Relationships between population spatial occupation and population dynamics

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Abstract

Population dynamics is commonly described non-spatially using parameters of population demography and vital traits. Population spatial organisation is therefore considered implicit and its importance in the population dynamics ignored. The present study evidences on a variety of stocks correlation between population spatial distribution indices, population abundance, recruitment and mortality. Series of research fisheries monitoring surveys were considered for a range of different stocks (cod, herring, anchovy, hake, mullet) in different regions of the North East Atlantic and Mediterranean (North Sea, Barents Sea, Baltic Sea, Bay of Biscay, Tyrrhenian Sea, Ionian Sea and Aegean Sea). For each population, each age and each year, 9 spatial indices were computed that characterised the spatial distribution in their centre of gravity, inertia, anisotropy, extension areas, number of patches and microscale structure. For each population and age, spatial indices were linearly regressed on the abundance, on the following recruitment, and on the mortality residuals (as a constant mortality has been fitted on cohort curves). A meta-analysis table was constructed that showed the number of times that correlations were significant. The result is that spatial indices provide additional indicators for assessing population status and could be helpful in the context of stock decline and habitat loss.

Key words: spatial indices; population dynamics, meta-analysis.

1. Introduction

Fishing has induced depletion on most exploited marine resources. Over fishing and overexploitation are now frequently encountered. The sustainability has become a key issue for the future of the world fisheries (Pauly, 2002). In that context, fisheries management based on single-species stock assessment has revealed limitations; one of them is that they have failed in a few important cases involving rapid stock decline. In particular, for the northern cod, *Gadus morhua*, off Newfoundland and Labrador, they have led us grossly underestimate the severity of the decline and the increasing impacts of fishing during the decline (Walters, 1996).

However, the scientific surveys would have been able to perceive this change. They are known to be an efficient means for monitoring species and understanding its temporal and spatial dynamics. But, the scientific surveys data are aggregated to form indices of relative

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abundance for stock assessments purposes. And the spatial dynamics of the resource is not used in the assessment process. With a better use, such data should have shown that cod collapse was associated with clearly defined spatial and temporal changes in density and biomass since 1989 (deYoung and Rose, 1993) and may have been prevented.

In this paper, we are looking for relationship between spatial indices that captures spatial pattern of European stocks and parameters of its dynamics in order to identify new indicators for assessment purposes.

2. Material and methods

2.1 Data surveys

Series of research fisheries monitoring surveys were analysed. For this study, 10 surveys were available which were carried out in different regions of the North East Atlantic and Mediterranean (North Sea, Barents Sea, Eastern Baltic Sea, Bay of Biscay, Tyrrhenian Sea, Ionian Sea and Aegean Sea).

Location and main characteristics of the surveys are found in Figure 1 and Table 1. The studied surveys were at once bottom trawl surveys and acoustic surveys. Stocks were of demersals (cod, hake and red mullet) and of small pelagics (herring and anchovy). Survey data series have produced numbers at age at sample location needed for the computation of the spatial indices and the population dynamics parameters. Most of the bottom trawls surveys follow known protocols: EVHOE series for Biscay hake (ICES, 1997; Poulard et al., 2003; Souissi et al., 2001), IBTS series for North Sea cod, MEDITS series for Central-Southern Mediterranean red mullet and hake of the Greek Seas (Bertrand et al., 2002). One can notice that red mullet population has been subdivided in two parts due to strait of Messina.

Concerning the acoustic surveys, Data have been treated in two different ways. Data from North Sea herring have been supplied by the North Sea acoustic survey (since 1989) and numbers at age have been aggregated by ICES statistical rectangle for each year, whereas they were available for every sailed nautical mile (ESDU) for the data from the Biscay anchovy supplied by the PELGAS acoustic survey series.

Table 2 presents the available ages collected during the surveys of each fish stocks. It also shows the corresponding ages or proportions of age used to determine the representative life stage (i.e. recruits, immatures, matures). Ogives of maturity at age were used when they were available.

2.2 Spatial indices

A series of spatial indices have been chosen to capture the spatial pattern of a population in a simple manner (Woillez *et al.*, 2005). Indices that are not dependent on an arbitrary delineation of the domain and on which the zero density values have a null contribution, have been favoured.

2.2.1 Centre of gravity and inertia

The centre of gravity (*CG*) is the mean location of the population and also the mean location of an individual taken at random in the field. The inertia which is the mean square distance between such an individual and the centre of gravity describes the dispersion of the population around its centre of gravity (Bez, 1997).

Let x be a point in a space at two dimension (2D) (short for the usual 2D notation *(x, y)*), *z(x)* the population density of population at location x. Then the total abundance of the population is:

$$Q = \int z(x)dx \qquad (1)$$

and the probability density function of the location x_I of a random individual I is $\frac{z(x)}{Q}$.

The centre of gravity is:

$$CG = E(x_I) = \int x \frac{z(x)}{Q} dx = \frac{\int x.z(x)dx}{\int z(x)dx} \quad (2)$$

and the inertia is:

$$I = Var(x_I) = \frac{\int (x - CG)^2 .z(x)dx}{\int z(x)dx} \quad (3)$$

In practice these statistics are estimated from data through discrete summations over the sample locations. In the case of an irregular sampling, surfaces of influence affected to samples are used as weighted factors. Practically, from sample values z_i at locations x_i, with surfaces of influence s_i, we have:

$$CG = \sum_{i=1}^{N} x_i.s_i z_i / \sum_{i=1}^{N} s_i z_i \quad (4)$$

$$I = \sum_{i=1}^{N} (x_i - CG)^2 .s_i z_i / \sum_{i=1}^{N} s_i z_i \quad (5)$$

Note: The surface of influence of a sample location is the sum of points of the space that are closer to this sample than the others. It can be evaluated by overlying a very fine regular grid and counting grid points that are closer to this sample. Know or supposed boundaries (land, limit distance of influence from sample location) for the sampled population may be used.

2.2.2 Anisotropy

In 2D, the total inertia of a population can be divided in two orthogonal components according to the main structuring directions of the population distribution which represent the maximum and the minimum of the overall inertia. The square root of the inertia along a given axis gives the standard deviation of the projection of the location of the population along this axis. Anisotropy exists when the two components of the total inertia are different. This can be summarized by the anisotropy index equal to the square root ratio between maximum and minimum of inertia. Its value is higher than 1, higher is the anisotropy, higher is the contrast between the two directions.

$$Anisotropy = \sqrt{\frac{I \max}{I \min}} \quad (7)$$

2.2.3 Number of spatial patches

The spatial distribution of a fish population in a given area may be heterogeneous. Local aggregations of fish, i.e. spatial patches which are bigger than a fish school, may be present. An algorithm has been written to identify spatial patches: a sample is attributed to a patch according to the value observed and the distance to an existing patch. The algorithm starts from the richest value and considers each sample in decreasing sample values order. The richest value initiates the first patch. Then, the current sample value is attributed to the nearest patch, providing the distance to its centre of gravity is smaller than a threshold distance. Otherwise, the current sample value defines a new patch. Are retained at the end the spatial patches whose biomass are higher than 10% of the total biomass. The summarizing index is then the number of patches.

2.2.4 Positive area

The positive area is the area covered by fish densities greater than zero. It is estimated from data as the sum of the areas of influence of the fish densities greater than zero.

$$PA = \sum_i s_i 1_{z_i > 0} \quad (8)$$

The zero values of density have no contribution to the positive area. However the positive area is very sensitive to the low density values, since a very small density value has a similar contribution to the positive area as a high value.

2.2.5 Spreading area

The spreading area is an index related to the Gini index (Gini, 1921), but which has the advantage over Gini index of having no contribution from zero density values. The Gini index (ranging from 0 to 1) is equal to twice the area between the Lorenz curve (the graphical representation of the cumulated proportion of abundance versus the cumulated proportion of densities) and the line to which it would be reduced if all densities were the same (the first bisector). It depends on the proportion of zero-density values within the domain considered. By contrast, we define the spreading area (expressed in nm^2) simply as twice the area below the curve giving the cumulated proportion of abundance Q(F)/Q versus the cumulated density areas F when the densities values are ranged from the highest to the lowest density values:

$$2\int \frac{Q(F)}{Q} dF \tag{9}$$

The zero-density area that may be considered has no contribution to the spreading area. As Q(F)/Q is monotonic between 0 and 1 and convex, the spreading area is lower than the positive area. It is equal to the positive area when the population is spread with a constant density (Lorenz curve equals the first bisector).

2.2.6 Equivalent area

The transitive geostatistical approach (Matheron, 1971) can be used to describe the spatial distribution of a fish population when it includes a few large density values, and when delimitating a domain with homogeneous variations is difficult (Bez *et al*., 1995; Bez *et al*., 1997). The spatial structure is then represented by the (transitive) covariogram, function of the distance between two locations:

$$g(h) = \int z(x)z(x+h)dx \tag{11}$$

Here, the equivalent area is defined as the integral range of the covariogram:

$$EA = \frac{\int g(h)dh}{g(0)} = \frac{Q^2}{g(0)} = \frac{Q^2}{\int z(x)^2 dx} \tag{12}$$

As it can be written:

$$EA = \frac{Q}{\int z(x)\frac{z(x)}{Q}dx} \tag{13}$$

It represents the area that would be covered by the population, if all individuals had the same density, equal to the mean density per individual.

The equivalent area ranges from 0 to the positive area. It would be equal to the positive area if all positive density values were the same.

2.2.7 Microstructure index

The microstructure index is taken as the relative decrease of the covariogram between distance h = 0 and a distance h0 chosen to represent the mean lag between samples:

$$MI = \frac{(g(0) - g(h0))}{g(0)} \tag{16}$$

It measures the relative importance of the structural components at scale smaller than the sample mesh resolution (including random noise). It lies between 0 and 1. Values close to 0 correspond to a very regular, well structured, density surface. On the contrary values close to 1 correspond to a highly irregular, poorly structured, density surface.

2.3 Population dynamics indices

2.3.1 Abundance index

The total abundance of the population is:

$$Q = \int z(x)dx \tag{13}$$

In practice these quantities are estimated from data through discrete summations over the sample locations with surfaces of influence affected to samples. Practically, from sample values z_i at locations x_i, with surfaces of influence s_i, we have:

$$Q = \sum_{i=1}^{N} z_i s_i \tag{14}$$

2.3.2 Recruitment index

The recruitment index is the abundance index of the recruits. Age group of the recruits does not always correspond to age 0. It depends of the time when survey fishing gear starts to recruit the new cohort. Moreover the first age to be recruited can not be representative of the real strength of the new cohort, even if the reproduction occurs before the survey. Therefore abundance of age 1, as well as age 2, can be considered as representative of the recruitment index. Table 2 presents the ages used to compute the recruitment index.

2.3.3 Mortality index

Total mortality rate can be defined in simple manner as:

$$Z(t) = \log(\frac{N(t)}{N(t+1)}) \tag{14}$$

Where *N(t)* is number *N* of fish at time *t* for a same cohort.

We have decided to work on residuals of the mortality instead of mortality it self, in order to have a more robust estimator. Therefore the method used to estimate total mortality was based on a modified catch curve analysis (Sinclair, 2001). A catch curve is constructed by plotting natural logarithms of abundance estimates of a year class at each age (Ricker, 1975). The curve shows a decreasing slope with the age, only if the year class has fully complete recruitment. Before the descending part, the year class recruits to the sampling and fishery and can not be considered as representative of the age. If mortality and recruitment to the sampling gear remain constant, the descending part is linear. Z may be estimated from the slope of the descending part.

We were interested in obtaining a constant estimate of the total mortality over the period. Therefore a linear regression was done on log abundance at age vs. age and allowing for separate intercepts for each year class. A common slope was estimated for all year classes and this was used as an estimator of Z. The analytical model was:

$$\ln A_{ij} = \beta_1 Y + \beta_2 I + \varepsilon \tag{13}$$

where A_{ij} = the abundance of age i in year j; Y = a class variable indicating year class Y (i.e. log of the recruitment); I = the covariate age.

The parameter vector β_1 gives separate intercepts for year classes which were treated as fixed effects. The parameter β_2 was the estimator of total mortality for the time period. Then residuals of total mortality were available.

2.4. Data analysis

Bivariate plots between spatial indices and population dynamics indices have been done. For each population and age, spatial indices were linearly regressed on the abundance, on the following recruitment (i.e. delay depends on which age is considered as representative of the recruits), and on the mortality residuals. Then meta-analysis tables were constructed that showed the correlations considered as significant (i.e. P-Value below or equal to 0.05).

3. Results

3.1 Spatial indices and stock abundance

For each population, and each year, 9 spatial indices and 3 parameters of the population dynamics were computed per age or representative life stage. Table 3 gives the ages and representative life stages with R^2 where the correlation is considered as significant at P-Value 0.05. There are numerous relations for most populations.

The positive area is the spatial index that is the most correlated through ages (or stages) and populations. For instance, positive area is significantly correlated to all ages and representative life stages of the North Sea cod. Bay of Biscay hake and Eastern Baltic cod show also significant correlations for almost all ages and representative life stages. Correlations on all ages could be considered as significant if a level of significance is increased to a P-value of 0.051 for the immature hake and a P-Value of 0.072 or below for mature and immature cod (Fig. 2). Barents Sea cod and Aegean hake are populations where many ages present also significant correlations with the positive area. After the positive area, spreading area followed by equivalent area are the indices that show the most numerous relations with a population.

North Sea cod is the population where the number of correlated spatial indices is the largest (i.e. 7). North Sea herring, as well as the red mullet of the Central-Southern Tyrrhenian Sea (GSA 10a) are coming next with 6 different indices responding.

Finally, some indices respond for almost all populations and other are more specific. In the other hand, there are populations were most of the indices respond and other where few answer. The spatial patterns of the European stocks are linked to their level of abundance through various indices: the mean location, the dispersion, the anisotropy, the area of extension, the microscale structure and the number of patches.

3.2 Spatial indices and recruitment

Significant correlations between population spatial distribution of mature and abundance of the following recruits are less frequent (Table 4). Only 6 stocks present significant relations, with a total of 10 relations. With a higher threshold P-Value (P-Value ≤ 0.1), the number of relations rises to 16 and 7 stocks out of 10 show relations. Three spatial indices (the spreading area, the equivalent area and the longitude of the centre of gravity) do not present correlation with a population (P-Value ≤ 0.05).

No significant correlation for a P-Value of 0.05 was found for the Biscay anchovy, the Central-Southern Tyrrhenian Sea red mullet (GSA 10a), the Ionian hake and the Biscay hake. However one can tone this negative result of Biscay hake down a bit. Actually, positive correlations appear with positive area and latitude of the centre of gravity, if level of significance is increased to a P-Value ≤ 0.1. Recruitment may be stronger when matures occupy a reduced area than in average and their mean location is rather south on the eastern continental shelf of the Bay of Biscay.

Aegean hake shows significant relationship between the numbers of patches of matures and the abundance of the following recruits. The higher the number of patches of matures, the better the recruitment. To a smaller extent, a negative correlation appears with the anisotropy, but with a P-Value of 0.06. Recruitment of hake may be better if the population is also distributed in a non preferential direction in the Aegean Sea.

Central-Southern Tyrrhenian Sea red mullet (GSA 10b) shows significant negative correlations with inertia and number of patches, and in a smaller extent, a positive correlation with the longitude of the centre of gravity (P-Value = 0.059). Recruitment of red mullet is better when matures present a low dispersion (inertia) and few patches. When the population is rather at the eastern side of the Sicily coast (high longitude of the centre of gravity), recruitment may be better.

North Sea herring presents a significant negative correlation with the inertia. The recruitment is better when mature herring are not too dispersed (low inertia).

North Sea cod presents a positive correlation between the recruitment and the positive area of the mature. The higher the area covered by the mature cod, the better the recruitment. To a smaller extent, a negative correlation occurs with the latitude of the centre of gravity (P-Value = 0.099). The recruitment is also larger when the location of the population is more southern than on average.

The Eastern Baltic cod is the population where the number of spatial indices that answer is the highest. Anisotropy, inertia and positive area of mature cod are positively correlated with the recruitment. The recruits present a high level of abundance when mature cod presents a high dispersion (high inertia), occupies a large area (high positive area) with a strong anisotropy (indeed, they cover totally the surveyed area which presents a preferential geometry).

The Barents Sea cod shows significant negative correlations with the microstructure index and the latitude of the centre of gravity. To a smaller extent, inertia is also negatively correlated, but with a P-Value of 0.069. Recruitment are better, when matures are well structured (low microstructure index) with a smaller dispersion than on average. The location of the population is also expected to be rather south.

3.3 Spatial indices and mortality

For each population, each year class, the mortality were estimated (Fig. 3) and residuals of the fit were used for regression with the spatial indices (Table 5). Some indices do not respond or respond very little. There is no index that emerges by responding for all stocks. The number of patches, and then the latitude of the centre of gravity are the indices that answer the best (respectively 6 and 5 responding stocks). All stocks respond, but some better than other (e.g. North Sea herring with 4 responding indices).

4. Discussion

4.1 Spatial indices and stock abundance

This meta-analysis has shown that there is a clear relationship between spatial pattern of a population and abundance. This relation can be detailed in various characteristics through our spatial indices. However, in the literature, fewer criterions are used in the models that describe the local response of density to a global change in abundance. They look how behave local densities and area covered by the population to a global change of abundance. The constant density model refers to constant densities and area varying with the abundance (Iles and Sinclair, 1982; Hilborn and Walters, 1992). The proportional density model refers to constant area and densities varying proportionally to abundance (Houghton, 1987; Myers and Stokes, 1989; Hilborn and Walters, 1992; Petitgas, 1997). The basin model developed by MacCall (1990) refers to densities varying 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). The relation of abundance with area indices (positive area, equivalent area and spreading area) informs us about the model to refer to, if any. In the model with constant density, densities would be expected to be proportional to any area index. In the proportional density model, the scatter plot would be vertical. In the case abundance increases with an area index, the intersection of the regression with the abscissa axis, if positive, would give a minimal area covered by the population at low abundance. Other cases where densities and areas are variable also exist, that corresponds to the basin model.

An important result is that there is a strong relationship between positive area and abundance. This result was already known for some stocks. For instance, Casey and Pereiro (1995) suggest that the distribution of *Merluccius merluccius* recruits in the North–East Atlantic varies with year-class strength, contracting for the poorer year-classes and expanding for good ones. Results presented here show also an expansion of the nursery areas surface in the case of good year-

classes, which contrasts with results reported in Sanchez and Gil (2000) and in Petitgas (1998), who state that the spatial distribution of recruits follows the criteria of fixed geometry and variable density. In Mediterranean Sea, the area occupied by 0-year old hake juveniles expands with increasing abundance and biomass (Abella et al., 2005) and comforts our result.

Strong relationship between range (i.e. positive area) and abundance appears in various kinds of stocks: demersal and pelagic. However, Atkinson et al. (1997) suggest that this relationship is tenable only for populations exhibiting strong associative behaviour. In these cases, local densities (those within aggregations or within areas occupied by groups of aggregations) remain almost constant related to and over a range of abundance levels (the "hyperstability" concept of Hilborn and Walters, 1992). For demersal populations, when densities are more limited by physical habitat than by behavioural causes, changes in abundance will not necessarily produce changes in nursery surface areas. Observed relations in the demersal populations of the meta-analysis may favour that those species do not behave as expected as they are under exploitation. They are no longer restricted by the physical habitat.

4.2 Spatial indices and recruitment

Most of studies on recruitment are looking for correlation between nursery area and size of the population. Thus, Rijnsdop et al. (1992) found a positive relationship between relative recruitment and the surface area of the nursery grounds for sole stocks. The "Nursery size hypothesis" seems to be also valid for other species such as plaice (van der Veer et al., 2000), cod (Rose and Leggett, 1991) and juveniles of haddock (Crecco and Overholtz, 1989). Riou et al. (2001) provided a relative index of juvenile abundance based on the extension of the respective geographic surfaces for some benthic species.

However, we are looking for something different were spatial pattern of mature individuals will affect the following recruitment. It may be considered as another condition that influences this key step of the population dynamics. For instance, in Biscay hake population, recruitment appears to be stronger when matures occupy a reduced area than in average and when their mean location is rather south on the eastern continental shelf of the Bay of Biscay, i.e. area of matures differs from that of the recruits. It could be partly explained that this particular spatial pattern of matures reduces the cannibalism on the recruits (Guichet, 1995) and favours the recruitment in this manner.

One can note in the literature other studied aspects. Thus, Iles and Sinclair (1982) state that population size mostly depends on the retention area available for larvae and juveniles. Timing and variation in environmental conditions at the time when larvae shift to the nursery areas should be critical. Sometimes larvae do not reach the nursery areas and that results in recruitment failures. Knowledge about the transport of spawning products is important for the understanding of the processes, which determine year-class strength.

4.3 Spatial indices and mortality

To our knowledge there has been no previous attempt to correlate mortality rate and spatial organization at age in a fish population.

4.4 About the significance of correlations

In our analysis, a correlation between a pair of variables was considered to be significant by reference to a chosen P-Value, e.g. 0.05. This means that a computed correlation would appear as significant with a probability equal to 0.05 in the case the true correlation is zero.

So if we are looking for correlations for 90 pairs of variables with a P-Value of 0.05 as in Table 4, we should expect to consider on average 0.05 x 90 = 4.5 correlations as significant in the case all true correlations would be zero. The fact that we find 10 significant correlations to recruits is in favour of the significance of those results (it would be difficult to test statistically if

10 deviates significantly from 4.5 in this example, as the pairs of variables are not independent from each other).

Now if we combine the 10 populations for each index (row of Table 4) or the 9 indices for each population (line of Table 4), we should expect on average 0.5 or 0.45 correlations to recruits considered as significant for P-Value = 0.05, in the case all true correlations would be zero. Observing 2 or 3 significant correlations to recruits in a line or a row is in favour of actual correlations: this applies to inertia, positive area and number of patches, and to Eastern Baltic cod, Barents Sea cod, and red mullet in Central-Southern Tyrrhenian Sea (GSA 10b).

For Tables 3 and 5, we have to consider the different ages. So for each cell (one index for one population having N ages), we should expect 0.05 N significant correlations in the case the true correlations would be zero. For the 10 populations, totalizing 60 different ages for the different fish of Table 5, we should expect 0.05 x 60 x 9 = 27 correlations to mortality considered as significant if the true correlations were zero. Observing 34 correlations considered as significant is not really in favour of significant relations with mortality.

In Table 3, the Immature and Mature groups are added to the ages (the Recruit has not to be added as it coincides with one of the ages), giving a total of 80 different pairs. This would give 0.05 x 80 x 9 = 36 correlations considered as significant if the true correlations were zero for the whole Table 3, and 0.05 x 80 = 4 for each index. Observing 97 significant correlations for the whole Table 3 is meaningful, highlighting the results obtained for Positive Area, and to a lesser extend for Spreading Area then Equivalent Area. Taking into account the range of their ages, some populations answer better to these indices (the cod and hake populations, then anchovy), and some answer badly (herring and red mullet).

5. Conclusion

This study provides a rather complete analysis of the spatial determinism of the fish population dynamics by investigating relationship between key parameters (abundance, recruitment and mortality) and a variety of spatial indices.

Numerous relations occur and could be used in assessment process. Indices might be used in indicator based approach that would hopefully take into account the spatial organization of the population, as well as biological and abundance status. Constructing synthetic indices for spatial distributions could also be investigated and used as spatial indicator in assessment procedures (Babcock *et al.*, 2005).

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Table 1. Species, areas and surveys considered in the meta-analysis.

Target species	Survey locations (areas)	Survey years	Survey names	Institutes
Anchovy	Bay of Biscay: SW France	1989 to 2005	PELGAS	IFREMER, Nantes, France
Cod	North Sea	1985 to 2005	IBTS	RIVO, Ijmuiden, Netherlands
Cod	Eastern Baltic Sea	1994 to 2004		SFI, Gdynia, Poland
Cod	Barents Sea	1989 to 2004		IMR, Bergen, Norway
Herring	North Sea	1989 to 2002		FRS, Aberdeen, Scotland
Hake	Ionian Sea	1994 to 2003	MEDITS	HCMR, Athens, Greece
Hake	Aegean Sea	1994 to 2003	MEDITS	HCMR, Athens, Greece
Hake	Bay of Biscay: W France	1987 to 2004	EVHOE	IFREMER, Nantes, France
Red Mullet	Central-Southern Thyrenean Sea: GSA 10-a	1994 to 2003	MEDITS	SIBM-COISPA, Bari, Italy
Red Mullet	Central-Southern Thyrenean Sea: GSA 10-b	1994 to 2003	MEDITS	SIBM-COISPA, Bari, Italy

Table 2: Available ages and representative life stages for each fish stock. For some stocks, ogive of maturity at age has been used to determine the representative life stage (recruits, immatures and matures)

Species	Ages	Recruits	Immatures	Matures
Biscay Anchovy	1, 2, 3	1	-	1 + 2 + 3
North Sea Cod	1, 2, 3, 4, 5, 6	2	1*0.99 + 2*0.95 + 3*0.77 + 4*0.38 + 5*0.14 + 6*0.00	1*0.01 + 2*0.05 + 3*0.23 + 4*0.62 + 5*0.86 + 6*1.00
Eastern Baltic Sea Cod	1, 2, 3, 4, 5	2	1*1.00 + 2*0.87 + 3*0.64 + 4*0.17 + 5*0.06	1*0.00 + 2*0.13 + 3*0.36 + 4*0.83 + 5*0.94
Barents Sea Cod	1, 2, 3, 4, 5, 6, 7, 8, 9, 10	2	1*1.0000 + 2*1.0000 + 3*0.9963 + 4*0.9906 + 5*0.9206 + 6*0.6344 + 7*0.2981 + 8*0.1363 + 9*0.0225 + 10*0.0012	1*0.0000 + 2*0.0000 + 3*0.0038 + 4*0.0094 + 5*0.0794 + 6*0.3656 + 7*0.7019 + 8*0.8638 + 9*0.9775 + 10*0.9988
North Sea Herring	0, 1, 2i, 2m, 3i, 3m, 4, 5, 6, 7, 8, 9	1	1 + 2i + 3i	2m + 3m + 4 + 5 + 6 + 7 + 8 + 9
Ionian Sea Hake	0, 1, 2, 3, 4, 5	1	1*1.0 + 2*1.0 + 3*0.5	3*0.5 + 4*1.0 + 5*1.0
Aegean Sea Hake	0, 1, 2, 3, 4, 5	1	1*1.0 + 2*1.0 + 3*0.5	3*0.5 + 4*1.0 + 5*1.0
Biscay Hake	0, 1, 2, 3, 4, 5	0	0*1.0 + 1*1.0 + 2*1.0 + 3*0.8 + 4*0.4 + 5*0.1	3*0.2 + 4*0.6 + 5*0.9
Central-Southern Thyrenean Sea: GSA 10-a Red Mullet	0, 1, 2, 3	1	-	1 + 2 + 3
Central-Southern Thyrenean Sea: GSA 10-b Red Mullet	0, 1, 2, 3	1	-	1 + 2 + 3

Table 3: Correlations between spatial indices and abundance of the year. Ages (number) and representative life stages (R, I, M), sign of the correlation and then coefficients of correlation (R^2) are shown when correlations are found significant (P-Value ≤ 0.05).

Species	A	I	PA	SA	EA
Biscay Anchovy	-	-	1 (R), M (+) .47,.54	1 (R), M (+) .65,.51	1 (R), M (+) .47,.54
North Sea Cod	4, M (+) .42,.27	-	1, 2 (R), 3, 4, 5, 6, I, M (+) .61,.80,.80,.44,.66,.67,.75,.32	2 (R), 6 (+) .21,.25	4, I (-) .27,.22
Eastern Baltic Sea Cod	-	-	1, 2 (R), 3, 4, 5 (+) .64,.43,.66,.40,.42	3 (+) .40	-
Barents Sea Cod	2 (R) (-), 7 (+) .40,.33	-	1, 3, 4, 8, 9, 10 (+) .36,.36,.43,.31,.68,.86	1, 4, 5, 9, 10 (+) .25,.27,.26,.60,.83	9, 10 (+) .38,.72
North Sea Herring	M (+) .36	-	-	1 (R), 6 (+) .32,.34	6 (+) .42
Ionian Sea Hake	-	0 (+) .46	0, 3, 5 (+) .58,.48,.61	M (-) .51	M (-) .49
Aegean Sea Hake	5 (-) .64	4 (+) .47	0, 2, 3, 4, 5, M (+) .46,.50,.82,.67,.78,.65	-	-
Biscay Hake	-	-	0 (R), 1, 2, 3, 4, 5, M (+) .41,.63,.77,.60,.86,.30,.74	2, 4 (+) .56,.34	2 (+) .44
Central-Southern Thyrenean Sea: GSA 10-a Red Mullet	2 (-) .42	0 (+) .99	0, 1 (R) (+) .94,.46	0 (+) .86	0 (+) .88
Central-Southern Thyrenean Sea: GSA 10-b Red Mullet	-	-	2 (+) .40	-	-

Species	xcg	ycg	NOP	MI
Biscay Anchovy	-	-	-	-
North Sea Cod	4, 5, 6, M (-) .37,.23,.36,.55	4 (+) .40	-	I (+) .28
Eastern Baltic Sea Cod	1, I (-) .52,.38	-	-	-
Barents Sea Cod	5 (+) .36	-	-	2 (R) (-) .30
North Sea Herring	9 (-) .57	0 (-), 3, 4, M (+) .48,.52,.47,.38	-	3, 5, 6 (-) .37,.33,.39
Ionian Sea Hake	-	-	-	-
Aegean Sea Hake	-	-	5 (+) .53	-
Biscay Hake	-	-	2 (+) .27	-
Central-Southern Thyrenean Sea: GSA 10-a Red Mullet	-	3 (+) .52	-	-
Central-Southern Thyrenean Sea: GSA 10-b Red Mullet	-	-	-	-

Table 4: Coefficient of correlations (R^2) between spatial indices of matures and abundance of the following recruits. Cells are shaded in dark grey when relations are below a P-Value of 0.05, and in light grey, when relations are between P-Values of 0.1 and 0.051. Cells also present the sign of the significant correlations.

Species	A	I	PA	SA	EA	xcg	ycg	NOP	M
Biscay Anchovy	.62	.00	.11	.00	.07	.15	.00	.13	.07
North Sea Cod	.00	.08	.29 (+)	.09	.01	.01	.16 (-)	.00	.00
Eastern Baltic Sea Cod	.58 (+)	.51 (+)	.50 (+)	.21	.26	.07	.26	.24	.01
Barents Sea Cod	.05	.27 (-)	.03	.05	.00	.03	.32 (-)	.07	.32 (-)
North Sea Herring	.00	.34 (-)	.07	.16	.06	.03	.00	.12	.09
Ionian Sea Hake	.18	.27	.13	.04	.14	.06	.17	.23	.23
Aegean Sea Hake	.54 (-)	.11	.43	.32	.23	.05	.01	.57 (+)	.06
Biscay Hake	.00	.01	.29 (-)	.05	.03	.02	.30 (-)	.00	.23
Central-Southern Thyrenean Sea: GSA 10-a Red Mullet	.00	.10	.05	.12	.19	.11	.09	NA	.17
Central-Southern Thyrenean Sea: GSA 10-b Red Mullet	.05	.68 (-)	.00	.21	.17	.47 (+)	.17	.63 (-)	.14

Table 5: Correlations between spatial indices and mortality residuals. Ages (number), sign of the correlation, then coefficients of correlation (R^2) are shown when correlations are found significant (P-Value ≤ 0.05).

Species	A	I	PA	SA	EA	xcg	ycg	NOP	M
Biscay Anchovy		1 (+) .96						3 (-) .99	
North Sea Cod					1 (+) .67		2 (+) .30	5, 6 (-) .31,.37	
Eastern Baltic Sea Cod	2 (+) .78		2 (-) .51			3 (-) .47			
Barents Sea Cod							3, 4, 5, 6 (-) .43,.43,.89,.52	8 (-) .58	
North Sea Herring	2 (+), 8 (-) .34,.66	5 (-) .44			1 (-) .34		4, 8 (+) .38,.68		
Ionian Sea Hake						0 (-) .97		3 (-) .59	
Aegean Sea Hake			4 (+) .80				5 (-) .80		
Biscay Hake		5 (+) .42	3, 4, 5 (+) .44,.36,.49					1 (+) .37	
Central-Southern Thyrenean Sea: GSA 10-a Red Mullet				1 (-) .75	1 (-) .71		1 (-) .77		
Central-Southern Thyrenean Sea: GSA 10-b Red Mullet		3 (+) .51						3 (+) .50	

Figure 1. Map of the area surveyed by the different institutes who collaborated in the present study.

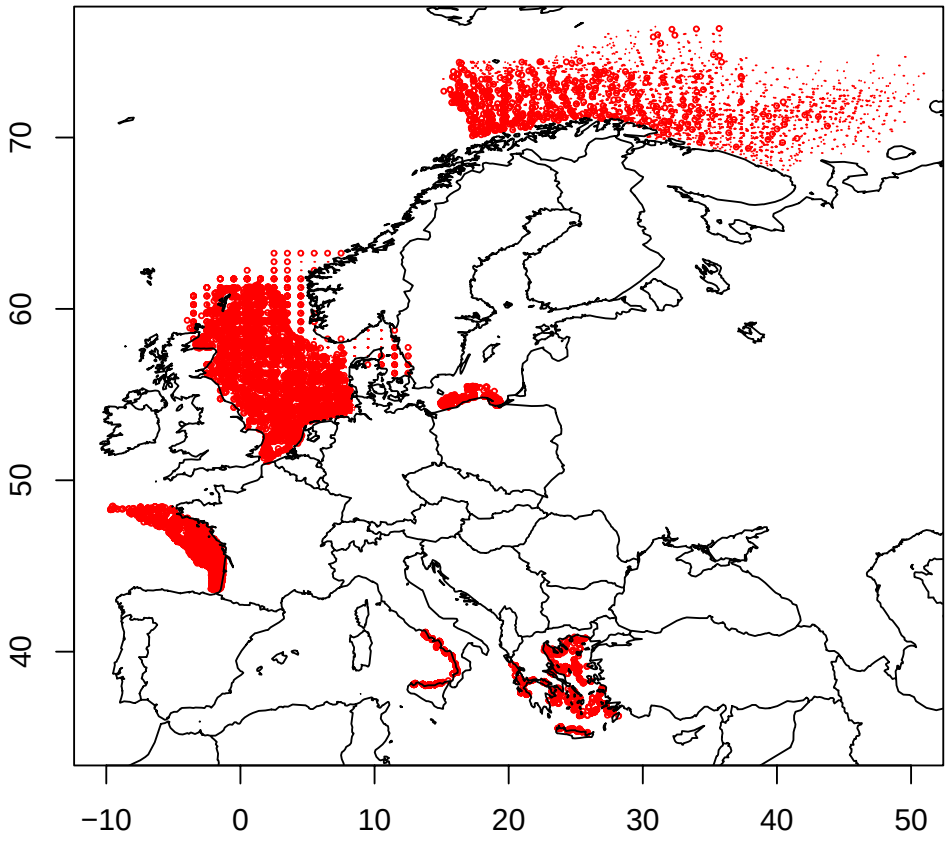

Figure 2. The linear relationship between the positive area and the abundance for ages and representative life stages of the European Hake of the Bay of Biscay.

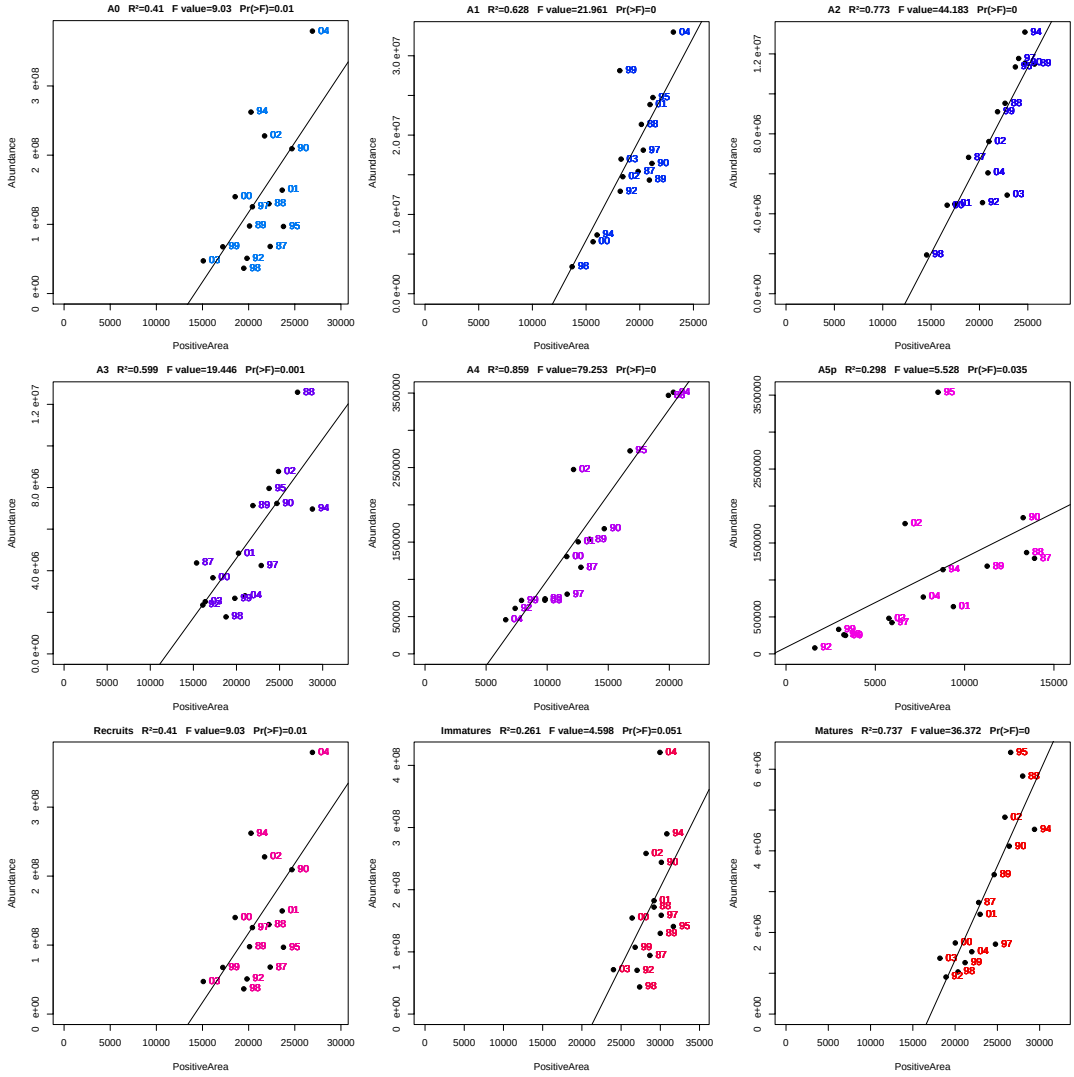

Figure 3. Example of the model fitting for two cohorts of the North Sea cod stock.