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FEEDING AND MIGRATION OF NORWEGIAN SPRING SPAWNING HERRING IN THE NORWEGIAN SEA

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ABSTRACT

After spawning on the shelf off Møre, Western Norway, the spawning stock of Norwegian spring spawning herring migrates to the Norwegian Sea for feeding. Simultaneously, the adolescent part of the stock leaves the wintering areas in fjords and coastal areas of northern Norway and starts feeding in the Norwegian Sea. During two cruises in April and June 1994, a transect from coastal water over the Norwegian continental shelf across the frontal zone into Atlantic water in the central Norwegian Sea was covered. Distribution and development of major prey species of the herring, *Calanus finmarchicus* and *C. hyperboreus,* were described in relation to hydrography and phytoplankton spring bloom dynamics.

In April, all year-classes of herring were found in Atlantic water where zooplankton biomass was high in the upper 50 m of the water column. *C. finmarchicus* occurred in the overwintering stages CV and adult females, and feeding conditions were probably good. The older year-classes of herring showed a westerly movement along the transect from April to June, and the oldest herring were found farthest to the west. The herring did not cross the Polar front into Arctic water masses in June, although feeding conditions, judged from zooplankton biomass distributions, seemed far better than in Atlantic water. The herring in June was distributed in Atlantic water masses with low biomass of small stages of the new generation of *C. finmarchicus,* and feeding conditions were probably not optimal.

The young year-classes of herring, which were found in Atlantic water in April, occurred over the shelf in June. There the zooplankton biomass was intermediate, but the new generation of *C. finmarchicus* had developed into late copepodite stages and adults and served as potential large particle food items for the herring.

INTRODUCTION

In May and June 1986 herring belonging to the strong 1983 year class of Norwegian spring spawning herring undertook a feeding migration from the nursery areas in the Barents Sea to the eastern part of the Norwegian Sea (Røttingen 1990). This was the first time in 15 years that Norwegian spring spawning herring were observed on the feeding areas in the Norwegian Sea. Since then this herring stock has wintered in fjord and coastal areas in northern Norway, spawned on the coastal banks of Norway, and utilized feeding areas in the Norwegian Sea during summer. Year classes younger than the 1983 year class have adopted the same migration pattern, part of the adolescent herring stock spend their first winter after the emigration from the Barents Sea in the same areas as the adult stock, another part is distributed in more outer coastal areas. Thus, the Norwegian spring spawning herring again, as was the case before the stock collapse in the late 1960-ies, utilizes the Norwegian Sea as a feeding area.

The feeding migration into the Norwegian Sea commences in March-April when the adult stock migrates from the spawning areas and the adolescent herring migrate out from the wintering areas. This is shown schematically in Fig. (1).

Prior to the stock collapse in the late 1960-ies many investigations were carried out to map the herring distribution in relation to plankton and environmental conditions (Pavshtiks 1956, Østvedt 1965, Rudakova & Kaverina 1969). It was found that during the feeding migration of the herring the production of the zooplankton biomass spread from south east towards north west in the Norwegian Sea (Pavshtiks & Timokhina 1972). The overwintered population of *Calanus finmarchicus* which concentrates towards the surface to feed and spawn during the phytoplankton spring bloom (e.g. Melle & Skjoldal 1994), are the most important food items probably governing the migration of the herring (Pavshtiks 1956, Østvedt 1965). However, there are not so many investigations on the first stages of the herring feeding migrations, i.e. the migration from the coastal shelf, over the continental slope and into the Norwegian Sea.

In the present study environmental conditions and herring distribution is investigated along a transect from the Norwegian coast and approximately 500 km into the Norwegian sea in April and 1000 km in June 1994. During this time period both adult and adolescent herring migrate westward into the Norwegian Sea. How is the feeding migration of the herring related to the feeding conditions? How is temporal and spatial variability of the feeding conditions for the herring along the transect related to the production cycles of the zooplankton stocks?

MATERIAL AND METHODS

Several cruises have been conducted (March and May 1992, April, July and August 1993, and April to June 1994) in order to map large scale distribution and migration of the Norwegian spring spawning herring, hydrographic conditions, nutrients and plankton development and distribution.

During two of the cruises with R/V "G. O. Sars", from 19 April to 6 May and from 30 May to 27 June 1994, more or less the same transect from the Norwegian shelf across the slope and into the deeper parts of the Norwegian Sea was covered (Fig. 2, 3). The transect was covered in late April during the first cruise and in early June during the last cruise, and will be termed the April and June transects. Temperature, salinity, and chlorophyll fluorescence were recorded continuously along the transects in the water intake of the ship at about 5 m depth. Temperature and salinity were determined with a Meerestechnik-Elektronik GmbH ctd 1500 (Mini-CTD) in a flow-through system. Fluorescence was determined with a Turner Design fluorometer equipped with a flow-through cuvette. At selected stations vertical profiles of temperature and salinity were obtained with a CTD down to 300 or 1000 m (or the bottom in shallow areas). A rosette sampler equipped with water bottles mounted on the CTD was used to provide water samples from 11-12 depths. Water samples at the surface were collected with a bucket. In June, sub-samples for determination of chlorophyll *a* and nutrients were taken from all water samples. In April, samples for chlorophyll *a* were limited to the upper 100 m. Storage and analyses of the samples were done as described by Føyn *et al.* (1981) and Rey (1991).

Distribution of herring was mapped with a hull mounted 38 kHz transducer coupled to the Bergen Echo Integrating System (BEI; Foote *et al.* 1991). Results are presented as area backscattering coefficient which to some extent is proportional to the biomass. However, the relationship between biomass and the acoustic coefficient will vary with size of the herring, and possibly also with the depth distribution of the herring due to its open swim bladder (Ona 1990).

At predetermined positions or according to acoustic registrations, herring were caught with a mid-water trawl. For sampling near the surface the trawl was equipped with 4 large additional floats (Anon. 1994). On a sub-sample of the herring (usually 100 individuals) standard biological analyses were performed, including body length, weight, fat content, stomach content index, and age readings from shells. From each sub-sample a total of 30 stomachs were fixed in 10% formaldehyde solution and 20 stomachs were frozen at -20°C for subsequent identification and enumeration of prey items in the laboratory.

Vertical distribution of zooplankton and micronekton were obtained with a 1-m^2 MOCNESS (Wiebe *et al.* 1985) in profiles from maximum depths of 600-700 m or 300 m (or close to the bottom in shallower water). Samples were split in two halves, one was fixed in 4% formaldehyde solution for species identification and enumeration and the other was separated into three size fractions (>2000, 2000-1000, and 1000-180 μm) by sieves. The size fractions were dried and burned for determination of dry weight and ash free dry weight biomass.

The continuous measurements of temperature, salinity and fluorescence were calibrated against recordings of temperature and salinity at 5 m depth with the CTD, and content of chlorophyll *a* in sub-samples from water bottles at 5 m (Fig. 3).

The stomach content analyses of the herring stomachs collected in 1994 are not finished yet, and therefore the results from stomachs collected on a similar cruise in April 1993 have been included here.

RESULTS AND DISCUSSION

Cruises conducted in March 1992 and in April 1993 and 1994 showed that the spawning stock had left the shelf waters at this time. Only a small part of the stock was still found off Møre in March 1992. In April 1993 and 1994, the year-classes that spawned on the shelf at Møre were found along the shelf from Møre to Lofoten, and some of the herring were already far into the Norwegian Sea. In April the spent herring of the spawning stock underwent extensive diurnal vertical migrations from ~400 m depth during day to the surface layer during night. Off the shelf break the herring were observed in layers 20-30 m thick and of more than 15 nm width at 3-400 m depth during day. During night the herring aggregated in schools at ~200 m depth or within the upper 50 m. Adolescent herring were found in highest concentrations above the shelf break in April. Small schools were also found in sheltered areas near the coast and a few over the shelf. The results from these cruises are used together with earlier investigations to indicate the migration routes of the herring from the Norwegian coast into the Norwegian Sea (Fig. 1), as a background for the interpretation of the herring distribution along the transect.

The transect covered in April and June crossed from the coast through the coastal current water mass at distance about 900 km (measured as distance from the western most point, of the transect in June), with salinity values increasing from less than 34 to 35 (Fig. 5a). The core of Atlantic water was found roughly between 400 and 700 km both months, as indicated by salinity above 35 (Fig. 5a, 6a). In the western end, the transect in June crossed the polar front and salinity dropped below 34.6. Temperature in April was below 6^{0}C in the coastal water. Across the front into Atlantic water temperature increased to more than 6^{0}C in the core of Atlantic water, while it decreased to ~4.5^{0}C in the western end. The low temperatures in coastal water in April reflect the low winter temperatures of this water mass compared to Atlantic water (Fig. 5b). However, in June the temperature in coastal water was similar to the temperature in Atlantic water (Fig. 6b). Towards west surface temperatures in Atlantic water decreased (Fig. 5b, 6b), probably mainly due to lower air temperatures.

Before the phytoplankton spring bloom can start there must be a stabilization of the water column over deep and well-mixed areas (Sverdrup 1953, Halldal 1953, Sambrotto *et al* 1986, Skjoldal and Rey 1989). Over the shelf this is achieved by light coastal water lying on top of Atlantic water, causing a marked salinity stratification. In Atlantic water stabilization is due to the formation of a thermocline which needs to build up every spring (Halldal 1953, Melle & Skjoldal 1994). Therefore, an earlier bloom is observed over the shelf and in the front than in the Atlantic water (Melle *et al.* 1993). Over the inner parts of the shelf, where a layer of coastal water covered the Atlantic water mass, chlorophyll concentrations in April were below 1 mg m^{-3} (Fig. 5c). Nitrate concentrations of 5-6 μM reveal that the spring bloom had not culminated in this area. Winter values of nitrate can be low in coastal water (Melle *et al.* 1993) so the low chlorophyll concentrations may indicate that the spring bloom was in an early phase. In the front between coastal and Atlantic water, medium to high chlorophyll concentrations were observed (3-6 mg m^{-3}), and although nitrate concentrations were reduced, the bloom was probably not limited yet (4c). In Atlantic water which still was homogeneous, the bloom had not started as shown by chlorophyll concentrations near zero and nitrate concentrations close to the typical winter concentration of Atlantic water (4c, d).

In June chlorophyll concentrations were low over the shelf and in the front between coastal water and Atlantic water (Fig. 6c). Low nitrate concentrations showed that this was because the bloom was over (Fig. 6d). In the Atlantic water, nitrate concentrations were still between 4 and 6 μM, while chlorophyll concentrations were low, less than 3 mg m^{-3} (6c, d). This was probably due to a less intense and prolonged bloom in this water mass compared to the bloom in the front. In the polar front region between Atlantic and Arctic water in the western part of the transect, intense blooms were observed in June. At the western most station of the transect, no nitrate was left at 5 m.

Fig. 7 shows vertical distributions of chlorophyll and nitrate concentrations along the transect in April and June. The main horizontal features of the continuous measurements are reproduced, but with less resolution in these plots based on point observations from the CTD stations. High concentrations of chlorophyll were limited to the upper 50 m both in April and June.

The dominance and distribution of zooplankton species and their developmental stages in the three size fractions of the biomass caught by the MOCNESS show a relatively simple and predictable pattern in this region. The highest biomass is usually found in the size fraction from 1000 to 2000 μm, and this is mainly due to CV copepodites and adults of *Calanus finmarchicus.* In the 180-1000 μm size fraction the younger copepodites (CI to CIV's) are found. *Metrida* spp. show a similar distribution of copepodite stages between the fractions, while *Pseudocalanus* spp. are usually found in the smallest size fraction. These species, however, usually occur in lower numbers than C. *finmarchicus* in spring and early summer. Other small copepods are found in the smallest size fraction, but they also contribute relatively little to the biomass compared to the new generation of C. *finmarchicus* which develops during spring and summer. The largest size fraction is usually predominant in the deeper parts of the water column and is dominated by *Euchaeta norvegica* and chaetognaths. In Arctic water, however, *Calanus hyperboreus* dominates this fraction, and may show high biomass near the surface as well when the new generation develop.

At stations in Atlantic water in April (St. 582-589) the size fraction 1000-2000 µm dominated in the upper 400 m (Fig. 8). Species enumeration of the preserved samples from the upper 100 m at stations 582/583 and 586 showed that *Calanus finmarchicus* in stages CIV, CV and adult females dominated by numbers, representing most likely the overwintering population (Fig. 8). *Calanus finmarchicus* was distributed throughout the upper 400 m, but tended to be concentrated in the upper 25 or 50 m at some stations (Fig. 8). The shallowest distribution was found at station 580, which was located in an area where the spring bloom was developing. Therefore, the population of *Calanus finmarchicus* in Atlantic water was in a transition from a deep winter distribution to a shallow spring distribution where spawning occurs during the spring bloom. On the coastal side of the front, the situation was different. Here the smallest size fraction dominated the biomass, which was low and showed a shallow distribution (Fig. 8). Stage distribution of C. *finmarchicus* at station 577 showed that in the coastal water over the shelf, spawning had taken place, and the new generation dominated in stages CI to CIII (Fig. 8). A few adult females may either have been remnants of the overwintered population or indicate that a second spawning was about to start. Zooplankton biomass was much higher in Atlantic water than in the water masses over the shelf.

In Atlantic water (st. 800-808) in June, the spawning of *Calanus finmarchicus* was over and the new generation was in stages CI to CIV as shown by the stage distribution at station 802 (Fig. 9). Biomass in the size fractions 180-1000 and 1000-2000 µm were mainly found in the upper 50 m (Fig. 9). The total biomass values were similar to or less than in April. Over the shelf and in the frontal zone between coastal and Atlantic water, a shallow distribution of biomass was found at station 809. This was dominated by the new generation of *Calanus finmarchicus* in a more advance state of development, mainly stages CV and adult females (Fig. 9). At station 810 over the shelf a deeper distribution of the biomass (probably C. *finmarchicus*) may indicate a beginning of the overwintering for a part of the population. Biomass was low over the shelf, as in April, but relatively high in the frontal zone.

In Arctic water in June, biomass values were high and showed a shallow distribution, except at the western most station (st. 797; Fig. 9). High biomass in the largest size fraction (>2000 µm) were due to *Calanus hyperboreus* which occurred in high numbers in stages CII-CV (Fig. 9). C. *finmarchicus* was in the overwintering stages in spite of high chlorophyll concentrations and exhausted nitrate in the upper 20 m (Figs 7, 9). This may indicate a mis-match between the spring bloom and the spawning of *C. finmarchicus* in cold water, a situation similar to what was described from the colder areas of the Barents Sea (Melle & Skjoldal 1994).

Other taxa like euphausiids, shrimps, and mesopelagic fishes were also caught in the MOCNESS. However, the catches were small and variable compared to the catches of copepods. This is in part due to avoidance of the MOCNESS by these motile species. The highest biomass of these larger forms was of krill over the shelf break (~6 mg m^{-3} ; data not shown). On a few occasions krill were caught together with herring during pelagic trawl hauls in the upper 30 m.

In April 1994, herring were found in Atlantic water west of the bloom conditions in the frontal zone (Fig. 5e). This coincided with the highest biomass of zooplankton. The dominant species, *C. finmarchicus*, occurred there in the oldest and largest stages, and at many stations the maximum in zooplankton biomass was found in the upper 25 m. Therefore, herring were found in the area where the feeding conditions seemed to be optimal.

The stomachs from 1994 have not been analyzed yet, therefore, we have no possibility of comparing actual feeding between areas yet. Data from April 1993 are available, however, and these results are given in Fig. 10. Unfortunately, most stations where herring were caught were on the shelf, and the stations off the shelf were deep hauls from ~200 m to 400 m, except for two stations with hauls from 80 to 110 m and 40 to 50 m, respectively. Therefore, differences in feeding of the herring off and on the shelf need to be interpreted with caution. On the shelf the stomach contents reflected the main features of the zooplankton distributions. In the stomachs dominated by copepods *Calanus finmarchicus* in stages CII to CV prevailed (Fig. 10), and these were also the stages most frequently found at station 577. The herring on the shelf in April 1993 were caught off Møre, farther to the south than the transect presented here. Euphausiids were also found in herring stomachs from some of the stations on the shelf. The herring caught at greater depths off the shelf had generally very little stomach content.

The herring caught at the shelf break and two stations further west in Atlantic water in April 1994 showed similar length and age distributions (Fig. 11). The 1983, 1989, and 1990 year-classes dominated the catches.

In June 1994 the herring distribution along the transect were separated in two areas (Fig. 6e). Over the shelf young herring of the 1991 year-class dominated and the older year-classes of adult herring were not present. This eastern concentration was farther east than in April. However, this may be due to young herring coming from other areas. In the western parts of the Atlantic region an increasing fraction of older herring were found, while the youngest herring were not present. Herring did not cross the front into the colder Arctic water (Fig. 6e).

In June the young herring over the shelf could feed on large specimens of the *C. finmarchicus* population in stages CIV to CVI (Fig. 8). The zooplankton biomass was generally low, however, at least in coastal water where the herring registrations were highest. The western concentration was found in an area with low biomass, and the *C. finmarchicus* population was dominated by young and small stages (CI-CIII). East of the herring concentration zooplankton biomass was several times higher. The low biomass of zooplankton in the area where herring was abundant may have been caused by the herring feeding (Fig. 9).

In the colder water across the polar front (station 799) zooplankton biomass was high and large specimens of *C. hyperboreus* and older stages of *C. finmarchicus* were present in high numbers. This water mass may not have been available to the herring, however, before later in the season when the upper the water layer becomes warmed up, and then the zooplankton situation probably would have been different with young stages dominating.

In the situation observed in 1994 feeding on the overwintered population of *Calanus finmarchicus* in April, May and early June appears to have been an important part of the herring feeding season. Later on the feeding conditions may be temporarily less favourable during the growth of the early stages of *C. finmarchicus* in Atlantic water, and when the Arctic water is still too cold for the herring to enter. However, when the new population of *C. finmarchicus* in Atlantic water grows into the older stages, feeding conditions may improve again. This is probably a short lasting event, since an early descent by the older stages of *C. finmarchicus* to the overwintering depths seem to be common in the Norwegian Sea (Østvedt 1955).

Østvedt (1965) found that adult herring in the waters north and northeast of Iceland were confined to areas where the old stages of the overwintered population of *Calanus finmarchicus* predominated. Later, when the new *Calanus* generation developed into late copepodite stages, also these areas were invaded by the herring. This was a situation similar to what we found in the shelf and frontal areas in the eastern part of the transect, where young herring in April were found in Atlantic water where the overwintering population dominated and over the shelf in June when the new generation there had developed into late copepodite stages.

In the western part of the transect, however, the herring had the probable advantage of feeding on the overwintered population in April, but were still confined to the same water mass when the new generation predominated in June. The adult herring did not migrate across the front into colder water, although herring have been observed to move into even colder areas to feed (Østvedt 1965). This may be related to herring stock size and zooplankton production which may have influence on the extension of the feeding area. In 1994 the feeding conditions in May and June may have been good and thus a feeding limited to the Atlantic water masses, and an early return to the overwintering areas in North Norwegian fjords may have been the result. In July and August 1991 and 1993 the herring in the Norwegian Sea had already returned to the areas near the Norwegian shelf, and food intake was low (Holst & Iversen 1992, Anon 1994). In the 1960's, however, the herring were still feeding in the areas near the Polar front in September and October and overwintered east of Iceland (Rudakova & Kaverina 1969).

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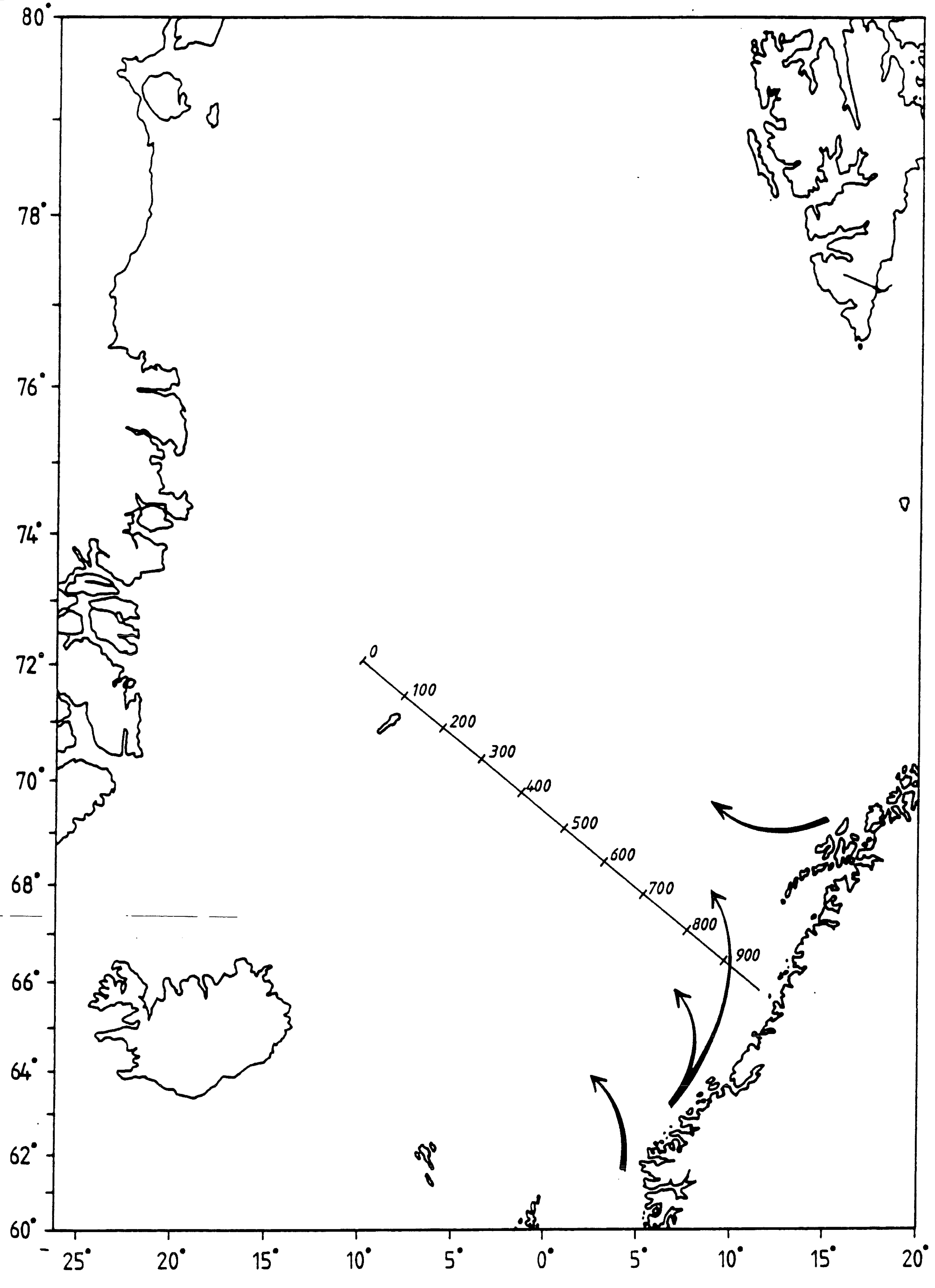

Fig. 1. Position of transect covered in April and June 1994. Anticipated migration routes of Norwegian spring spawning herring from the Norwegian coast into the Norwegian Sea.

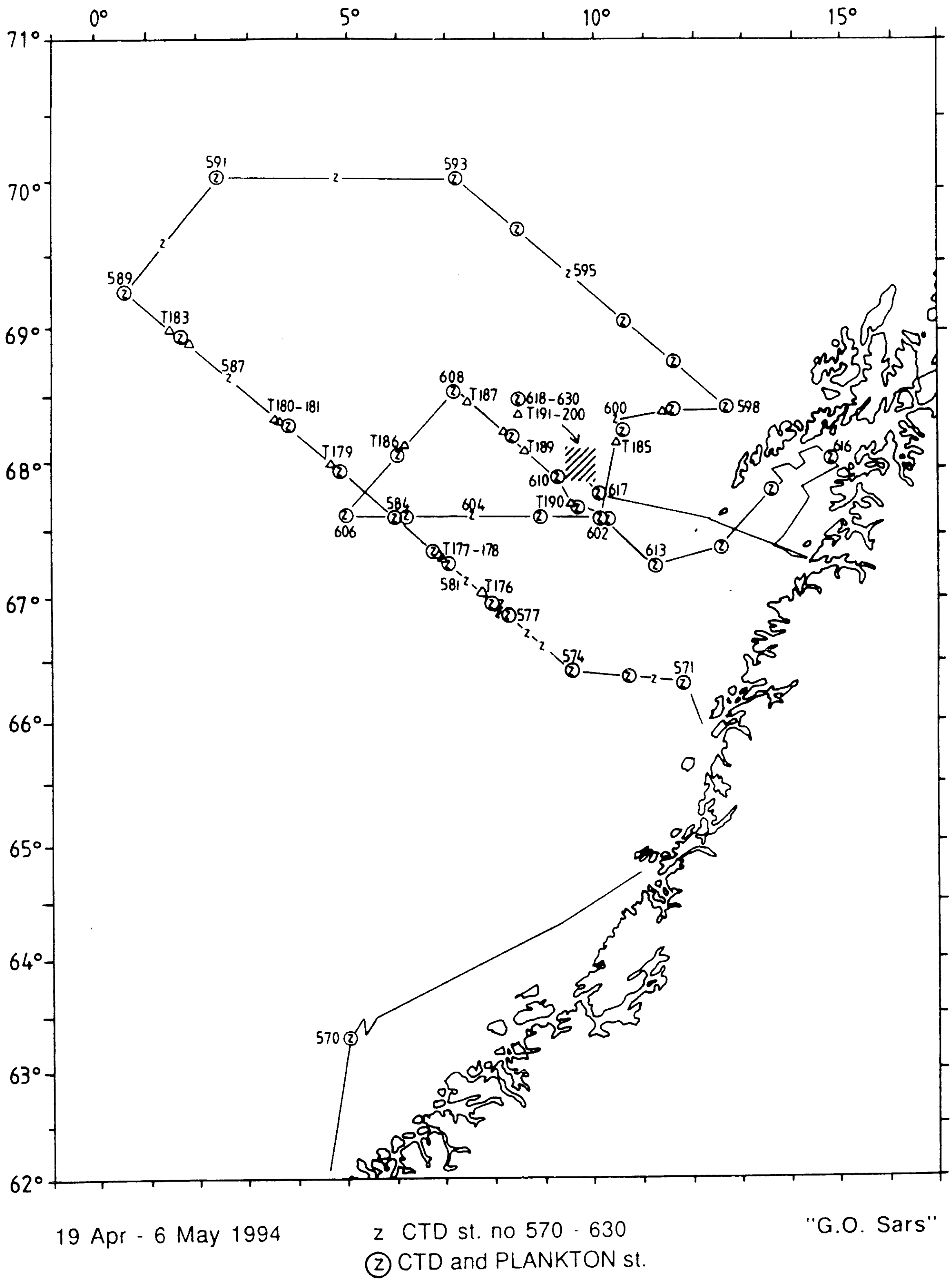

Fig. 2. Cruise lines and sampling stations in April 1994. Transect from about CTD-station 571 to station 589.

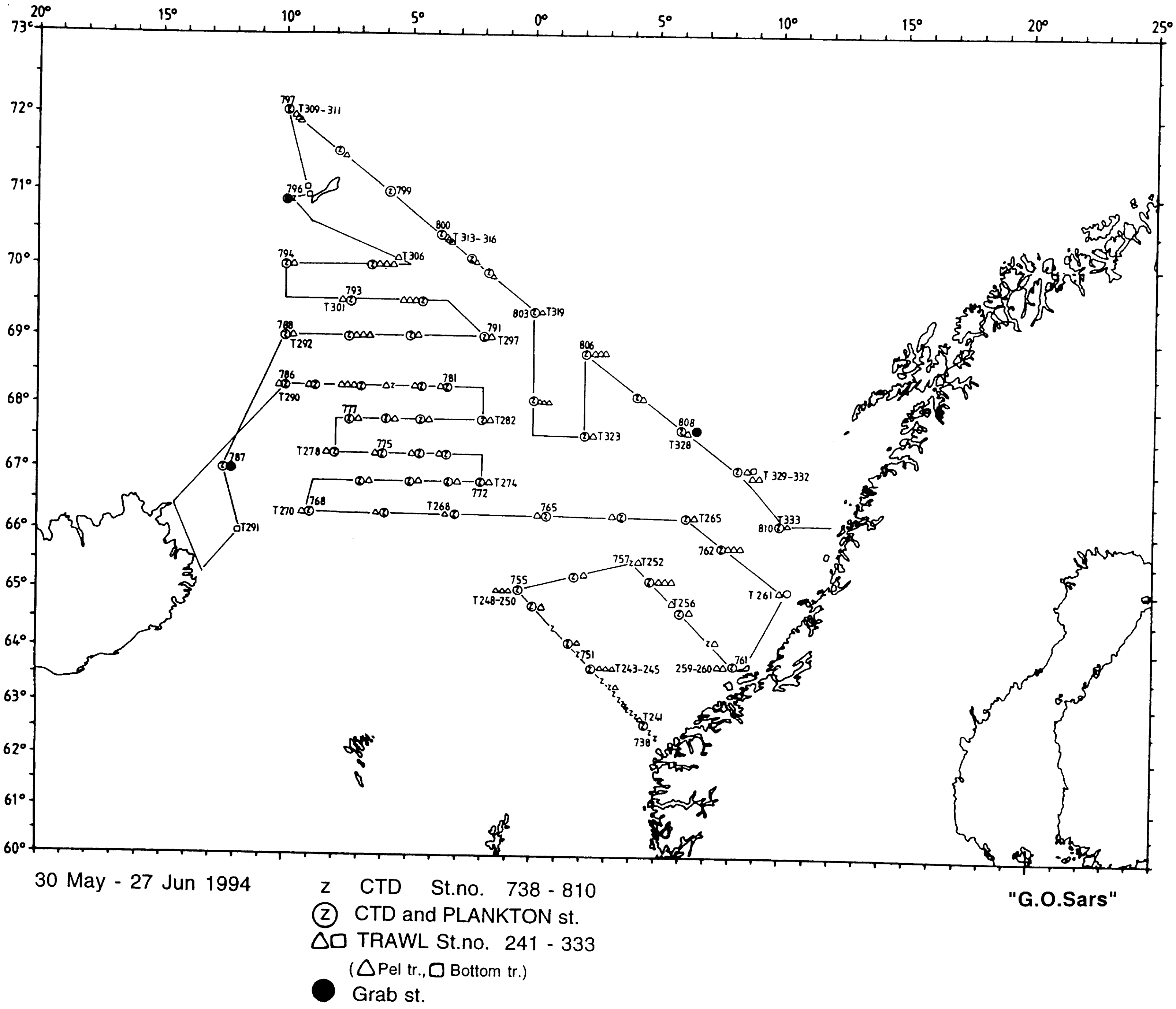

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Fig. 3. Cruise lines and sampling stations in June 1994. Transect from CTD-station 810 to station 797.

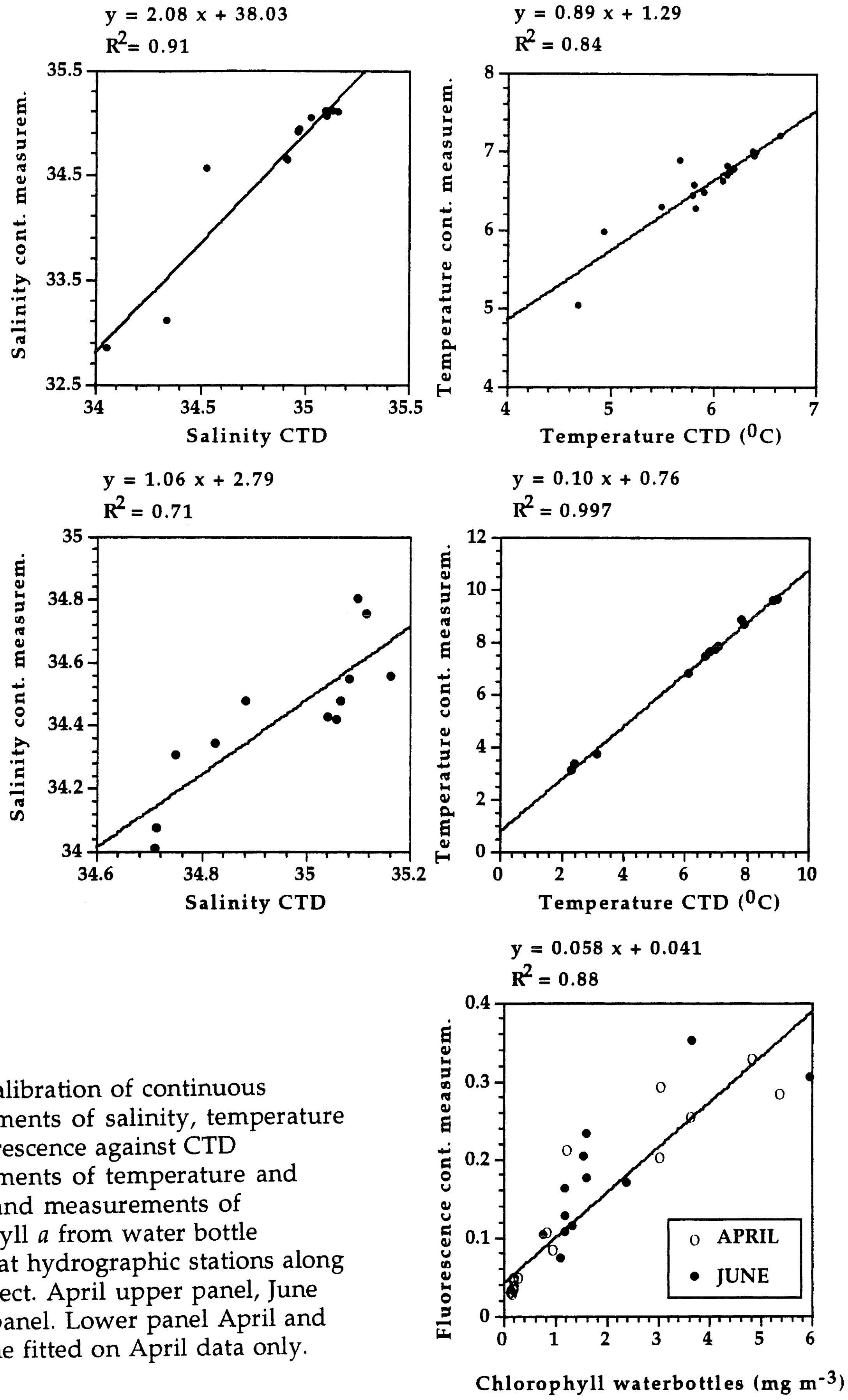

Fig. 4. Calibration of continuous measurements of salinity, temperature and fluorescence against CTD measurements of temperature and salinity and measurements of chlorophyll *a* from water bottle samples at hydrographic stations along the transect. April upper panel, June middle panel. Lower panel April and June. Line fitted on April data only.

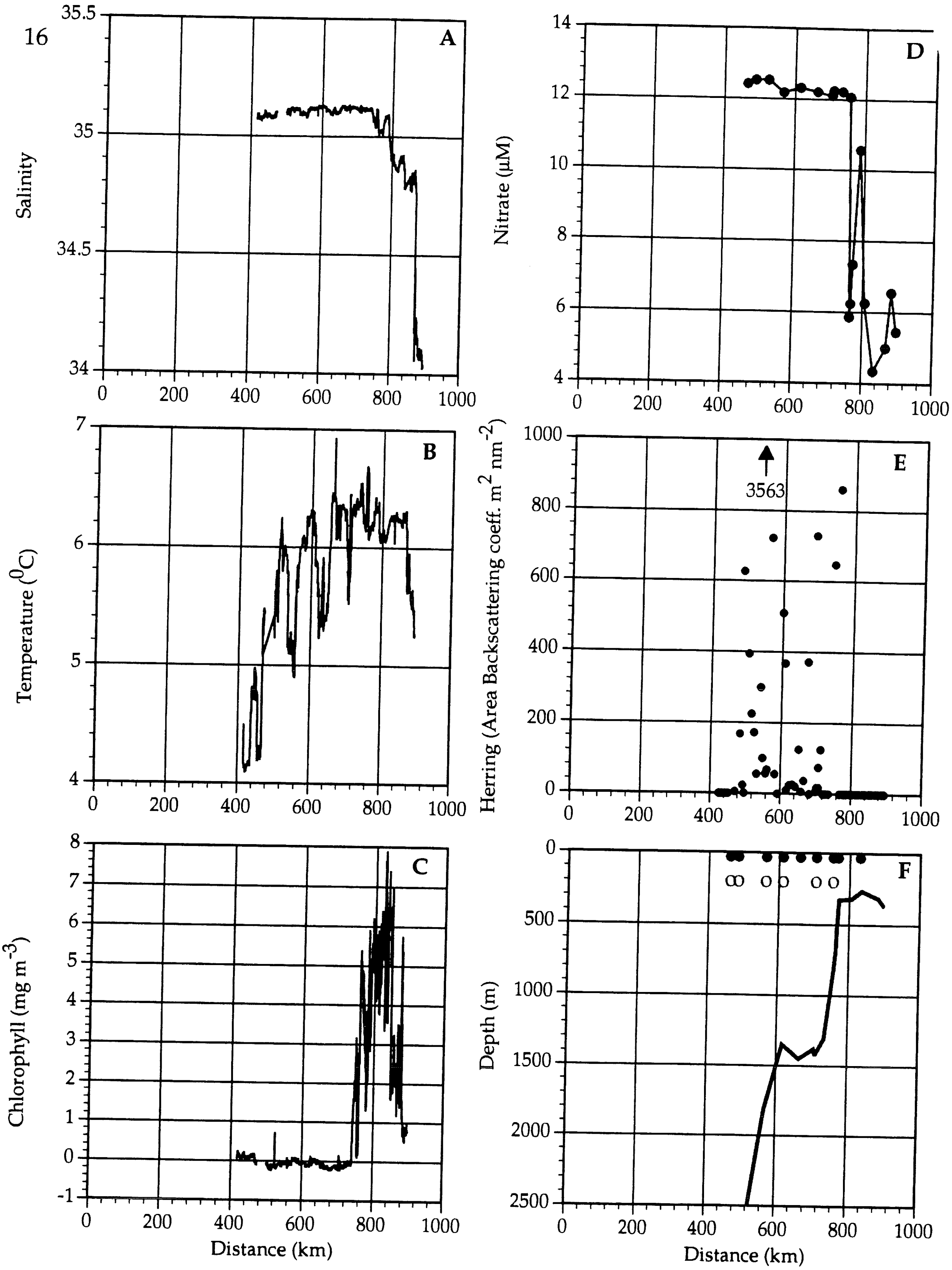

Fig. 5. April 1994. Distribution of salinity (A), temperature (B), fluorescence (C), nitrate (D), acoustic integrator values of herring each 5 nm (E), bottom topography (line), hydrographic stations 574-589 (filled circles), and trawl stations 176-183 (open circles) (F). See Fig. 1.

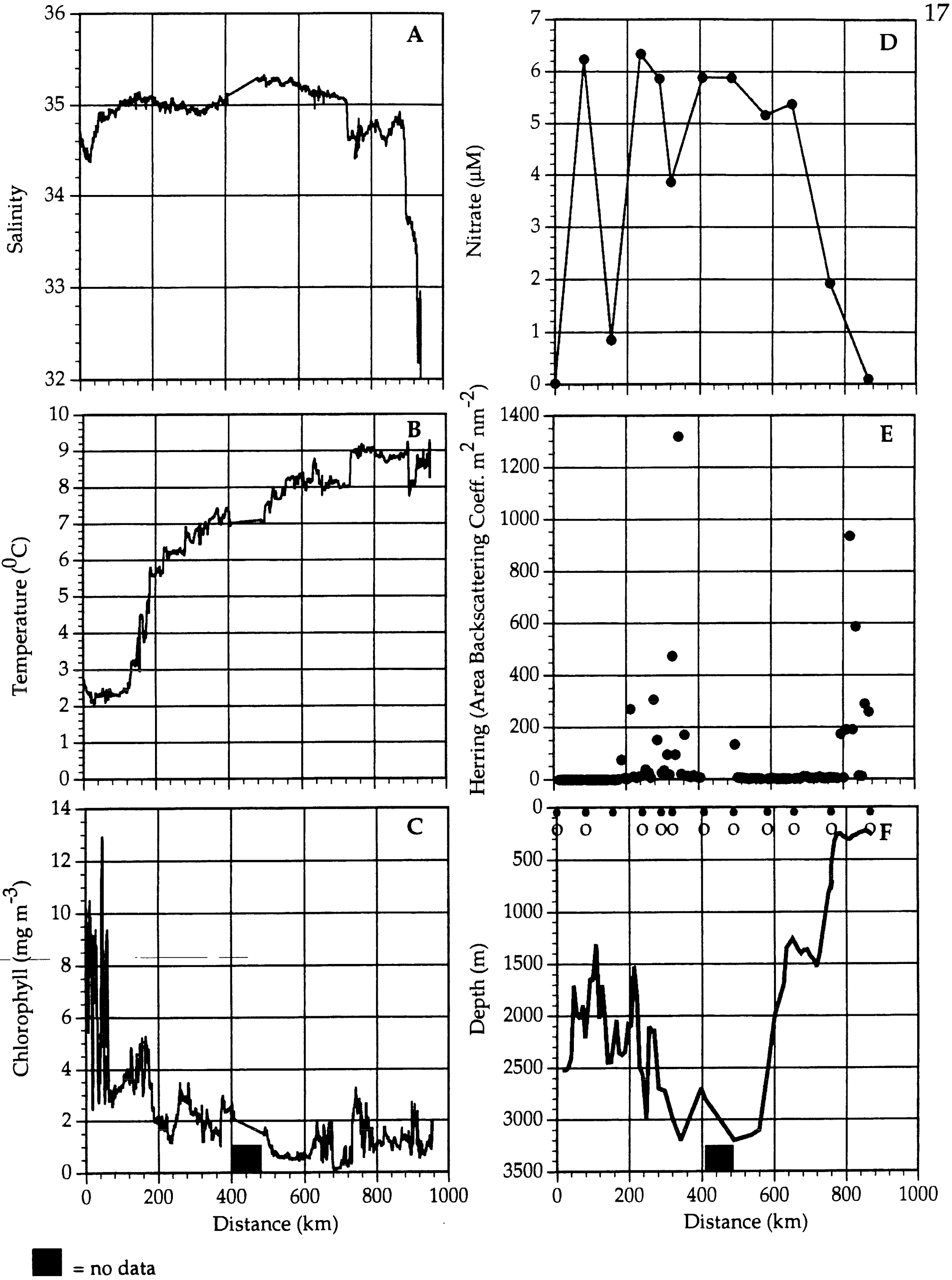

Fig. 6. June 1994. Distribution of salinity (A), temperature (B), fluorescence (C), nitrate (D), acoustic integrator values of herring each 5 nm (E), bottom topography (line), hydrographic stations 810-797 (filled circles), and trawl stations 333-309 (open circles) (F). See Fig. 1.

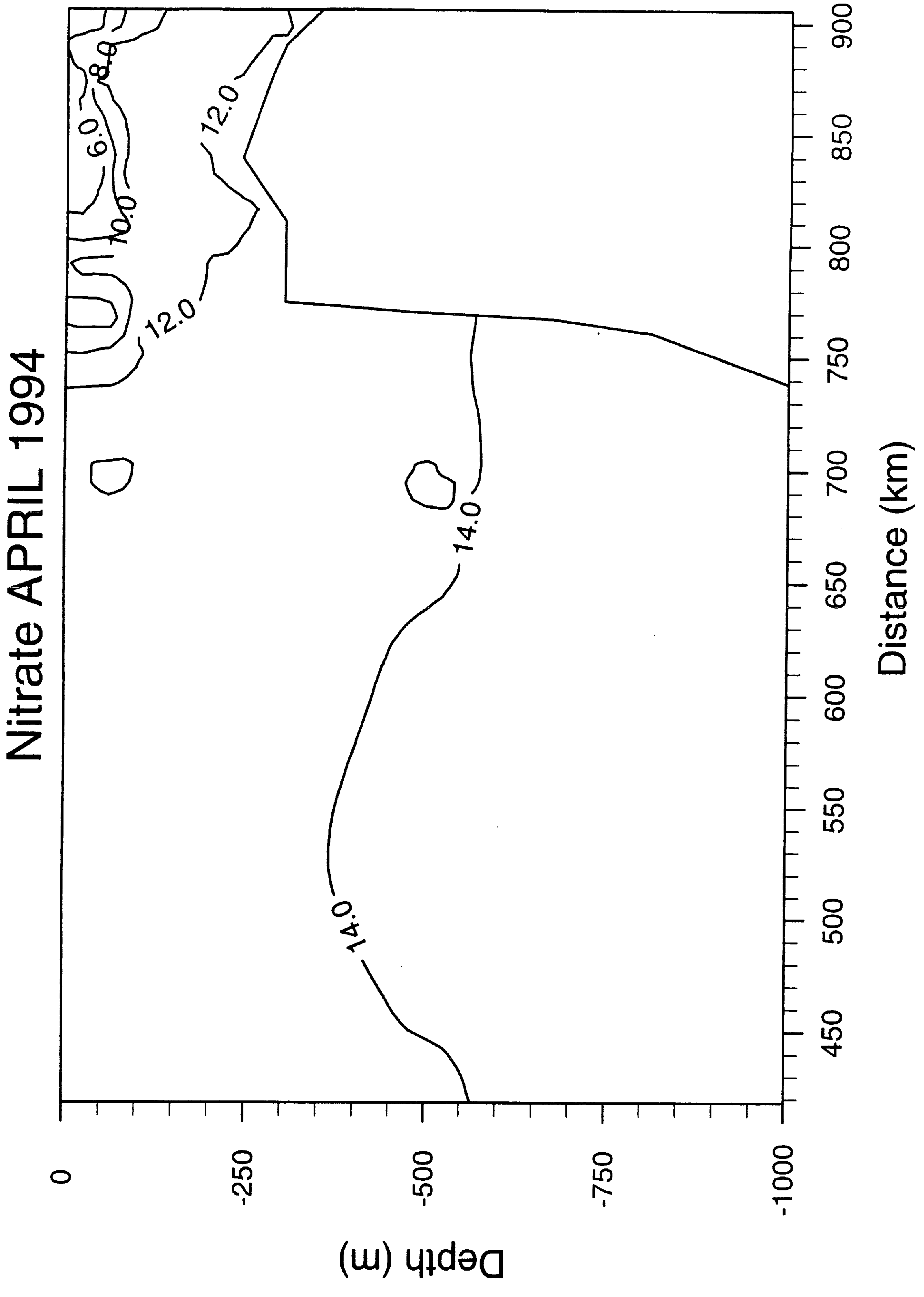

Fig. 7. Vertical distribution of nitrate (µM) along transect in April.

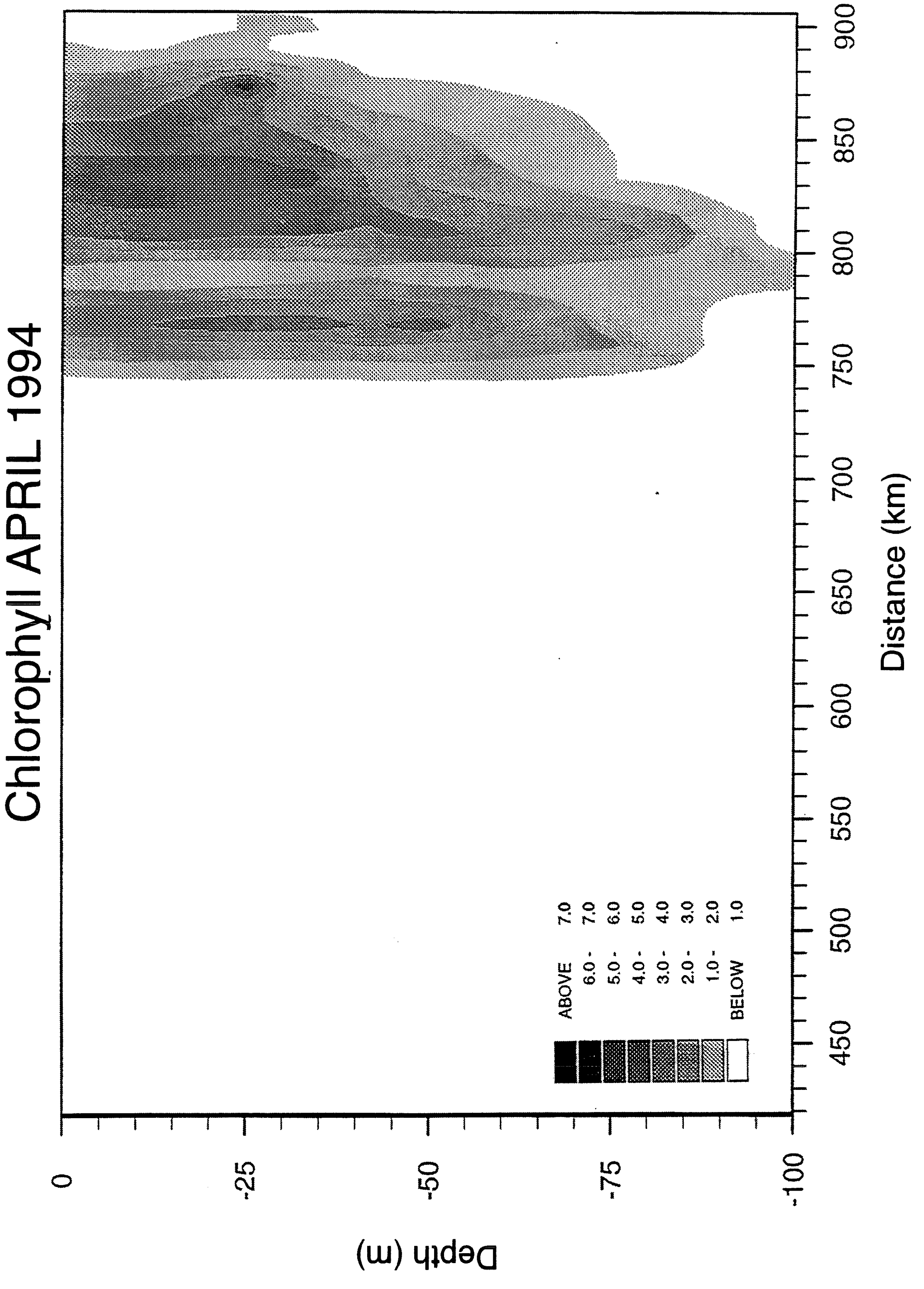

Fig. 7 cont. Vertical distribution of chlorophyll *a* (mg m^{-3}) along transect in April.

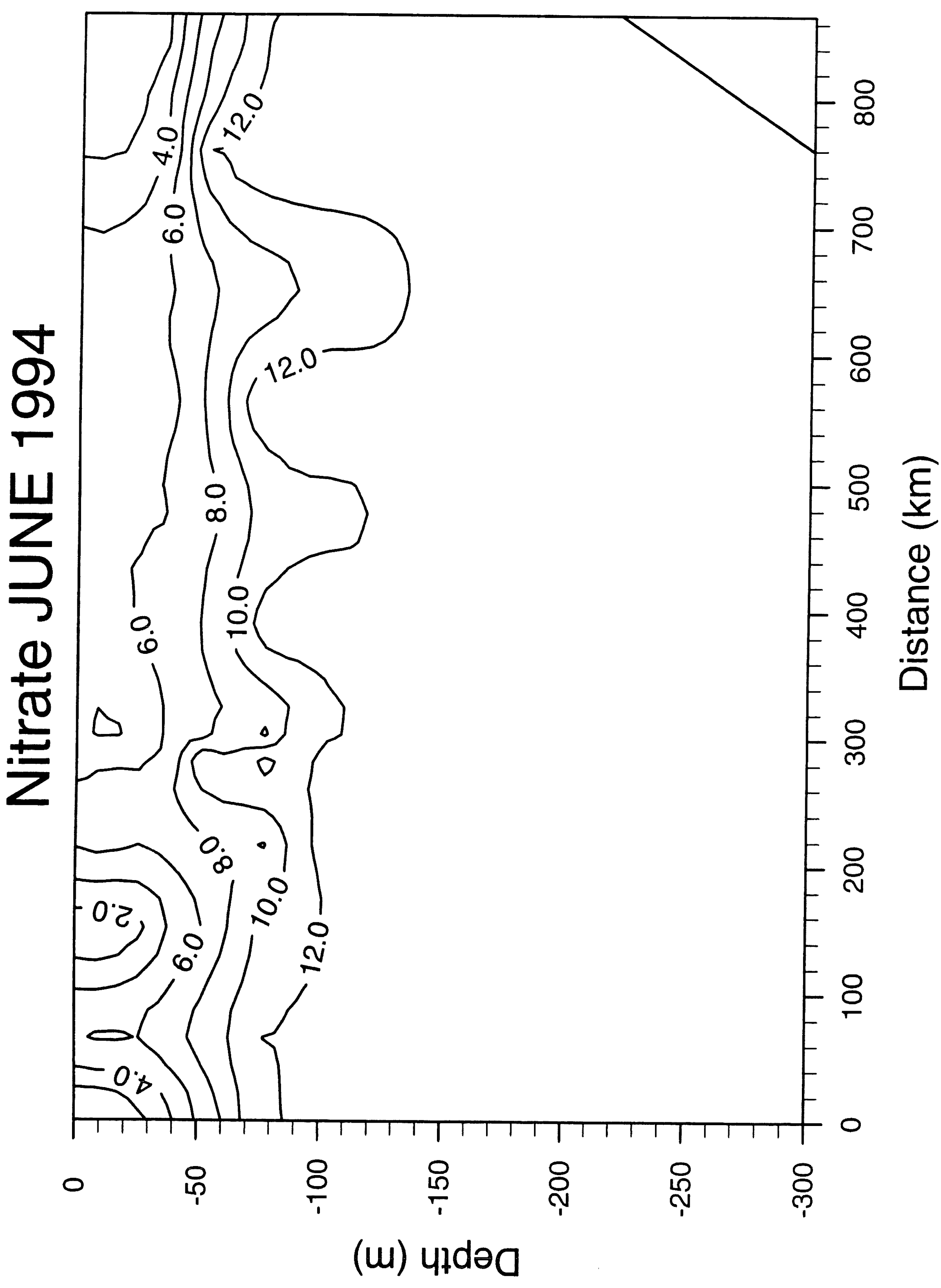

Fig. 7 cont. Vertical distribution of nitrate (μM) along transect in June.

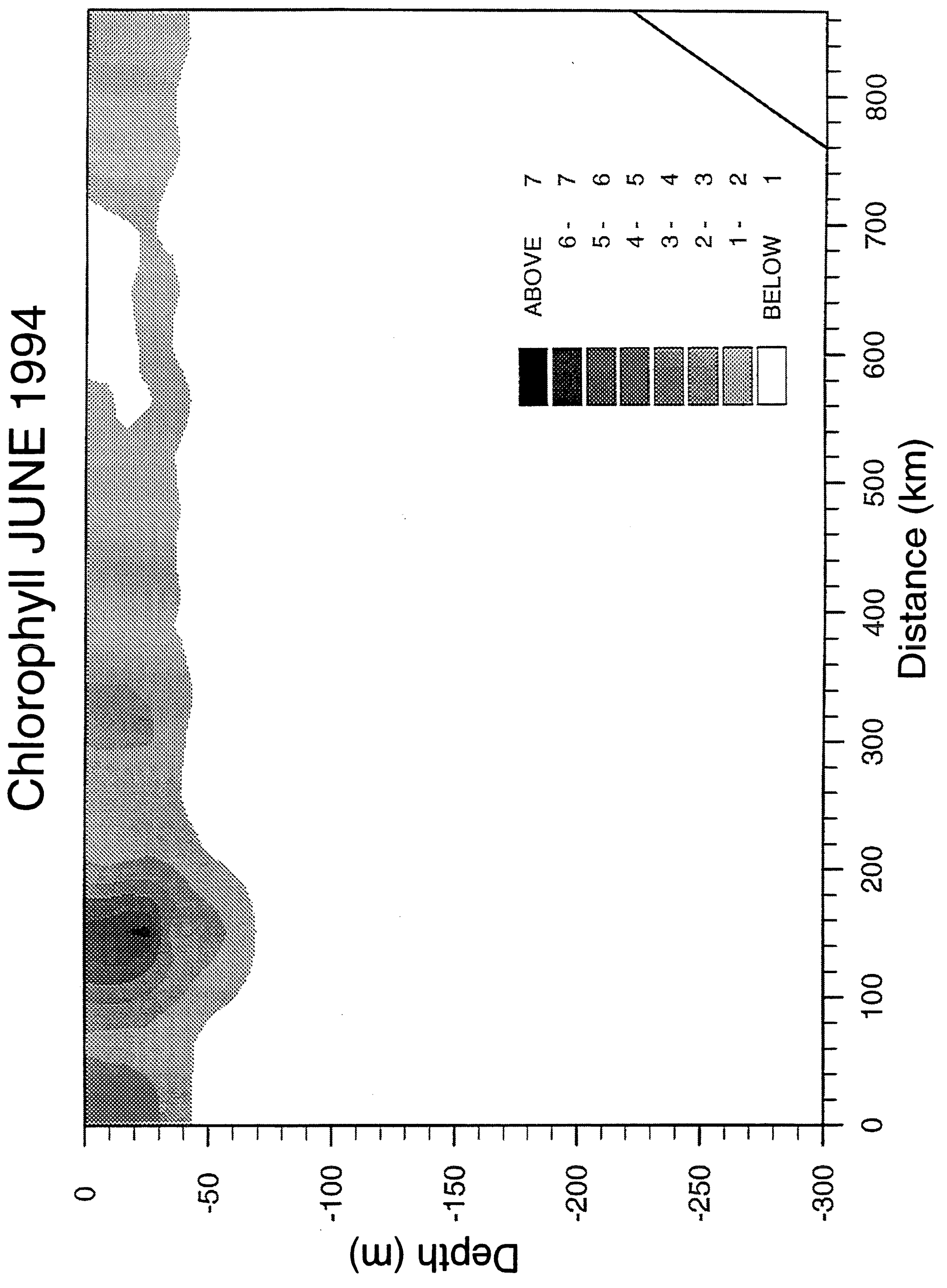

Fig. 7 cont. Vertical distribution of chlorophyll (mg m-3) along transect in June.

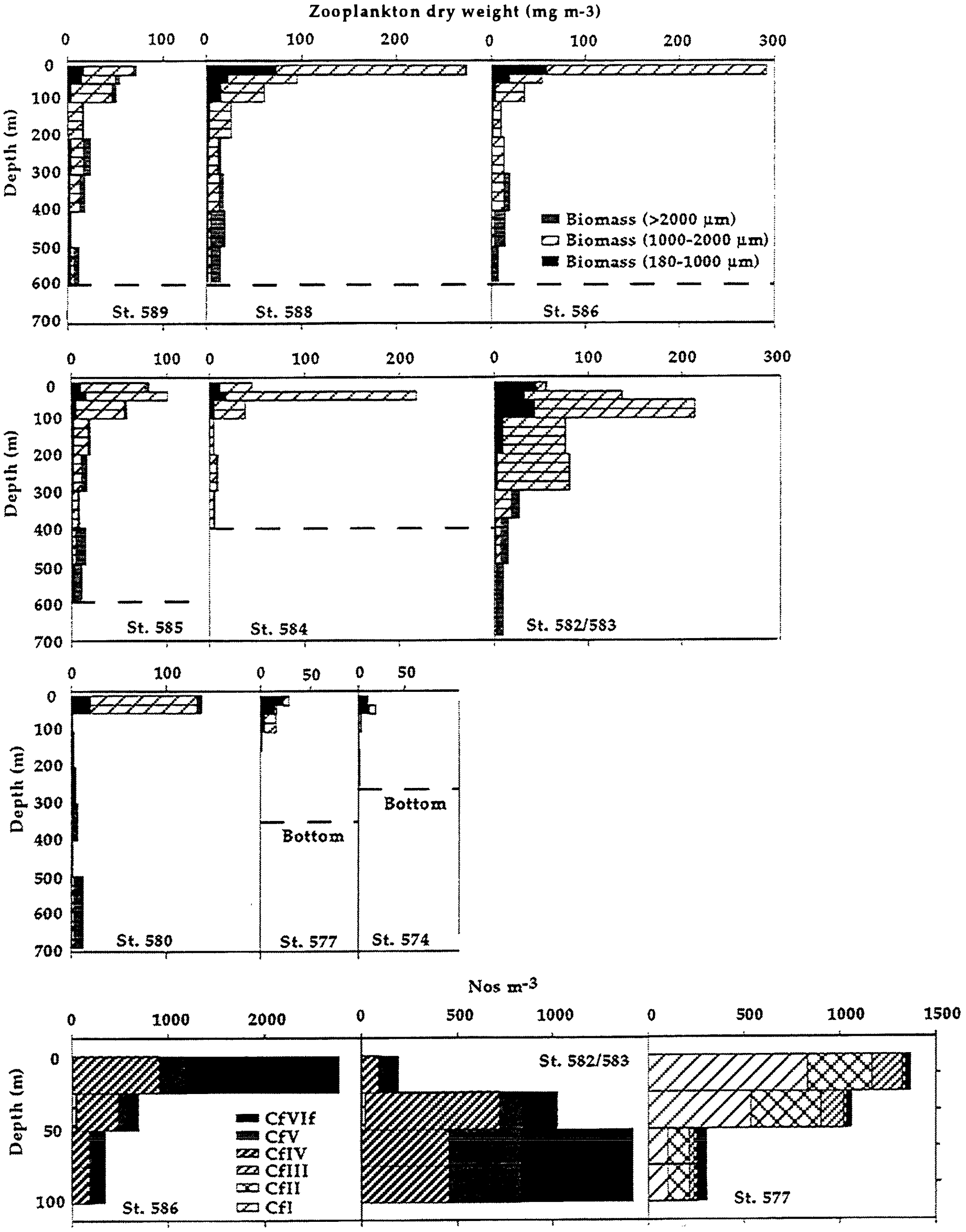

Fig. 8. Vertical distribution of biomass size fractions and abundance of *Calanus finmarchicus* at MOCNESS-stations along transect in April.

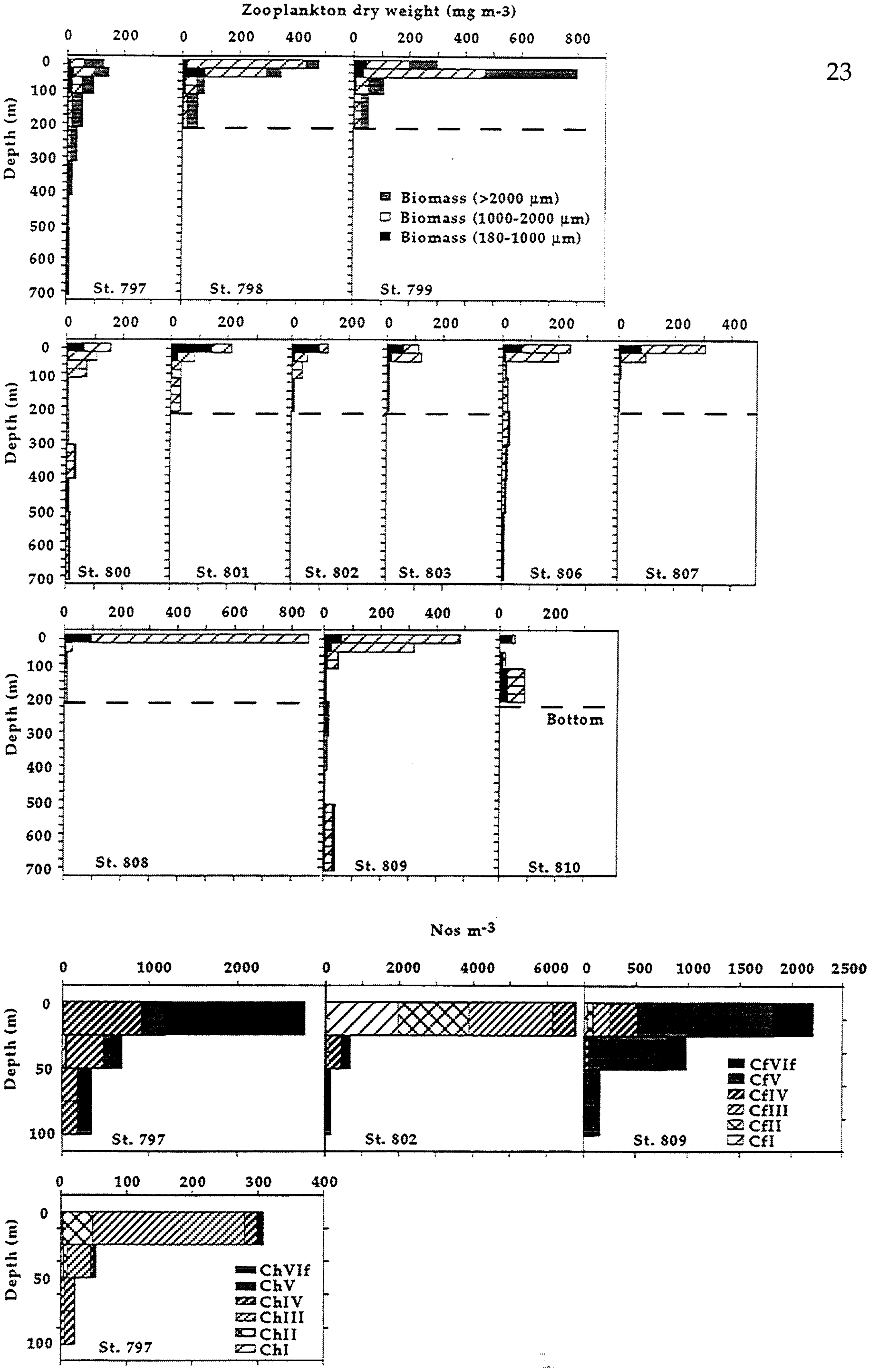

Fig. 9. Vertical distribution of biomass size fractions and abundance of *Calanus finmarchicus* at MOCNESS-stations along transect in June.

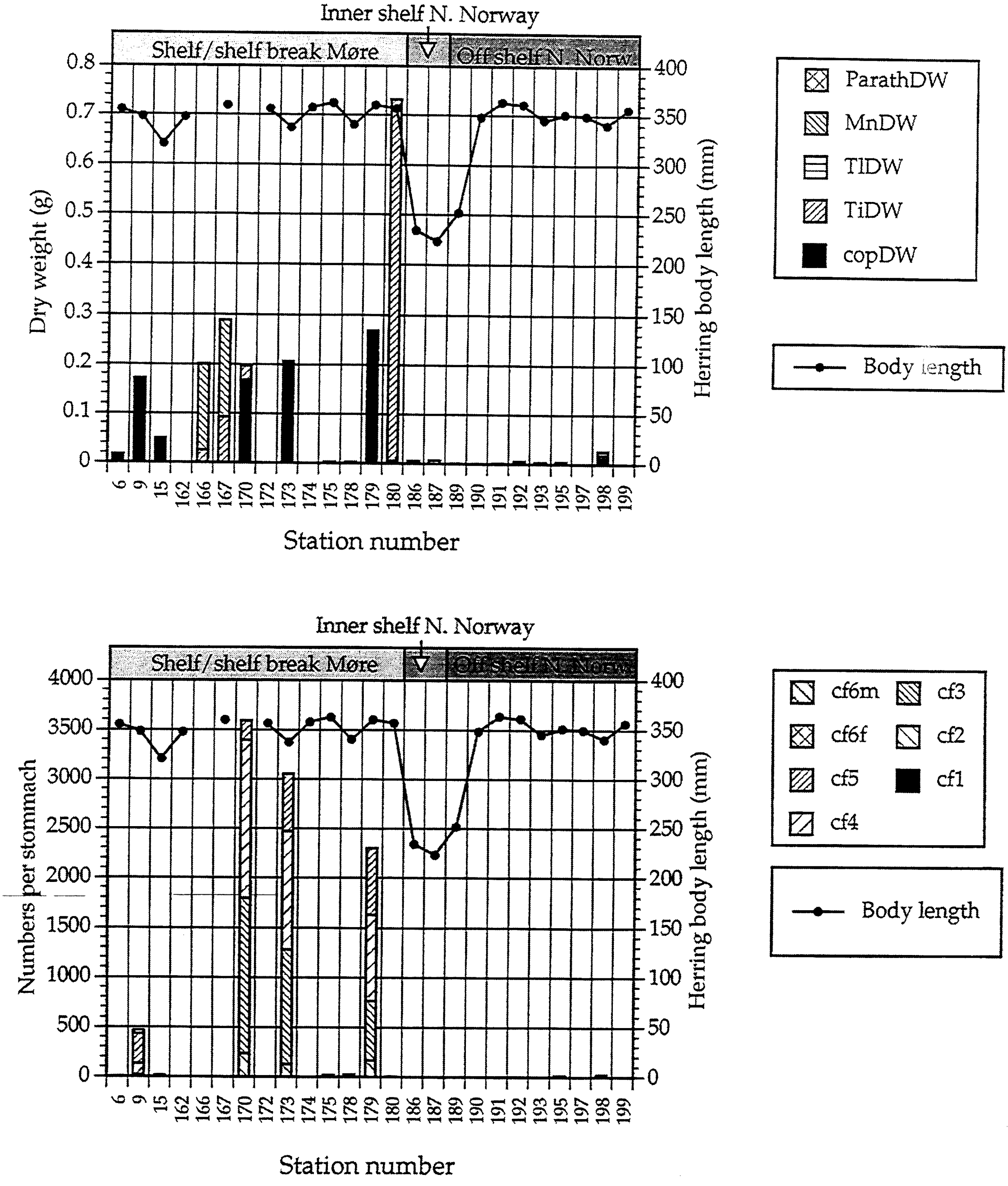

Fig. 10.Stomach content of herring in April 1993. Average dry weight of copepods, *Thysanoessa inermis, Thysanoessa longicaudata, Meganyctiphanes norvegica* and *Parathemisto* spp. in stomachs (Upper panel). Stage distribution (average number per stomach) of *Calanus finmarchicus* (Lower panel).

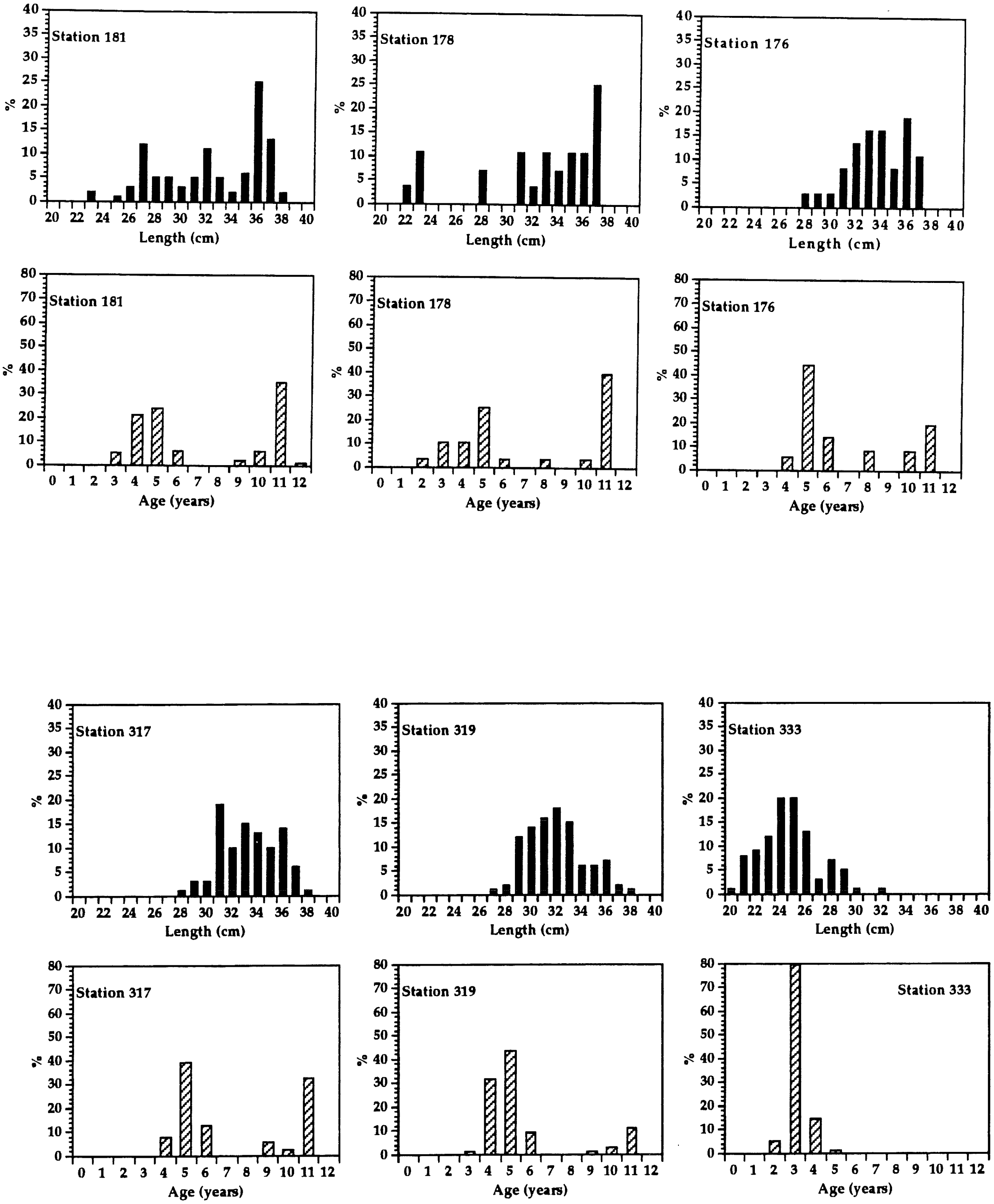

Fig. 11. Age and length distribution of herring at selected trawl stations along transect in April (Upper panel) and June (Lower panel).