

Density-dependent Changes in the Spatial Distributions of Atlantic Cod (*Gadus morhua*), American Plaice (*Hippoglossoides platessoides*), and Greenland Halibut (*Reinhardtius hippoglossoides*) on the Flemish Cap during 1988–2002

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Hendrickson, L. 2005. Density-dependent changes in the spatial distributions of Atlantic cod (*Gadus morhua*), American plaice (*Hippoglossoides platessoides*), and Greenland halibut (*Reinhardtius hippoglossoides*) on the Flemish Cap during 1988–2002. *J. Northw. Atl. Fish. Sci.*, **37**: 53–72.
doi:10.2960/J.v37.m566

Abstract

The Flemish Cap is an isolated bank located east of the Grand Banks in the Northwest Atlantic Ocean. Research bottom trawl surveys of the Flemish Cap have been conducted in July by the European Union since 1988. Data from these surveys were used to assess changes in the spatial distributions of Atlantic cod (*Gadus morhua*), American plaice (*Hippoglossoides platessoides*), and Greenland halibut (*Reinhardtius hippoglossoides*) during 1988–2002. Kriging and indices of collocation and co-occurrence indicated that cod and plaice distributions have a high degree of overlap and that density-dependent range contraction of both stocks occurred during a time when Greenland halibut, a more common inhabitant of deep water, exhibited range expansion into shallow water on the Cap. However, the timing and locations of these distributional changes were such that little overlap occurred between the distributions of Greenland halibut and either cod or plaice. The range expansion of Greenland halibut was also density-dependent and primarily attributable to young fish (ages 1 and 2 from the 1994 and 1995 year-classes) which prefer shallow water. The range contractions of cod and plaice have persisted since the mid-1990s, and despite fishing moratoria implemented for plaice in 1994 and for cod in 1999, neither stock has shown signs of recovery. Biological and stock assessment implications of these distribution changes are discussed in relation to the lack of recovery.

Key words: American plaice, Atlantic cod, collocation, Flemish Cap, *Gadus morhua*, Greenland halibut, *Hippoglossoides platessoides*, kriging, range contraction, range expansion, *Reinhardtius hippoglossoides*, spatial distribution.

Introduction

The Flemish Cap is an isolated bank, centered at 47°N 45°W, which is separated from the Grand Banks of the Newfoundland continental shelf by the deeper waters (up to 1 500 m) of the Flemish Pass. The Cap is a dome-shaped feature that consists of a shallow central area (125 to 150 m) and a steeply sloped perimeter.

Since 1988, multi-species bottom trawl surveys of the Flemish Cap have been conducted in July by the European Union (EU). During 1988–2002, survey biomass indices indicated a shift in the predominant groundfish species from American plaice (*Hippoglossoides platessoides*) and

Atlantic cod (*Gadus morhua*) to Greenland halibut (*Reinhardtius hippoglossoides*) (Saborido and Vázquez, MS 2003). The Flemish Cap populations of American plaice (Pitt, 1963) and Atlantic cod represent discrete stocks, and during July, both species are distributed entirely within the depth range sampled during the EU survey, 125 to 730 m (Saborido and Vázquez, MS 2003). Plaice are also distributed within this depth range during winter and are most abundant at depths of 200 to 400 m with few individuals found at 550 to 728 m (Bowring and Brodie, 1994). In both summer and winter, plaice are most abundant at depths of 100 to 200 m on the northern Grand Banks (Morgan and Brodie, 1991). Although plaice have been found in the deeper waters of the Flemish Pass (Iglesias

et al., 1996), there is no evidence of mixing between the Flemish Cap and Grand Banks populations (Morgan and Bowering MS, 2004). The summer depth distributions of cod populations located within the general latitudinal range of the Flemish Cap tend to be shallow. During summer, cod are distributed at median depths of 144 to 181 m in the northern Gulf of St. Lawrence (Castonguay *et al.*, 1999) and 46 to 51 m in the southern Gulf of St. Lawrence (Swain *et al.*, 1998).

Greenland halibut is a deep-water species that generally occurs at depths of 300 m to 1 600 m (Templeman, 1973). The depth distribution of the Greenland halibut stock extends beyond the boundaries of the Flemish Cap survey area (Dwyer and Bowering, MS 2003). During the late 1980s, a substantial portion of the stock was distributed in the Flemish Pass and on the slope of the Flemish Cap, at depths of 750 to 1 500 m; possibly due to a large-scale migration of the stock from northern areas (Bowering and Power, 1995).

All three stocks are under quota management by the Northwest Atlantic Fisheries Organization (NAFO). During 1960–88, cod landings from the Flemish Cap generally ranged between 10 000 and 57 000 tons and were estimated to range from 29 000 to 48 000 tons during 1988–95 (Cerviño and Vázquez, MS 2004). Historically, American plaice were primarily taken as by-catch in directed fisheries for cod and *Sebastes* sp., but catches increased during the late 1980s due to increased freezer trawler effort (Bowering and Brodie, 1994). Thereafter, fishing moratoria were implemented for both stocks, in 1994 for plaice (NAFO, 1994) and in 1999 for cod (NAFO, 1999). Just after the plaice moratorium, in 1995, a fishery for Greenland halibut developed on and around the Flemish Cap (NAFO, 2003). Despite the fishing moratoria, the Flemish Cap stocks of cod and plaice have yet to show signs of recovery from overfishing (Alpoim and Ávila de Melo, MS 2004; Cerviño and Vázquez, MS 2004).

The spatial distributions of demersal fish species affect the catch composition of bottom trawl fisheries (Alverson *et al.*, 1994) and also have important life history and ecological implications. Therefore, an understanding of the temporal changes in the spatial distribution of the three species, before and after implementation of the fishing moratoria, may provide insight into why the Flemish Cap cod and plaice stocks have not recovered. In this study, we use 15 years of research survey data to assess whether the spatial distributions of the three species are associated with changes in abundance and to characterize spatial overlap between their distributions. The potential effects of these distributional changes on the recovery of Flemish Cap cod and plaice stocks are also discussed.

Materials and Methods

Catch rate data from research bottom trawl surveys conducted during a single season were used to characterize interannual changes in the spatial distribution and relative abundance of Atlantic cod, American plaice and Greenland halibut on the Flemish Cap. Relative abundance (stratified mean number per tow) and biomass (stratified mean kg per tow) indices were computed for each species based on catch rate data from bottom trawl surveys of the Flemish Cap conducted during 1988–2002. The surveys were conducted by the European Union (EU) during a 2.5 to 3-week period in July and incorporated a stratified-random sampling design with stratification based on depth (Doubleday, 1981; Saborido and Vázquez, MS 2003). Sampling was conducted in nineteen strata ranging in depth from 125 m to 730 m, encompassing a total area of 36 203 km² (Fig. 1). Station allocation was proportional to stratum area and consisted of a minimum of two stations per stratum. Standardized tows were conducted at 3.5 knots for 30 minutes (a tow distance of 3.24 km) and 113 to 121 stations were sampled per year (Fig. 2). Survey gear, vessel characteristics, and sampling methods are described in Saborido and Vázquez (MS 2003).

We used the GLM procedure in SAS (SAS Institute, 1985) to test whether interannual changes in the distribution of each species were density-dependent and associated with depth. The model included log-transformed density data (number per tow) as the dependent variable and year and stratum depth range as independent class variables. Stratum depth ranges included: 127–146 m, 147–183 m, 184–256 m, 257–366 m, 367–549 m, and 550–730 m. Maps of density data, aggregated across years, were created for each of three length classes, corresponding to ages 1, 2 and 3+ (Alpoim *et al.*, MS 2002), in order to determine whether depth preferences varied by size-class. Annual trends in percent abundance by depth range were also examined. For each species, percent abundance (P) during year (i) in depth range (j) was computed as:

$$P = \left(\frac{\bar{N}_{i,j} A_j}{\sum \bar{N}_{i,j} A_j} \right) * 100$$

where A_j is the area of depth range j .

Evaluation of Spatial Structure

The Geostatistical Analyst extension of ArcGIS v8.2 (ESRI, 2001) was used to model interannual changes in the spatial distribution of each species and to produce prediction maps that illustrate such changes. The "ordinary kriging" method (Cressie, 1993) was used to model changes in spatial structure based on density data (number per tow) from the EU surveys. An omni-directional, spherical

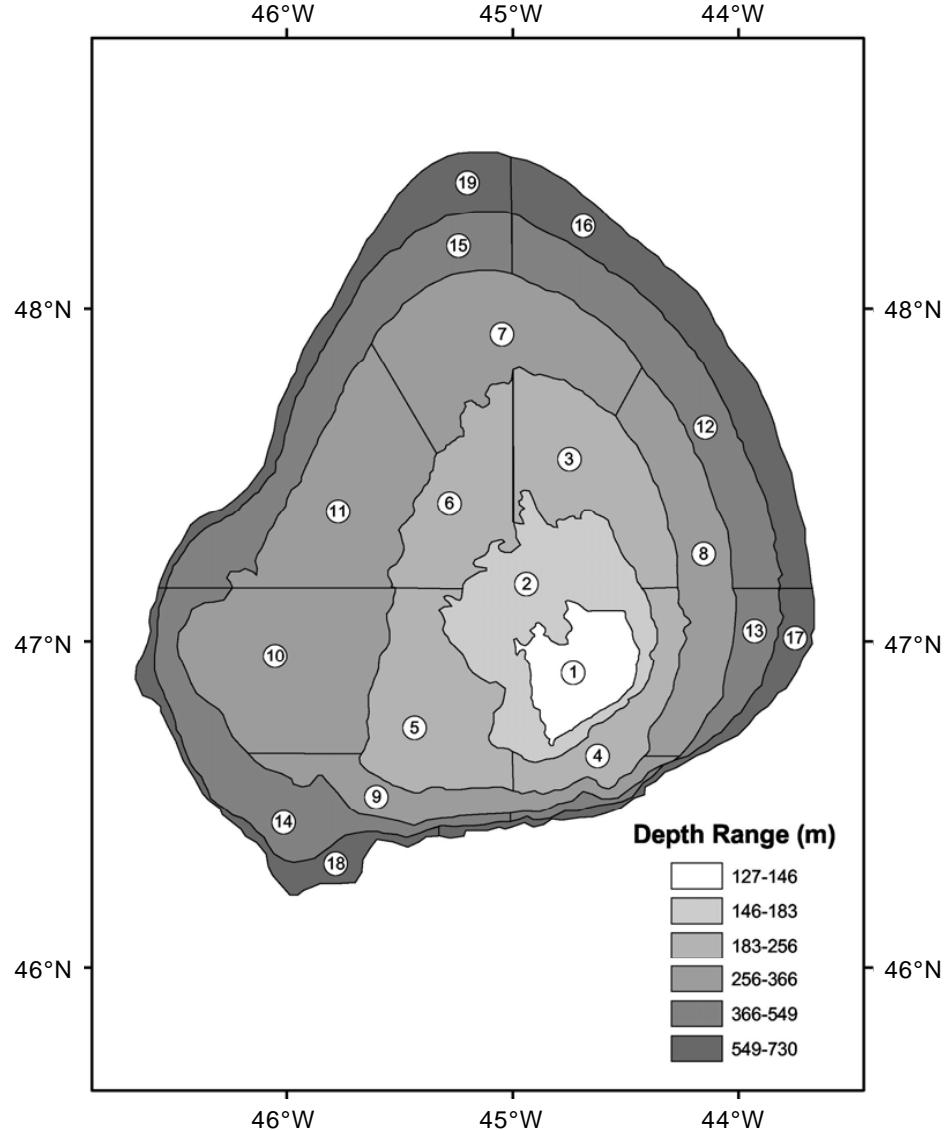


Fig. 1. Depth strata sampled during the July EU bottom trawl surveys of the Flemish Cap in 1988–2002.

semivariogram model was fit to empirical semivariograms of detrended, log-transformed density data (numbers per tow) from the EU survey, by year, for each of the three species. A least squares fit was performed to estimate the parameters of a spherical model defined as:

$$\gamma(h) = \begin{cases} \theta_s \left[\frac{3}{2} \frac{b}{\theta_r} - \frac{1}{2} \left(\frac{b}{\theta_r} \right)^3 \right] & \text{for } 0 \leq b \leq \theta_r \\ \theta_s & \text{for } \theta_r < b \end{cases}$$

where θ_s is the sill, h is the lag vector and b is the length of h (distance between two locations), and θ_r is the range.

For each year, the assumption of stationarity of variance was met by log transformation and detrending of the catch rate data. Detrending was necessary because three-dimensional graphs of catch densities by latitude and longitude showed persistent, second-order polynomial spatial trends for all three species. Examination of the influence of directional changes on annual semivariogram clouds did not indicate the presence of anisotropy for any of the three species analyzed. The software uses the sector method to define the search neighbourhood, which consisted of a four-sector ellipse that contained a minimum of three neighbours per sector. Following detrending, point kriging

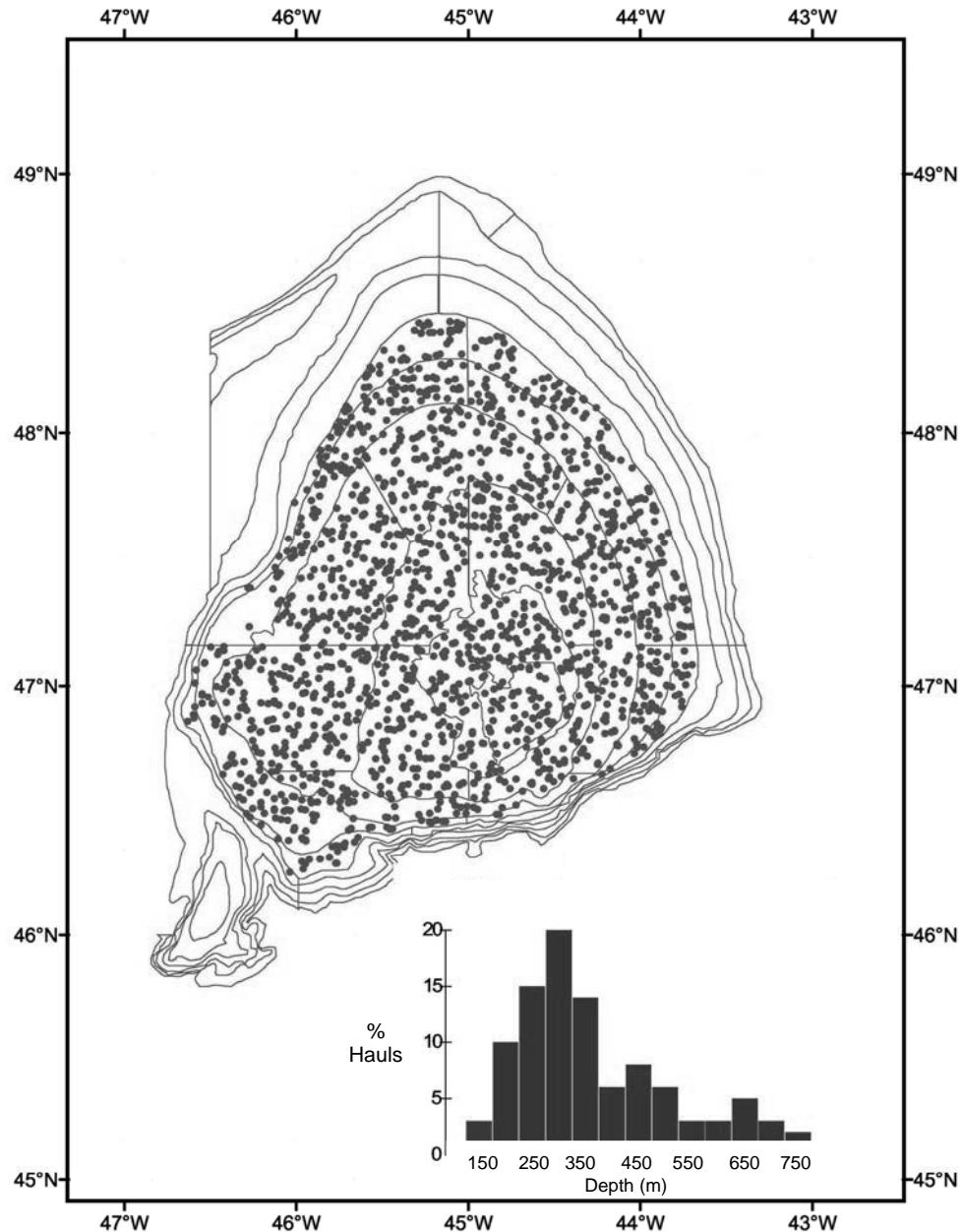


Fig. 2. Stations and depth strata sampled during the July EU bottom trawl surveys of the Flemish Cap in 1988–2002.

was carried out on the residuals. Polynomial trends were added back to the output surface and kriging estimates were back-transformed prior to calculating the final predictions using the following equation (Cressie, 1993):

$$\hat{Z}(s_0) = \exp\{\hat{Z}(s_0) + \sigma_{Y,k}^2(s_0)/2 - m_Y\}$$

where

$$m_Y = -(1 - 1'\Gamma^{-1}\gamma - 1)/1'\Gamma^{-1}1$$

and $\gamma \equiv (\gamma(s_0 - s_1), \dots, \gamma(s_0 - s_n))'$ and Γ is the $n \times n$ matrix

whose $(i,j)^{\text{th}}$ element is $\gamma(s_i - s_j)$. The software computed optimal lag distances and numbers of lags in addition to providing semivariogram parameter estimates for each year and species.

Relationships Between Species Distributions

The EU survey data were used to evaluate inter-annual relationships between species distributions on global and local scales. Relationships between cod and plaice distributions were evaluated on a global scale using

a collocation index. Local-scale relationships between all three species were evaluated by computing the co-occurrence of species pairs in survey tows. For each tow where more than four individuals of both species were caught, the degree of co-occurrence was computed as a percentage of the density of species A divided by the combined density of both species. The percentage of tows with co-occurrence for each pair of species, as well as the percentage of cod (in numbers) in tows with halibut co-occurrence and the percentage of plaice (in numbers) in tows with halibut co-occurrence were summarized by year and stratum. In addition, we examined the percentage of survey tows with positive catches of each species, by year, as a measure of dispersion because spatial overlap between species distributions is affected by the degree of dispersion of each population.

Collocation of Cod and Plaice

Annual changes in the collocation of cod and plaice populations were assessed using the method of Bez and Rivoirard (2000). Collocation refers to the way in which two spatial distributions are positioned relative to one another (e.g. between species A and B) and accounts for more than just the degree of spatial overlap between them. The method is robust because it is based on the computation of a distance-based spatial index, the global index of collocation (*GIC*), which is unaffected by the inclusion of stations where catch rates are zero. Determining whether such stations should be included or excluded can be problematic when defining habitat domains (Rivoirard *et al.*, 2000) and can result in comparing within-habitat zeros of species A with those outside the habitat domain of species B. Geo-referenced abundance data (number per tow) from the EU surveys were used to compute annual *GIC* values using R software and geostatistical routines developed by the Centre de Géostatistique in Fontainebleau, France. The *GIC* is based on computing both the center of gravity and the inertia of a population. The center of gravity (*CG*) is the mean location of an individual (*i*) sampled at random from a population, the coordinates of which are computed as:

$$CG = \begin{cases} \frac{\sum_i u_i \cdot z_i}{\sum_i z_i} \\ \frac{\sum_i v_i \cdot z_i}{\sum_i z_i} \end{cases}$$

where u_i is the longitude, v_i is the latitude and z_i is the observed density at each sample location. Inertia can be represented as an ellipse drawn around two axes that define the directions in which a population is most and least dispersed around its center of gravity (the intersection

of the two axes). Thus, inertia produces a symmetric ellipse around the center of gravity even if the distribution is skewed. Inertia (*I*) is calculated as the mean square distance between an individual sampled at random (x_i) and the center of gravity of the population (*CG*), and is computed in surface area units as:

$$I = \frac{\sum_i (x_i - CG)^2 z_i}{\sum_i z_i}$$

GIC values can range from 0 to 1, representing populations that are distributed in two separate locations (*GIC* = 0) and populations with confounded centers of gravity (*GIC* = 1), respectively. Annual *GIC* values were computed as:

$$GIC = 1 - \frac{\Delta CG^2}{\Delta CG^2 + I_1 + I_2}$$

where ΔCG is the distance between the centers of gravity for population A and population B, while I_1 and I_2 represent the respective inertias of each population.

Results

During 1989–98, the relative biomass of cod and plaice declined sharply and was coincident with a sharp

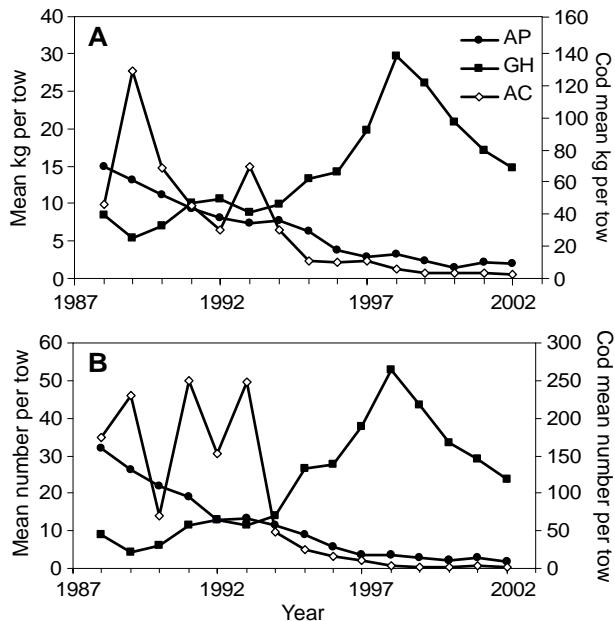


Fig. 3. Relative biomass (A) (stratified mean kg tow), and (B) abundance indices (stratified mean number per tow) of Atlantic cod (AC), American plaice (AP), and Greenland halibut (GH), during 1988–2002, from the July EU bottom trawl survey of the Flemish Cap.

increase in Greenland halibut biomass (Fig. 3A). Thereafter, during 1998–2002, cod and plaice biomass indices remained at levels near zero, while Greenland halibut indices declined to their 1996 level. With the exception of cod during 1989–92, relative abundance indices mirrored relative biomass trends (Fig. 3B).

Interannual changes in density were associated with changes in the spatial distributions of the three species. Densities of all three species were significantly associated with stratum depth range and this relationship varied significantly by year (Table 1). Year and depth range explained large percentages of the variability in the densities of cod (78%), American plaice (71%) and Greenland halibut (77%) during 1988–2002. Residuals plotted by year and depth range varied without trend for all three species. Prior to 1993 and 1994, cod and plaice, respectively, were most abundant at 183–256 m (Fig. 4). Thereafter, both species were more abundant in shallower areas, at depths less than 183 m. During this same time period, Greenland halibut moved into shallower water and became more abundant at depths of 256–549 m than 549–730 m. After 1995, halibut were most abundant at 256–549 m, while cod and plaice were most abundant at depths less than 256 m. However, halibut abundance at 183–256 m gradually increased from 2% to 13% after 1995.

Maps of kriged abundance indicate that persistent, long-term changes in the distribution of all three species occurred during 1988–2002. For cod and plaice,

semivariogram models indicate a gradual shift from a well-defined spatial structure to one that is more random. Examples of semivariogram models fit to cod and plaice abundance data from the early, middle and latter part of the time series highlight this shift (Fig. 5). The range, which can be considered as an indicator of the size of fish aggregations, was greater for both species during the beginning of the time series than during the end. Densities at stations located further than the range distance are not spatially-correlated. For example, plaice were distributed over a larger area prior to 1995 than after. The range of plaice averaged 176 km during 1988–95 then declined sharply thereafter, averaging 38 km during 1996–2002 (Table 2). Annual cod distributions were characterized by ranges that were shorter and more variable than those of plaice. Cod ranges fluctuated between 14 km and 44 km and were characterized by a series of rises and falls. The range of cod increased during 1988–92, and then declined from 44 km in 1992 to 19 km in 1996. During 1997 and 2000, the range of cod declined from 39 km to 22 km, respectively. Range estimates were high during 1997, 1998 and 2001 due a large nugget effect (random component), indicating little or no spatial structure. The nugget effect quantifies the amount of small-scale spatial structure that is unknown because it is attributable to inter-sample distance and measurement error. As expected, shifts toward a more random semivariogram generally resulted in greater variability in the kriged estimates. An expansion in the range of Greenland halibut occurred coincident with the range contraction observed for cod and plaice.

TABLE 1. General linear model results for the effects of year and depth range on the densities (number per tow) of Atlantic cod, American plaice and Greenland halibut on the Flemish Cap during 1988–2002. Depths ranges, which correspond to the survey strata, are: 127–146 m, 147–183 m, 184–256 m, 257–366 m, 367–549 m, and 550–730 m.

Model effects	df	Type III SS	Mean square	F	P > F	r^2
Atlantic cod						
Year	14	1 144.40	81.74	44.85	0.0001	0.78
Depth range	5	6 025.16	1 205.03	661.21	0.0001	
Year × depth range	70	1 307.89	18.68	10.25	0.0001	
American plaice						
Year	14	458.89	32.78	23.68	0.0001	0.71
Depth range	5	3 563.98	712.79	514.93	0.0001	
Year × depth range	70	521.62	7.45	5.38	0.0001	
Greenland halibut						
Year	14	362.54	25.90	21.27	0.0001	0.77
Depth range	5	4 391.37	878.27	721.48	0.0001	
Year × depth range	70	581.92	8.31	6.83	0.0001	

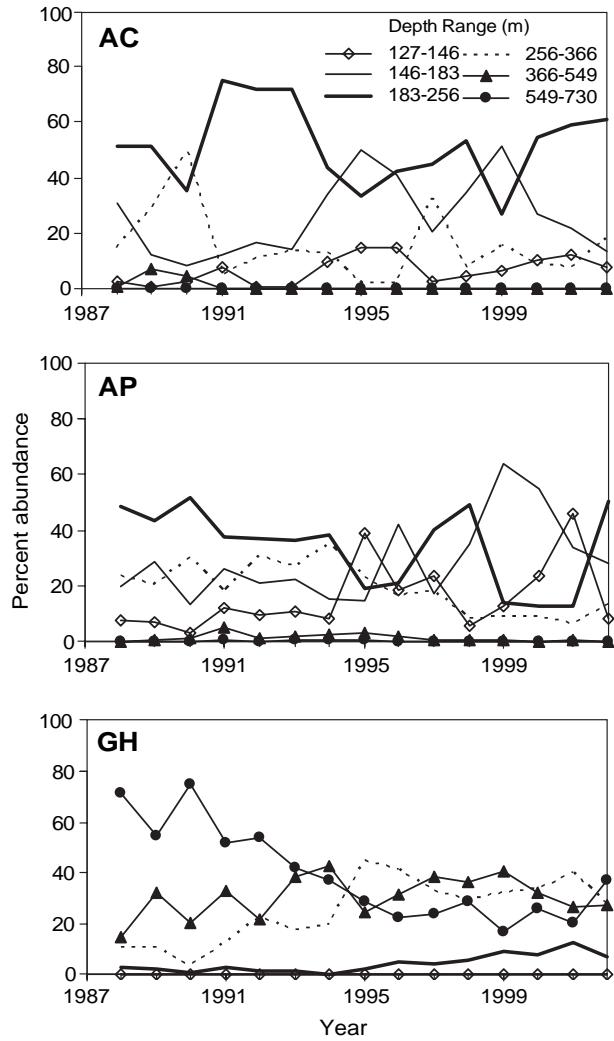


Fig. 4. Trends in annual percent abundance, by depth range, for Atlantic cod (AC), American plaice (AP), and Greenland halibut (GH) on the Flemish Cap during 1988–2002.

The range of Greenland halibut mirrored its abundance trends, exhibiting an increase during 1990 through 1999, from 23 km to 73 km, then declining thereafter to 45 km in 2002 (Table 2, Fig. 6).

Maps of kriged abundance indicate that the Flemish Cap stocks of cod and plaice exhibited severe contractions in their distributional areas during 1988–2002. During 1988–94, cod were distributed across a large portion of the Cap and were most abundant at depths of 150 m to 350 m, where large areas of dense aggregations could be found (Fig. 7). During 1995–2002, the area of cod distribution decreased severely in size and became concentrated on the shallowest portion of the Cap, where aggregations were smaller and less dense, and eventually nonexistent.

Similarly, a sharp contraction in the area of plaice distribution occurred during 1988–2002 (Fig. 8). Unlike the patchy distribution of cod, plaice were more evenly distributed and characterized by a series of concentric density rings that decreased with increasing depth. During 1988–94, the area and density of the plaice distribution changed from a large area of high density, located across a broad depth range (125 m to 300 m), to a small area of low density within the 150-m isobath. During 1995–2002, plaice occurred at very low densities with only one very small, high-density aggregation present within the 150-m isobath during some years.

An expansion in the range of Greenland halibut occurred concurrent with the range contraction of cod and plaice. For all three species, distributional trends can be divided into two periods separated by a transition period during 1993–95. The range of Greenland halibut gradually expanded onto the perimeter of the Cap, from a small area of high abundance at the northernmost tip in 1988, to an area encompassing most of the perimeter of the Cap (to the 600-m isobath) in 1995 (Fig. 9). During 1996–99, the area of distribution expanded further onto the Cap in the form of a circular band. In 1999, this band reached its maximum width and occupied the entire circumference of the Cap. Abundance increased with depth, particularly along the northern perimeter. The area of distribution completely encircled the 250-m isobath, within which was the bathymetric limit of cod and plaice distribution during this time (Fig. 7 and Fig. 8). During 2000–02, the area of Greenland halibut distribution shrank in size, but this reduction did not occur uniformly around the perimeter of the Cap. Instead, large patches of very low abundance occurred within a horseshoe-shaped band of moderate abundance, particularly on the northern portion of the Cap.

The range expansion of Greenland halibut into shallow water, during 1995–98, was primarily attributable to age 1 and age 2 fish from the 1994 and 1995 year-classes (Fig. 10C). These small fish (≤ 31 cm TL) were most abundant at depths of 250 m to 350 m, while fish larger than 31 cm were most abundant at depths of 300 m to 700 m (Fig. 11). There were very few catches of Greenland halibut at depths less than 200 m. Most of the Greenland halibut caught on the Flemish Cap were immature because few fish were larger than 60 cm (Alpoim *et al.*, MS 2002), the lower end of the range of L_{50} values reported for females sampled near the Cap (Morgan and Bowering, 1997).

A consistent decline in abundance occurred in all three length classes of American plaice (Fig. 10B). Fish

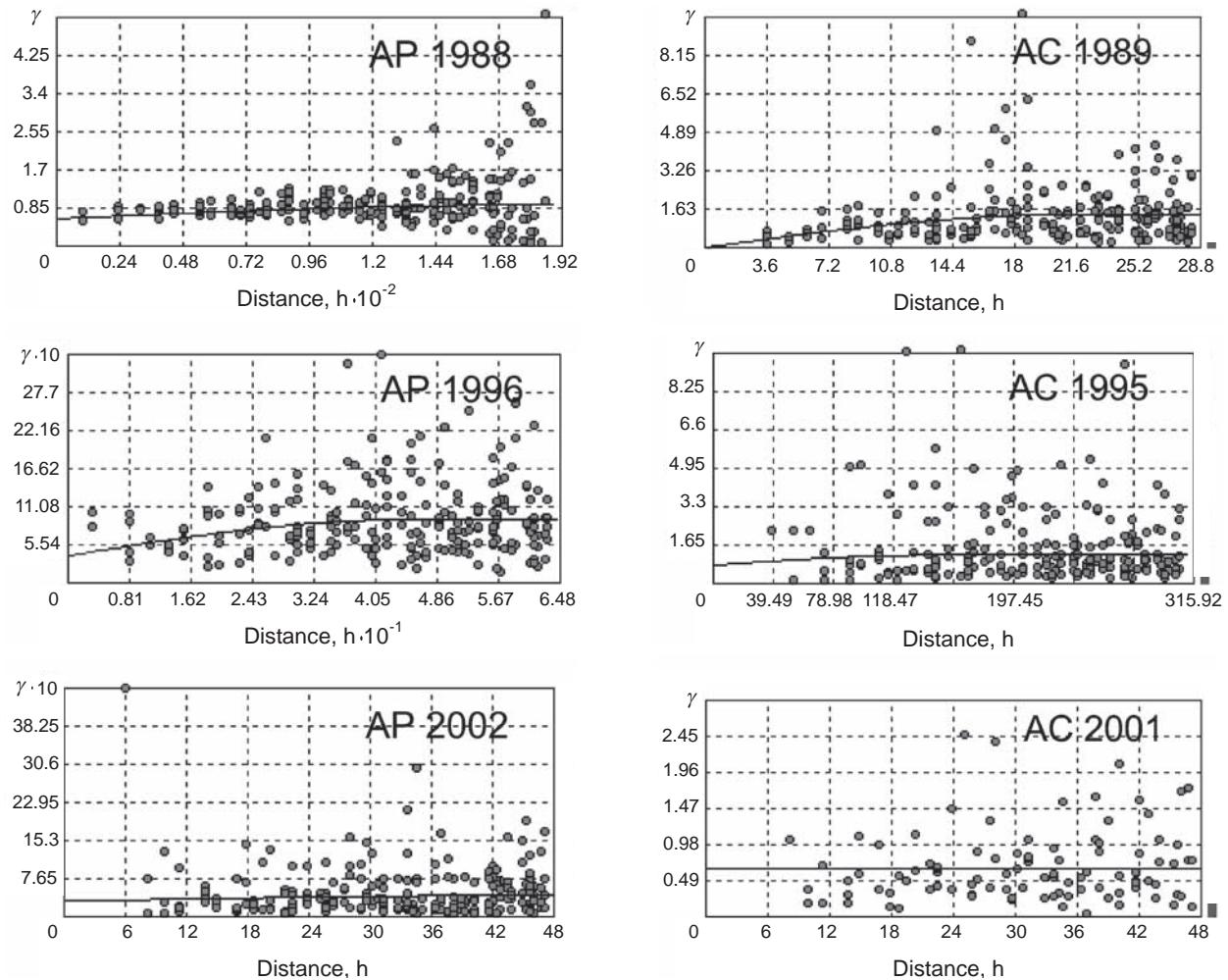


Fig. 5. Examples of semivariograms for spherical models fit to American plaice (AP) and Atlantic cod (AC) density data during a period of rapid decline in abundance for both species on the Flemish Cap.

TABLE 2. Parameter estimates for spherical semivariogram models fit to July abundance data for Atlantic cod, American plaice and Greenland halibut on the Flemish Cap during 1988–2002.

Year	Atlantic cod			American plaice			Greenland halibut		
	Range (km)	Nugget	Sill	Range (km)	Nugget	Sill	Range (km)	Nugget	Sill
1988	26.2	0.51	1.44	186.8	0.61	0.93	47.4	0.58	0.62
1989	21.0	0.00	1.40	176.9	0.49	0.61	91.0	0.28	0.60
1990	24.4	0.37	1.01	185.1	0.69	1.00	23.0	0.00	0.61
1991	31.0	0.63	1.85	67.7	0.48	0.90	40.0	0.09	0.44
1992	44.3	0.32	2.93	178.5	0.64	0.74	27.7	0.24	0.71
1993	36.1	1.50	2.64	196.6	0.51	0.79	63.0	0.45	0.67
1994	18.8	0.00	1.83	192.3	0.55	0.89	29.0	0.62	0.83
1995	14.8	0.79	1.23	220.7	0.75	1.04	52.0	0.15	0.95
1996	19.3	0.00	1.27	44.2	0.39	0.92	49.0	0.30	0.85
1997	39.1	0.43	0.94	23.2	0.09	0.88	37.0	0.15	0.78
1998	39.7	0.27	0.60	37.0	0.68	1.36	69.0	0.18	0.73
1999	25.0	0.00	0.56	45.0	1.09	1.09	73.0	0.37	0.59
2000	22.5	0.00	0.47	34.2	0.00	0.75	70.0	0.23	0.68
2001	45.6	0.66	0.66	33.3	0.00	1.08	64.0	0.01	0.92
2002	13.5	0.00	0.83	47.0	0.32	0.43	45.0	0.18	0.84

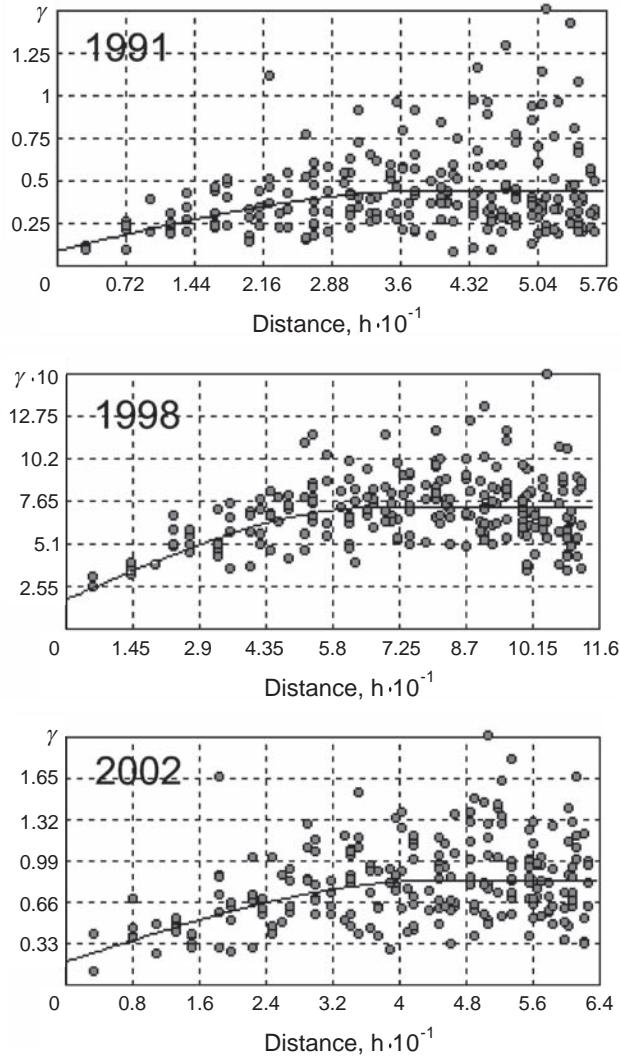


Fig. 6. Examples of semivariograms for spherical models fit to Greenland halibut density data during a period of increasing abundance, in 1989–98, followed by a gradual decline.

larger than 30 cm TL (age 3+), which dominated the survey catches, showed a preference for the shallow water and were most abundant at depths less than 200 m (Fig. 12). Unlike American plaice and Greenland halibut, cod did not show depth preferences by size-class (Fig. 13). During 1991–93, most of the cod caught in the survey were smaller than 40 cm (Fig. 10A) and appeared as high-density aggregations (Fig. 7) of age 1 and age 2 fish from the 1990 and 1991 year-classes (Fig. 10A). After 1994, all three length classes were at similarly low levels of abundance.

Relationships Between Species Distributions

Collocation indices suggest a high degree of similarity between cod and plaice distributions. During 1988–

2002, annual ellipses of inertia for both species showed a high degree of overlap (Fig. 14A) and GIC values were consistently at or near 1.0 (Fig. 14B). The spatial distributions of cod and plaice became more aggregated while the distribution of halibut became more dispersed. The percentage of survey tows with catches of cod decreased from 85% in 1990 to 33% in 2002 (Fig. 15). American plaice showed a similar trend but the decrease occurred later. The percentage of tows with plaice catch decreased from 85% in 1993 to 35% in 2000. In contrast, the distribution of Greenland halibut became more dispersed, and between 1994 and 1998, this species was found in 61% and 90% of the tows, respectively.

Cod and plaice co-occurred more frequently, in 24% of the survey tows conducted during 1988–2002, than did either species with Greenland halibut. Cod and halibut co-occurred in 4% of the tows and plaice and halibut co-occurred in 3% of the tows. Co-occurrence varied by year and stratum for all three stocks. The co-occurrence of cod and plaice declined from 59% in 1988 to near 0% in 2000 (Fig. 16). This trend was due to a shift, after 1993, from frequent co-occurrence in a large number of strata (strata 1–11 at depths of 127–365 m) to co-occurrence in only a few of the shallowest strata (strata 1–5). After 1998, co-occurrence was only present in stratum 2 (144–181 m), the only stratum where the two species consistently co-occurred throughout the time series. Greenland halibut were never caught on the shallowest part of the Cap (in stratum 1), where cod and plaice frequently co-occurred. Greenland halibut and plaice co-occurred in few strata (7–11 and 14) and there has been no co-occurrence since 1998. The percentage of plaice in tows with halibut co-occurrence declined over time, particularly on the southwest side of the Cap in stratum 10 (Fig. 17A). Greenland halibut co-occurred with cod across a broader area, in more strata, on an annual basis than with plaice. The percentage of cod in tows with halibut co-occurrence also declined over time and progressed from deep water (strata 7–15) during 1988–95 to shallower water (strata 3–6, Fig. 17B) thereafter.

Discussion

Density-dependent changes in the spatial distributions of Atlantic cod, American plaice and Greenland halibut occurred on the Flemish Cap during 1988–2002. For all three species, distributional trends can be divided into two periods, pre- and post-1995. Declines in the abundance of cod and plaice were accompanied by severe range contraction and a breakdown in the spatial structure of both stocks. A similar trend has also been documented for the northern cod stock (*Gadus morhua*) in NAFO Div. 2J+3KL during 1985–92, coincident with its collapse

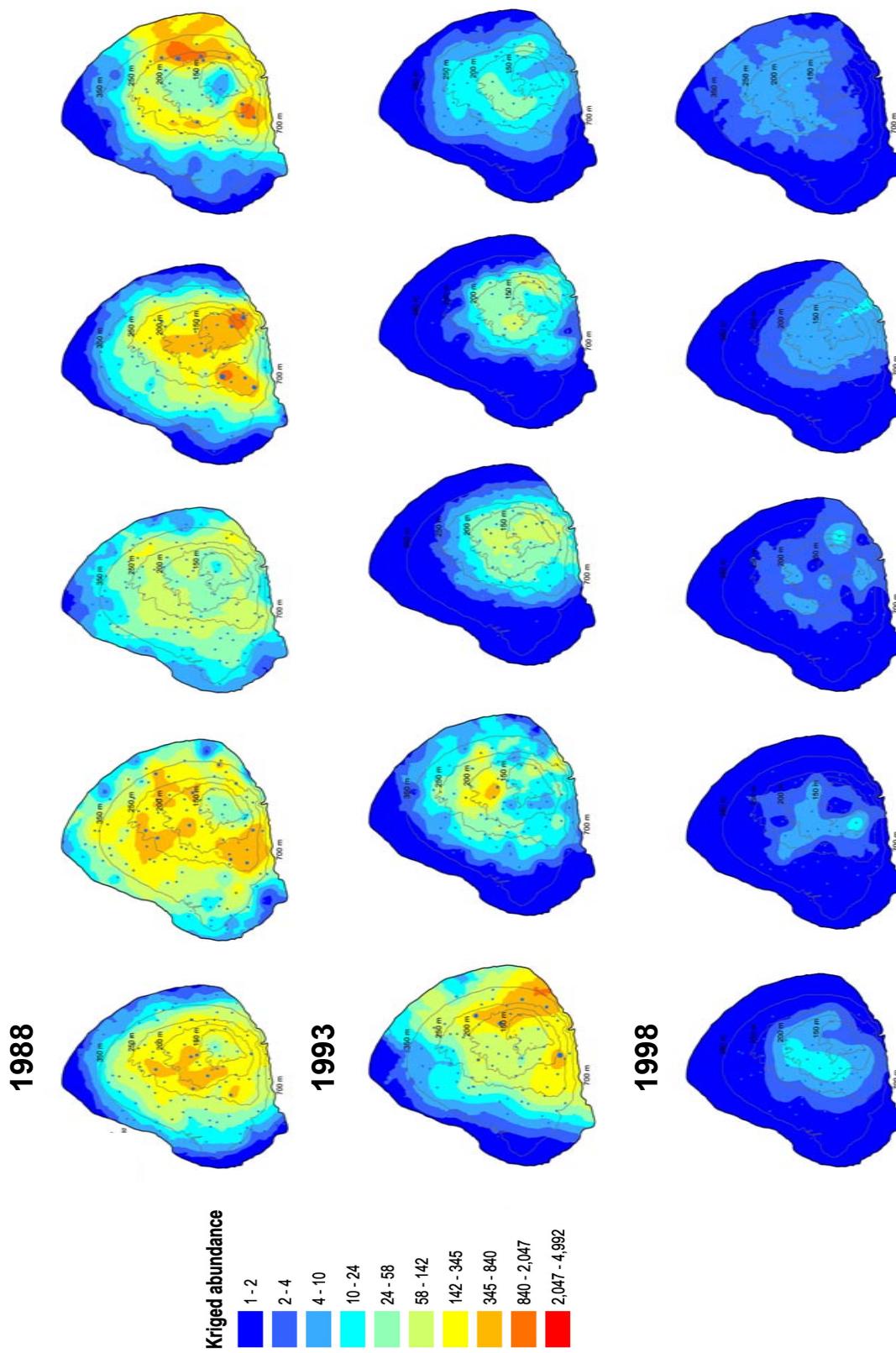


Fig. 7. Maps showing the kriged abundance of Atlantic cod on the Flemish Cap during 1988-2002.

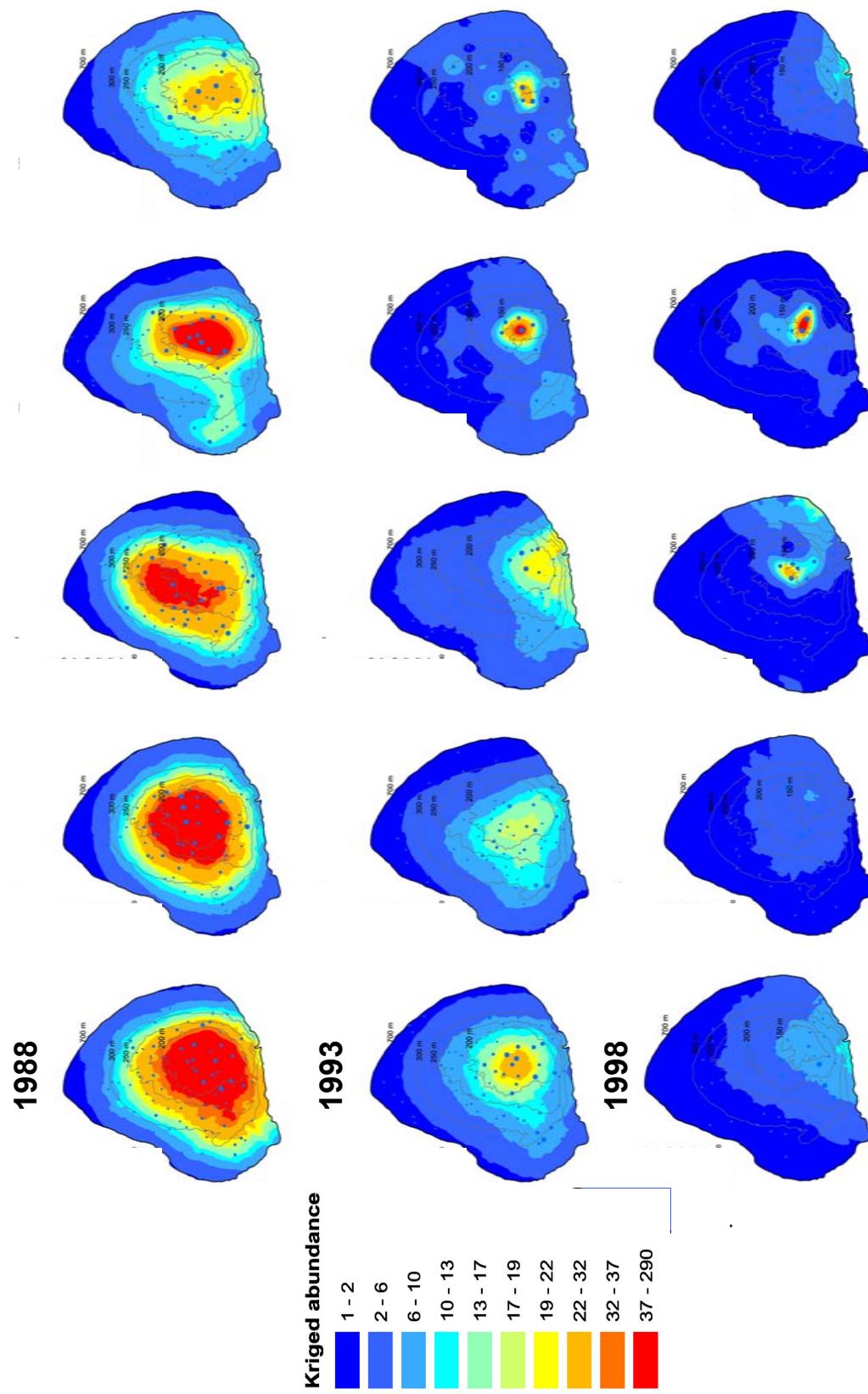


Fig. 8. Maps showing the kriged abundance of American plaice on the Flemish Cap during 1988–2002.

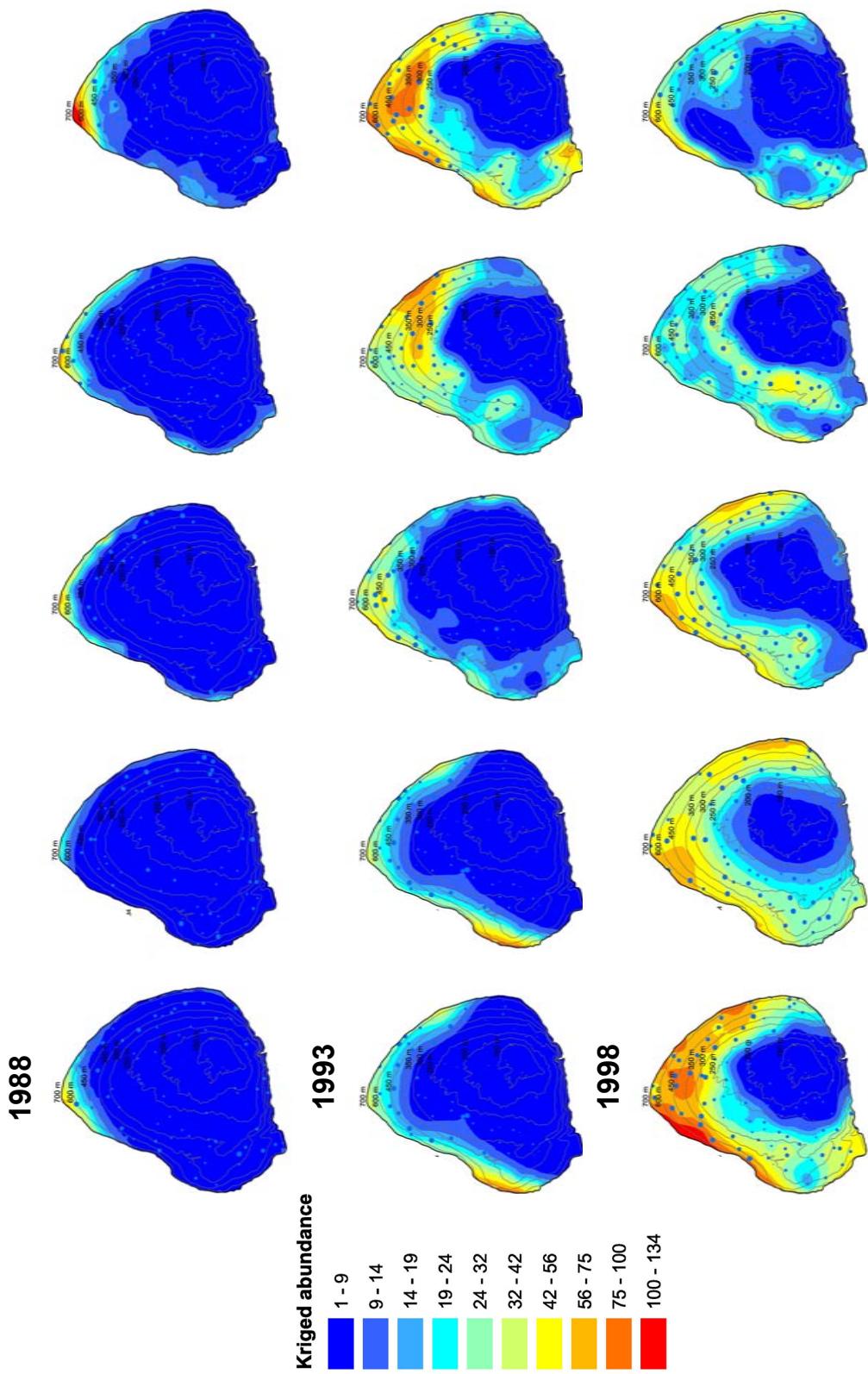


Fig. 9. Maps showing the kriged abundance of Greenland halibut on the Flemish Cap during 1988–2002.

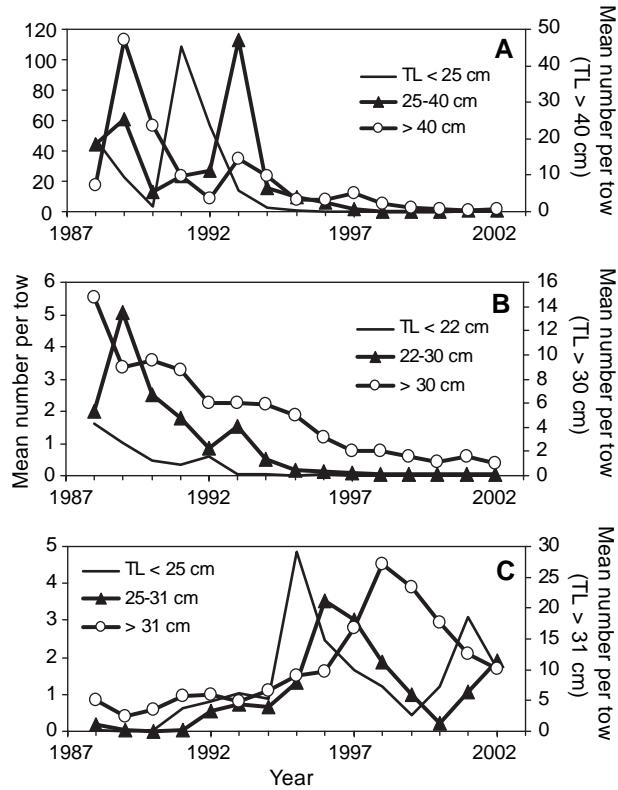


Fig. 10. Relative abundance (stratified mean number per tow), by length class, of (A) Atlantic cod, (B) American plaice, and (C) Greenland halibut on the Flemish Cap during 1988–2002. For each species, the three length classes correspond to ages 1, 2 and 3+.

(Warren, 1997). Global indices of collocation indicate that the Flemish Cap cod and plaice stocks were distributed in similar locations during 1988–2002. However, a more localized index of co-occurrence suggested a decline in the distributional overlap between the two species during this time period and that persistent co-occurrence was limited to depths of 147 to 183 m. During 1988–2002, decreases in the abundance of both stocks coincided with decreases in their areal distributions and both species became concentrated on the shallowest part of the Cap. Prior to 1988, during 1978–85, American plaice were distributed across a broader area and were most abundant on the Cap at depths of 200 to 400 m (Bowring and Brodie, 1994).

Coincident with the range contraction of cod and plaice, Greenland halibut expanded its range on the Cap into shallower areas that were previously inhabited by cod and plaice. Such broad-scale, within-season distribution shifts can be associated with changes in food and/or space competition or environmental conditions. However, the timing of these shifts was such that the areas in which cod and plaice were distributed showed little overlap with the

distribution of Greenland halibut. Thus, it is unlikely that the range contraction of cod and plaice occurred as a result of food and/or space competition with Greenland halibut. On the Flemish Cap, cod and plaice have similar prey preferences (Torres *et al.*, 2000). However, co-occurrence of the two species declined during the study period, suggesting a reduction in food and/or space competition.

Shifts in the spatial distribution of cod may reflect density-dependent changes in temperature preference. Swain and Kramer (1995) found that cod occupy shallow, warm areas when abundance is low and colder, deeper areas when abundance is high in order to reduce metabolic costs as food rations decline. However, such shifts are not likely for American plaice (Swain and Morin, 1996), because plaice prefer cold temperatures regardless of whether rations are high or low (Morgan, 1993). In either case, the distributional shifts of cod and plaice have persisted across years during the summer, when thermohaline conditions near the bottom of the water column are fairly constant on the Cap. A seasonal thermocline is present on the Cap during May through late August (Gil *et al.*, 2004). There is no seasonal cycle in temperature or salinity at depths below 100 m (Colburne and Foote, 2000), and at depths below 200 m, average temperature and salinity values recorded during the 1988–2000 EU surveys exhibited little interannual variability (Gil *et al.*, 2004). These trends suggest that factors other than changes in thermohaline conditions are the primary reason for the persistence of the observed distributional changes.

Since the fishing moratoria, neither the cod nor plaice stocks have shown signs of recovery. Post-moratoria levels of spawning stock biomass have continued to remain extremely low, total biomass has continued to decline, and there has been no appreciable recruitment in either stock (Alpoim and Ávila de Melo, MS 2004; Cerviño and Vázquez, MS 2004). Recruitment can be affected by the environment as well as spawning stock size. However, unless the natural mortality rate of mature fish has increased, these negative trends combined with the persistent pattern of range contraction suggest that fishing mortality rates on both stocks continue to be problematic.

Extremely low spawning stock size may be the primary reason for the lack of recovery of cod and plaice stocks. However, the persistent range contraction observed in both stocks also has biological implications that may be linked to stock recovery. The most obvious is the potential for increased vulnerability of aggregations to trawl fisheries (Kulka *et al.*, 1995). In addition, geographic fragmentation of the spawning stock, whereby spawners are concentrated in small patches located further apart, may hinder stock recovery due to: a) reduced demo-

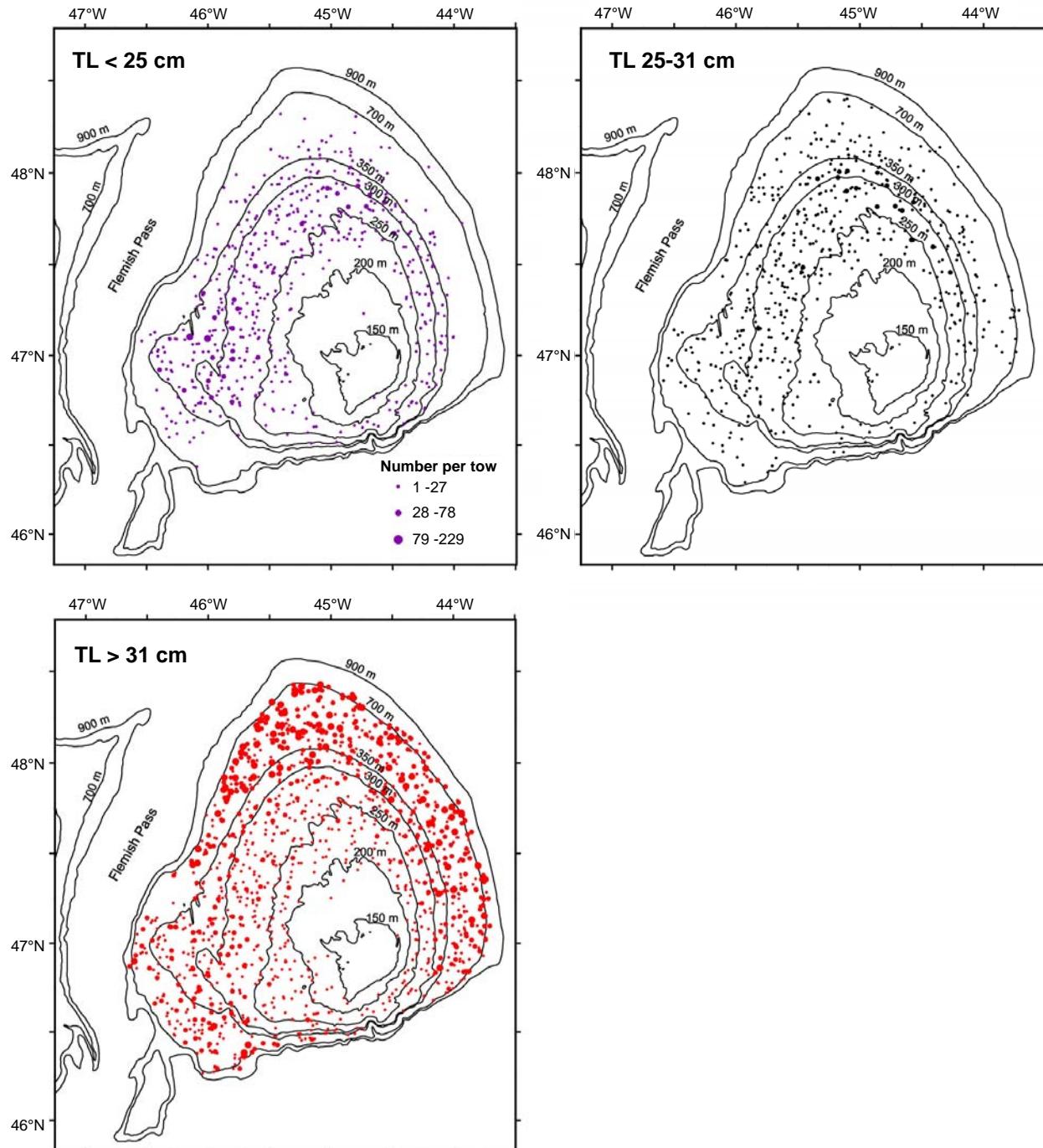


Fig. 11. Distribution of Greenland halibut abundance (number per tow) on the Flemish Cap, by length classes corresponding to ages 1, 2 and 3+, during EU bottom trawl surveys conducted in 1988–2002.

graphic variation in stock spawning characteristics (Murański *et al.*, 2001); b) reduced genetic diversity (Berkley *et al.*, 2004); c) reduced areas over which eggs and larvae are dispersed and dispersal into less favorable habitats, and (d) restricted environmental conditions for growth and reproduction. For example, an anticyclonic gyre is a

semi-permanent hydrologic feature on the Flemish Cap (Kudlo and Borokov, MS 1975) and its presence presumably affects primary productivity levels as well as larval dispersal and retention. During the period of 1988–2000, a well-developed anticyclonic gyre was present on the Cap during 1991, 1993 and 1995–2000, with the strongest

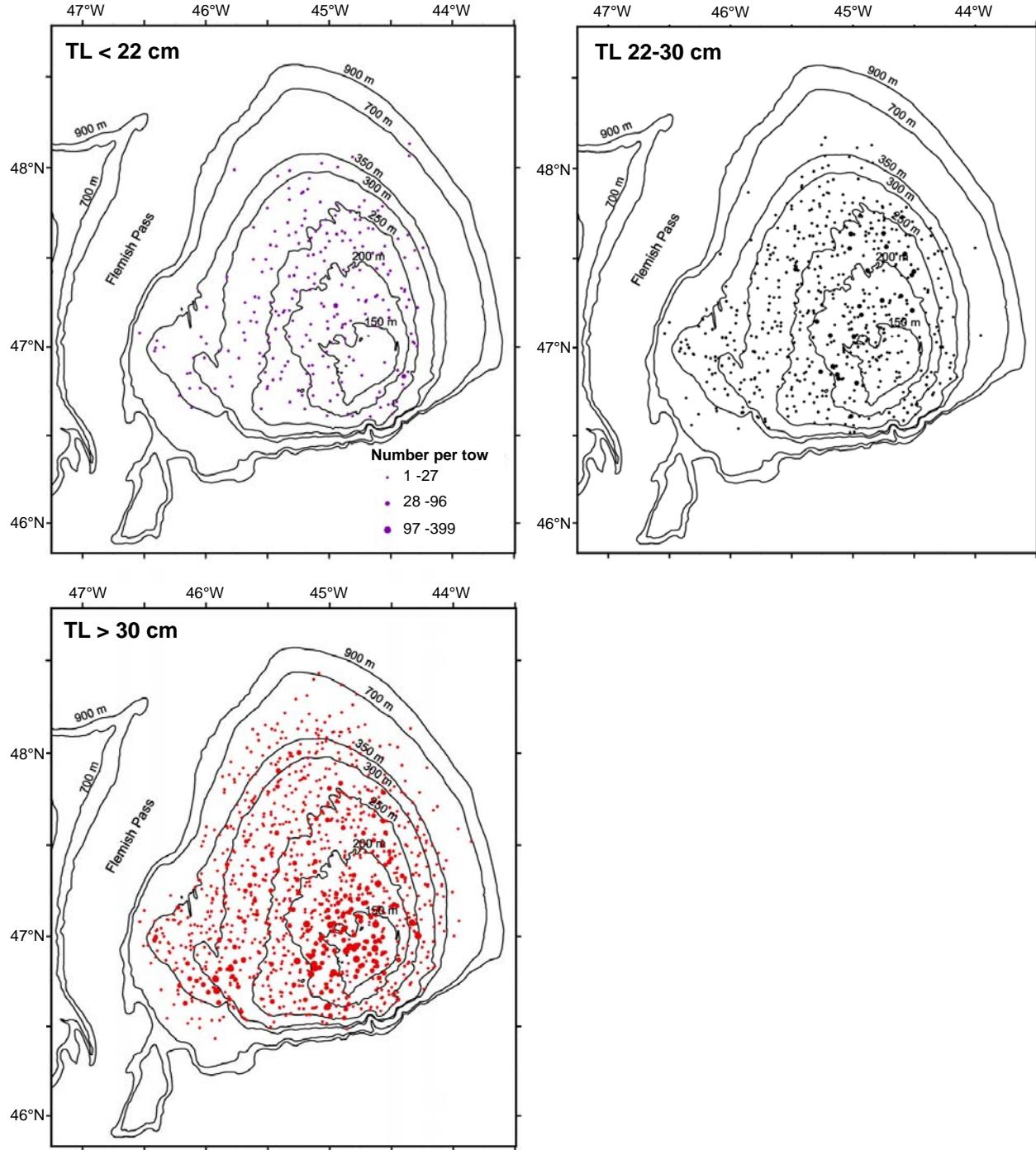


Fig. 12. Distribution of American plaice abundance (number per tow) on the Flemish Cap, by length classes corresponding to ages 1, 2 and 3+, during EU bottom trawl surveys conducted in 1988–2002.

gyre present in 1998 (Gil *et al.*, 2004). Presence of the gyre affects thermal and salinity conditions on the Cap whereby the core contains warmer, less saline waters. During July, the amplitude of mean geostrophic velocities

in the gyre tends to be highest along the eastern edge of the Cap and is associated with a southward flow off the Cap (Fig. 18). During periods when the anticyclonic gyre was well-developed, throughout most of the 1990s, the

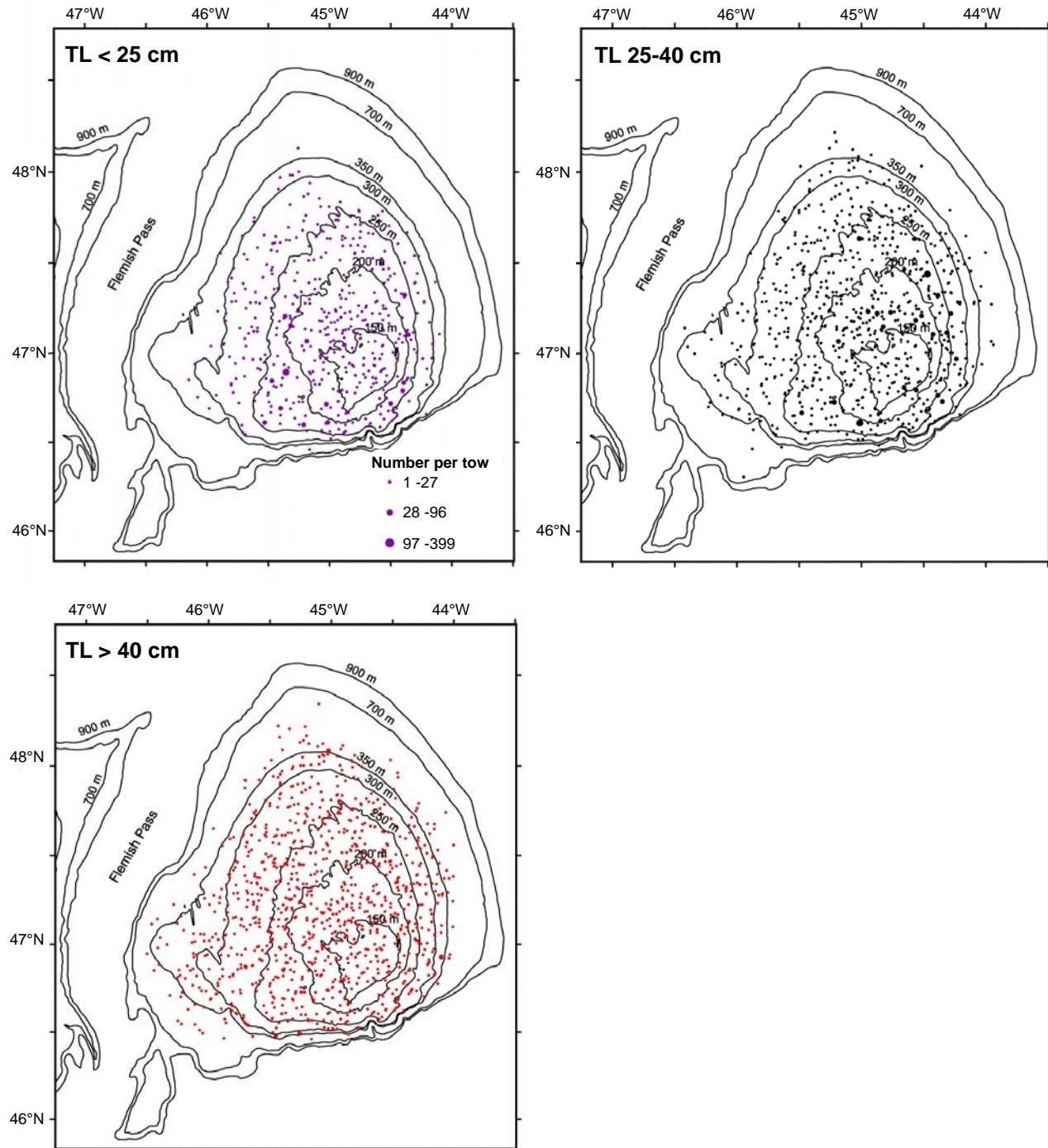


Fig. 13. Distribution of Atlantic cod abundance (number per tow) on the Flemish Cap, by length classes corresponding to ages 1, 2 and 3+, during EU bottom trawl surveys conducted in 1988–2002.

location of the high-amplitude flow off the Cap coincided with the area where cod and plaice were concentrated during this time and where the egg densities of American plaice are highest during July, near the center of the Cap at depths of 150 to 200 m (Nevinsky and Serebryakov, 1973). Therefore, the presence of strong gyres during the

1990s may have resulted in the loss of plaice eggs and larvae from the Flemish Cap ecosystem.

Range contraction also has important implications for stock assessments. For example, research survey biomass and abundance indices will be estimated with less

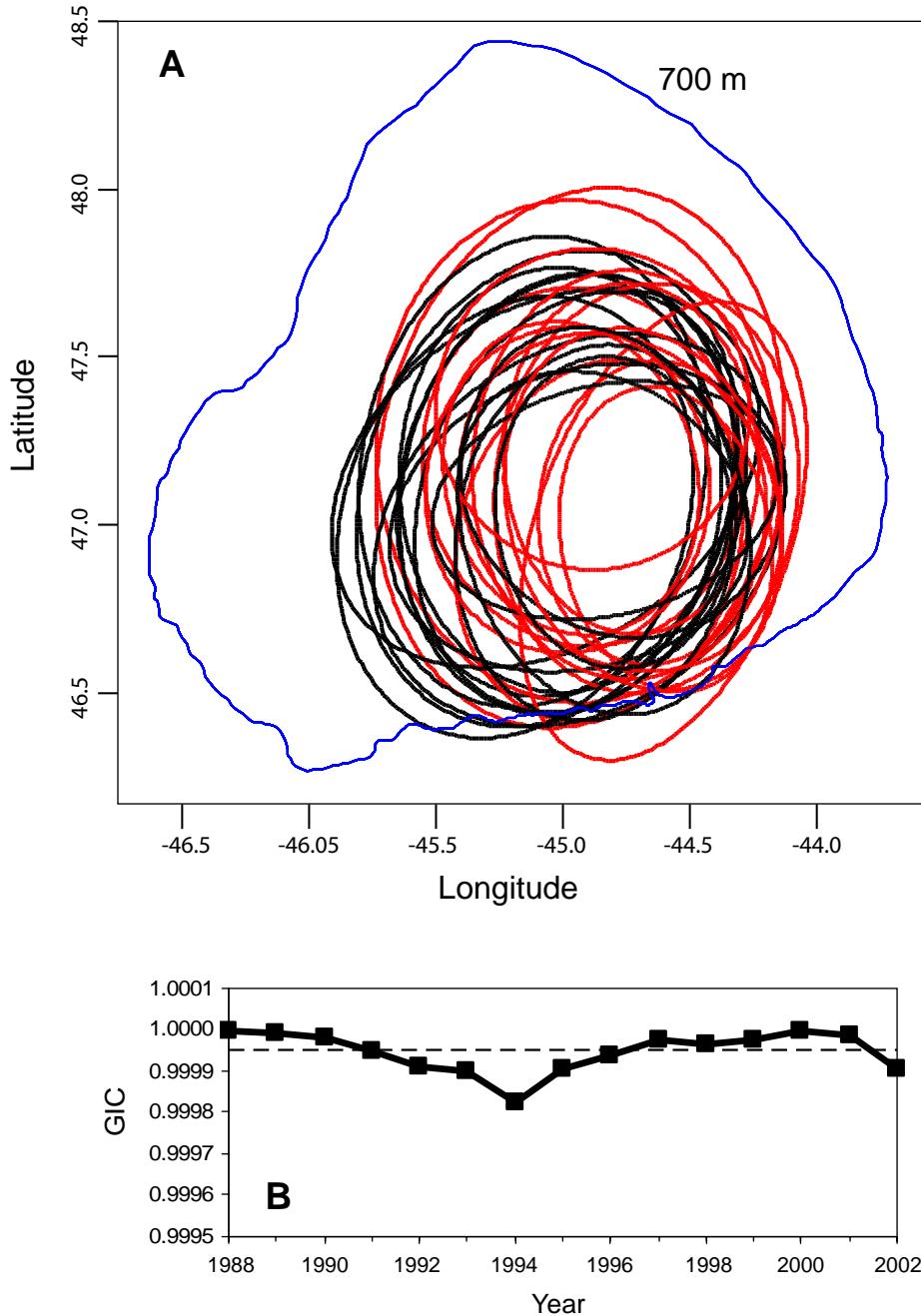


Fig. 14. Ellipses of inertia (A) indicating the annual areal distributions of Atlantic cod (red) and American plaice (black) and (B) global (GIC) indices of collocation for the two species on the Flemish Cap during 1988–2002.

precision when the spatial distribution of a population becomes distributed across a smaller area because the population will be sampled less frequently. In addition, annual trends in stratified mean weights per tow, where the mean is computed as an arithmetic mean, may mask declines in stock biomass because only a few high-density

tows can have a large effect on the arithmetic mean, and as range contraction occurs, the mean becomes more dependent on fewer tows. Geometric means are more robust to infrequent high-density survey catches, but may be overly sensitive to changes in fish distribution and should therefore be compared with annual trends in

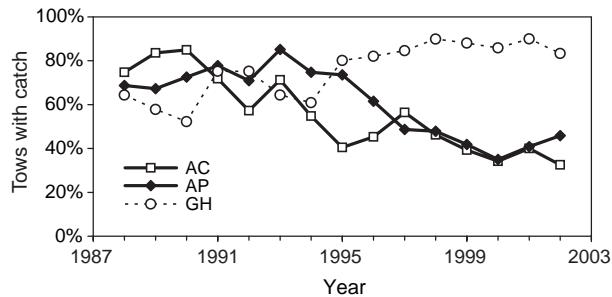


Fig. 15. Percentages of research survey tows, on the Flemish Cap, with catches of Atlantic cod (AC), American plaice (AP) or Greenland halibut (GH) during 1988–2002.

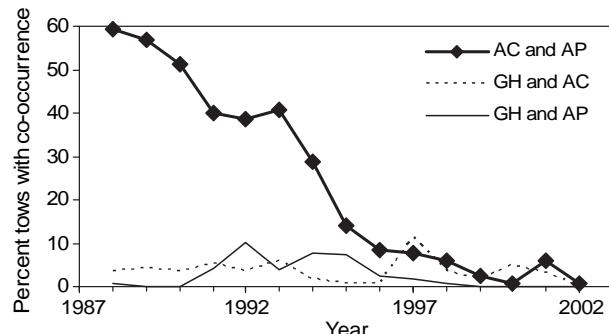


Fig. 16. Percentages of research survey tows with a co-occurrence Atlantic cod and American plaice (AC and AP), Atlantic cod and Greenland halibut (AC and GH), and American plaice and Greenland halibut (AP and GH) on the Flemish Cap during 1988–2002.

arithmetic means when examining abundance or biomass trends (Hutchings, 1996). The concentration of a population in a smaller area may also result in an increased vulnerability to mobile fishing gear. Swain *et al.* (1994) documented density-dependent changes in the catchability of cod in survey and fishery bottom trawls. Hutchings and Myers (1994) reported a negative relationship between cod catchability and stock biomass that was attributable to catch rate differences between low-density and high-density areas of cod distribution (Hutchings, 1996). Consequently, fisheries catch-per-unit effort data should not be considered proportional to stock size for stocks that

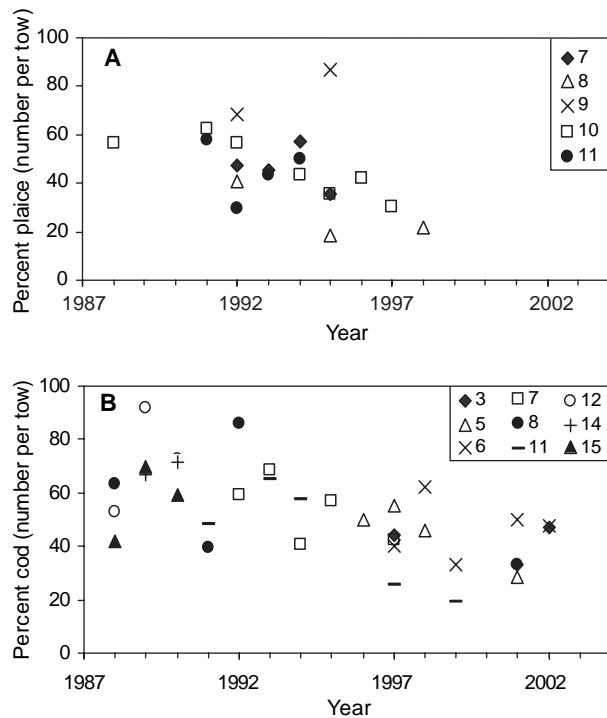


Fig. 17. Average percentages of (A) American plaice (number per tow) in survey tows with catches of both American plaice and Greenland halibut and (B) Atlantic cod in tows with catches of both Atlantic cod and Greenland halibut, by year and depth stratum, on the Flemish Cap during 1988–2002. Stratum depth increases with stratum number.

exhibit range contraction. Given the density-dependent changes that have occurred in the spatial distributions of cod and plaice on the Flemish Cap, it is recommended that alternative indices of abundance and biomass be used to monitor stock status, including geometric means and indices of spatial structure.

Acknowledgements

We would like to thank Ralph Mayo, Fred Serchuk and the anonymous reviewers whose comments and suggestions helped to improve the quality of the manuscript.

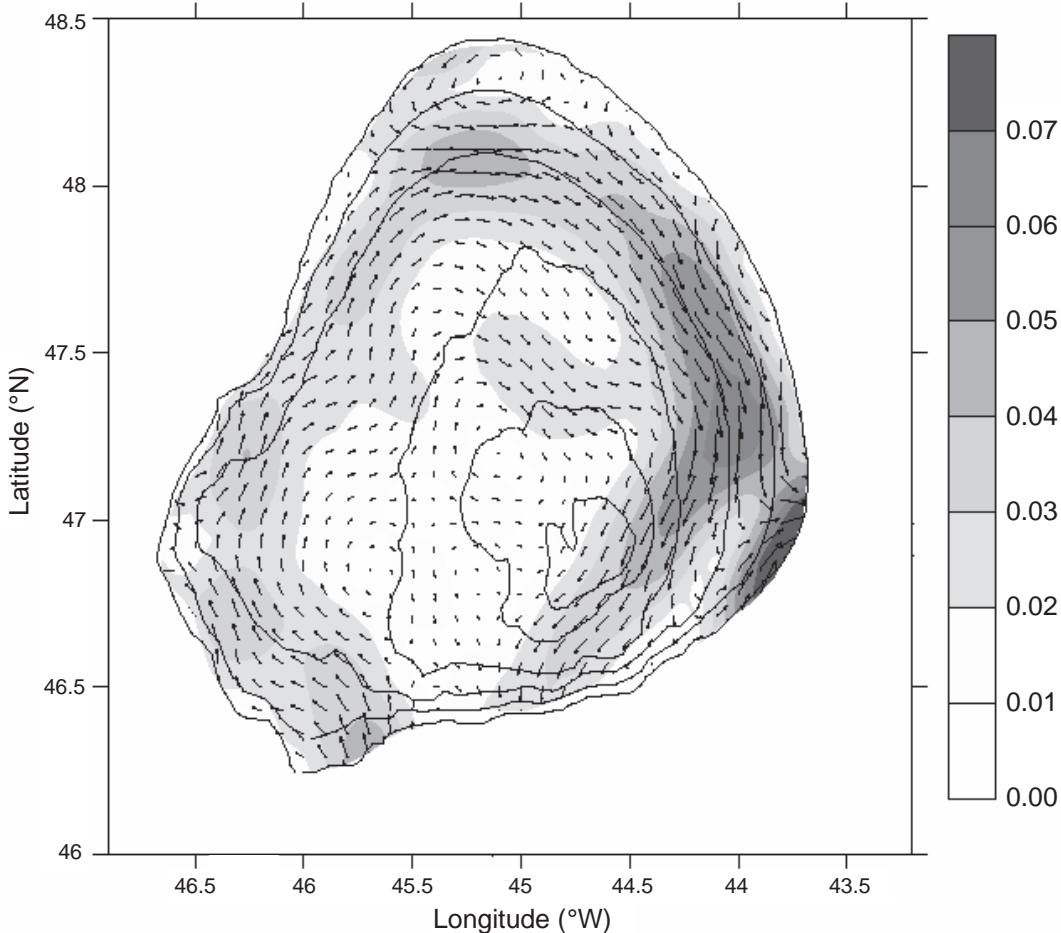


Fig. 18. Mean geostrophic velocity vectors and amplitudes (shaded areas, ms^{-1}) at a depth of 10 m, on the Flemish Cap in July, during 1988–2000 (from Gil *et al.*, 2004).

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