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C.M. 1993/L:43
Biological Oceanography Committee



UNDERWATER OPTICS AND BEHAVIORAL RESPONSES OF KRILL TO
PRESENCE OF FISH PREDATORS AFFECT FISH-PLANKTON
INTERACTIONS

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ABSTRACT

In clear oceanic waters off the Norwegian shelf and in outer shelf waters, mesopelagic fish (*Maurolicus muelleri*) were located at approximately 200 m by day. Across a front into water of lower light penetration, *M. muelleri* ascended about 100 m. Concurrently, a layer of krill (*Thysanoessa inermis*) appeared at between 150-200 m, i.e. below their potential predator *M. muelleri* and generally about 100 m above the bottom. The bottom associated fish Norway pout (*Trisopterus esmarkii*), occasionally ascended from the benthic boundary layer, foraging in the lower part of the krill layer. However, evidence was found that *T. inermis* responded to their presence by upward swimming. These results indicate that optical properties of water masses may be prominent in governing plankton and fish distributions and their predator-prey interactions. They furthermore suggest instantaneous behavioral responses in fish and krill to the presence of their respective prey and predator.

INTRODUCTION

The role of fish in the ecosystem, and how fish influences zooplankton distribution and behavior, have been extensively analyzed in freshwater (e.g. Stick & Lampert 1981, Gliwicz 1986, Carpenter 1988, Levy 1990), but have been less frequently studied in marine systems. Interactions between plankton and marine fish have traditionally been addressed by means of stomach analysis, with the purpose of revealing the fish diet. Additionally, some studies of fish-plankton interactions have evaluated predator-prey relationships in theoretical, rather than empirical terms (e.g. Giske & Aksnes 1992, Giske et al. 1992, Aksnes & Giske 1993). In these exercises, the visual capability of the fish and the optical properties of the environment are considered key properties for the foraging success. Recently, a few studies have shown that occurrence of fish may influence the distribution and behavior of marine zooplankton. For example, it appears that the presence of pelagic fish (visually foraging predators) in some cases stimulates diel vertical migration of zooplankton, i.e. downward swimming by day, to avoid the predators (e.g. Bollens & Frost 1991, Bollens et al. 1991, 1992).

Above continental shelves, sufficient light may reach the bottom for visual predators to detect their prey throughout the water column. Accordingly, plankton is faced both with the threat of predation by pelagic fish from above and by bottom associated fish from below. Predation by bottom fish apparently is prominent on shallow banks (e.g. Isaacs & Schwartzlose 1965, Hobson & Chess 1986, Genin et al. 1988, Hobson 1989). Here, fish may feed on vertically migrating individuals, that, after having been carried by currents over the shelf-bank within the surface waters at night, are trapped by the relatively shallow bottom when in the morning they descend towards their normal daytime depths. Apparently, plankton from oceanic populations are especially vulnerable to predators in this setting, which is very different from their normal daytime habitat (Hobson 1989).

However, banks and continental shelves are also inhabited by more or less endemic plankton populations (e.g. Hobson & Chess 1986, Barange & Pillar 1992, Kaartvedt 1993). Assumingly, such shelf species would be better adapted to their relatively shallow habitat, having evolved behavioral traits to counteract the treat of both pelagic and benthic predators. Successful avoidance of predators nevertheless will depend on the physical setting of the habitat, of which the optical properties (i.e. light transmission of the water mass) could be critical in constraining plankton distribution in the presence of visual predators.

In this paper, we present results on mesopelagic fish (*Maurocliticus muelleri*), krill (*Thysanoessa inermis*), and bottom fish (Norway pout; *Trisopterus esmarkii*) distribution in a transect from open oceanic waters onto the Norwegian shelf, and through a front on the shelf. We suggest that the light

transmission of water masses may be essential in governing fish distribution and constraining krill distribution, and we report on krill behavior that may reduce interactions with their fish predators.

MATERIAL AND METHODS

The study was carried out off northern Norway (at approximately 66 °N) in April 1993. The distribution of macroplankton and fish were continuously recorded acoustically by ship mounted SIMRAD EK 500, 38 KHz and 120 KHz split beam transducers, during a transect from oceanic water and onto the shelf. Concurrent continuous registrations were made of salinity, temperature and fluorescence in water from the ships sea water pump (taken at 5 m). Vertical profiles of salinity, temperature, fluorescence and light extinction were established at selected stations by a Neil Brown CTD and a Biospherical light meter, measuring light on separate wavelengths, and also being equipped with CTD and a fluorometer. The transect was covered twice; with R/V "Johan Hjort" at about 2 pm and with R/V "G.O. Sars" at about 5 pm (GMT). From the last transect we only present acoustic data.

For identification of acoustical targets, sound scattering layers (SSL's) were sampled by a midwater trawl (Harstad trawl; Nedreaas & Smedstad 1987), MOCNESS (Wiebe et al. 1985), and a Methot Isaac Kidd midwater trawl (MIK).

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 AND DISCUSSION

Offshore registrations on the 38 KHz sounder consistently revealed two SSL's. An upper layer was situated at about 200 m by day, and a deeper layer between 300-500 m (the deeper SSL will not be further discussed in this paper). Sampling in the upper layer on this and previous cruises identify the mesopelagic fish Müller's pearlside (*Maurolicus muelleri*) as the main target (unpublished results). The pearlside performed diel vertical migrations, swimming towards the surface at night.

During the first cross shelf transect at about 2 pm, the vertical distribution of *M.muelleri* suddenly (in the course of about 1 nautical mile) ascended approximately 100 m (Fig. 1a). This change in vertical distribution was associated with the passage of a front, as demonstrated by concurrent drops in salinity and temperature, and increased fluorescence (Fig. 2). Light extinction inside the front was much higher than in oceanic water (Fig. 3), and light levels at depth decreased accordingly. Roughly corresponding

light levels in the pearlside layer in oceanic waters (200 m) and in the coastal waters (100 m) indicate that the rapid change in vertical distribution could be explained by change in light intensity. Previous studies have shown that pearlsheds are very sensitive to fluctuating light conditions, for example rapidly adjusting their vertical distribution in response to variable cloudiness (Giske et al. 1990, Balino & Aksnes 1993).

When the front was passed three hours later the same changes in vertical distributions were observed (Fig. 1b). The vertical structures, however, generally showed a more shallow distribution probably due to a lower surface light level later in the afternoon.

As *M. muelleri* ascended, a new SSL appeared at depths inhabited by *M. muelleri* outside the front (Fig. 1a,b). Trawl catches in this new layer consisted almost exclusively of the euphausiid *Thysanoessa inermis*, and comparison between the two acoustical frequencies further verified the identity of the targets as relatively small organisms. While this particular layer ascended into the upper 100 m at night, i.e. came within the range of the 120 KHz sounder, it was more distinctly revealed by the higher frequency (in contrast to fish). Krill is in the lower detectable size range of a 38 KHz transducer, but is recorded when occurring in aggregations (multiple targets).

Possibly, *Thysanoessa* could exist inside the front since an appropriate depth zone became vacant when the pearlside ascended. Due to the lower light penetration in this coastal water mass, *Thysanoessa* found a habitat below visually foraging pelagic predators, while still above bottom associated fish. In the clear water outside the front, any krill might have been easily spotted by visually hunting bottom fish.

Accordingly, the optical properties of water masses appears to be essential in delineating pelagic habitats. Whereas water mass characteristics like temperature and salinity are often used as basis in evaluations of distributional patterns, concurrent changes in optical properties may well be as important, and sometimes the decisive factor. Some macro-plankton populations may occur in coastal water masses of reduced transparency, while otherwise corresponding habitats in adjacent shelf regions of clear water may be too shallow due to predation from fish.

Bottom fish clearly represented a treat to the krill. The continuous acoustical records showed that fish occasionally swam up from the benthic boundary layer, penetrating into the lower part of the krill layer (Fig. 4). Trawl catches in this ascending fish layer consisted of Norway pout (*Trisopterus esmarkii*), with stomachs full of krill (Table 1). Net feeding can probably be disregarded, as much of the stomach content consisted of well digested individuals. In other locations the fish stayed close to the bottom and thus lived vertically separated from this potential prey. This indicates a

small-scale/short-term spatial or temporal variation in predation pressure on the krill.

Table 1. Stomach content of a subsample of 9 Norway pout from a midwater trawl catch. Bottom depth 295m, sampling depth 170-200m, time: 0745 pm (GMT), position 66°29'N, 10°46'E.

Fish length (cm)	Stomach content (g)	Dominating prey item/Nos	Stomach fullness	State of digestion
11	empty			
11	0.334	<i>T. 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	Euphausiids/2	3	3
14	empty			
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	Euphausiids/2	3	3
17	1.128	<i>T. inermis</i>	4	3

Interestingly, *T. inermis* seemingly responded to the approaching fish by upward swimming, on one occasion by about 75 m (Fig. 4). Apparently, *T. inermis* could sense the treat from below, trying to escape to shallower water. In spite of this escape response, many were eaten, as evidenced by the stomach analysis. The krill apparently became squeezed between fish swimming up from the benthic boundary layer, and pelagic fish above (e.g. *M.muelleri*), which are potential predators on krill (Gjøsæther 1981). However, there also seemed to be a slight upward displacement of the pearlside layer, which may have been induced by the upward swimming of organisms from below. Alternatively to an explanation favoring biological interactions, the Norway pout, *T. inermis* and *M. muelleri* might have responded to a common factor, e.g. small scale fluctuations in light conditions. However, the ascent and subsequent descent was not accompanied by corresponding fluctuations in surface light conditions, and the same pattern was seen when repeating the transect in the opposite direction to trawl in the fish layer for the stomach analysis. Neither were any small scale variations detected in salinity, temperature and fluorescence from the continuous registrations.

In recent years, instantaneous responses in plankton vertical distribution in the presence of predators have been repeatedly documented, especially in studies from freshwater (e.g. Neill 1990, 1992, Dawidowicz & Loose 1992) but also in marine environment (e.g. Bollens & Frost 1991, Bollens et al. 1992, Frost & Bollens 1992). However, so far, marine investigations have favored "bottom-up" explanations like temperature, salinity and prey distribution in evaluations of distributional patterns. An increased emphasis on the fish's role in structuring marine ecosystems depends on a proper and concurrent mapping of both fish and plankton. These results demonstrate the ability of using acoustics for simultaneous studies of predator and prey

distributions and implied promise for evaluations of predator/prey relationships between fish and larger zooplankton.

ACKNOWLEDGEMENTS

We thank professor Egil Sakshaug for access to data on light extinction.

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FIGURE LEGENDS

Figure 1a. Printout from the 38 KHz echosounder on R/V "Johan Hjort" at about 2 pm (GMT), showing ascendance of the pearlside layer when passing the front from oceanic into coastal water (left to right), with subsequent introduction of a krill layer (*Thysanoessa inermis*) below the pearlside and above concentrations of bottom fish (*Trisopterus esmarkii*).

Figure 1b. As Fig. 1a when R/V "G.O.Sars" passed the front described in Fig. 1a at about 5 pm (GMT).

Figure 2. Continuous registrations of salinity, temperature and fluorescence at 5 m depth when passing the front from oceanic into slightly fresher and colder coastal waters with higher concentrations of phytoplankton (left to right).

Figure 3. Vertical profiles of a) sigma T, b) fluorescence, and c) transmission of blue light, in open oceanic waters (1) and just inside the front (2). Considerable higher light extinction and fluorescence, and slightly lower sigma T (but without a distinct density stratification) are apparent in coastal waters.

Figure 4. Printout from the 38 Khz sounder, showing Norway pout ascending from the bottom stratum and into the lower part of the krill layer, and a subsequent rise of the krill.

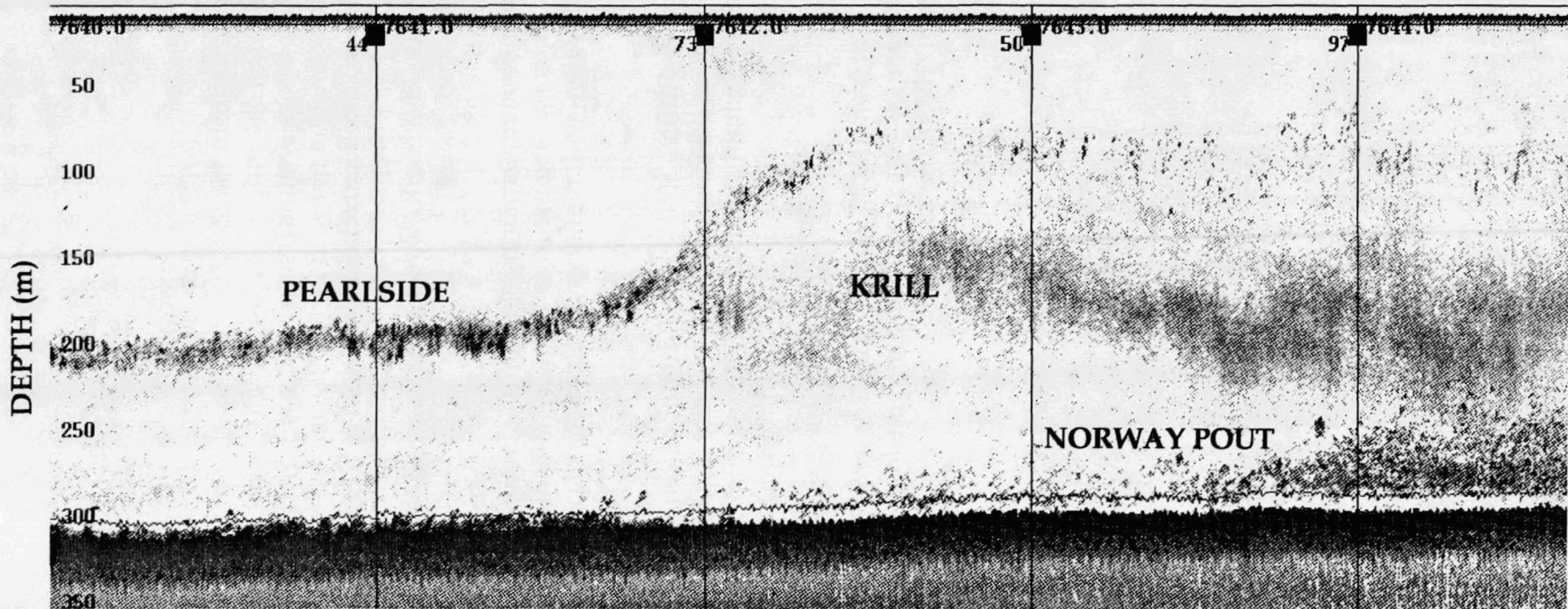


Figure 1a.

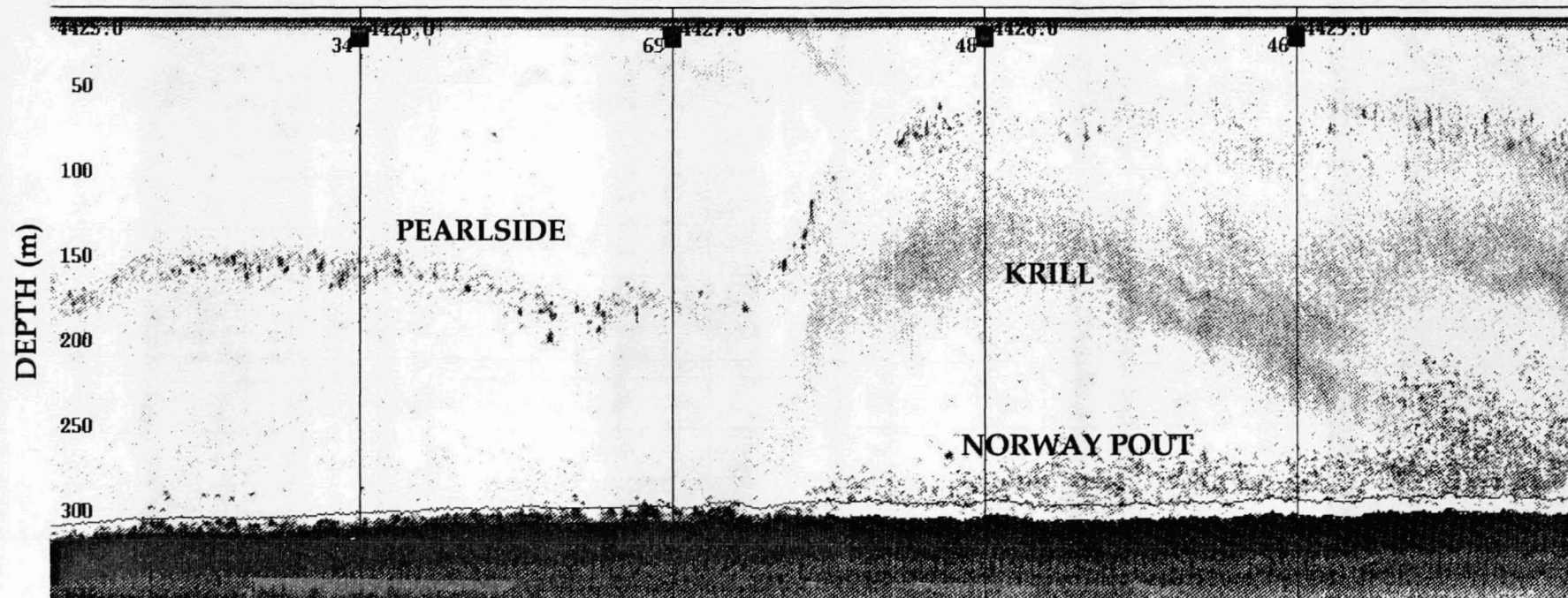


Figure 1b.

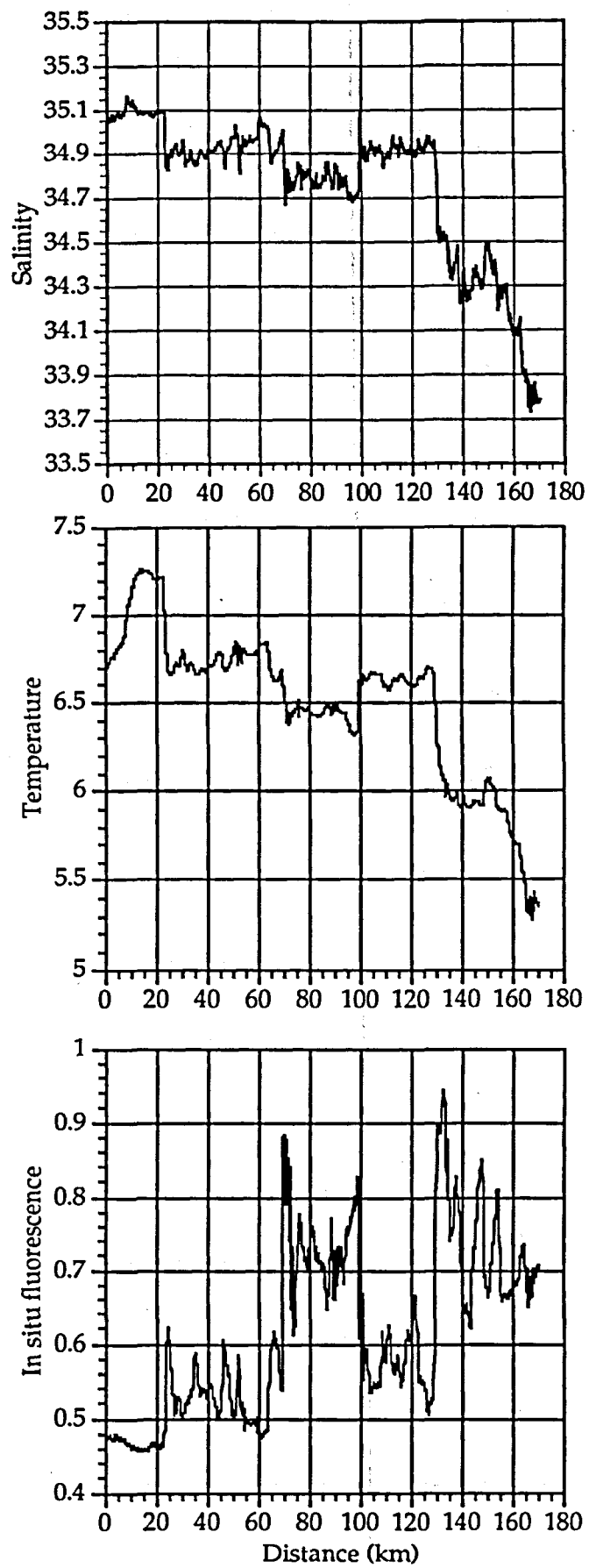


Figure 2.

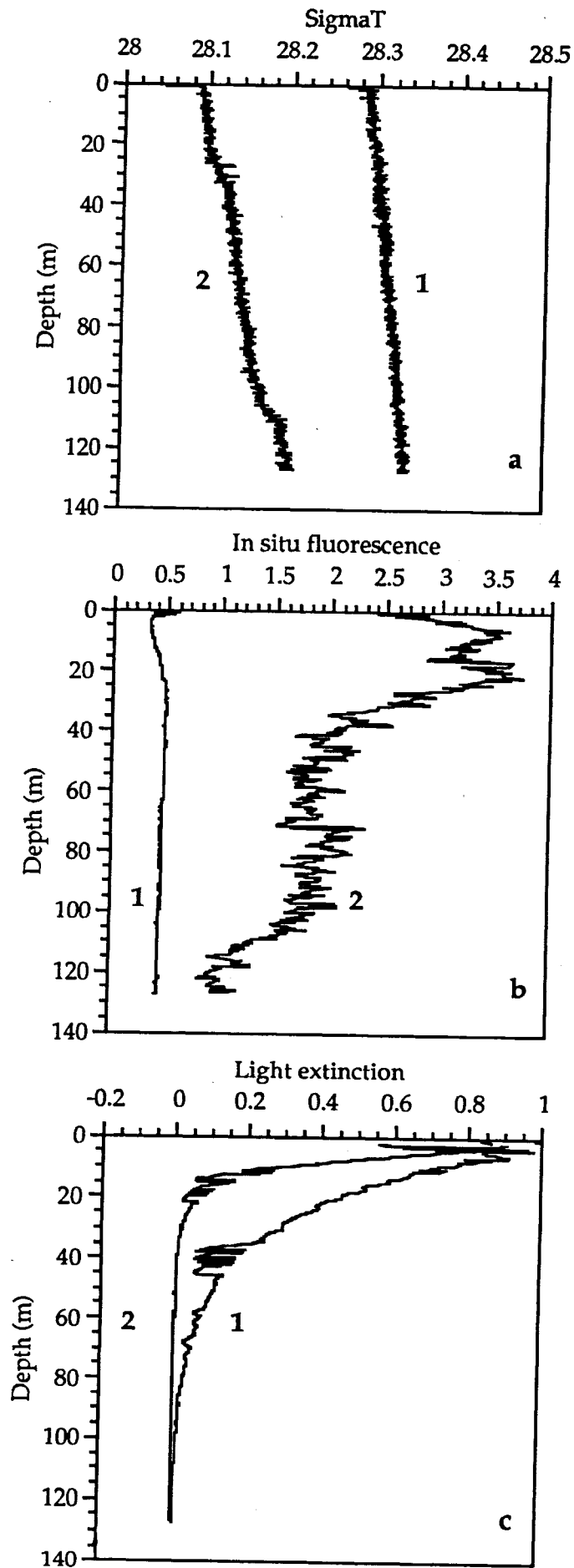


Figure 3.

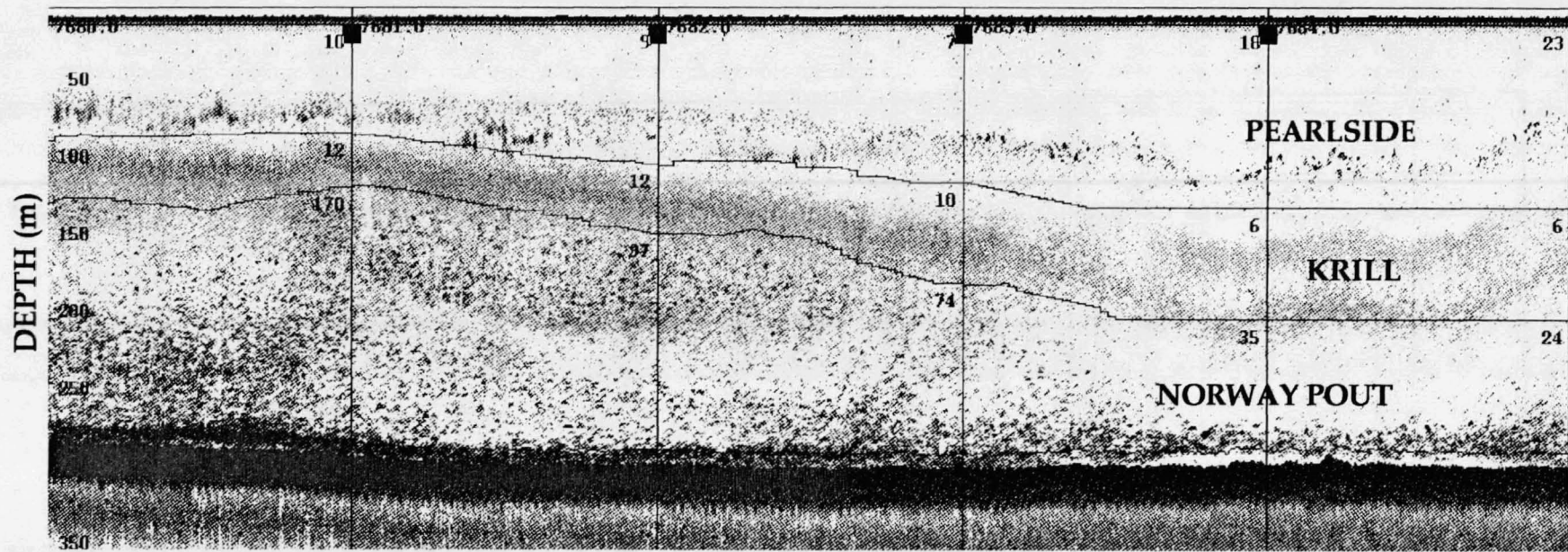


Figure 4.