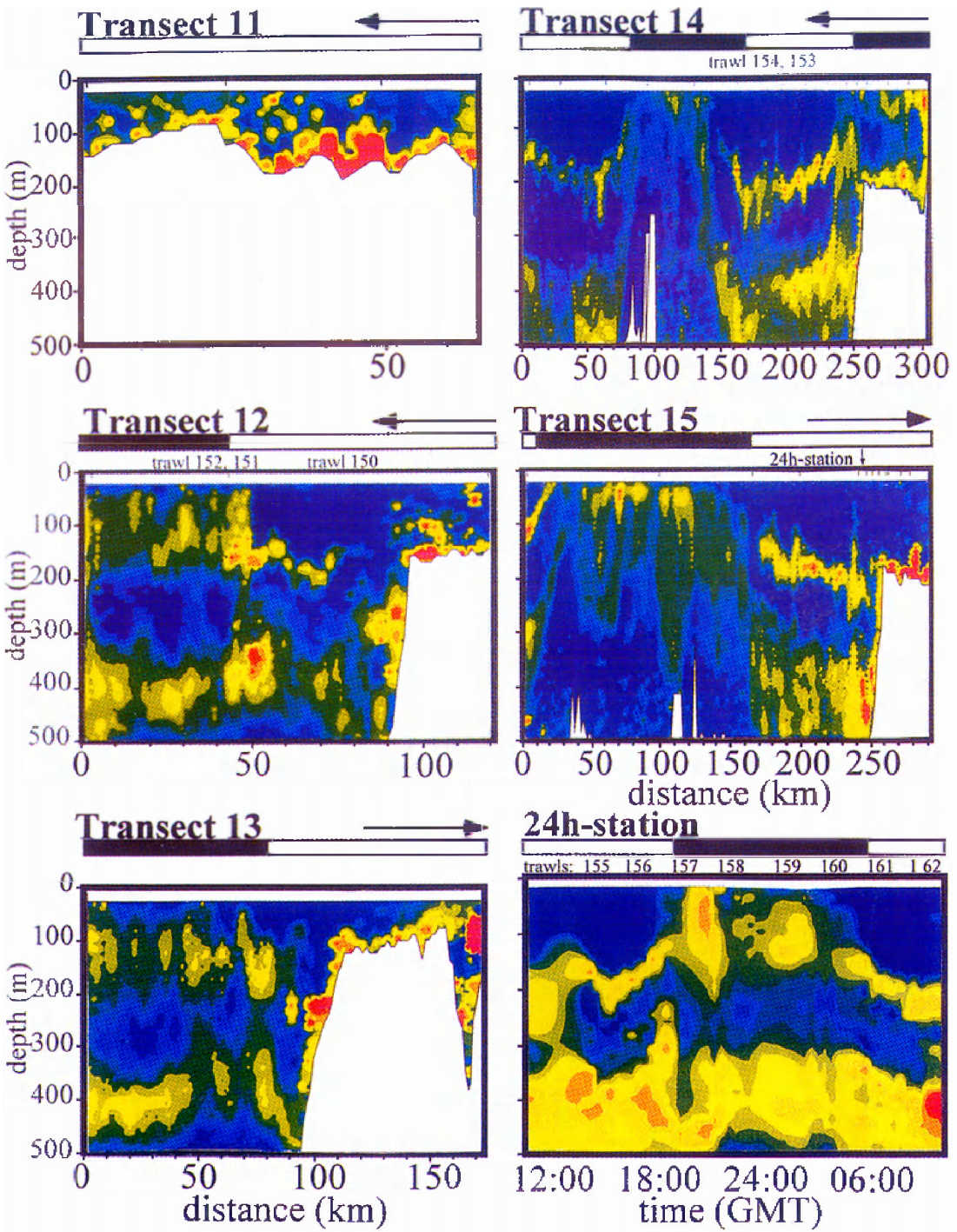


Figure 1 continued.

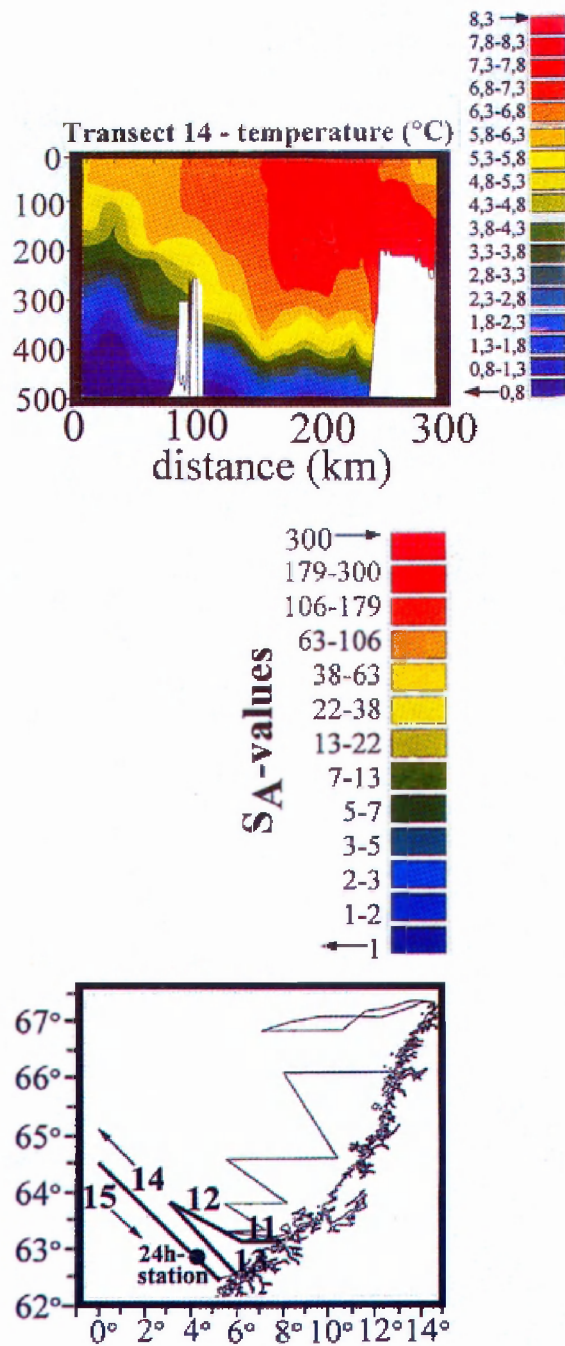


Figure 1 continued.

southern regions, and some Norway pout were then caught pelagically (mainly at transect 11, Table 1). On the contrary, these targets resided close to the bottom both day and night in northern regions.

DISCUSSION

Identification of acoustic targets

Pearlsides were the only fish caught in trawling aimed at the upper mesopelagic layer. That pearlside is the major target in this kind of acoustical structure is in accordance with other offshore (BERGSTAD 1990, MELLE & al. 1993, KAARTVEDT & al. 1996) and fjord (GISKE & al. 1990, SKJOLDAL & al. 1993b, RASMUSSEN & GISKE 1993, BJELLAND 1995, GOODSON & al. 1995) sampling. Layers of pearlside are characterized by narrow vertical extension and considerable horizontal patchiness, as apparent in ping based prints from the present investigation. Also the vertical distribution and diel migration behavior unequivocally point to pearlside.

The deep scattering layer outside the shelf seems to be characteristic for the eastern Norwegian sea (MELLE & al. 1993). The main species components are known (MELLE & al. 1993, this study), but their relative abundance and distribution within the layer remain undescribed. The presence of many, relatively small (<~ 5 cm) organisms in a large ensonified volume (e.g. 600 m³ at 300 m depth using the present settings) causes diffuse echo registrations. This prevents the use of acoustical signatures to identify the different organisms by hull mounted transducers, except for registrations of larger fish (identified as blue whiting by trawling) in the upper part of the layer.

Herring prevailed in trawl catches from the dense schools on the shelf, and the dense schools are characteristic for herring. Herring may, however, occasionally be confused with blue whiting, which also may form relatively dense aggregations. While we ascribe the shelf registrations to herring, the shelf break registrations probably were mainly due to blue whiting. They inhabited deeper water, were less dense than the herring schools, and differed in behavior by not carrying out diel vertical migration. Also several other species are common at the shelf break (e.g. greater argentine *Argentina silus* and redfish *Sebastes* spp; BAKKEN & al. 1975) and probably contributed to the high backscattering as revealed by the compressed plots.

Both the color code, trawl catches and comparison with previous studies (e.g. KAARTVEDT & al. 1996) suggest that the demersal registrations of smaller fish at the shelf may represent Norway pout.

Distribution and behavior

Pearlsides were distributed wherever the bottom depth exceeded their requirements for a daytime habitat, but not at shelf regions shallower than about 200 m. This either implies behavioral mechanisms to maintain their distribution outside shallow regions, or high mortality for individuals that become transported shelfward during their vertical migration by night (e.g. ISAACS & SCHWARTZLOSE 1965, HOBSON 1989). The fish caught in the pearlside layer were small (about 3 cm with a mean weight of 0.24 g; TORGERSEN 1995), while scarce catches deeper than 200 m included larger individuals (an upper mode of about 6 cm; TORGERSEN 1995). This vertical segregation between size classes corresponds to results for fjord populations, and has been ascribed to a different trade-off between foraging and antipredation behavior among juvenile and adult fish (GISKE & AKSNES 1992, ROSLAND & GISKE 1994).

The diel migration pattern of pearlside was roughly similar to reports on fjord populations (GISKE & al. 1990, GISKE & AKSNES 1992, BALIÑO & AKSNES 1993, GOODSON & al. 1995), though the nocturnal descent was more extensive in the oceanic locations. The dusk and dawn ascent fits the 'antipredation window' theory by CLARK & LEVY (1988), which ascribes twilight migrations to a positive trade-off between sufficient light to detect prey, though dimly enough to reduce risk of predation by piscivores. For fjord populations, the nocturnal descent in between has been ascribed to increased fitness obtained by residing near sub-surface temperature maxima due to faster digestion (GISKE & al. 1990, GISKE & AKSNES 1992). Our results, however, do not fit this scheme. Maximum temperature increase obtained by the oceanic populations associated with their nocturnal descent was 0.2 °C and sometimes the pearlside even experienced reduced temperatures by this behavior. Antipredator behavior or prey distribution represent alternative explanations.

The behavior of the deep scattering layer differed between locations. Organisms of this layer barely displayed diel migration in northern regions and close to the shelf in southern regions, but carried out pronounced diel migrations further offshore (Fig. 1). Direct impact by varying physical factors, or associated changes in distribution of food or predatory regime, may have caused organisms to behave differently among locations. Alternatively, the taxonomic compositions of the layer may differ.

The vertical temperature profile represented one important environmental difference between these locations. The mainly non-migrating layer near the shelf spent the daytime in warm Atlantic water, while the migrating layer further offshore spent daytime in cold

Arctic intermediate water ($< 3^{\circ}\text{C}$), and migrated into Atlantic water ($\sim 8^{\circ}\text{C}$) by night. To establish whether temperature *per se* (e.g. WURTSBAUG & NEVERMAN 1988), or associated changes in taxonomic compositions may explain the deviating behavior, requires specially designed studies.

Blue whiting living pelagically off the shelf carried out diel vertical migrations, in contrast to aggregations of blue whiting at the shelf break. This difference in behavior has not been addressed in previous studies and causes are not known.

The herring at the shelf were heading from their spawning grounds to oceanic feeding areas (MELLE & al. 1994, DALPADADO & al. 1996). Scarce stomach content (some krill) suggested limited feeding during this horizontal migration (TORGERSEN 1995). This is in accordance with results presented by MELLE & al. (1994) and DALPADADO & al. (1996), who also found little feeding and krill as the only prey. Like the herring, krill on the shelf performed diel vertical migrations (MOCNESS-catches). We can not, however, say if the corresponding behavior of predator and prey represents a causal relationship. The hypothesis that herring, by staying in upper waters, may exploit northward flowing currents to aid migrations to oceanic feeding grounds will be evaluated (MELLE & al. in prep). The deep day-time distribution could be related to antipredator behavior. Killer whales (*Orcinus orca*) are major predators on herring along the Norwegian coast (e.g. SIMILÅ & al. 1996). The following spring we observed killer whales on the shelf, preying on herring which possibly had been herded to the surface layer from deep daytime habitats.

Norway pout is known to migrate vertically (GORDON 1977, ALBERT 1993). KAARTVEDT & al. (1996) showed that vertical distribution by day (and inferred feeding rhythms) of this primarily demersal planktivore varied in association with optical properties of the water, and we have even caught Norway pout in the surface layer by day (unpublished result, Institute of Marine Research). Previous investigations have given few clues on flexibility in the diel migration pattern, but the results of the present study (vertical migrations to the south, apparent lack of vertical migrations to the north) suggest a plastic diel vertical migration pattern.

Echo registrations as an index for predation pressure on zooplankton

The compressed echo plots mainly reflect large scale distribution of planktivorous fish and thus envisage one element of the patchy predatory regime encountered by zooplankton. Considerable additional small scale patchi-

ness is concealed by these condensed plots. Predation pressure exerted by these planktivores depends on factors like light intensity, antipredator behavior/presence of piscivores, food preferences and their spawning behavior. Nevertheless, these large scale plots provide some visualization of how predation pressure on zooplankton may vary as a function of depth, between north and south, between shelf and the open ocean, and throughout the day.

The variability and dynamics in predation pressure imply that zooplankton will benefit from flexible behavioral patterns. Predator induced variability in diel vertical migrations has recently received much attention. There is an increasing number of field studies unveiling correlation between diel vertical migrations and abundance of planktivorous fish as well as experimental studies documenting that diel vertical migrations may be induced by presence of predators (e.g. BOLLENS & FROST 1989, 1991, BOLLENS & al. 1992, FROST & BOLLENS 1992, NEILL 1992, HAYS 1995). Most efforts to study behavior of zooplankton related to predators have been made in lakes and enclosed marine systems. Acoustics provides a useful tool for addressing these questions on the larger scales represented by open oceanic systems.

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