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# SPATIAL STRATEGIES OF FISH POPULATIONS

by

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By spatial strategy we mean the relation between local density and population abundance. How does the fish density surface changes over the years when the population abundance varies? This question is thought critical because the relevant use of c.p.u.e. data as abundance indexes over the years depends on the type of strategy as the fishing effort is not homogeneously applied in space.

Three models are proposed to characterize how the density surface may change when population abundance varies. Geostatistical selectivity curves are used and a simple test is given in order to determine which model to choose. Such investigation is applied on two spatio-temporal series of monitoring surveys. One is made of bottom trawl surveys. The other concerns pelagic echointegration surveys.

Relatively to the population mean, the bottom trawl survey data show time invariant characteristics of the relative histogram and of the relative density surface. The local densities are thus related to the population abundance. Relatively to the population mean, the acoustic pelagic data show a great variability of the relative density surfaces. The relative histogram is time invariant only for medium and high population abundance. The relative histogram for low population abundance is skewer.

It is argued that the fishing effort is applied specifically on the tail of the population histogram of fish densities. Thus an abundance index estimated from c.p.u.e. data will be biased in the case of low pelagic abundance. The use of the histogram of fish density as estimated from monitoring scientific surveys is discussed for correcting such bias.

This study gives arguments to think that the values of local densities are influenced by the value of the global abundance. Thus a population has a specific strategy for occupying its habitat.

INTRODUCTION

Consider the fish spatial distribution as a density surface in a given area. The density surface can be interprated as a realisation on the area, of a process that has a spatial structure and an histogram. Scientific surveys that sample homogeneously over the entire surface enable to estimate the statistical and geostatistical characteristics of the density surface. But the fishing effort at sea is preferentially applied on high fish densities that fishermen encounter. Thus c.p.u.e. data integrated over time are relevant of the histogram tail of densities and of local spatial means. Can these data be used to built population abundance indexes? This raises the question of how high and low values are related in their proportions and how these vary when the population mean varies.

Consider that the catch in a trawl tow or in a purse seine is proportional to what was in the sea. We write: $d(x,t) = \dfrac{c(x,t)}{q\,f(x,t)}$, where c is the catch at point x and time t, f is the fishing effort, q is the catchability and d the fish density in the sea. The catchability q may vary with space, time, fish density, environmental conditions... We shall consider that q is constant. This to exhibit the consequences of an inhomogeneous application of fishing effort in space. If f was applied homogeneously over the area of fish presence, then the integration of c over space and time could serve to estimate the population abundance. But if we consider that f is selectively applied in specific sub areas and selectively applied on the tail of the histogram of fish densities, we can use c.p.u.e. data to estimate total population parameters only if we can characterize how the density histogram varies when the population mean varies and/or how the spatial distribution varies when the population mean varies.

Mac Call (1976) and Ulltang (1980) have investigated the relation between biomass and catch for pelagic stocks and have shown that the catch may increase when the biomass decreases. In their studies the term catchability was used to define a resulting global parameter, the way the fish population lets itself be caught by the fishing fleet. Thus what these authors call catchability includes three major components, a technical component (the efficiency of the gear), a behavioural component (the behaviour of the fish in front of the gear) and a spatial component (the spatial structuring of the fish densities). In the previous formula catchability refered to the behavioural component. We believe that the spatial component has a major effect on the final catchability. We shall characterize different types of spatial strategies of the fish and their possible consequences in the use of c.p.u.e. data for estimating abundance indexes.

## I- GEOSTATISTICAL SELECTIVITY CURVES AND SPATIAL STRATEGIES

Spatial heterogeneity can be measured by the skewness of the histogram of densities. We want ot study how the histogram varies in shape when the mean varies. But monitoring surveys provide histograms with different means and variances which are not easily comparable because of the effect of the variance on the mean. To compare the shapes of histograms with different means and variances we use the geostatistical selectivity curves (Matheron 1981, Lantuéjoul 1990). These enable to characterize three types of relation between spatial heterogeneity and population abundance.

### 1.2. SELECTIVITY CURVES, Q(T), P(T):

Let z(x) denote the fish density at point x. The set ($z(x_1)$, ..., $z(x_n)$, ...) is a realisation of a random function Z. Let m be the mean of Z and F(z) the cumulative frequency curve of Z: $E(Z) = m\,;\ F(z) = \mathrm{Prob}(Z \le z)$ where z is a threshold value of the density z(x).

T(z) denotes the surface where Z takes values greater than z: $T(z) = \int_z^{\infty} dF(u) = E(1_{Z\geq z}) = 1 - F(z)$.

(In mining studies, T(z) represents is a tonnage, thus the letter T for denoting what is here a surface). Q(z) denotes the fish quantity that is standing on the surface T(z): $Q(z) = \int_z^{+\infty} u\,dF(u) = E(Z\,1_{Z\geq z})$. The graph Q(T) gives the cumulative integrated fish quantity Q(z) as a function of the occupied surface T(z). Q(z) varies between 0 and m; T(z) varies between 0 and 1. (Fig.1)

The concavity of the curve Q(T) is a parameter that is analogous to the skewness of the density histogram. The hatched area that separates on Figure 1 the curve Q(T) from the diagonal mT is called the selectivity S: $S = 2\int_0^1 (Q(T) - mT)dT = \int_0^{+\infty} F(u)(1-F(u))du$. The selectivity is a measure of the concavity of Q(T). The selectivity is a dispersion parameter but has two advantages in comparison to the variance. First, S may characterize the dispersion of a process that has no variance (infinite variance). Second, S is less sensitive in practice to the high density values.

Let F1 and F2 be two cumulative frequency curves that have the same mean. The associated selectivity curves Q1(T) and Q2(T) enable to rank the dispersions of F2 and F1:

F2 is said more selective than F1 if: $Q_2(T) > Q_1(T), \forall T \in [0,1]$

Consider two years, 1 and 2, where the spatial dispersions differ but the not the population means. The sentence "year 2 is more selective than year 1" means that on any surface T(z) the fish quantity in year 2 is higher than in year 1. When years have different means, we may compute P(T) curves where P(z) is defined by: $P(z) = \frac{Q(T)}{m}$. P(z) represents the percentage of the population abundance that is standing on the percentage T(z) of total surface. T(z) is defined by the densities greater than z.

The curves Q(T) and P(T) are easily computed as follows. For each survey, rank the data in descending order. Then compute for each threshold $z_p$: $Q(z_p) = \sum_{i=p}^{n} \frac{n_i}{n} z_i$ ; $P(z_p) = \frac{Q(z_p)}{m}$; $T(z_i) = \sum_{i=p}^{n} \frac{n_i}{n}$ , with $n_i$ being the number of data in class i, n the number of data in the survey, $z_i$ the mean of class i.

## 1.2. SPATIAL STRATEGIES

The variations in shapes of the Q(T) and P(T) curves associated with variations of the population abundance enable to characterize what we here call strategies for the occupation of space. Three different spatial strategies are thought of and characterized by the selectivity curves.

Strategy 1:

The increase of population abundance is associated with an increase of fish density in one (or several) specific sub zone(s) and the other densities elsewhere do not vary. The total area of fish presence stays constant. Some years the habitat gets permissive in some areas and these allow very high densities. This is thought to be a spatial version of Cushing's match/mismatch larval survival hypothesis (Cushing 1972). This type of strategy could be interprated by a lognormal model: the medium stays constant and the increase in the arithmetic mean is due to an increase in the logarithmic variance.

Strategy 3:

The density in the area of fish presence stays constant whatever the population abundance. When the population abundance varies, the surface over which the population is present varies consequently. This situation is inspired by the one observed by Iles et al. (1982) on herring spawning grounds: the bigger the spawning area the bigger the larval population. The reduction of the area of fish presence has also been observed for low stock sizes in pelagic stocks of herring and anchovies (Mac Call 1976, Ulltang 1980).

Strategy 2:

Here the total area of fish presence stays constant. When the population abundance increases all point densities increase but the contribution of each local density to the population mean stays constant. Myers et al. (1989) have observed a similar strategy on gadoids in the north sea. Houghton (1987) names it consistent spatial pattern.

Figure 2 explains the test for distinguishing between the three strategies. Two years are represented, one where the abundance is low (year 1) and one where the abundance is high (year 2). For strategy (S2) the curves Q(T) are strictly proportional as the relative densities $\frac{z(x)}{m}$ stay constant when m varies. The curves P(T) thus superpose. For strategy (S3) the curves Q(T) superpose at the origin as the density on the habitat stays constant when m varies. For strategy (S1) neither curves Q(T) nor the curves P(T) superpose. The strategies (S1) and (S2) can be distinguished on the curves P(T). For strategy (S1), the low abundance year is less selective where as for strategy (S3) it is the high abundance year that is less selective.

The selectivity curves enable to characterize easily the variations of the histogram shape when the population mean varies but they do not enable to characterize changes in the spatial distribution and in the spatial structure of the densities. In addition to the selectivity curves we shall produce maps of fish density.

## II- SPATIAL STRATEGY OF HAKE-0 IN THE BAY OF BISCAY

Since 1987 IFREMER has carried out yearly monitoring bottom trawl surveys in the bay of Biscay to map and assess the groundfish resources in that area. Details on the program (EVHOE) and on its realisation can be found in Poulard (1990). We shall be concerned by the age class 0 of Hake (Merluccius merluccius) during the autumn surveys as the young fish can be considered fully recruited on the nursery grounds in autumn. The nursery grounds are known to be muddy and sandy sediments particularly in the north of the Bay (Dardignac 1988) where there is a great muddy bank. Age was defined by length. The youngs of Hake were considered of the 0-year class when their length was lower than 19cm. This is the maximum length encountered by Guichet (1988) for 0 year classes.

The sampling is performed according to a random stratified scheme where depth and latitude define the strata limits and where the number of trawl stations per strata is proportional to the strata surface. We therefore consider that the scheme disperses homogeneously the trawl stations over the entire surface of the bay so that the simple average of the data for each survey is used as the population mean estimate for that year. The fish density we work on is the number of individuals of Hake-0 per 30 minutes trawl tow.

The basic statistics are:

| Year | Nb. trawl stations | simple average, m | coeff. variation, $\sigma / m$ |
|---|---|---|---|
| 1987 | 131 | 44 | 2.41 |
| 1988 | 142 | 83 | 2.07 |
| 1989 | 134 | 57 | 1.97 |
| 1990 | 136 | 131 | 2.16 |

The abundance varies from a factor 3 at the most during the four years. The relative dispersions measured by the coefficient of variation (standart deviation over mean) are of the same order of magnitude.

Figure 3 shows the proportional representations of the data in space for each year. Each representation is scaled by the maximum value for that year. The maximum value in each year is represented by a circle of a fixed radius. All the other values for that year are represented by circles whose radii are deduced by proportionality to the maximum: $r_i = \frac{z_i}{z_{\max}} r_{\max}$, where $r_i$ is the radius of the circle representing the value $z_i$. Zero values are represented by stars. The spatial distributions are very similar over the years. In particular the high densities are localized in the same areas of the northern part of Biscay between 48N and 46N where the regionalisation is domy shaped.

The selectivity curves Q(T) and P(T) are computed and shown on Figure 4. The curves Q(T) are not superposed at the origin and the curves P(T) are very close to each other. Hake-0 shows a strategy of type (S2). Whatever the total quantity, the relative histogram stays constant, the same percentage (in number) of the year class occupies the same percentage (in surface) of the bay of Biscay.

Relatively to the year total, the young fishes occupy the same grounds each year and are dispersed on the grounds in the same way. Thus the spatio-temporal variability can be modeled as follows:
$\frac{Z(x,t)}{M_q(t)} = M_w(x) + R(x,t)$, where Z(x,t) is the density at point x and year t, Mq(t) is the population mean of year t, Mw(x) is the time invariant expected relative density at point x and R(x,t) are the residuals.

The spatial strategy characterized here is one in which the local densities are linked to the total abundance in the same way each year whatever this abundance. Thus even if the fishing effort is applied specifically on one part of the histogram of densities or in one sub area , c.p.u.e. data will give comparable indexes of abundance over the years. More over, as the relative density surface is time invariant, a spatial managment of the resource can be thought about.

Petitgas (1991) estimated $M_W(x)$. A variogram for each year was computed and a map for each year was derived by kriging. The interpolation grid was the same for each year, with say a mesh size of a. Then for each point of the grid, the kriged value, $z^k(x,t)$, was divided by the estimated population abundance, $a\sum_x z^k(x,t)$.

Then at each point, averages of these percentages were computed over time: $M^*_w(x) = \frac{1}{n_t}\sum_t \frac{z^k(x,t)}{a\sum_x z^k(x,t)}$.

Figure 5a shows a map of the estimated time invariant relative density surface. Figure 5b shows the area T(z) corresponding to a P(T) of 80%. Figure 5b shows the area where 80% of the year class stands each year, whatever the strength of that year class. The zone has been superposed on the great muddy sediment bank of north Biscay. The correspondance is clear.

When the variance of the residuals R(x,t) calculated in time at each point x is a function of $M_W(x)$, then the model can be factorized and gives a GLM model. If: $R(x,t) = a\, M_W(x) + Y(x,t)$ then: $Z(x,t) = M_q(t)\, M_W(x)\, U(x,t)$ with $U(x,t) = 1 + a\, Y(x,t)$. Such situation was characterized by Petitgas (1991) on a sery of monitoring icthyoplanktonic surveys for stage-1 sole eggs in the bay of Biscay (program SOLDET of IFREMER, Koutsikopoulos 1991). The residuals U(x,t) showed a well structured variogram but not interaction between time and space (cross variograms between maps of U were flat).

## III- SPATIAL STRATEGY OF PELAGIC FISH IN SENEGAL

Since 1984, the senegalese oceanographic research center, CRODT, has carried out in cooperation with ORSTOM, yearly monitoring acoustic surveys of the pelagic resources on the continental shelf of Senegal and Gambia by means of the echo-integration technique. Details about the monitoring program (ECHOSAR), the acoustic instrumentation can be found in the survey technical reports, for example in Levenez, Samb et al. (1985).

The calibration and the equipment adjustments were the same for each year thus the echo integrated values are directly comparable between surveys. No specie identification of the echoes was performed. The data are mean backscattering echo energy per nautical mile square of sea surface. They are converted to fish density units by using the same arbitary TS every year. The elementary distance sampling unit along the transects (ESDU) is 1 nautical mile. Day and night values are used together without corrections as it is assumed that there are similar percentages of night and day data each year and that high density areas are not systematically sampled during day or night for some years.

South of Cap Vert the sampling is performed along E-W transects 5 degrees apart in latitutde. Some years the inter transect distance is 10 degrees in latitude in front of the Gambian coast. As the sampling is regular, the simple average of the data is used to estimate the population abundance.

The basic statistics are:

| Year | Nb.data | m | $\sigma$/m | Nb.zeroes | max |
|---|---|---|---|---|---|
| 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 |

The abundances vary greatly between years. The greater difference is by a factor of 7.6. The coefficient of variations are of similar orders of magnitude and are useless here to characterize differences in dispersion. The population mean is well correlated with the value of the maximum. The low abundance year is associated with a high percentage of zeroes.

The Figures 6,7 show the proportional representations of the data in space for each year. Each representation is scaled to the value 1500 to ensure good visibility. The radius of the circle representing the value 1500 is fixed for all surveys, $r_{ref}$. The radius representing the value $z_i$ is given by: $r_i = \frac{z_i}{1500} r_{ref}$ .Here, the high densitites are not encountered in the same areas year after year. The spatial distribution does not show a time invariant component.

The selectivity curves are shown on Figure 8. The curves Q(T) do not superpose. The curves P(T) superpose well excepted for the low abundance year 1989. This low abundance year 1989 shows a relative density surface that is more selective than for any other year. All the other years can be characterized by the strategy (S2). The selectivity of the curves P(T) was computed: the values are very close for all years exepted for 1989 where the selectivity is higher.

| Year | 1985 | 1986 | 1987 | 1988 | 1989 | 1993 |
|---|---|---|---|---|---|---|
| Selectivity of P(T) | 0.78 | 0.77 | 0.75 | 0.76 | 0.84 | 0.75 |

The pelagic community south of Cap Vert exhibits a strategy of type (S2) for medium and high population abundances. For low population abundance, the few high values occupy a small surface and represent a great percentage of the population abundance thus the biomass is much more concentrated in space. When changing from a low abundance year such as 1989 to a high abundance year such as 1993, we observe an increase in occupied surface and an increase in the mean density over this surface. The strategy is a mixed one between S(3) and (S1).

When the population has a medium abundance that does not vary more than by a factor of 3 (values in the range 50-150), the relative histogram stays constant (P(T) curves superpose). Thus local densities are linked to the global abundance in the same way, whatever the abundance. Even if the fishing effort is applied on the tail of the density histogram, this tail will represent the same percentage of the total biomass year after year and c.p.u.e. data give indexes of abundance that can be compared. But for low abundance the spatial strategy is different. The high values integrated over the space they occupy represent a greater percentage of the total biomass than for other years. There is in this case a real risk that c.p.u.e. data overestimate the abundance.

The use of the geostatistical selectivity curve P(T) could help correct for this bias. But more information is needed on the fishing strategy of the fishermen because this approach requires the knowledge of the threshold under which fishermen do not operate. Fréon (1991) has observed that this threshlod varies in the senegalese pelagic fishery. Marchal (1993) has shown that this threshold diminishes during the ivoirian fishing season as if the fishing fleet was progressively exploiting the histogram starting from the tail.

In space, the high values do not appear systematically in the same zones. Thus the model for the years showing strategy (S2) is: $\frac{Z(x,t)}{M_q(t)} = R(x,t)$ , the notations being the same as previously in section II. There is no time invariant spatial distribution of the relative densities. Any given percentage of total surface will hold the same percentage of the total abundance over the years (strategy (S2)) but here, these occupied areas are not agregated in the same manner year after year.

## DISCUSSION AND CONCLUSION

The interaction between the spatial distribution of the fish densities and the spatial distribution of the fishing effort may introduce bias when estimating with c.p.u.e. data the time sery of population abundance over the years.

The geostatistical selectivity curves derived from monitoring survey data enable to characterize the way the population disperses its densitites when occupying space. It turns out from the examples examined that both groundfish and pelagic fish show similar strategies for medium and high population abundances: year after year, the same percentage of total biomass occupies the same percentage of space. Thus, even if the fishermen go for the high values and apply the fishing effort on the histogram tail of the densities, the c.p.u.e data should provide reliable and comparable indexes of abundance through time.

The risk of bias in the estimation of population abundance form c.p.u.e. data arises for low population abundance. Such case has been observed here only for the pelagic data set. The selectivity curves P(T) could help correct for this bias but more knowledge is presently needed on the fishing strategy itself for performing this correction.

The difference observed between groundfish and pelagic fish spatial strategies is in the temporal variability of the spatial distribution of the relative densities. The spatial distribution of the young hake is determined by the relation of the fish with the muddy sediments. These have a fixed location over the years. This generates a time invariant domy shaped component in the spatial distribution of the fish. We believe that the pelagic fish distribution is determined by a fixed relation with hydrographic parameters. But as the regionalisation of these vary greatly in time, the spatial distribution of the fish varies.

Such study needs to be made on other fish populations in different waters in order to see wether the superposition of the P(T) curves in a certain range of population abundances is a general rule for both pelagic and groundfish populations. If this was true, this would mean that in any population, the local density is influenced by the value of the global abundance and not only by the immediat local environmental factors.

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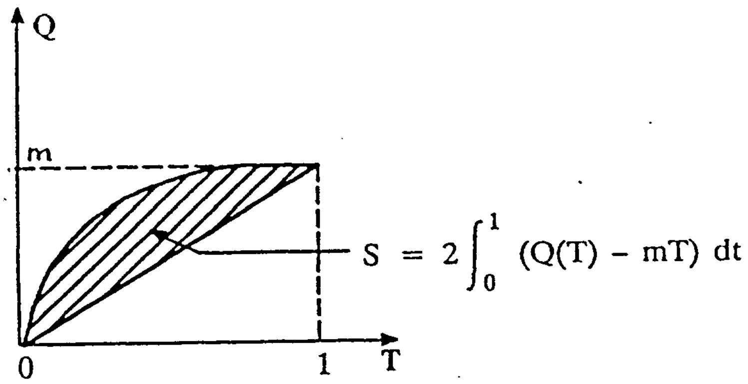


Geostatistical selectivity curve Q(T)

Fig. 1

# SPATIAL STRATEGIES AND SELECTIVITY CURVES

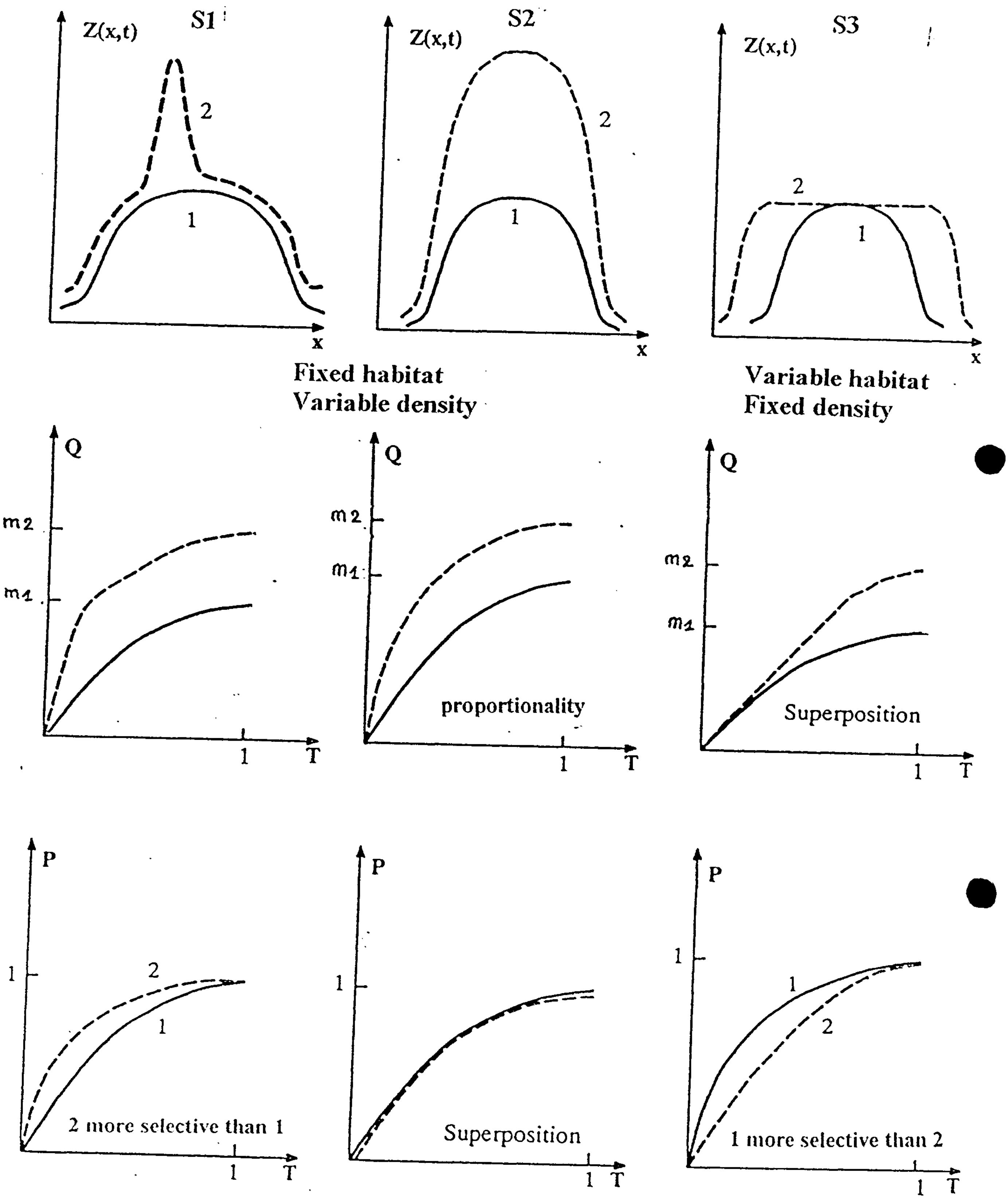
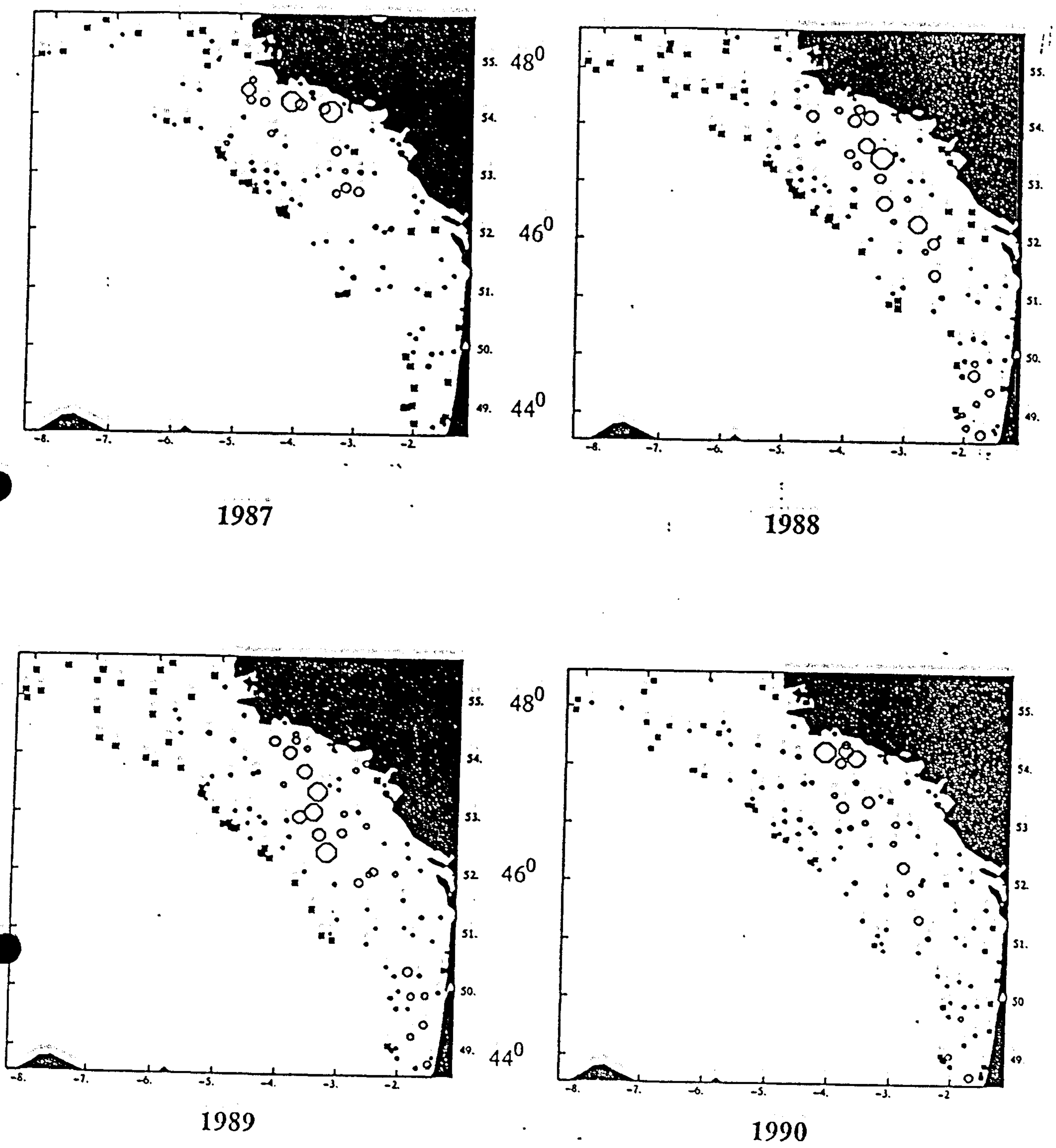


Fig. 2



1987

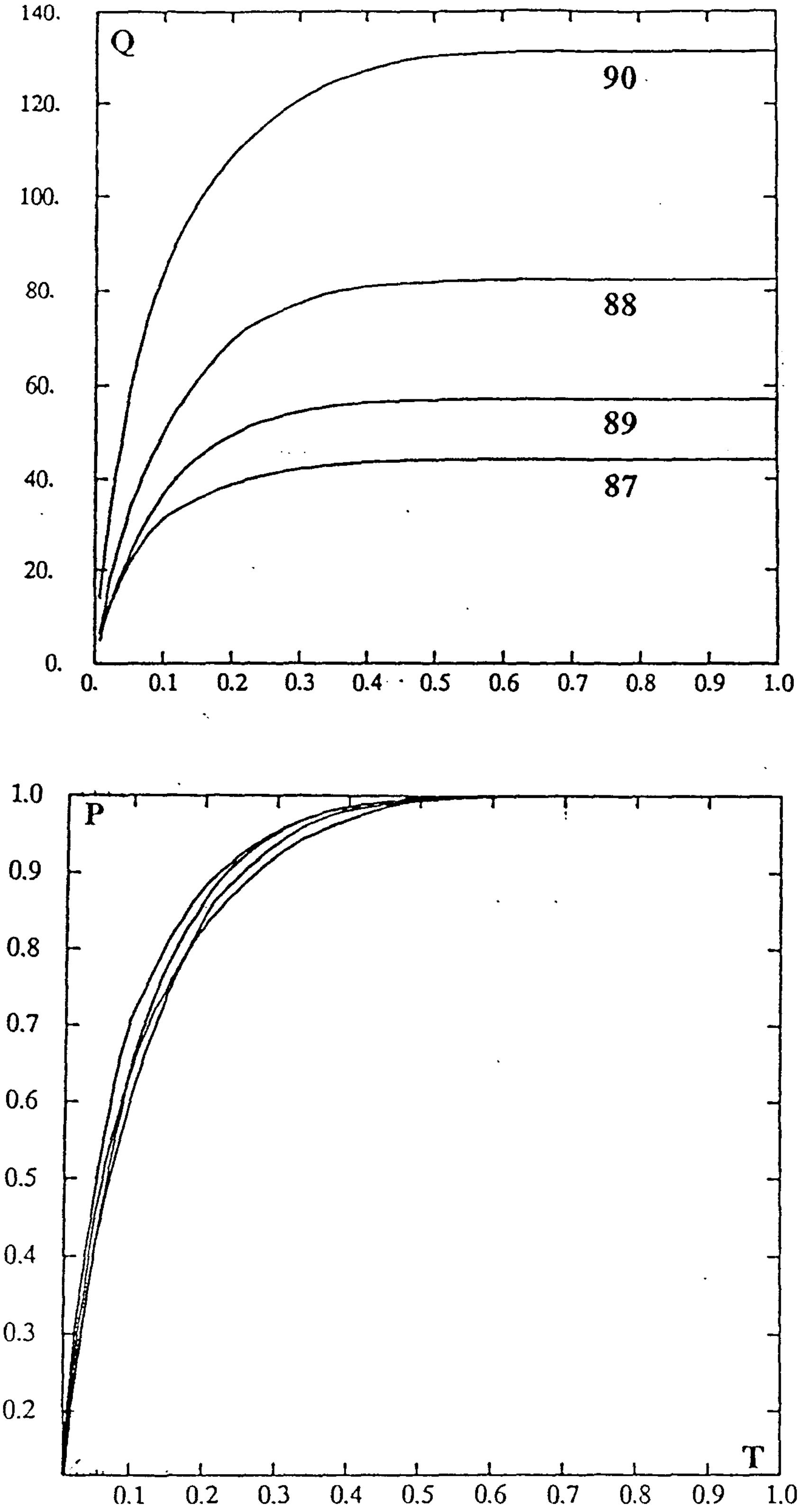
1988

1989

1990

Proportional representation of sampled Hake-0 densities in the Bay of Biscay

Fig 3



Selectivity curves for the Hake-0 data in Biscay Bay

Fig 4

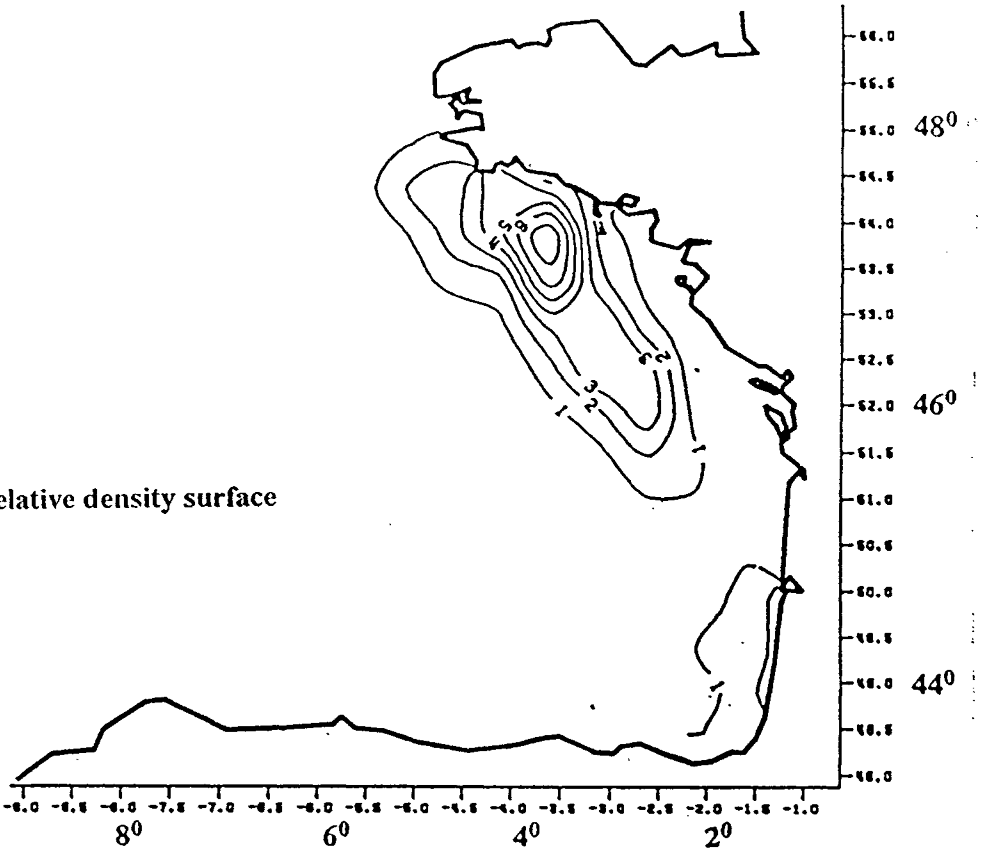


Fig 5a

Map of the time invariant relative density surface of Hake-0 in Biscay Bay

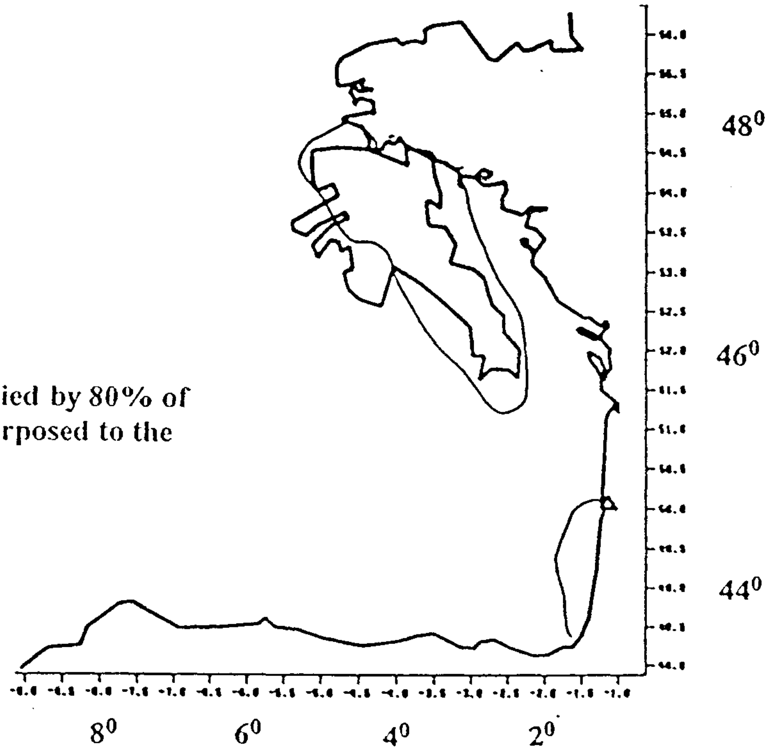
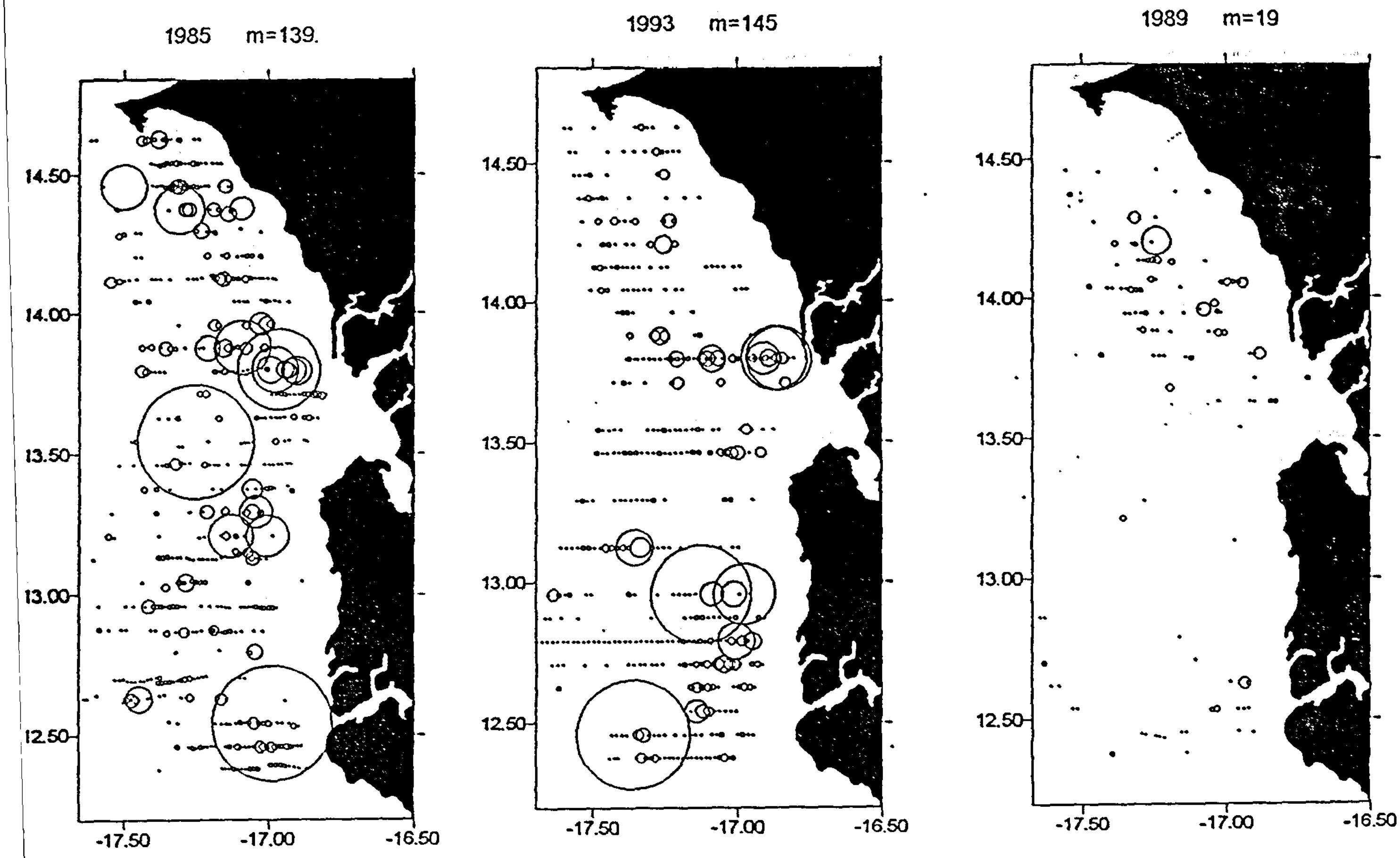


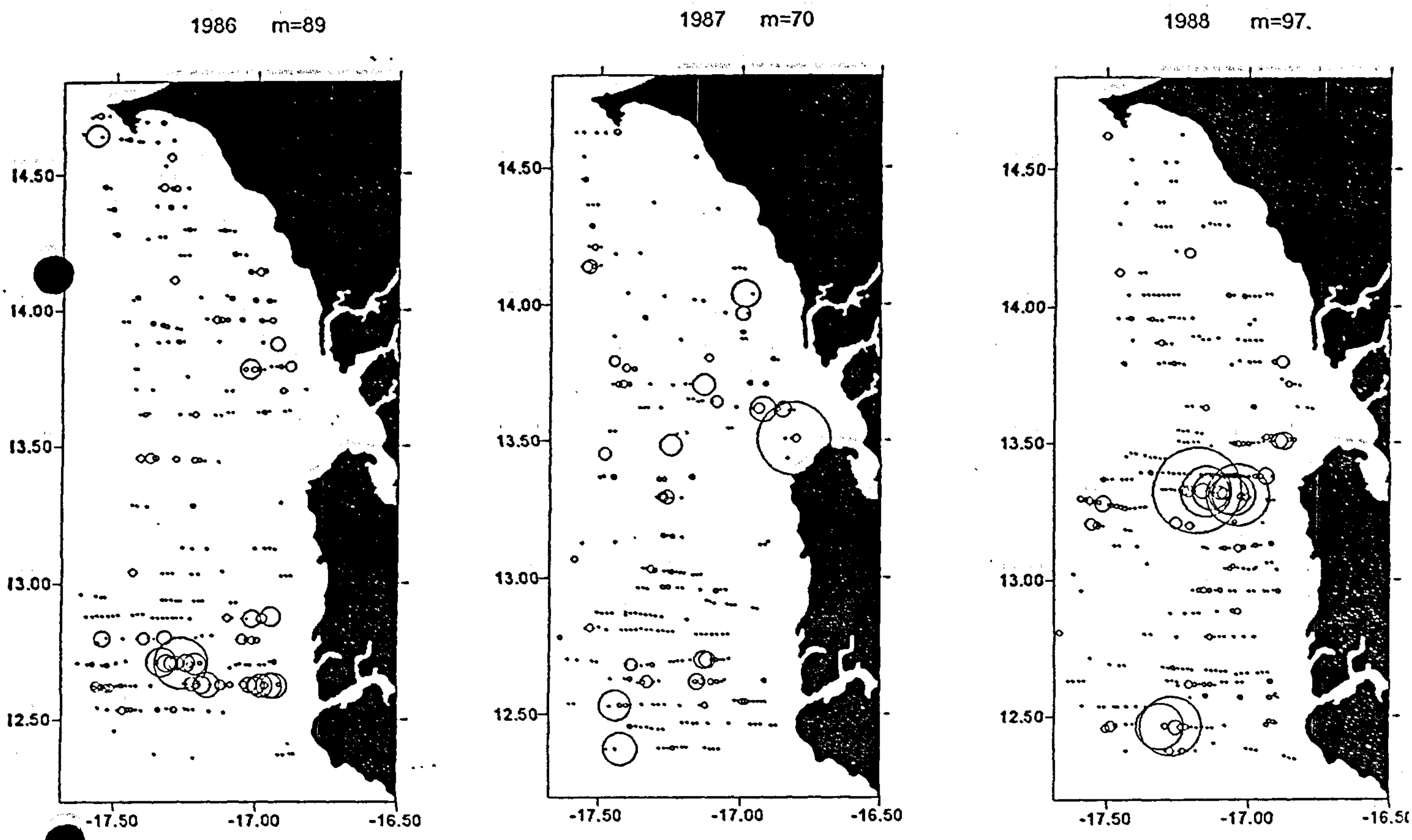
Fig 5b

Representation of the average surface occupied by 80% of the year class-0 of Hake. The surface is superposed to the great muddy bank of Biscay bay.



Proportional representation of pelagic echointegration values
from Cap Vert to Cap Roxo.
Bare areas are areas of zeroe or very low values.

Fig. 6



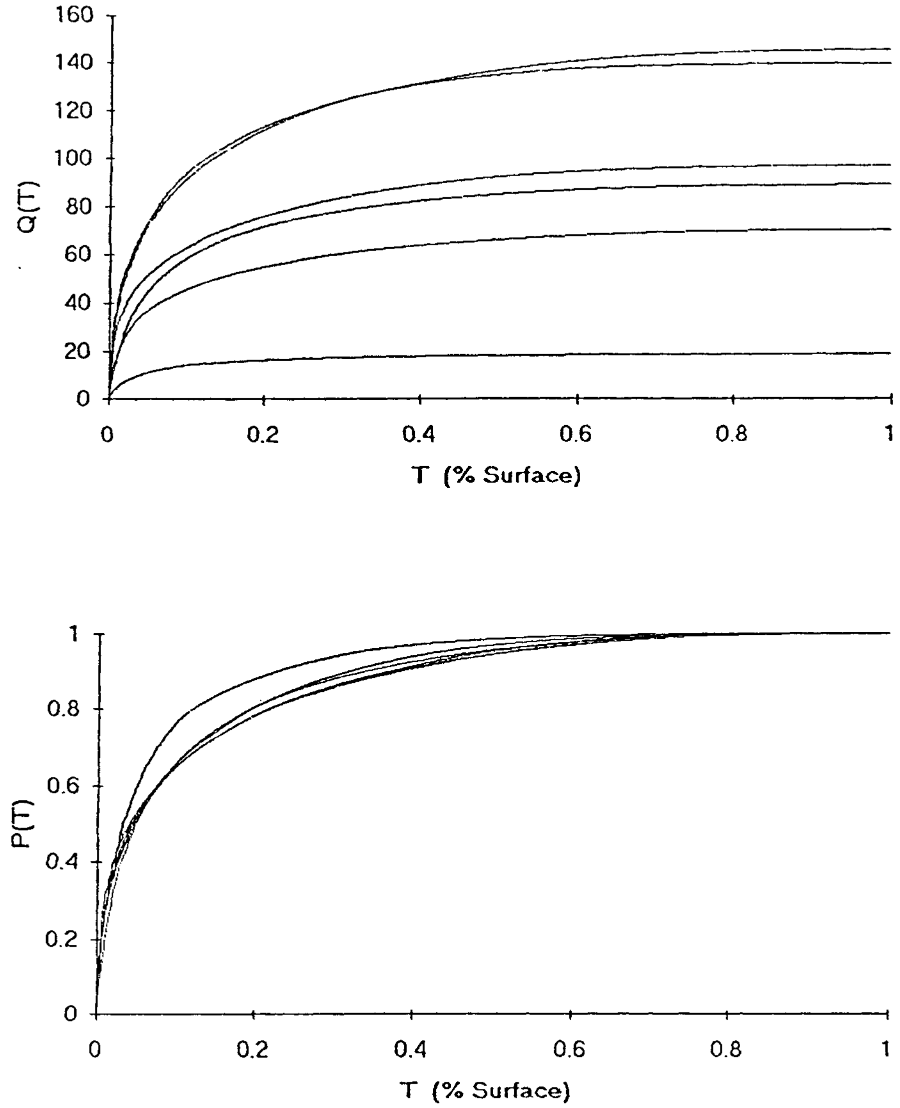
1986 m=89

1987 m=70

1988 m=97.

Proportional representation of pelagic echointegration values
from Cap Vert to Cap Roxo.
Bare areas are areas of zeroe or very low densities

Fig 7



Selectivity curves for the pelagic acoustic senegalese data

Fig. 8