

Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves

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I present here methods for describing how spatial distribution changes as population abundance varies. Four models for biomass-dependent spatial dynamics are described and characterized by geostatistical aggregation curves. These curves provide a simple way to choose between models when characterizing spatio-temporal variability of survey data. A test of significance is proposed based on a bootstrap resampling algorithm. The analysis is applied to two spatio-temporal series of monitoring surveys; a groundfish bottom trawl survey and a pelagic echointegration survey. Relative to the population mean, the relative histograms in both series are time invariant for medium and high observed abundances. But for low population abundance, the relative histogram is more skewed. I then discuss the use of commercial CPUE data for deriving time series of comparable abundance indices when the density histogram changes with abundance.

Key words: spatial distribution, geostatistics, abundance, CPUE.

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Introduction

Commercial catches result from the interaction between a heterogeneous fish spatial distribution and a heterogeneous application in space of fishing effort. Fishermen perform a special sampling of the density histogram. In a sense, CPUE data represent the density histogram tail and/or local spatial means of the spatial distribution of the fish population. Can these data be used to build time series of comparable population abundance indices? This raises the question of how the density histogram varies when the population mean varies, which is the subject of this paper. It also raises the question of how fishing tactics vary with fish spatial distribution, a question that will only be discussed here.

Paloheimo and Dickie (1964) first raised the issue that variations in the aggregative behaviour of the fish may cause variations of stock catchability. For anchovy and herring, two schooling pelagic fishes, an increase of stock catchability at low stock size has been described by different authors (MacCall, 1976; Ulltang, 1980; Winters and Wheeler, 1985; Csirke, 1989). This increase was attributed to a decrease in occupied area at low stock size with constant average density. These authors stress the danger of using CPUE as an abundance index

without information on the spatial distribution of the stock. More recently, a similar inverse relation between stock size and catchability has been reported for cod and haddock, two schooling demersal fish species (Crecco and Overholtz, 1990; Marshall and Frank, 1995; Myers and Cadigan, 1995). Decrease in occupied area at low stock abundance has been reported for these species from analysis of survey data (Swain and Wade, 1993; Marshall and Frank, 1995; Swain and Sinclair, 1994; Myers and Cadigan, 1995). No relation between geographic distribution and abundance was reported for plaice (Swain and Morin, 1996).

Different dispersion indices of geographic distributions have been used and can be grouped into three categories: geometrical, areal or distributional and model-based. Geometrical indices are based on the computation of the centre of gravity of the geographic distribution (Murawski and Finn, 1988) and inertia around it (Atkinson *et al.*, 1997). They have been used to show shifts in the spatial distributions from survey data. Model-based indices assume a relation between stock abundance as measured by VPA and local density as measured by survey catches. Myers and Stokes (1989) used a power relation as have Marshall and Frank (1995). Such indices were used to test for a local

response to a change in abundance. Areal or distributional indices have been used for survey data. Areal indices are based on the estimation of an area for which density values exceed a threshold. This threshold can be taken in absolute value (Swain and Wade, 1993) or as a percentage of the zonal mean (Swain and Sinclair, 1994). Areas supporting 50% to 90% of the abundance can be derived. Distributional indices characterize the spatial distribution as a cumulative frequency. Marshall and Frank (1994) have also used cumulative frequency plots while Myers and Cadigan (1990) have used Lorenz curves which relate a percentage of biomass to the area that contains it. Areal and distributional indices have been used to show decreases in area coverage of fish stocks with decreases in abundance.

Three models have been proposed to describe the local response of density to a global change in abundance: (i) the constant density model where density stays constant and the area covered by the stock varies with abundance (Iles and Sinclair, 1982; Hilborn and Walters, 1992); (ii) the proportional model where the area occupied stays constant and local density varies proportionally to abundance (Houghton, 1987; Myers and Stokes, 1989; Hilborn and Walters, 1992; Petitgas, 1997); and (iii) the basin model where density and area vary with abundance (MacCall, 1990). In the basin model, density changes in all areas with abundance as a result of relationships between habitat suitability and local density. This model is a fisheries application of the ecological theory on density dependent habitat selection (Sutherland, 1983).

In the present paper, I propose a simple analysis of survey data to identify which model describes best the variations in the geographic distribution. I also propose a fourth model where only some local areas change their density with population abundance. The approach proposed uses a geometrical analysis and a distributional index based on geostatistical aggregation curves (Matheron, 1981). The analysis proposed is applied on two series of monitoring surveys, a demersal and a pelagic survey.

Methods

A spatial distribution has three major characteristics; patterns in the location and shape of high density areas, roughness of the density surface, and global statistics like zonal mean and variance. Patterns can be analysed by geometrical indices mentioned in the introduction and this will not be our present concern. Roughness is summarized in the skewness of the density histogram, in the correlation structure, or in a power law of Taylor (1961) between mean and variance computed on small blocks of the area. Changes in the density histogram with the zonal mean are analysed here with geostatistical

aggregation curves (Matheron, 1981; Lantuéjoul, 1990; Petitgas, 1997) because they allow simple comparison of histograms with different means and variances.

Geostatistical aggregation (or concentration) curves $Q(T)$ and $P(T)$

Let $z(x)$ denote the fish density at point x and A the total area occupied by the fish population. Let I define the set $(z(x_1), \dots, z(x_n), \dots)$ to be a realization of a random function Z over A . Also let m be the mean of Z and $F(z)$ its cumulative frequency curve where z is a threshold value of the density $z(x)$.

The curve $Q(T)$ of Matheron (1981) (geostatistical "selectivity" curve) relates the abundance $Q(z)$ to the area $T(z)$ occupied by densities greater than the threshold z (Fig. 1). The term selectivity is here confusing as it has another meaning in fisheries. I suggested (Petitgas, 1997) calling these curves geostatistical aggregation or concentration curves because $Q(z)$ measures the maximum abundance that can be on any area $T(z)$ in the survey area.

More precisely $T(z)$ denotes the proportion of the total area A where density is greater than z :

$$T(z) = \int_z^{\infty} dF(u) = 1 - F(z). \quad (1)$$

$T(z) \times A$ measures the cumulative surface of the areas where density is greater than z . $Q(z)$ is the fish biomass in these areas:

$$Q(z) = \int_z^{+\infty} u dF(u). \quad (2)$$

$Q(z)$ measures the maximum fish biomass that is in any proportion $T(z)$ of A . $Q(0)$ corresponds to the total fish abundance. $Q(z)$ varies between zero and $Q(0)$. $T(z)$ varies between zero and unity.

The concavity of the curve $Q(T)$ is a parameter that is analogous to the skewness of the density histogram. It is twice the area separating the curve $Q(T)$ from the diagonal mT , which is the $Q(T)$ curve for a homogeneous spatial distribution. The concavity of the curve $Q(T)$ is called selectivity in the field of Mining. I suggest using the term space selectivity or space concentration index. It is given by:

$$Ss = 2 \int_0^1 (Q(T) - mT) dT = \int_0^{+\infty} F(u)(1 - F(u)) du. \quad (3)$$

The index Ss is a dispersion parameter but has two advantages compared to the variance. First, Ss can characterize the dispersion of a spatial process for which the variance is not defined. Second, Ss is less sensitive in practice to high density values.

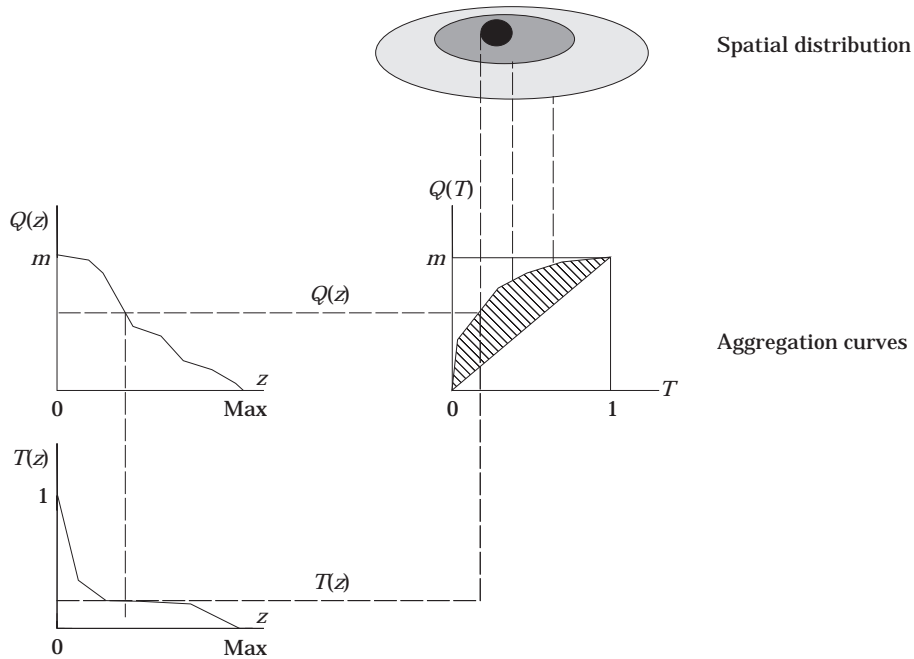


Figure 1. Graphical construction of the geostatistical aggregation curve $Q(T)$ with the curves $Q(z)$ and $T(z)$ for a schematical spatial distribution. Density values are denoted by z . $T(z)$ is the proportion of the total fish presence area where the density is greater than z . $Q(z)$ is the fish biomass that is on the area $T(z)$ where density is higher than z . The curve $Q(T)$ relates $Q(z)$ to $T(z)$ and gives the maximum biomass that can be in any proportion T of the total area. The hatched zone under the $Q(T)$ curve represents half of the space selectivity (concentration) index S_s .

When years have different means, I suggest computing $P(T)$ curves where $P(z)$ is defined as a proportion of the abundance varying between zero and unity:

$$P(z) = \frac{Q(z)}{Q(0)} \tag{4}$$

$P(z)$ is the proportion of population abundance in the areas where density is greater than z . It is the maximum proportion of abundance in any area $AT(z)$. A space selectivity index for the curve $P(T)$, S_{sp} , is defined as twice the area between $P(T)$ and the diagonal line. It can be seen to be analogous to a logarithmic variance.

The curves $Q(T)$ and $P(T)$ can be computed for survey data as follows. Compute for each of the n sampled density values z_i its area of influence a_i and rank the densities z_i in descending order, from maximum to minimum. The curves are given by:

$$Q(z_p) = \sum_{i=1}^p a_i z_i; P(z_p) = \frac{\sum_{i=1}^p a_i z_i}{\sum_{i=1}^n a_i z_i}; T(z_p) = \frac{\sum_{i=1}^p a_i}{\sum_{i=1}^n a_i} \quad \text{where } z_1 > z_2 > \dots > z_n \tag{5}$$

In this paper, the surveys consisted of sample points homogeneously distributed over the same surveyed area,

A. Thus, we used the following formulae as estimates of the previous ones:

$$Q(z_p) = \sum_{i=1}^p \frac{n_i}{n} z_i; P(z_p) = \frac{Q(z_p)}{m}; T(z_p) = \sum_{i=1}^p \frac{n_i}{n} \tag{6}$$

where n_i is the number of data in class i , n the number of data in the survey, z_i the mean of class i and m the simple average of the data. $Q(z)$ will thus vary between zero and m .

Spatial dynamics characterized

I refer to the relationship between local density and population abundance as the spatial dynamic. The three models of spatial dynamics reviewed in the introduction can be characterized by the behaviour of the curves $Q(T)$ and $P(T)$. I add to the list another dynamic, (D1).

Dynamic (D1): The area of fish presence, A , stays constant. An increase in population abundance is associated with an increase of fish density in one (or several) specific subareas and densities elsewhere do not vary. This can be considered to be a spatial expression of Cushing's match-mismatch larval survival hypothesis occurring locally at one or several spots in the plankton (Cushing, 1972). In this case, local environmental effects

favour an increase in local fish density. This results in an increase in variance and consequently in the mean but not necessarily in the median. In this dynamic, local fish density is not related to total abundance but to local environment. This dynamic is compatible with a log-normal formalism where local effects would affect the logarithmic variance but not the median. Thus variations in the arithmetic mean would be due to variations in the logarithmic variance.

Dynamic (D2): The area of fish presence, A , stays constant. An increase in population abundance is associated with an increase in density at all points but the density at each point remains a constant proportion of the population abundance. This dynamic has been named the "consistent spatial pattern" by Houghton (1987) and the "proportional density model" by Hilborn and Walters (1992). This pattern has been reported for gadoids in the North Sea (Myers and Stokes, 1989), for young hake in Biscay (Petitgas, 1994) and for sole eggs on a spawning ground (Petitgas, 1997). In this dynamic local fish density changes at the same rate as population abundance.

Dynamic (D3): The area of fish presence varies with population abundance but the density histogram stays constant and consequently so does the average fish density. This situation was suggested by the spatial distribution of larval herring reported by Iles and Sinclair (1982) on spawning grounds: the bigger the spawning area the bigger the larval population. Hilborn and Walters (1992) named this dynamic the "constant density model". In this case, the maximum density stays constant and local fish density does not change at the same rate as population abundance.

Dynamic (D4): The area of fish presence, the maximum and average fish densities vary with population abundance. This dynamic has been reported for stocks when abundance collapsed. Ulltang (1980) reported this dynamic for herring, McCall (1990) for anchovies and Swain and Wade (1993) for cod. MacCall (1990) gave ecological grounds for such a dynamic based on habitat selection and carrying capacity and presented it in the form of the so-called basin model. Dynamic D4 is a mixed dynamic as it can be obtained by combining dynamic D2 with dynamic D3. In this dynamic, local density does not change at the same rate as population abundance and the maximum density increases with abundance.

The spatial dynamic of the relative density is biomass-independent in dynamic D2 and biomass-dependent in dynamics D3 and D4. In D3 and D4, biomass collapse is associated with range collapse in the spatial distribution. Dynamic D1 has a different status as it characterizes local effects.

Figure 2 gives a visual representation of the four dynamics with the corresponding behaviours of the geostatistical $Q(T)$ and $P(T)$ curves. Two years are

shown, one where the abundance is low (year 1) and one where the abundance is high (year 2). For dynamic D2 the curves $Q(T)$ are strictly proportional as the relative densities $z(x)/m$ stay constant when m varies. The curves $P(T)$ thus superpose. For dynamic D1, year 2 (high abundance) shows both $Q(T)$ and $P(T)$ curves that stay higher than year 1 curves (low abundance). For dynamic D3, $Q(T)$ curves superpose at the origin (consistency in the maximum density on the habitat) and $P(T)$ curve for year 1 is higher than for year 2. Dynamic D4 has the same behaviour as dynamic D3 for $P(T)$ curves but $Q(T)$ curves don't show any superposition. The ratio of their slopes at the origin equals the ratio of the two abundances.

Because aggregation curves are a way to compare histograms overall, they do not describe changes in the location of high densities. Charts of fish density need to be produced to look at changes in location.

Variation of the space selectivity index with population size

The curves $P(T)$ and their space selectivity indices, S_{sp} , play a major role as they enable us to distinguish between dynamics D1, D2 and the group D3–D4. Then the curves $Q(T)$ serve to distinguish between dynamics D3 and D4. In dynamic D2, the index S_{sp} stays constant and shows no variation with population abundance. In dynamic D1, the index increases when population size increases but in dynamics D3 and D4, the index increases when population size decreases. I propose testing the significance of variations in the index S_{sp} by a bootstrap resampling algorithm (Manly, 1996).

Consider the null hypothesis to be the dynamic D2. Under this hypothesis, the relative densities (z_i/m) of each survey are realizations of an underlying spatial distribution. The different survey data can be pooled together and resampled to estimate the S_{sp} index of the underlying $P(T)$ curve under the null hypothesis. It is not necessary to estimate the $P(T)$ curve for the pooled data set to estimate its S_{sp} index. Lantuéjoul (1990) proved that the space selectivity index S_s can be written as:

$$S_s = \frac{1}{2} E[|X - Y|]$$

where E denotes the expectancy and X and Y are two random variables with the same cumulative distribution F .

Therefore, it is only necessary to resample with replacement N pairs of independent values in the pooled data set and then compute half the average of the N absolute differences between the paired values. The statistical distribution of the index S_{sp} can thus be derived and its $t/2\%$ confidence limits on each side. A survey showing its S_{sp} outside these limits can be said

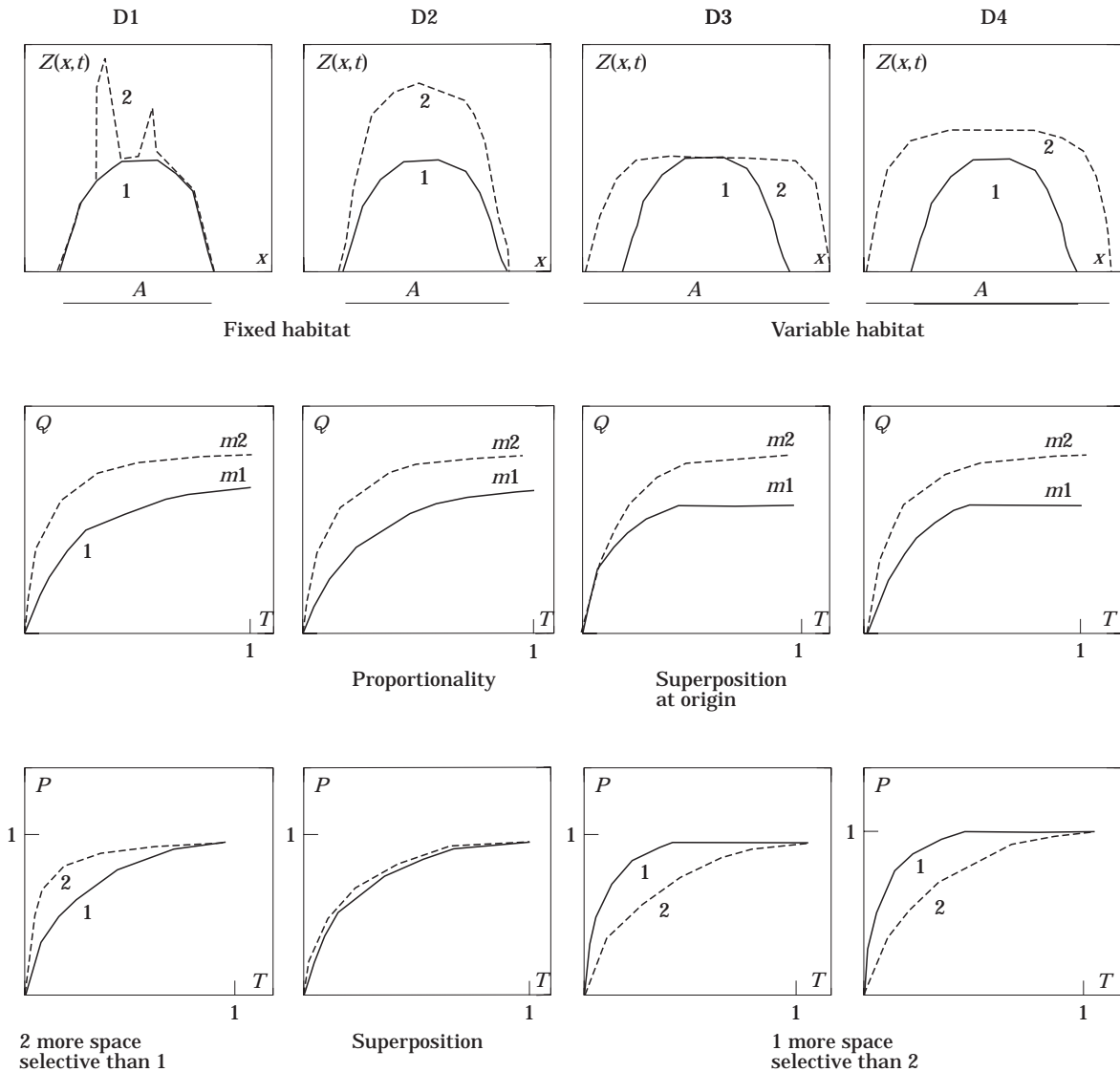


Figure 2. Four models of spatial dynamics characterized by geostatistical aggregation curves $Q(T)$ and $P(T)$. The lines marked (1) and (2) represent the dynamics of the density surface when biomass increases from year 1 to year 2. Abscissa (x), represents space. Ordinate, $Z(x,t)$, represents fish density at location x for year t . Graphs $Q(T)$ and $P(T)$ are plotted below the spatial dynamic they characterize. T represents a proportion of total area A . $Q(T)$ represents the maximum fish biomass that can be on any area of surface AT and $P(T)$ represents the maximum proportion of total biomass that can be on this area. Year 1 represents a low abundance year (continuous line) and year 2 a high abundance year (dotted line).

to depart significantly from dynamic D2 at the $t\%$ significance level.

Data and results

Spatial dynamic of young hake in Biscay Bay

The French Institute of Research for the Exploration of the Sea, IFREMER, has carried out yearly bottom trawl surveys since 1987, of young fish in the Bay of Biscay

(Poulard, 1990). We are concerned here by the age class 0 of Hake (*Merluccius merluccius* L.) during autumn surveys as the young fish are fully recruited on the nursery grounds. The nursery grounds are known to have muddy bottoms, in particular the great muddy bank in North Biscay (Dardignac, 1988). Age 0 fish were defined as those with length lower than 19 cm; the maximum length reported by Guichet (1988) for this age class. The sampling scheme was stratified random. Depth and latitude defined strata limits. In each stratum

Table 1. Basic statistics of age-0 hake densities in Biscay Bay, France. Data mean variance are denoted by m and σ^2 . Number of tows is n . Density is expressed as the number of individuals per 30 minutes trawl tow.

Year	n	m	σ/m
1987	131	44	2.41
1988	142	83	2.07
1989	134	57	1.97
1990	136	131	2.16

the number of trawl stations was proportional to the stratum area. Thus, trawl stations are considered homogeneously distributed in space and the data average in each survey was used to estimate the population mean for that year (recruitment index). The fish density is expressed as the number of individuals per 30-min trawl tow.

Abundance varied by a factor 3 during the years 1987 to 1990 (Table 1). The relative dispersions measured by the coefficient of variation (standard deviation over mean) are of the same order of magnitude. The spatial distributions were very similar over the years (Fig. 3). In particular, the high densities are localized in the same areas of the northern part of Biscay Bay between 48°N and 46°N latitude where the density surface is dome shaped.

The aggregation curves $Q(T)$ do not superpose at the origin and the curves $P(T)$ are close to being superposed (Fig. 4). This suggests that age-0 hake shows a dynamic of type D2. High density areas represent the same proportions of biomass and of total area, whatever the year and the abundance level.

Dynamic D2 and the absence of geometrical shift in the spatial distribution suggest that the spatio-temporal variability can be appropriately modelled as follows:

$$\frac{Z(x,t)}{M_q(t)} = M_w(x) + R(x,t) \quad (7)$$

where $Z(x,t)$ is the density at point x and year t , $M_q(t)$ is the abundance for year t , $M_w(x)$ is the time invariant expected relative density surface at point x and $R(x,t)$ are the residuals. Petitgas (1991, 1994) estimated $M_w(x)$ by kriging and related the area A_{80} corresponding to $P(T)=0.8$ to the muddy bottoms in Biscay Bay. A_{80} is the area where the highest densities summing to 80% of the age-0 hake stand each year, whatever its abundance. When the variance of the residuals $R(x,t)$ is a function of $M_w(x)$, then the model can be factorized and gives a multiplicative model (Petitgas, 1997).

Spatial dynamic of pelagic fish in Senegal

Since 1984, yearly acoustic surveys of the pelagic resources on the Senegalese continental shelf have been

carried out by the Senegalese Oceanographic Research Center of Dakar-Thiaroye, CRODT, and the French Institute of Scientific Research for Cooperation and Development, ORSTOM (Levenez *et al.*, 1985). I considered the surveys performed on the shelf, south of Dakar. Equipment settings were the same in all surveys. Echo-integration values were computed at regular intervals of one nautical mile. No species identification of echoes was performed. Main pelagic species fished in this area are Clupeoidea (*Sardinella* sp.) and Carangidea. Density values represent mean back-scattered acoustic energy per square nautical mile of sea surface and are proportional to fish density. Because day and night coverages represented similar percentages of the data in each survey, day and night data were used together to compute comparable statistics for all surveys. The survey was performed along parallel transects oriented east to west and crossing the entire shelf. Transects were 5 nautical miles apart in latitude, except for some years when the intertransect distance was 10 nautical miles off the Gambian coast. This was not thought to affect the estimation of the mean. As the sampling is regular, the data average is used to estimate population abundance.

The abundance varied greatly among years (Table 2). The coefficients of variations are of similar orders of magnitude. The population mean is well correlated with the maximum value and the low abundance year is associated with a high number of zero values. High densities are not encountered in the same areas each year and the spatial distribution shows no clear time invariant component (Fig. 5).

$Q(T)$ curves do not superpose at the origin and $P(T)$ curves superpose well except for the low abundance year of 1989 (Fig. 6). Space selectivity (concentration) indices for the $P(T)$ curves are close for all years except 1989 which has a higher index (Table 3).

The difference in space selectivity between year 1989 and other years was tested for using the bootstrap test discussed earlier. The relative densities were pooled for all years except 1989. The null hypothesis was that all years except 1989 have a spatial dynamic D2. The index S_{sp} for the pooled data set was estimated by randomly resampling 10 000 pairs of values. This was repeated 1000 times to generate the statistical distribution of the index S_{sp} under the null hypothesis. The distribution was dome shaped and 95% of the values were in the interval [0.71, 0.82] and the average was 0.77. Year 1989 is thought to be significantly different compared to the other years. Also, all other years can be described by dynamic D2.

When changing from a high abundance such as 1993 to a low abundance such as 1989, we observe a decrease in occupied area, a decrease in average density and an increase in the space selectivity of the relative density surface. The dynamics of this change can be represented

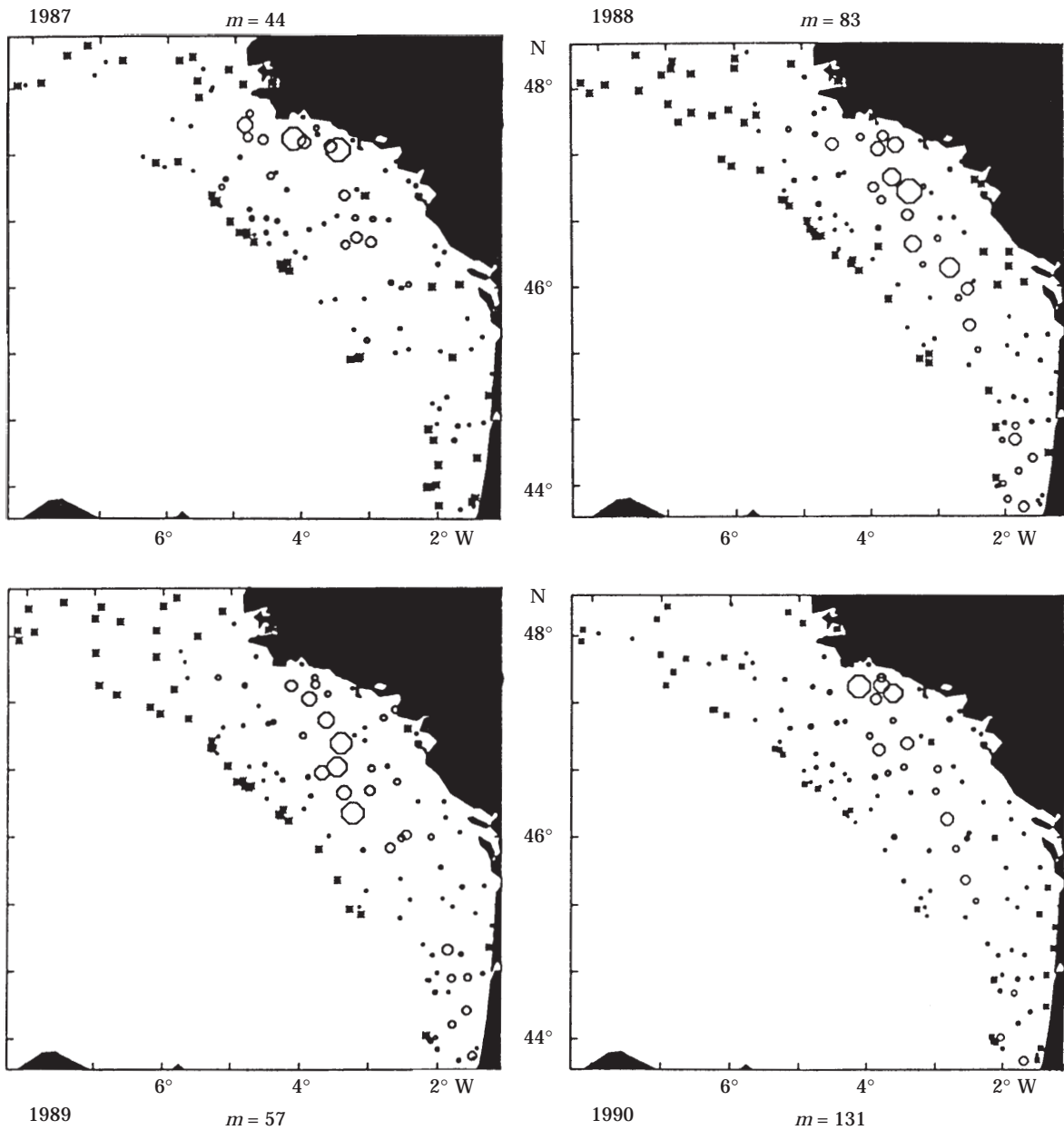


Figure 3. Age-0 hake densities sampled in Biscay Bay. Charts show the relative densities for each year. Circle radius for each value is proportional to fish density divided by the maximum density in the survey. Black squares denote zero values. m denotes the data simple average.

by the dynamic D4 (basin model). Thus the pelagic community shows two states of changes. The spatial distribution varies among high and medium abundance years with dynamic D2. Changes in spatial distribution associated with very low biomass follow dynamic D4.

For the years showing dynamic D2, high values do not appear systematically in the same zones. There is no time invariant spatial distribution of the relative density and the density surface can be modelled by a random

process, $R(x,t)$. Thus the model written with the same notations as previously is given by:

$$Z(x,t) = M_q(t)R(x,t).$$

The same proportion of population biomass will be on the same proportion of total area over the years (dynamic D2) but here these occupied areas are not aggregated in the same manner year after year.

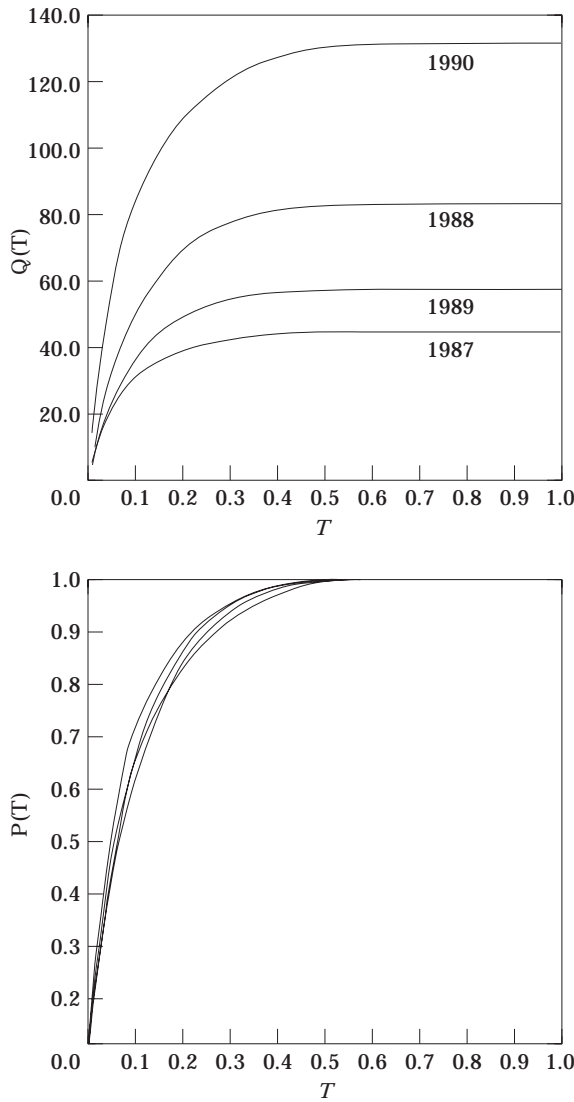


Figure 4. Geostatistical aggregation curves for the hake-0 data in Biscay Bay. Curves $Q(T)$ are scaled to the mean and not the abundance. Units for T and $P(T)$ are percents and kg per 30 min trawl haul for $Q(T)$.

Discussion and conclusion

The curve $P(T)$ is similar to a Lorenz curve $L(z)$ used by Myers and Cadigan (1995). Equations 1 to 6 can be used to estimate $P(T)$ and $L(T)$ but for a $P(T)$ curve, z values are ranked in descending order when they are in ascending order for $L(T)$. The space selectivity index for the $P(T)$ curve, S_{sp} , is similar to the Gini index defined for the $L(T)$ curve used by Myers and Cadigan (1995). Mapping the areas for $P(z)=0.5, \dots, 0.9$ corresponds to the approach used by Swain and Sinclair (1994).

I believe that it is more convenient in fisheries to use the geostatistical $P(T)$ aggregation curve than a Lorenz

Table 2. Basic statistics of pelagic acoustic density south of Dakar, Senegal. Data mean and variance are denoted by m and σ^2 . Number of sample values is n . Density is proportional to the mean acoustic backscatter per square nautical mile of sea surface.

Year	n	m	σ/m	Nb. zeroes	Maximum
1985	1115	139	3.22	3	7303
1986	889	89	2.60	17	3287
1987	967	70	3.29	0	4769
1988	958	97	3.51	2	5626
1989	928	19	3.37	72	1155
1993	804	145	3.17	1	7028

curve. The former approaches the problem by considering the high densities while the latter is conceived with the lowest densities. We are, I believe, more interested by how much abundance exists in high density areas rather than by how much is in low density areas. However, there is no theoretical difference between the two approaches.

In the present paper, the geographical distribution was studied at its largest scale. Starting from assumptions at a small scale between local density, number of shoals and biomass in the shoals, Gauthiez (1997) derives the corresponding Taylor variance-to-mean relations characterizing the spatial distribution at a larger scale. These relate to the dynamics described here. Dynamic D2 can be obtained for a constant number of shoals but a varying biomass in them. Dynamic D3 and D4 apply for a varying number of shoals but the former refers to a constant biomass while the latter characterizes varying biomass in the shoals. Dynamic D1 has a different status. For this dynamic, the spatial distribution is not the result of a selective occupation of the habitat by the population biomass. Rather, the population biomass is the result of local effects. Dynamic D1 could perhaps be more appropriate for the spatial distribution of larval survival.

In addition to time series of abundance indices, monitoring surveys provide useful information on spatio-temporal variability. Plots of density charts for each year and geostatistical aggregation curves provided a simple analysis of the spatio-temporal variability and enabled characterization of changes in the density surface and its histogram associated with changes in the abundance. The analysis lead to a spatio-temporal modelling approach.

In the examples examined, both demersal and pelagic fish showed similar spatial dynamic D2 for medium and high abundances: year after year, the highest values occupied the same proportion of total area and represented the same proportion of total biomass. However, the two examples differed in the yearly variation of the

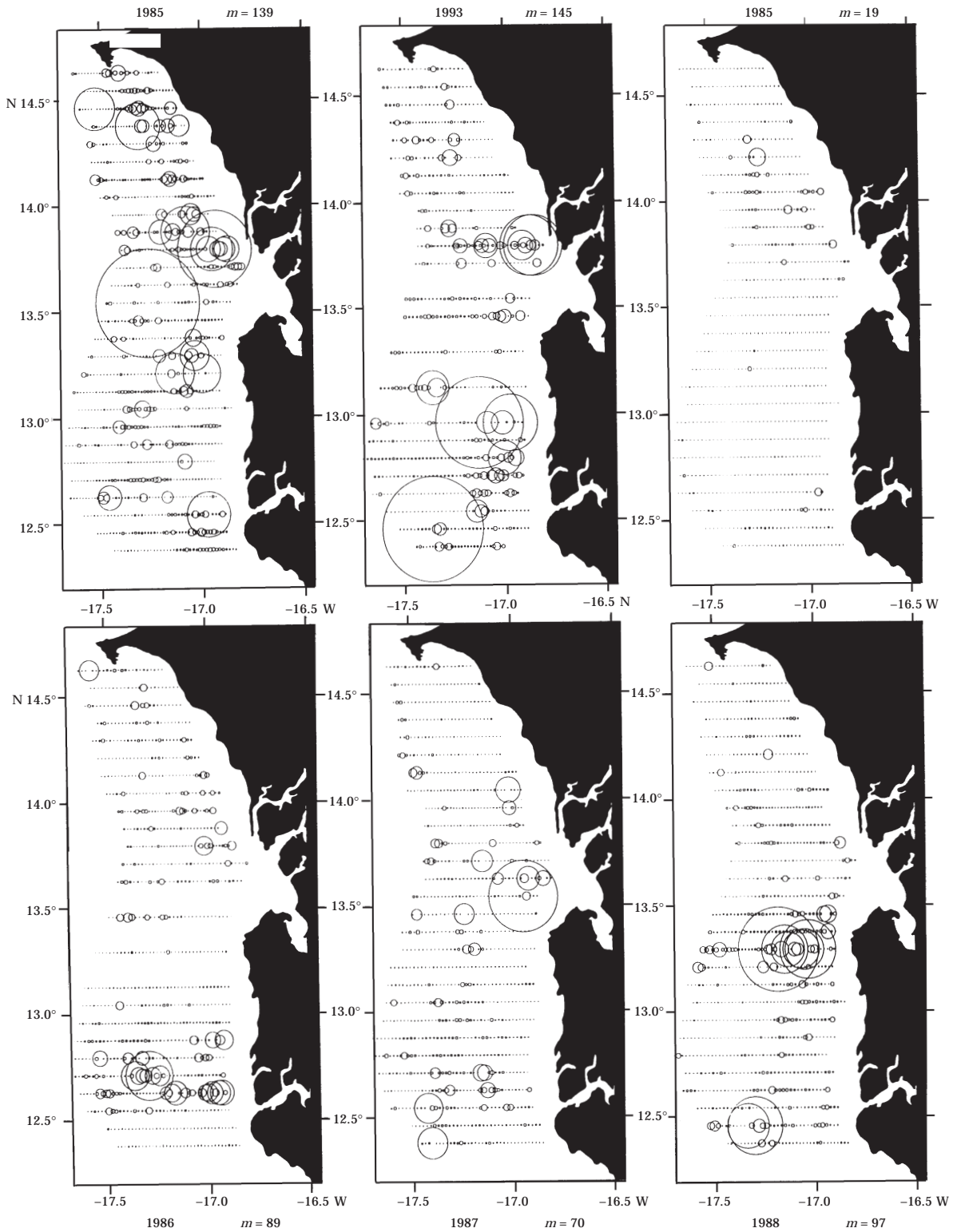


Figure 5. Pelagic echo-integration densities in Southern Senegal, from Dakar to Roxo Cape. Charts show relative densities scaled to a common value for all years. Circle radius for each value is proportional to fish density divided by 1500 echo integration units. m denotes the data sample average.

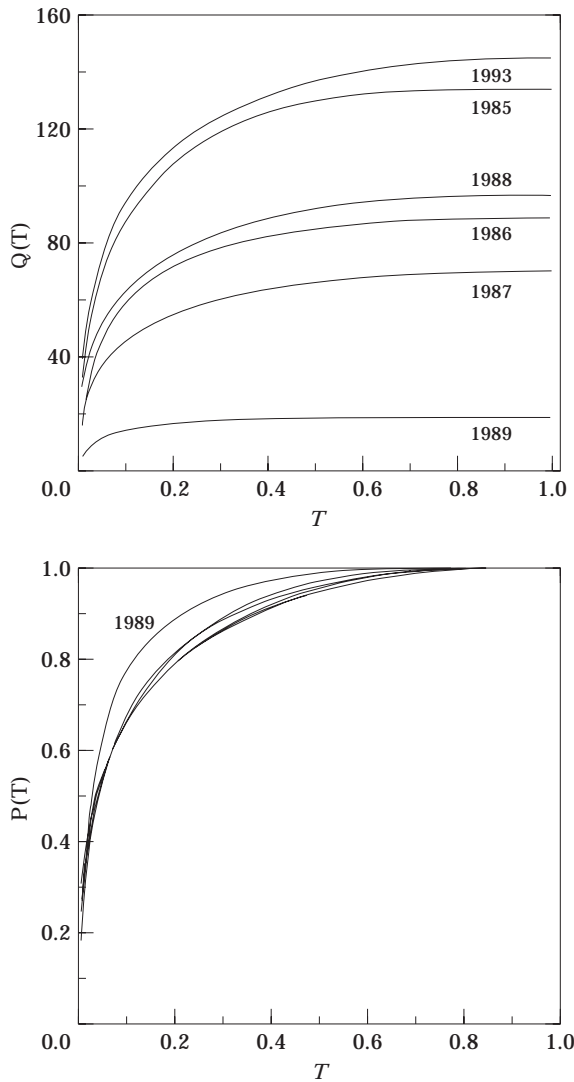


Figure 6. Geostatistical aggregation curves for the Senegalese pelagic data. $Q(T)$ curves are scaled to the mean and not the abundance. Units for T and $P(T)$ are percents and echo-integration units per square nautical mile for $Q(T)$.

Table 3. Space selectivity index S_{sp} of curves $P(T)$ for the Senegalese pelagic densities. $S_{sp} = 2 \int_0^1 P(T) dT - 1$. Units for S_{sp} are square percents.

Year	1985	1986	1987	1988	1989	1993
Index S_{sp}	0.78	0.77	0.75	0.76	0.84	0.75

density map. The spatial distribution of young hake is influenced by the distribution of muddy bottoms which have fixed location and area over the years. This generates a time invariant dome shaped component in

the fish spatial distribution. It is believed that the pelagic fish distribution is determined by a fixed relation with hydrographic and plankton parameters. But as the spatial organization of the pelagic habitat varies between years and within a season (e.g. wind induced upwelling), the fish spatial distribution varies. A switch in the spatial dynamic occurred in the pelagic data set when surveyed abundance was very low. This was reflected in an increase in the space selectivity of the relative histogram. Such a drop in surveyed abundance was not observed in the young hake data set and it is not known whether such a switch would also happen for hake at lower abundance.

In interpreting CPUE data, knowledge of variations in both the fish spatial distribution and fishing tactic are needed. Do the fishermen change their way of working and cooperating when the fish density surface changes with stock size? In particular, if fishermen develop a fleet tactic with increased cooperation between boats when occupied area has contracted at low stock size, fishing mortality can be greatly increased (Paloheimo and Dickie, 1964; Ulltang, 1980). But if a given fishing fleet samples the fish density histogram with a time invariant process, then CPUE will depend only on the fish spatial dynamic. Observations in tropical semi-industrial purse seine fisheries indicate that this last case may be occurring. Fréon (1991) and Marchal (1993) reported variations in the catch per seine haul between years and within a season, for the Senegalese and Ivorian purse seine fisheries of *Sardinella* sp. They argue that fishermen preferentially capture those schools that have a biomass larger than a given threshold and that fishermen seem to lower this threshold when big schools are too sparse. In these fisheries, schools are seen at the sea surface, then selected and captured. Also, technical constraints restrict major changes in fishing tactic as boats cannot stay at sea long and have limited storage capacity and communication facilities. If we consider a fish spatial dynamic of type D2 (constant relative histogram) and a fishing process that does not change (for example, fishermen exploit the 5% right tail of the density histogram resulting in an exploitation threshold that depends on population biomass), then CPUE data can be used to construct a time series of comparable abundance indices.

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