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On the site-specific role of the central Norwegian shelf for the recruitment strategy of the Norwegian spring spawning herring

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Introduction

The Norwegian Coastal Current originates primarily from the fresh water outflow from the Baltic and the fresh water run-off from Norway. This water mixes with the North Sea Water and Atlantic Water and flows northward along the coast of Norway as a wedge-shaped low-salinity current bordered by the Norwegian North Atlantic Current off the central and northern parts of Norway (Fig.1). Off central Norway between 62° and 68° N, the Norwegian continental shelf is at its widest with a complicated bottom topography consisting of several shallow banks separated by deeper channels (Fig. 2). A conspicuous feature in the circulation pattern of that area is the pronounced topographic steering of the current (SÆTRE, 1998).

The Norwegian continental shelf north of 62° N and the Barents Sea are often considered as closely linked ecosystems where important fish species spend their entire life cycles(DRAGESUND and GJØSÆTER,1988). The eggs , larvae and juvenile fish drift northward from the spawning ground at the Norwegian coast towards their nursing and feeding area in the Barents Sea . There is subsequently a counter-current spawning migration back to the spawning ground. This somewhat simplified picture is relevant to most commercial species except for the Norwegian spring spawning herring which, before 1970, had their feeding area in the Norwegian Sea(RØTTINGEN, 1992). BJØRKE and SÆTRE(1994) demonstrated that the above area is not an isolated system and they presented evidence for a transport of juvenile fish into the central Norwegian shelf from spawning fields outside the area, such as in the North Sea, off Iceland, west of Scotland and around the Faroes.

The central Norwegian continental shelf is the spawning and hatching area for the Norwegian spring spawning herring with a spawning stock presently of about 7 million tonnes. The herring have demersal eggs and spawn mainly at the southernmost coastal banks off central Norway in February-March. The larvae hatch after approximately three weeks and are transported in a northerly direction by the Norwegian Coastal Current into the nursery areas, mainly the Barents Sea(DRAGESUND,1970). The herring stock has shown great abundance fluctuations through historical time(Fig. 3) and the increase in exploitation rate by the end of the 1960s resulted in a collapse of the stock(DRAGESUND *et al.*,1980). During the first part of the recovery period up to the mid-eighties, the herring was feeding in Norwegian coastal waters while from the late 1980s when the stock increased further, feeding during summer again took place in the Norwegian Sea(RØTTINGEN, 1992) Before the collapse of the stock the wintering area was in the Norwegian Sea between Iceland and the Faroes. After 1970, however, the wintering area of the herring has been the inshore waters of northern Norway. A summary of the temporal variability in migration and abundance of the herring stock is given by DRAGESUND *et al.*(1997).

Most likely, the central Norwegian shelf has an important site-specific role for the recruitment strategy of the Norwegian spring spawning herring. Since the start of the recovery of the Norwegian spring spawning herring in the late 1979s, more than 90 % of the spawning stock spawned on a relatively restricted area of this shelf between 62° and 63°30'N (RØTTINGEN,1992). Based mainly on herring larvae distributions, data from Lagrangian drifters and a numerical model, the aim of this contribution is to elucidate how the general circulation pattern and physical processes of the area relate to the drift, dispersal and recruitment success of herring larvae

Material and methods

Herring larvae surveys covering the central Norwegian shelf have been carried out in March-April since the late 1950s (DRAGESUND, 1970). From 1985 the larvae sampling methods were harmonised and more environmental parameters included in the sampling programme and the results reported annually (e.g. SÆTRE, BJØRKE and FOSSUM, 1988, FOSSUM, 1996). The routinely sampled material on these cruises is herring larvae, phytoplankton, zooplankton, nutrients, as well as water temperature and conductivity. During 1985 - 1992 field studies on the distribution of herring larvae also were conducted in May, (NEDREAAS, 1995) and during 1978 - 1991 the post-larvae distribution of herring was covered in June-July(e.g. BJØRKE *et al,*1989). The International 0-group surveys in the Barents Sea have been carried out since 1965 and is reported annually(e.g. ANON, 1997).

Since 1981 the Institute of Marine Research in Bergen, Norway has deployed more than 200 drifting satellite-tracked Argos buoys during spring and early summer to study the upper layer circulation and follow the drift and dispersal of pelagic fish larvae and juveniles (SÆTRE, 1998). The surface drifter is attached to a 11 m^2 window-blind drogue usually by a 30 m tether The buoys deployed in or drifting into the geographical area defined by Fig. 2 were used in the present study. These included 69 drifters from the period 1986 - 1994 and 2 from 1982. All these drifters except one were recovered with their drogues intact. 80% of the deployments were in March-April, so the drift of these buoys is representative for the spring/ summer situation. Consequently, the material does not provide seasonal variations. No attempt has been made to correct the drifters for the possible influence of wind, i.e. the direct effect on the surface buoy or the indirect effect by setting up an Ekman current

The model results in this contribution is from the model and the runs described by SVENDSEN *et al.*,(1995). The model set up consist of the well-known POM hydrodynamic model (BLUMBERG and MELLOR,1987) coupled to a simple Lagrangian particle tracking model. The model is used to approximate the prognostic variables from 15 February to 15 September each year during the period 1976 - 1993. The particles assumed to represent herring larvae are released at the spawning ground according to the mean hatching curves and given a vertical migration pattern according to HEATH *et al.* (1988).Use and validation of the model set up for different areas of the north-east Atlantic is described in SVENDSEN *et al.*(1996), BERNTSEN *et al.*1996) and SKOGEN *et al.*(1997).

Results

Larvae distribution and recruitment variability

Based on the investigations referred to above, Fig 4 is a synopsis and an attempt to visualise typical distribution patterns of the different stages of the herring larvae; in mid-April, in mid-May, around 1 July and 1 September. The main spawning areas have in recent years been on the central Norwegian shelf between 62° and 66° N. As can be seen, the young herring drift northward with the persisting current system while at the same time its distribution area increase. At about 72° N the current and the transport split into two branches; one flows into the Barents Sea while the other one follows the continental shelf break towards the west coast of Svalbard (Fig. 1). There is large inter-annual variability in both the abundance and the distribution pattern of the young stages of herring. Some years may be characterised by a strong inflow to the Barents Sea while in other years the larval transport towards the Svalbard area will dominate. Fig 4, however, can be regarded as a conceptual climatic mean distribution.

Table 1. Stock and recruitment indices for the Norwegian spring spawning herring

References	1	2	3	4	5	6	7	8	9
YEAR	Larval index ≥ 12 mm	Larval index St. 2a	Larval product. index	Post larvae index	Log. 0-gr. Aug-Sep. index	0-gr. index Nov.	Age 3 in millions	Spawn. stock (thous. tonnes)	Recruit-ment succes (7/8)
1976	0.056				0.00	1888	669	135	4.96
1977	0.029				0.01	207	333	284	1.17
1978	0.015				0.02	603	409	355	1.15
1979	0.077			9	0.09	1729	807	385	2.10
1980	0.000			1	-	117	99	468	0.21
1981	0.007		0.3		0.00	134	71	503	0.14
1982	0.010		0.7		0.00	1469	152	501	0.30
1983	0.280		2.5	(93)	1.77	6866	24449	570	42.90
1984	0.120		1.4	(46)	0.34	701	1038	594	1.75
1985	0.200	1.67	1.1	(57)	0.23	502	2382	491	4.85
1986	0.072	0.26	0.7	(5)	0.00	204	602	409	1.47
1987	0.046	0.66	1.3	3	0.00	410	393	982	0.40
1988	0.110	3.40	9.2	86	0.32	1274	1839	3124	0.59
1989	0.340	2.60	13.4	(980)*	0.59	2890	5768	3838	1.50
1990	1.000	0.53	18.3	(571)*	0.31	1009	10754	3994	2.69
1991	2.600	3.30	8.6	2786*	1.19	2807	27613	4157	6.64
1992	1.700	2.90	4.6		1.06	2891	32195	4004	8.04
1993		13.00	24.7		0.75	827	12310	3864	3.19

( ) = Incomplete coverage of the distribution area * = aggregating in schools

References

1) KRYSOV, BJØRKE and SVENDSEN (1995) 2) FOSSUM (1996) 3) ICES (1998)
4) BJØRKE, BAKKEPLASS og HANSEN (1991) 5) ICES (1998) 6) ICES(1998) 7) ICES(1998)
8) ICES(1998)

The recruitment to the herring stock shows great variability as demonstrated by the number of recruits measured at an age of 3 years(Fig. 5). Table 1 lists some stock and recruitment indices for the Norwegian spring spawning herring for the period for which the model was run (1976 - 1993). A survival index (Column 9) was calculated as the ratio between the number of recruits at age 3 years and the corresponding producing spawning stock. The survival index for the period 1950 - 1993 is shown in Fig. 6. The index is varying within two orders of magnitude with the well known 1983 year class as having the outstanding best survival for the three years old herring for at least the last 50 years. Also at the 0-group stage the 1983 year class has its extreme high abundance (Table 1, Columns 5 and 6) while at an earlier stage the picture is not so clear (Table 1, Columns 1,3 and 4).

The plot of the spawning stock versus the corresponding number of recruits at three years age indicate some interesting features(Fig. 7): The chances to have a good year class from a low spawning stock (below 2 million tonnes) is very small - this happened in 1983 only. Also for high spawning stocks(above 8 million tonnes) there is only one good year class which is that of 1950.The nine years with spawning stock size above 8 million tonnes(1950 - 1958) had all a low survival index(Fig. 6). The best chances for a good recruitment seems to be at medium spawning stock size(Fig. 7).

Lagrangian drifters

The results from all the 69 drifters deployed or drifting into the area defined in Fig. 2 are presented as a trajectory plot in Fig. 8. Fig. 9 shows the parts of the trajectories where the daily mean drift speed exceeds 30 cm/s. Branching of the Norwegian Coastal Current around 63°30'N can clearly be seen with the main route close to the coast and a secondary route along the shelf break. The main route consists of sections characterised by rather high speed and directional persistence, such as between 64° and 65°N and 66° and 67°N, followed by areas of retention. The secondary route along the shelf break shows some mesoscale eddy-like features.

Fig 10 is an attempt to sum up the most conspicuous upper layer circulation features as revealed both from both historical hydrographic observations as well as from Lagrangian drifters (SÆTRE, 1998). The whole shelf area north of 63°N is covered by Atlantic water below 100-150 m and the effect of the topography is transferred from the Atlantic water to the Norwegian coastal water above. During the first two quarters of the year there seems to be no westward cross-current transport from the shelf into the deep parts of the Norwegian Sea.

As an effect of the topography, the Norwegian Coastal Current split into two branches at about 63°30'N; an outer one which follows the shelf break and an inner one at the coastal side of the banks(SÆTRE, 1998).The outer and secondary branch mixes with Atlantic water and gradually looses its coastal water identity. It is hardly traceable north of 65°N. Some meso-scale eddy-like features along this route could most likely be explained by meanders along the frontal zone between the Atlantic water and the Norwegian coastal water. The inner and main branch is the Norwegian Coastal Current proper or the Coastal Jet, with the highest values of mean current speed and directional stability. The wedge-shaped current flows in a narrow 20 - 30 km broad zone. The mean transport time between 63° and 68°N along the two routes is approximately the same but the inner route has the highest variability in current speed(SÆTRE,1998).

Several retention areas are identified on the shelf. These locations act as convergence zones, where marine organisms may accumulate. The anticyclonic retention areas are usually associated with banks while in others the rotation of circulation apparently depends more on other topographic features such as depressions, horizontal current shear or the local winds(SÆTRE, 1998).

Model results

SVENDSEN *et al.*(1995) compared the 18 years(1976-1993) of particle distributions from the model simulation of the larval drift with several years of measured larval distribution. There was a tendency for the larvae having progressed slightly further north and east than postulated by the model. However, they conclude that on a large scale the model seems able to quite realistically simulate several years of measured distribution pattern of herring larvae two and four months after hatching. Actual larval concentrations within the distribution area was not compared as larval mortality was not accounted for.

Fig 11 gives the modelled mean current vectors in 30 m depth for the spring month(April-June) for the period 1976-93 and Fig 12 isolines for the mean current speed. By comparing with Fig. 10 some of the important circulation features could be seen, such as the split of the Norwegian Coastal Current into two branches and other large scale topographic effects. The Coastal Jet and the influence of the smaller banks, however, are not apparent north of 65°N. The model is able to correctly identify the two areas of maximum current speed and seems to simulate the average strength of the current speed at the shelf area rather good. It miss, however, to reproduce the high current speed values in the Coastal Jet north of 65 °N

Model particles were released in 30 m depth at two positions; one at a coast-near location at the shelf(A) and the other one at the shelf break(B). 9 particles were released every ten days from 25 March to 25 April during the years 1989-1992 and the results depicted as trajectories up to 1 July (Fig. 13). The trajectories from the two locations show clear differences. The particles from the inner position are mainly found in a narrow band along the inner and main branch of the Norwegian Coastal Current while the particle from the shelf break position are spread more with less directional stability.

The model also calculate the centre of gravity of the particle distributions and σ^2 which is the mean squared distance from the particles to their centre of gravity or simply the *variance*. The unit for the variance is m^2 and σ^2 is proportional to the size of the distribution area. Fig 14 shows the temporal development of σ^2 for the years 1976 to 1993 from the start of the hatching at 5 March to approximately mid-September. The figure also includes the observed range of the size of the distribution areas for the same observation periods as referred to in Fig. 4. The best fit between the calculated σ^2 and the observed size of the distribution areas is obtained by applying 2 as the proportionality factor.

The inter-annual variability in the σ^2 development (Fig. 14) seem to be rather low the first 80 days and increase thereafter. As can bee seen, the expansion rate of the distribution field, $\partial\sigma^2/\partial t$, sometimes could be zero or even negative indicating an accumulative phase for the particles or the presence of retention areas. There is a reasonable coincidence between the calculated size of the distribution area applying 2 as proportionality factor and the observed size range. The largest discrepancy between the observed and the calculated values is found in May.

In Fig 15 the position of the calculated centres of gravity for the period 1976-1993 during four different surveys are compared with the observed gravity centres range from the same surveys. With the exception of April, all the observed centres of gravity is found north of the calculated ones from the model and the discrepancy between the calculated and observed values increase with time. This means that nature transports the herring larvae faster towards the Barents Sea than the model is able to do. Fig. 16 gives more detail for the different years for the calculated centres of gravity 1 July and 20 August. The years with the northernmost gravity centres 1 July(79,83,86,92) continued to be so also 20 August.

The model calculated the age of the particles found in three different zones of the central Norwegian shelf(64°-66°, 66°-68°, and north of 68° N) for 45, 75 and 117 days after the start of hatching. The results of these calculation are found in Table 2.

Table 2 Mean age of the herring larvae within each area after 45, 75 and 117 days after start of hatching for the years 1990-1992.

	Numbers of days after start of hatching								
Area	1990			1991			1992		
	45	75	117	45	75	117	45	75	117
68°N → N	45.0	67.2	100.1	-	66.2	100.1	-	70.3	96.4
66°N - 68°N	36.8	58.3	94.1	39.4	57.1	94.4	41.8	54.4	94.2
64°N - 66°N	23.0	49.4	91.1	23.1	50.7	92.9	25.0	49.8	90.8

45 days after the start of the hatching during the years 1990 to 1992 there is a clear north-south gradient in the age of the particles. This gradient is gradually reduced with time and at 117 days after hatching(1 July) it is insignificant. This is obviously an effect of horizontal mesoscale mixing. In nature, however, this process seems to be slightly stronger than simulated by the model (FOSSUM and MOKSNES, 1993, FOSSUM and MOKSNES, 1995).

Discussion

In the last fifty years of the herring stock history only two strong year classes, 1950 and 1959(Fig. 5), was produced before the collapse of the stock in the late 1960s(Fig. 3). During the recovery period several large year classes were produced with 1983, 1991 and 1992 as the most outstanding(Figs. 5 and 7). In Norwegian waters good year classes frequently occur simultaneously for several species, such as for herring, cod and haddock(SÆTERSDAL and LOENG,1987, ELLERTSEN *et al.*,1989). This is a clear indication of the presence of a climatic signal in the recruitment mechanisms as demonstrated by several authors. Large-scale variability in physical conditions thus set the frame within which the potential recruitment mechanisms can operate. The relative importance of these will probably vary between stock and species as well as with space and time. An important task is therefore to try to identify the most relevant ones and to elucidate in which part of the early life history of the studied fish stock the different mechanisms are of significance.

The spawning stock of the herring was 2-600 thousand tonnes during the period 1976-1986. With the recruitment of the strong 1983 year class the spawning stock biomass increased to about 4 million tonnes for the years 1989-1993(Table 1,Fig. 3). FOSSUM(1996) studied the first-feeding larvae during the period 1985-1993. It was evident from these investigations that there was a rather strict relationship between the size of the spawning stock and the number of larvae found, and most of the variability in the larval abundance could be explained by the concurrent change in the spawning stock biomass. The abundance of post-yolk-sac larvae(Development stage 2a) is believed to reflect the success of the first-feeding period. Based on this assumption successful first-feeding periods must have taken place to a certain extent in 1985, 1988-1989, and 1991-1993(Table 1, FOSSUM,1996). The highest larval survival was found in 1993 and this could be explained by the high prey density found this year(FOSSUM,1996).

KRYSOV, BJØRKE and SVENDSEN (1995) used the abundance of larvae larger than 11 mm as an index for the first-feeding larval survival(Column 1,Table 1). As could be expected, there is some minor discrepancies between this index and that of FOSSUM,(1996). The time series of KRYSOV, BJØRKE and SVENDSEN (1995) clearly indicate that during the period 1976-1984 only 1983 could be characterised as a year of good first-feeding larval survival(Table 1). Consequently, all three strong year classes(1983,1991,1992) after the start of the recovery period are included in the years of successful first-feeding larval survival. It seems as good first-feeding larval survival is a necessary but not sufficient condition for a strong year class. A similar conclusion is reached for the importance of the environmental signal on recruitment. SÆTERSDAL and LOENG,(1987), ELLERTSEN *et al.*,(1989) and SUNDBY,(1995) have all demonstrated positive correlation between the sea temperature and the formation of good year classes of species, such as herring, cod and haddock in Norwegian waters. However, in this system high temperatures is a necessary, but not adequate, factor to produce good year classes. As a tentative conclusion on this part of the discussion may be that the environmental influence on recruitment variability is primarily operating on the early larval phase by effecting the first-feeding larval survival.

For the Norwegian spring spawning herring there appear to be a rather strict relationship between the 0-group index in August-September and the number of recruits at age 3 years(Table 1) which means that the year class strength is to a large degree fixed when the larvae reach the 0-group stage. After the year class has successfully passes the first-feeding phase other important recruitment processes will determine whether a good year class is established. The present authors believe that these other processes are mainly predation.

Fish eggs and larvae are prey for a wide range of marine organisms, from algae to seabirds and mammals. Until the end of the first-feeding period the predation on herring larvae is probably of insignificant importance for the recruitment success. Later on, predation is a part of a size-selective process and the vulnerability of the fish larvae and 0-group fish in relation to year class strength increase dramatically. According to HAMRE and HATLEBAKK(1998) the herring is the key species at fish level of the food chain in the Norwegian Sea-Barents Sea ecosystem and the cod is its dominant predator. Based on their system model for the Norwegian Sea-Barents Sea ecosystem they conclude that the survival of 3 year old herring is mainly determined by predation of immature cod. Other important predators on herring larvae and juvenile are probably 3-4 year old herring(HOLST and RØTTINGEN,1994), blue whiting(T. Monstad,IMR, personal communication) and seabirds, such as puffins(ANKER-NILSSEN and LORENTSEN, 1990).The available data are inadequate to assess the total consume of herring as well as the relative importance of the different predators.

The 1983 year class was characterised by having the outstanding best survival for the three years old herring for at least the last 50 years. Why was this year unique in relation to the recruitment to the herring stock? Most likely, the drastically reduced mortality for the juvenile herring and consequently, an extraordinary good survival rate this year was due to a drastic reduction of predators. The 1982 year class of blue whiting was good and a potential predator but there was no herring and the cod stock was on its historically lowest level.

The central Norwegian shelf is characterised by a complicated bottom topography which has a pronounced effect on the circulation features. The currents in the area are split into several branches of which some have the character of a well defined jet current while other branches is more variable. During the first half of the year the whole shelf area act as a large retention area with actually no westward leakage of herring larvae into the deep Norwegian Sea. Fronts with frontal processes, transient and quasi-stationary eddies are all conspicuous features of this highly dynamic area.

The main spawning areas of the Norwegian spring spawning herring in recent years been the central Norwegian shelf between 62° and 66°N. This is also the area for the first contact between the northward flowing Atlantic Water and the Norwegian Coastal Water(Fig. 1). As a result, the highest winter and spring temperatures along the whole Norwegian coast are found her. Herring have demersal eggs and the most important spawning fields are usually found in areas of topographically induced quasi-stationary eddies. The whole shelf area north of 63°N is covered by Atlantic Water below 100 - 150 m with rather small temperature variability compared to the upper layers. This means only minor fluctuation in incubation time. The larvae are hatched in batches in retention areas where also the prey of the larvae, copepods eggs and nauplii, are concentrated. Various authors have described how the patchy distribution of both fish larvae and their prey in areas dominated by hydrographic structures such as eddies and fronts are positive for the larval survival.

The numerical model seem to be able to realistically simulate a number of pronounced feature of the circulation pattern and the herring larvae distribution. However, it clearly also missed to reproduce some important characteristics of both.

The model correctly identify the two areas of maximum current speed; along the shelf edge of 63°-64°N and 68°-70°N as well as the typical current values for the two area. It gives reasonable values for the current along the shelf break while the modelled current speed for the largest part of the shelf is to small. The model reproduce some of the large-scale circulation features, such as the split of the Norwegian Coastal Current at around 63°N and to a certain degree the influence of the larger banks such as Haltenbanken and Trænabanken(Fig.2) The model was not able, however, to include the influence of the minor banks or to identify and reproduce the inner coastal jet current. The main reason for these discrepancies is probably due to the grid size of the model(20x20 kilometre) being to coarse.

The model seems to able to describe the northern limit of the distribution area(SVENDSEN *et al.*,1995) and the expansion rate of the distribution area for the herring larvae reasonable good. For the centres of gravity, however, the model did not. All the observed centres of gravity are found north of the calculated ones and the discrepancy between the two sets of values increase with time. A possible explanation for this could be the way the model handle particles entering into the most coast-near grid box - the so-called coastal particles. These could be entrapped and perhaps later released to the open sea and will contribute to the retardation of the northward particle transport. If we recalculate the centres of gravity 1 July and delete the coastal particles the gravity centres will clearly move further north but still there will be a large discrepancy between the observed and the calculated values(Figs 15 and 17)

In the model runs the particles are given a vertical migration pattern applied for the North Sea herring(HEATH *et al.*,1988) which might not be representative for the Norwegian spring spawning stock. The particles released in a fixed depth of 30 m(Fig. 13), however, further demonstrate the model transports the particles northwards at a lower speed than the nature. ÅDLANDSVIK and SUNDBY(1994) are using a very similar model system to simulate the transport of eggs/larvae/juveniles of Arcto-Norwegian cod. From their comparison with survey data it was clear that the model transport was too fast in the initial phase along the coast of northern Norway. In the present study the result is the opposite; the model transport is slower than observed. In spite of that, the explanation for the discrepancies between model and observations in both cases could partly be explained by the lack of ability for the model to resolve small-scale topographic features such as retention areas over smaller banks and narrow and rapid jet currents. Another important explanatory factor is probably the absence of larvae mortality in the model. Introduction of an exponential mortality function would clearly contributed to the northward displacement of the modelled centres of gravity and thereby improved conformity between model and observations.

Finer spatial resolution in the hydrodynamic model and introduction of a larval mortality function are probably the most important factors for approaching more realistic model results in relation to transport of fish larvae and juveniles along the Norwegian coast.

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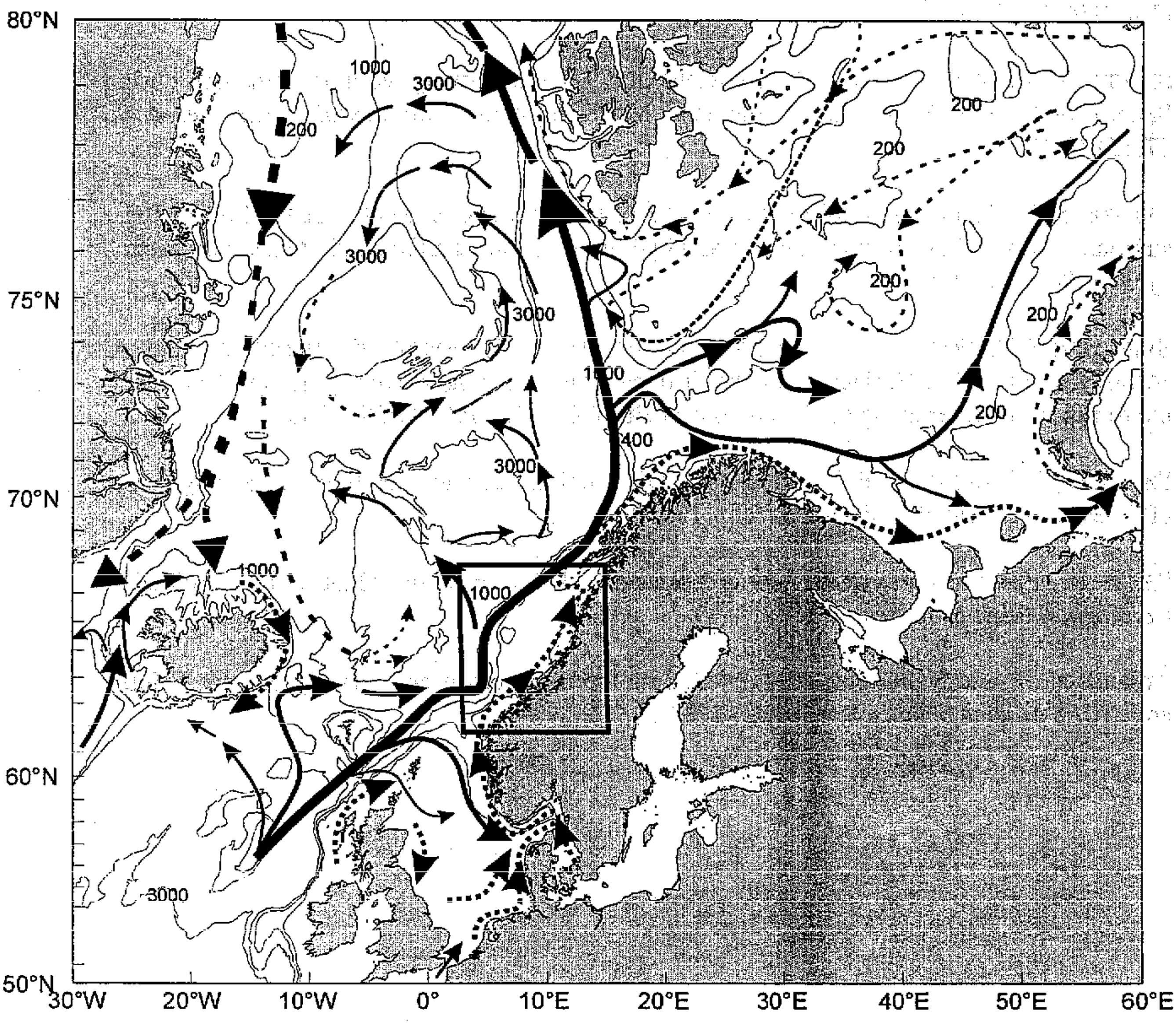

Fig. 1. Persistent currents in the northern NE Atlantic. Framed area is the central Norwegian shelf.

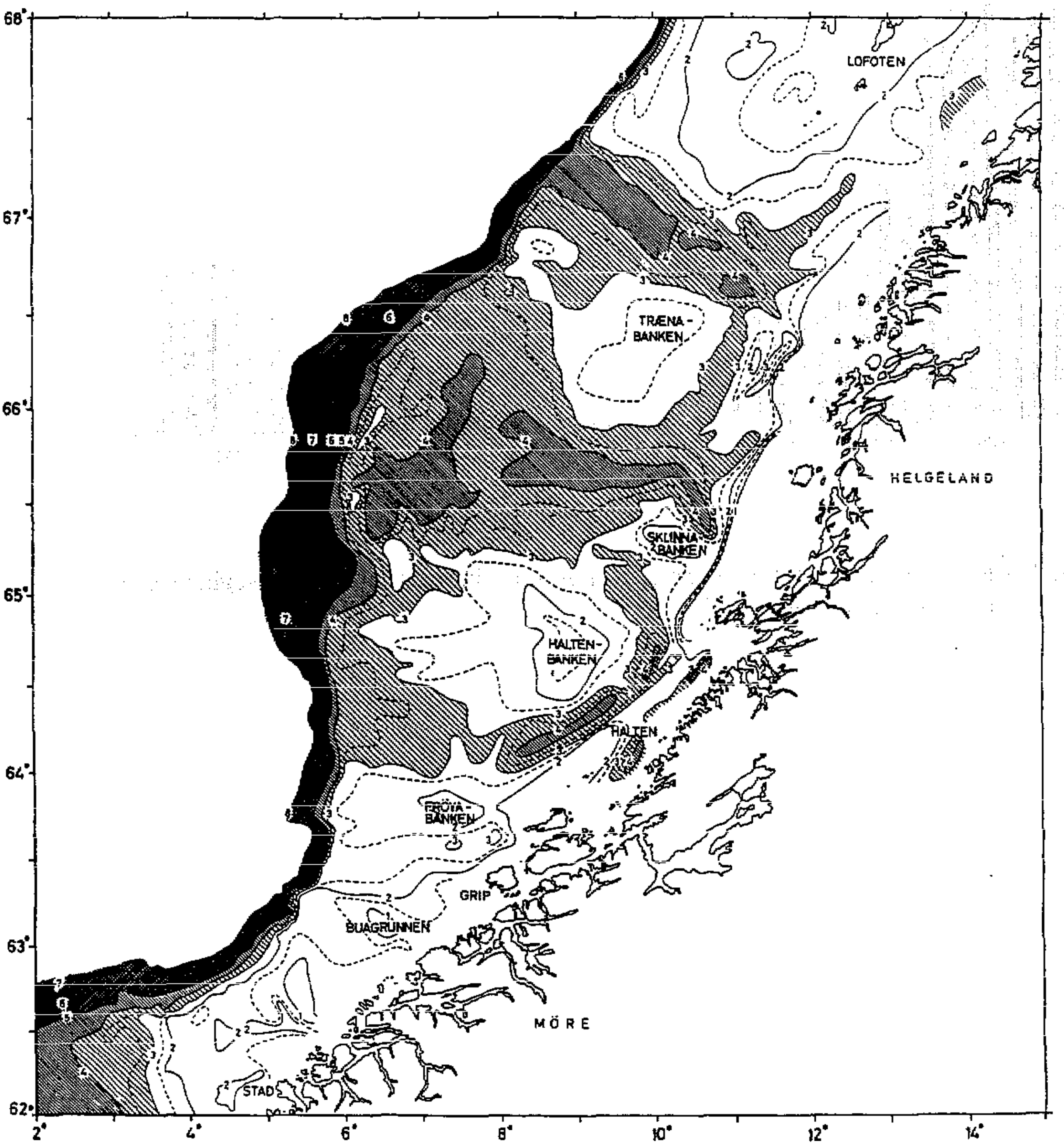

Fig. 2 Bathymetric map(in 100 meters) for the area of investigation.
(LJØEN and NAKKEN, 1969).

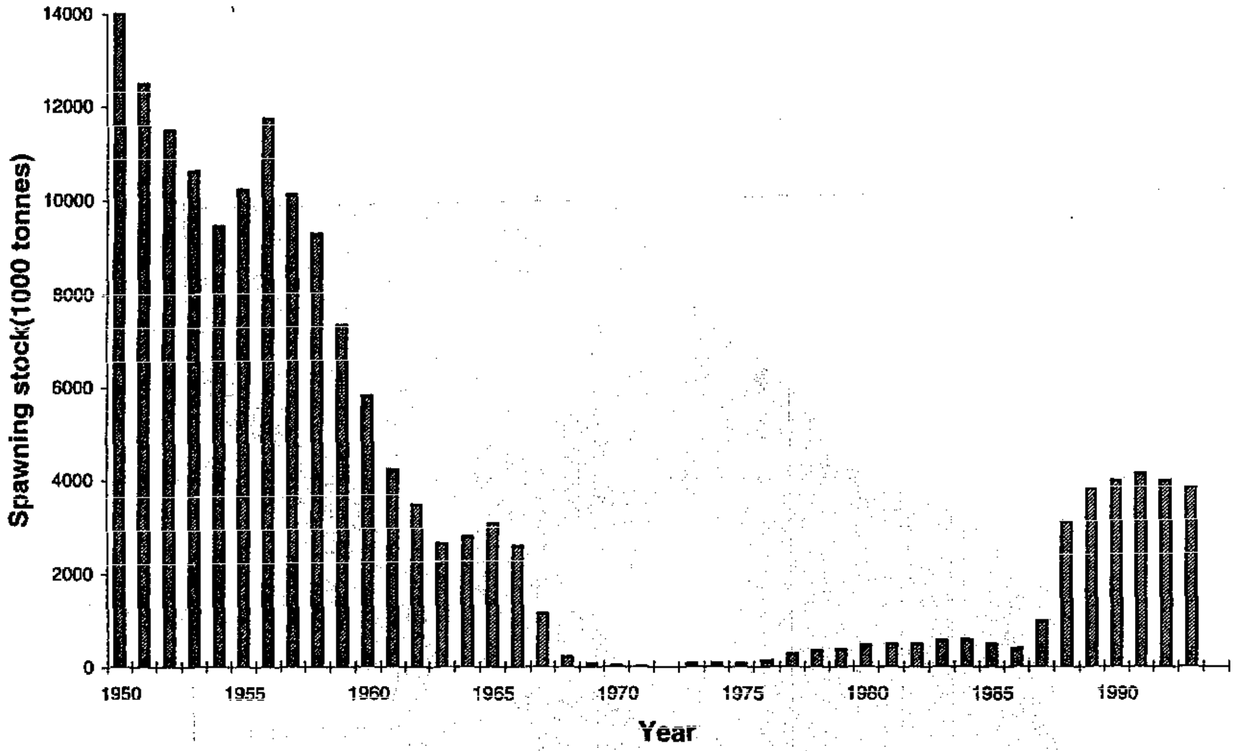

Fig. 3. The temporal fluctuation in the spawning stock biomass of the Norwegian spring spawning herring (ICES, 1998).

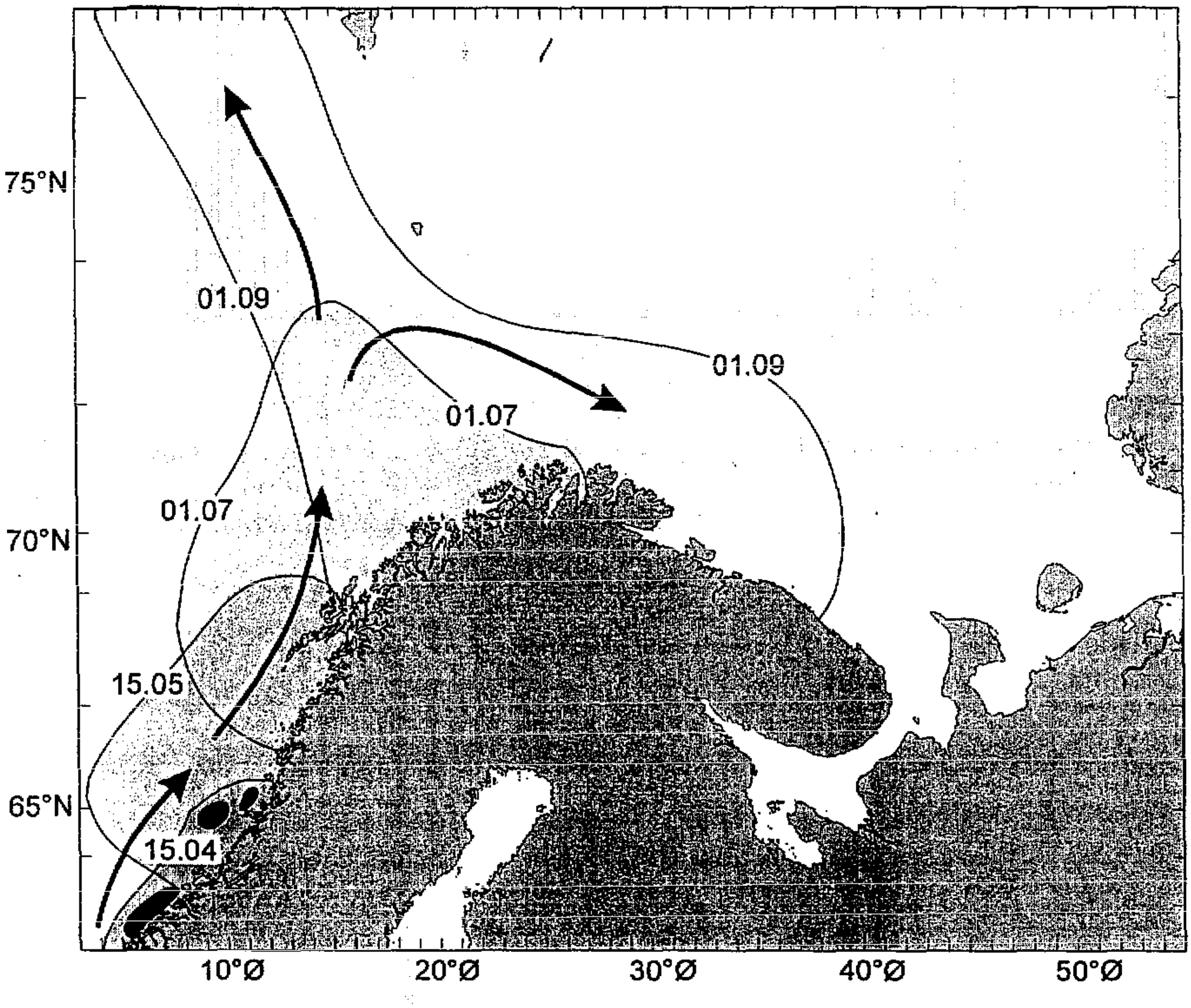

Fig. 4. The main spawning area and the typical distribution area of the herring larvae, post-larvae and o-group fish.

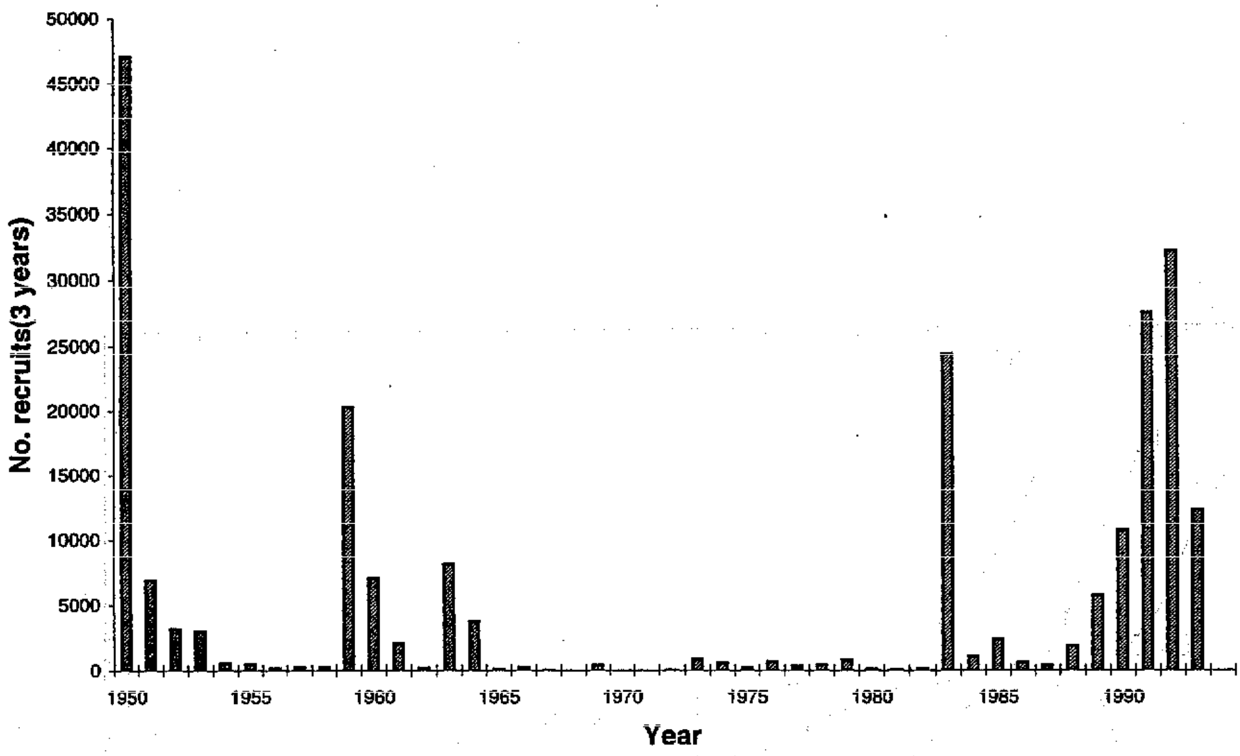

Fig. 5. The recruitment to the herring stock measured as number of recruits at 3 years age (ICES, 1998).

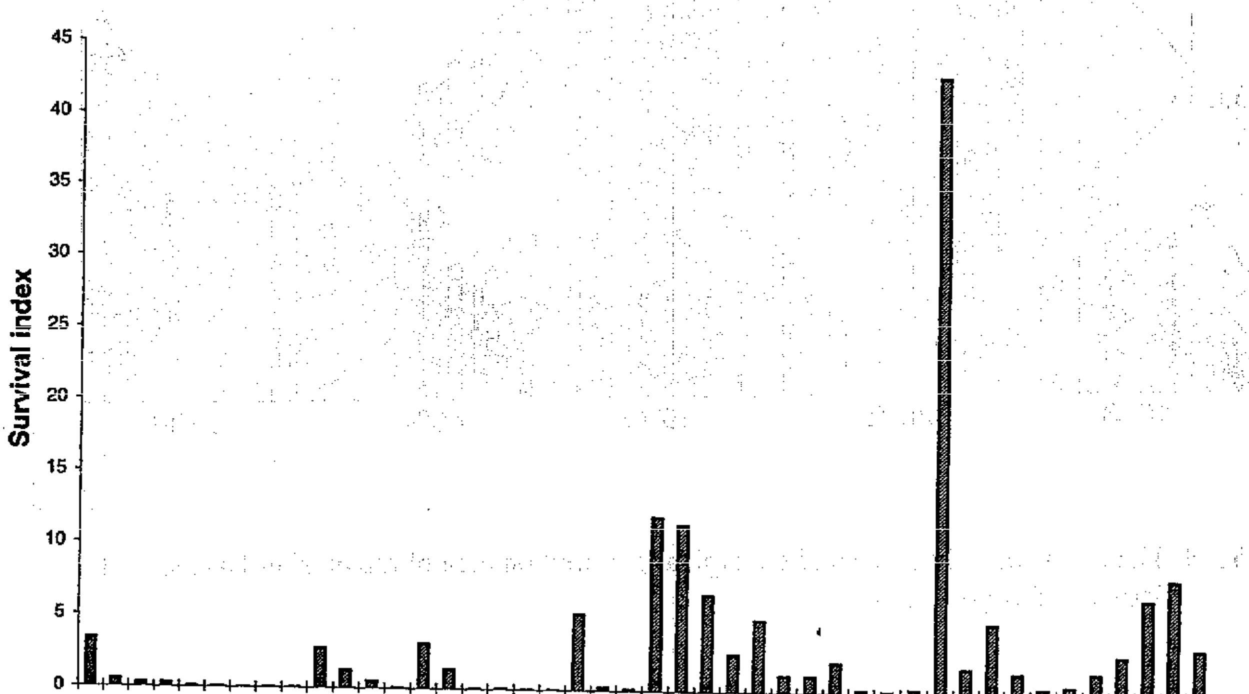

Fig. 6. The survival index of the herring calculated as the ratio between number of recruits at age 3 years and the biomass of the corresponding spawning stock.

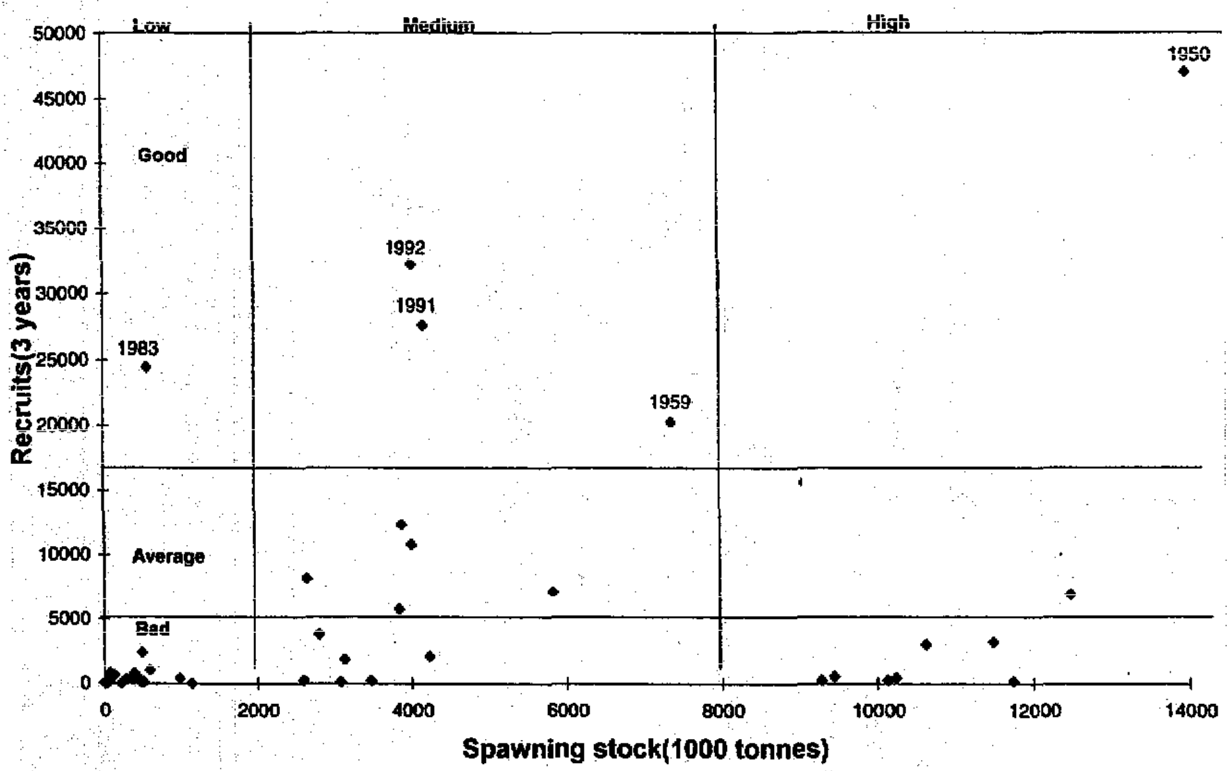

Fig. 7 The spawning stock size versus the corresponding number of recruits at 3 years age.

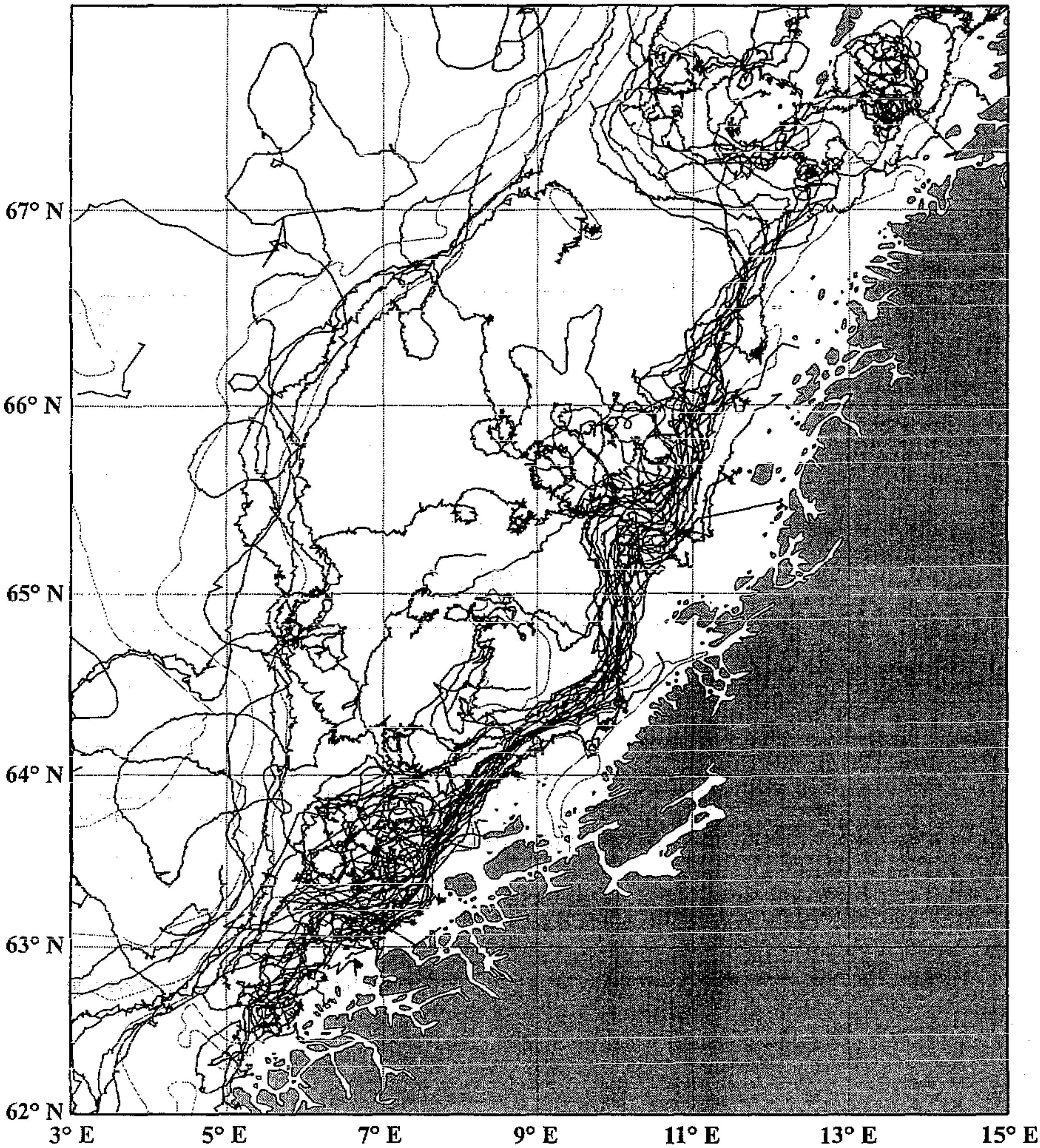

Fig. 8. Trajectory plot of all the drifters deployed or drifting into the area.

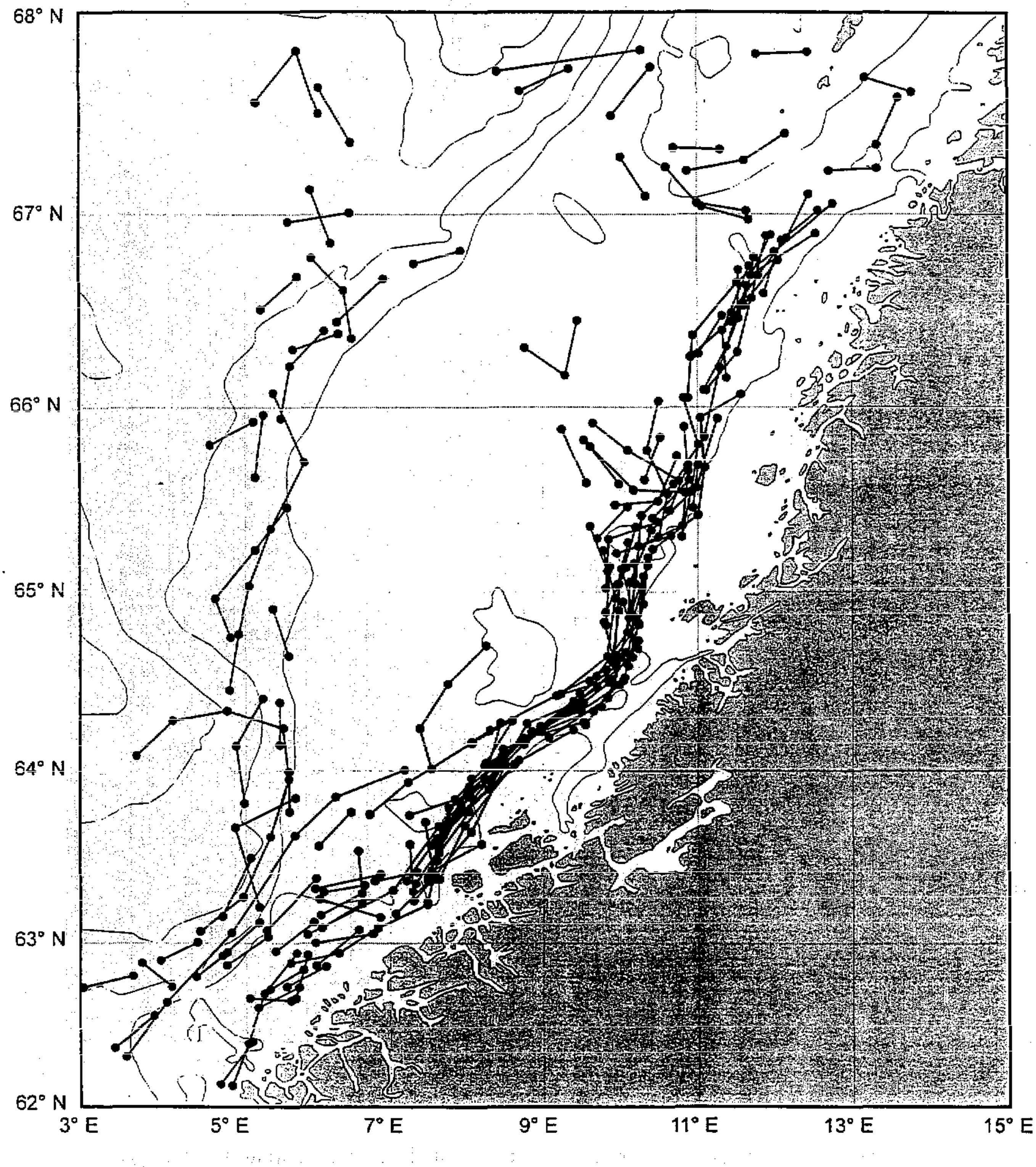

Fig. 9. Parts of the trajectories where the daily mean drift speed exceed 30 cm s^{-1}.

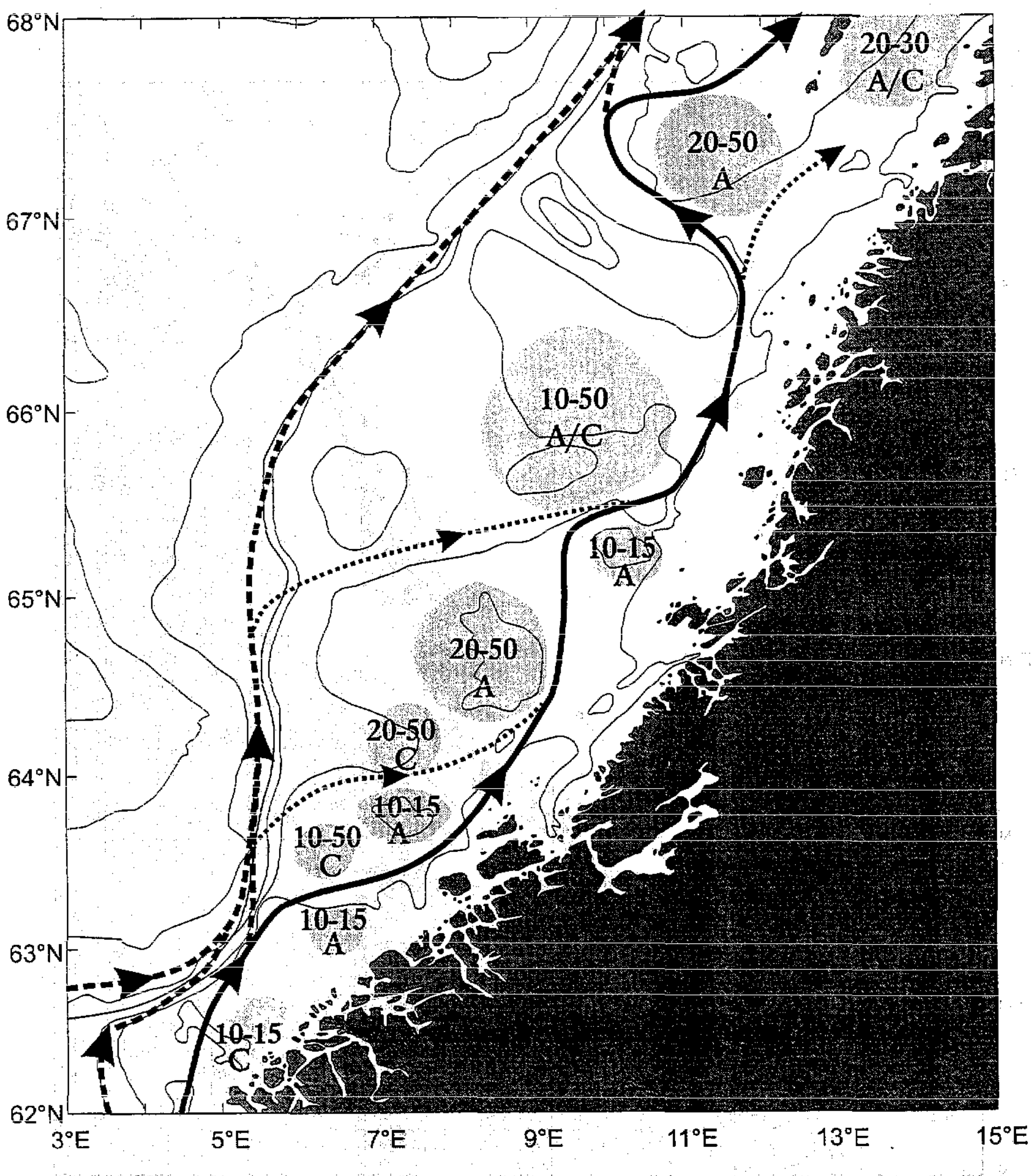

Fig. 10. Transport routes and retention areas. The number in the retention areas are average residence time in days.A) Anti-cyclonic movements dominate.C) Cyclonic movement dominate.

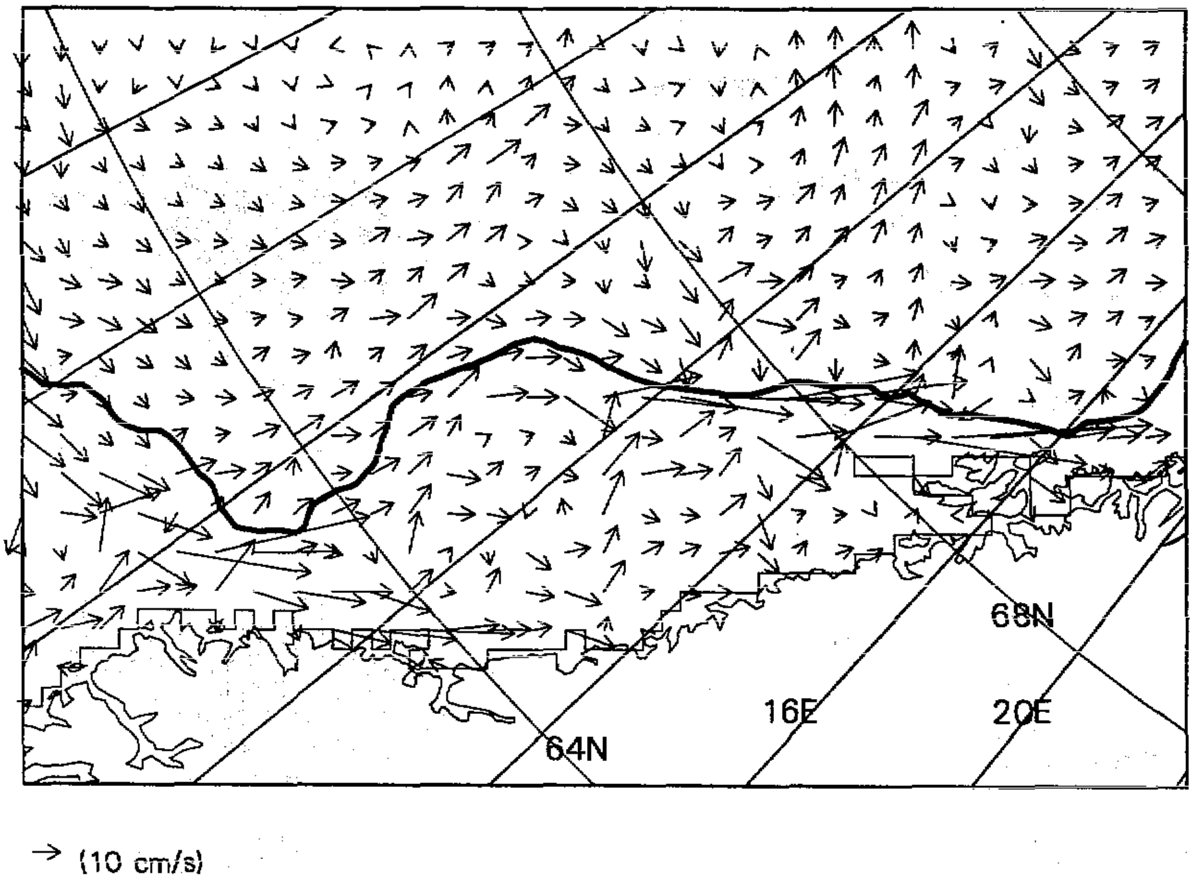

Fig. 11. Modelled mean current at 30 m depth for April-June 1976 - 1993.

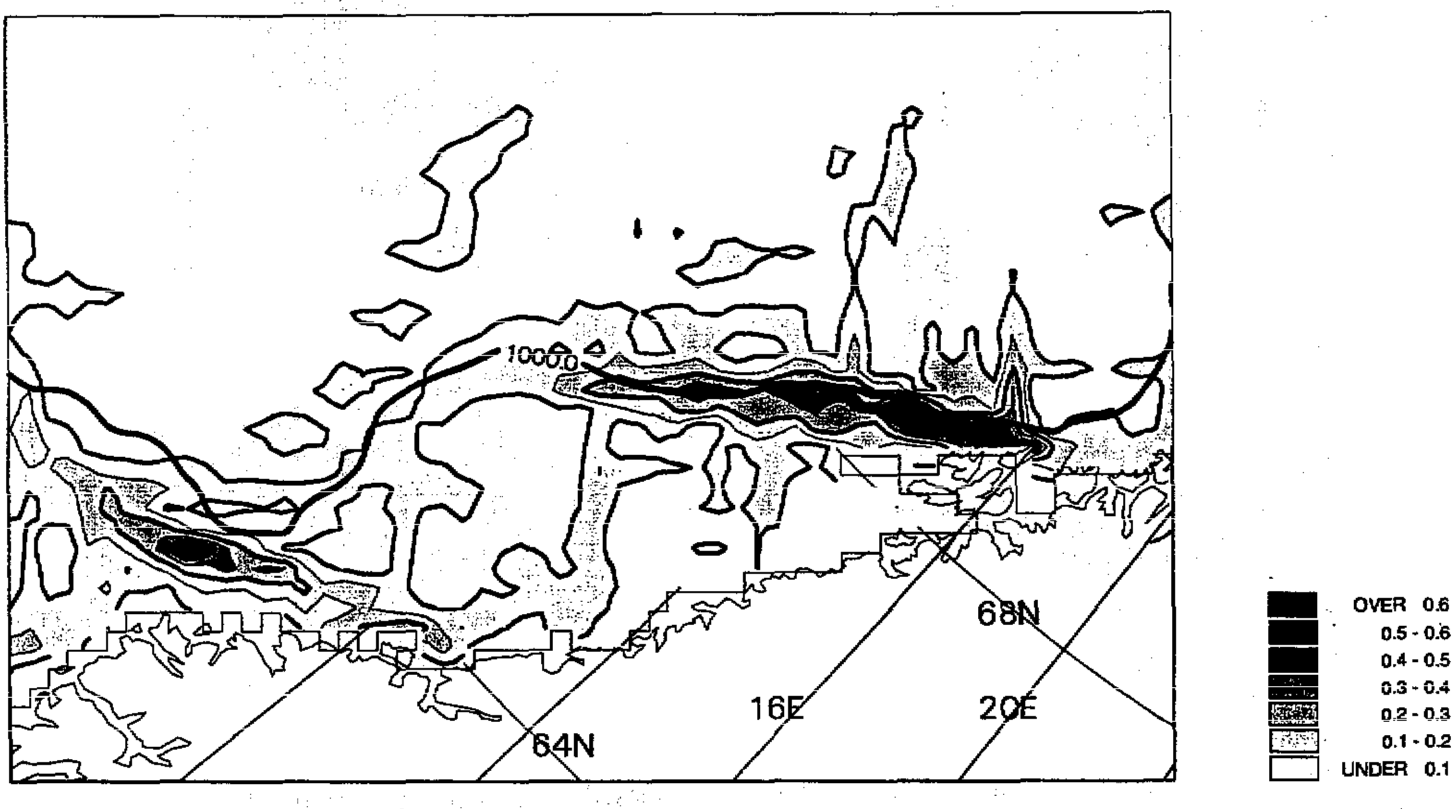

Fig 12. Isolines for mean current speed at 30 m depth for April-June 1976 - 1993

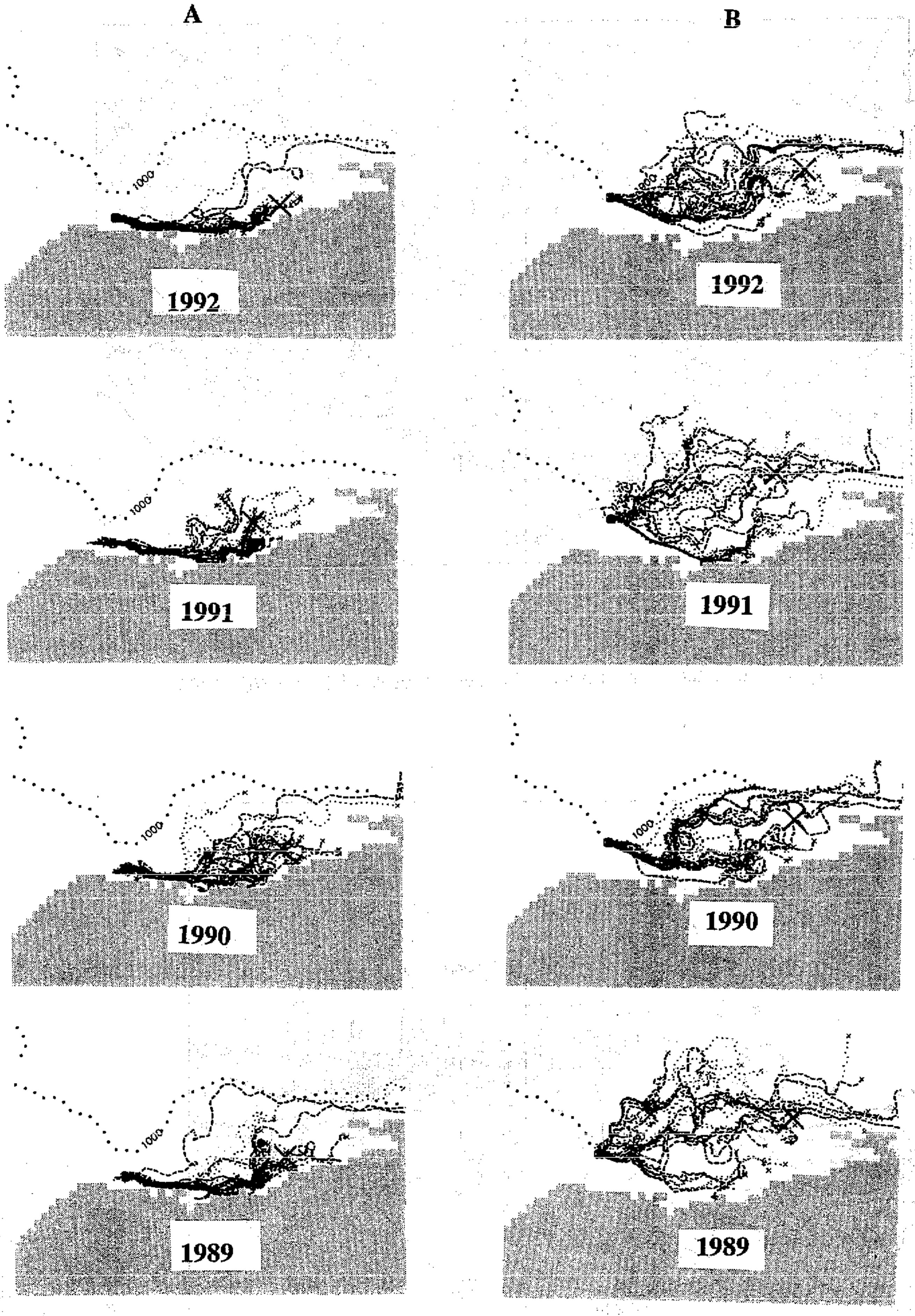

Fig. 13. Modelled trajectories up to 1 July for particles released in 30 m depth every ten days from 25 March to 25 April during the years 1989 - 1992.

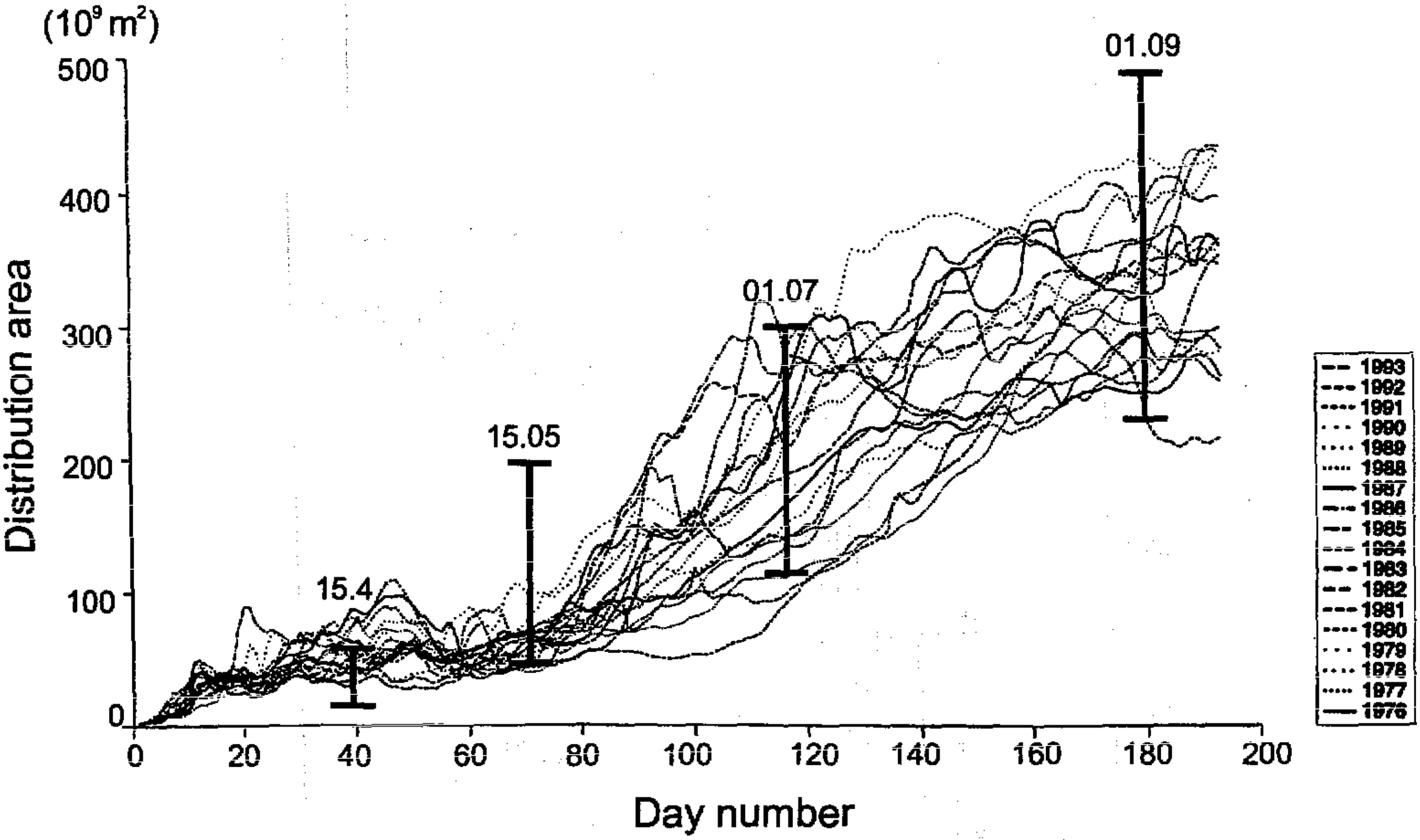

Fig. 14. Modelled temporal development of the size of the distribution area and the variance σ^2. Bars indicate the observed range of the size of the distribution area.

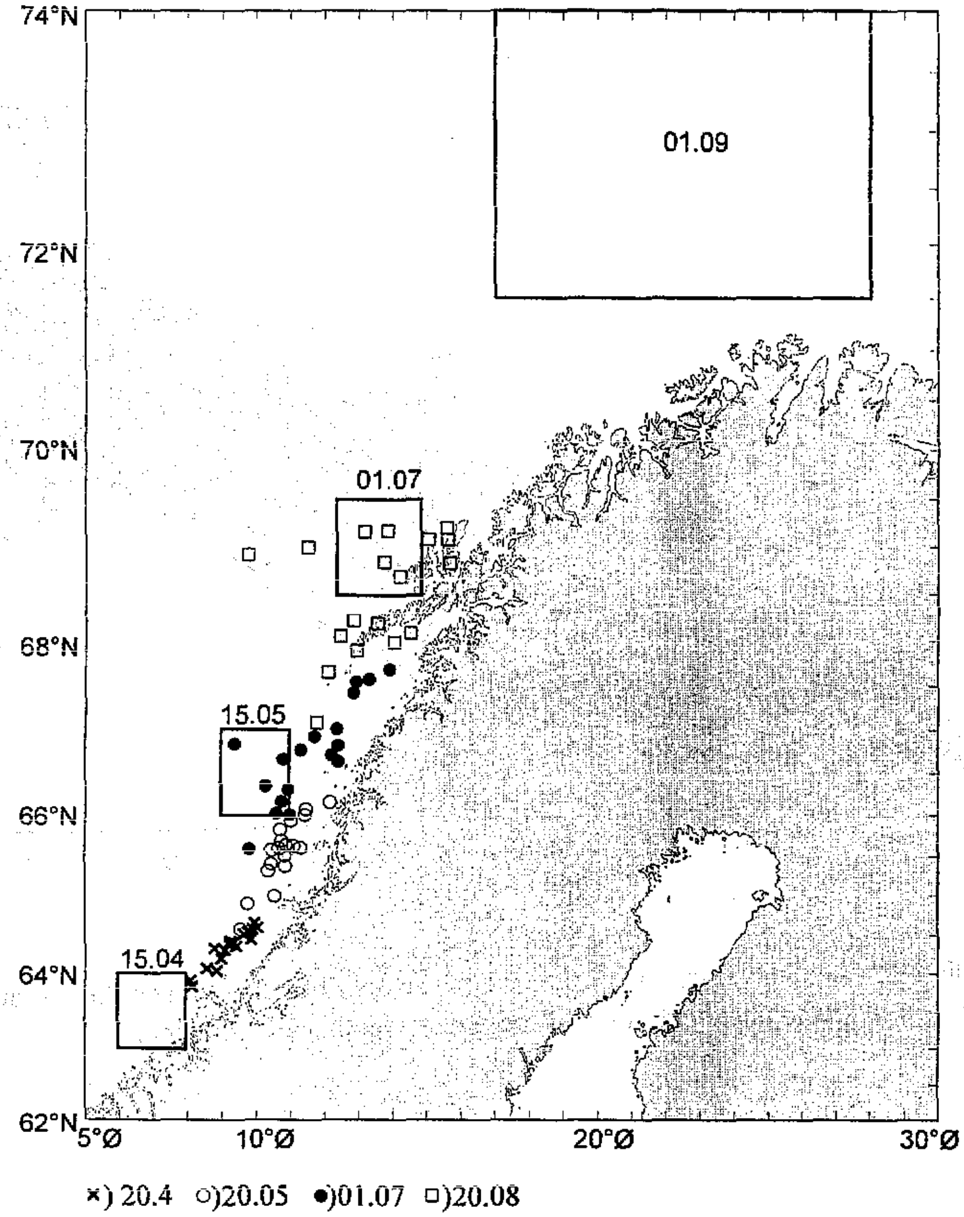

Fig. 15. Calculated centres of gravity during four different surveys for the period 1976-1993 compared with the observed gravity centres range (Rectangles).

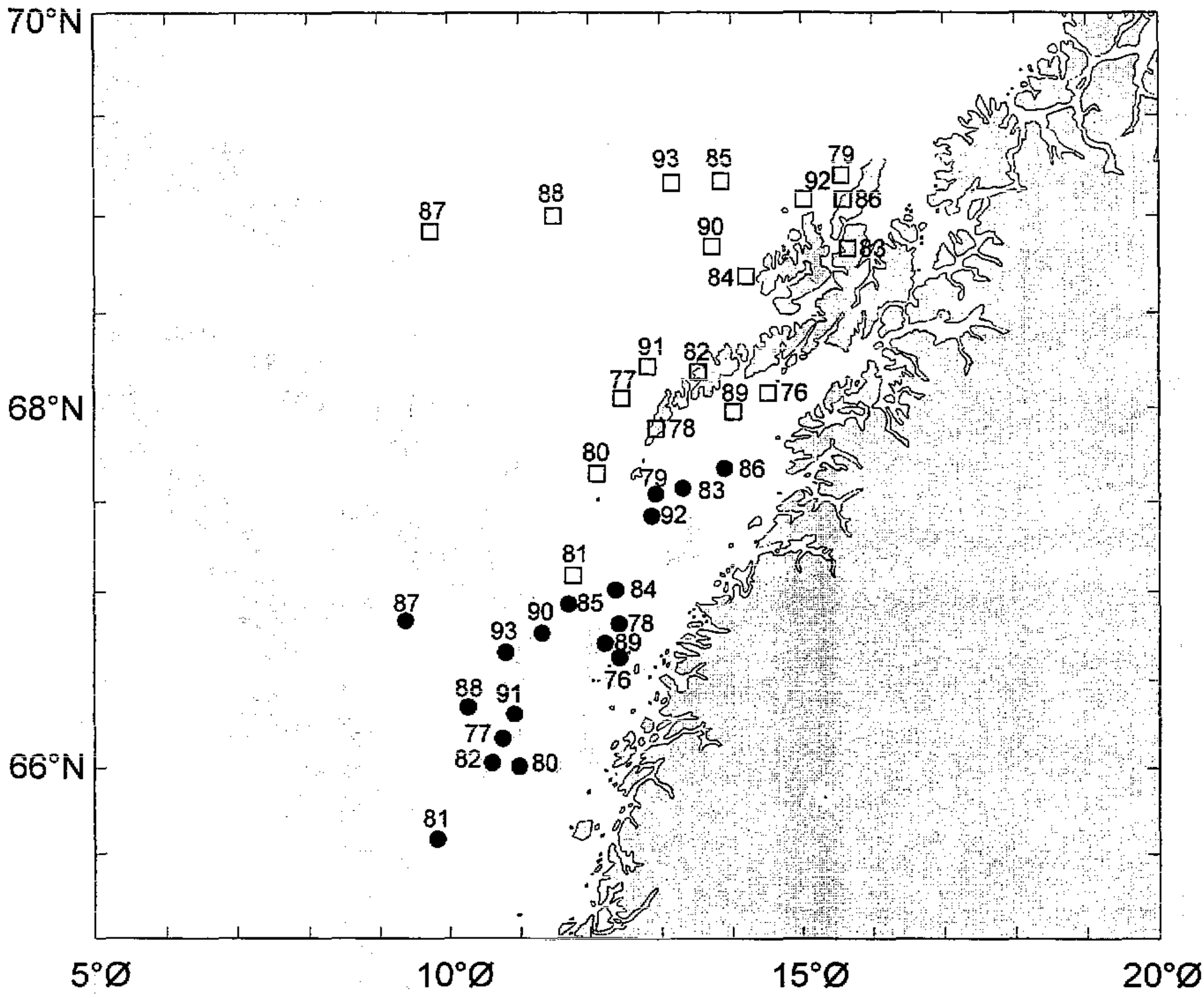

Fig. 16 Calculated centres of gravity 1 July(circles) and 20 August(squares) for the different years

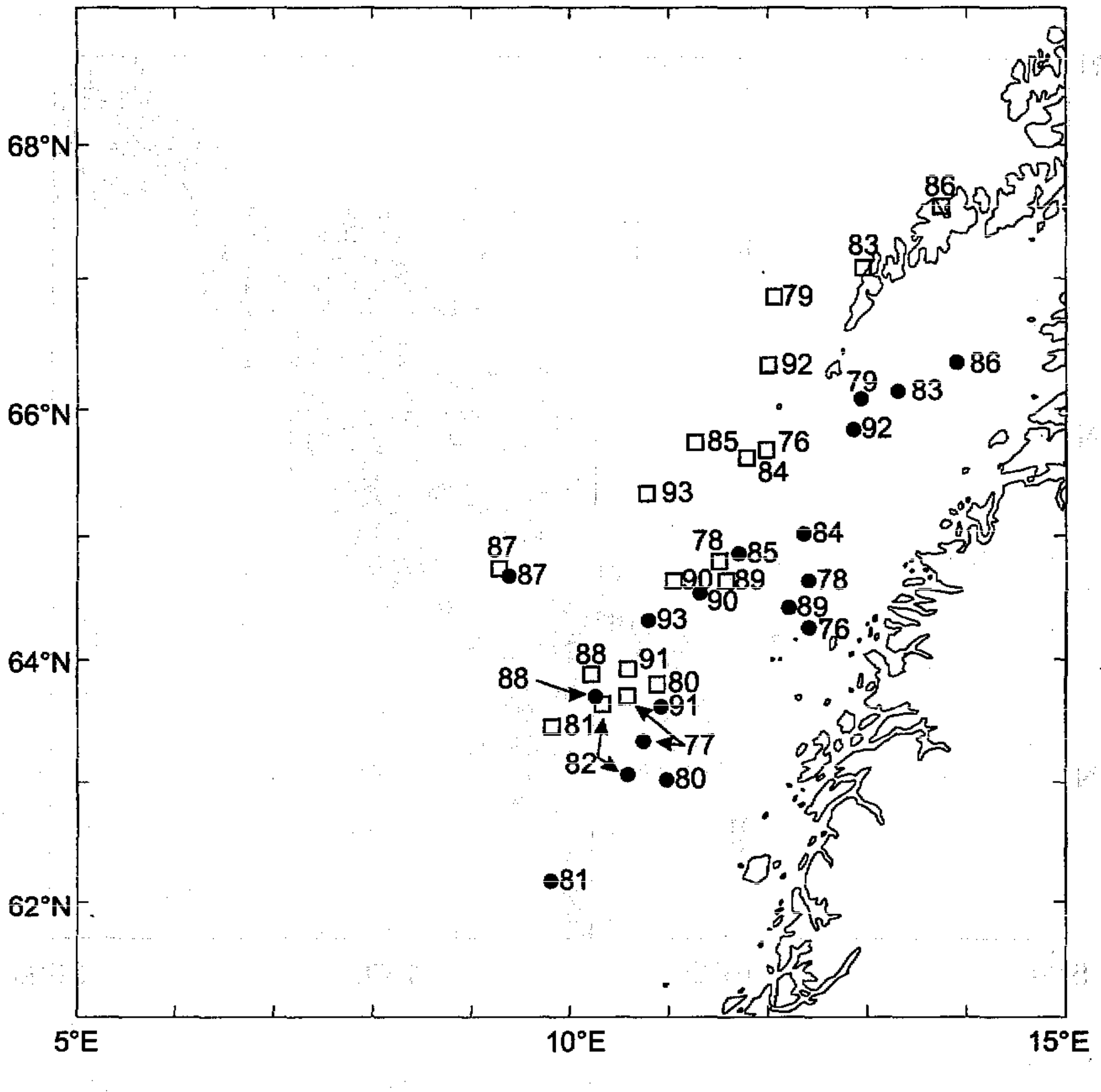

Fig. 17 Calculated centres of gravity 1 July with coastal particles included(circles) or excluded(squares).