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Usefulness of the spatial indices to define the distribution pattern of key life stages: an application to the red mullet (*Mullus barbatus*) population in the south Tyrrhenian sea

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Abstract

This study aims to explore the performance of the approach based on spatial indicators to characterise with quantitative metrics the spatial dynamics of red mullet life stages (recruits and adults), to identify areas where red mullet recruits are more concentrated, to establish relationships with the adult distribution and to detect the ability of spatial indicators to capture the stability of the spatial occupation of preferential areas across the years. Data are from the GRUND and MEDITS experimental trawl surveys. The methodological approach used in this study is based on the estimate of spatial indicators as developed within the EU Fisboat project. The results proved that many of the 9 examined spatial indicators and pairwise relationships, between indicators and abundance, enabled us to better understand the spatial distribution and interannual variability of the red mullet population life stages and the relationships between spatial distribution and abundance. In addition, we identified the geographical area (southwards, along the Calabria coast) where recruits of red mullet resulted mainly distributed and we also verified that these locations are stable across years.

Key words: spatial indices, Tyrrhenian sea, red mullet.

Introduction

Since a rather long time many Mediterranean demersal fish are characterized by heavy exploitation at small sizes (e.g. Caddy 1990). Often juvenile stages of these species pass their early life history in a restricted area, frequently but not always inshore. Thus, the protection of sensitive habitat, like nursery areas, is increasingly considered as a necessary complementary tool for fishery management.

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Explicit approach to juvenile fisheries management should hence recognize the need for seasonal or permanent closures of nursery areas and spawning refuge within MPAs, and should map biologically important 'critical habitats' (e.g. Caddy, 2006). This concept is based on the specific Mediterranean situation, but also on the perception that conventional fishery management techniques are insufficient or have failed to prevent overexploitation of target species (FAO 1995; Walters and Maguire, 1996; Beverton, 1998).

However, questions often rising from researchers and stakeholders are mainly related to the following considerations: which are the spatial indices enabling the characterization as 'nursery' of the areas where recruits are preferentially distributed? How is it possible to design management measures without sound information on the stability of the spatial location of nursery areas along time? In addition, how relationships between spatial indices that captures spatial pattern of stocks and parameters of its dynamics should be combined, in order to identify new indicators for a more comprehensive assessment purposes?

The approach of spatial indicators as descriptor of a) distribution patterns, b) changes across space and time, c) pairwise relationships with population indices and dynamics, has been developed within the EU FISBOAT project (Fisheries Independent Survey Based Operational Assessment Tools). The identified spatial indicators characterise location (centre of gravity of the distribution, inertia, patches), occupation area (positive area, equivalent area, spreading area), aggregation (microstructure) (Woillez et al., 2005; 2006; 2007). Bez and Rivoirard (2000a) proposed tools such as centre of gravity and inertia to summarise the spatial distribution of population, while Bez and Rivoirard (2000b) suggested the global index of collocation to examine how two populations are geographically linked or distinct, by comparing the difference of their centres of gravity to the mean distance between individuals, taken at random and independently from each population.

The aim of this study is to explore the performance of the approach based on spatial indicators to characterise the spatial dynamics of red mullet life stages, identify areas where red mullet recruits are more concentrated, establish relationships with the adult distribution and detect the ability of spatial indicators to capture the stability of the spatial occupation of preferential sites across the years.

The spatial indices mainly used are the centre of gravity (CG), the inertia (I) and the global index of collocation (GIC). This type of study intend also to be a propaedeutic step to estimate nursery areas or other grounds preferentially occupied by key life-stages (e.g. spawners) of red mullet across space and time.

Material and methods

Survey data

The time-series used in this study (1994-2004) are from GRUND and MEDITS experimental trawl-surveys (Spedicato et al., 1998; Relini et al., 2000; Bertrand et al., 2002) carried out in the south Tyrrhenian sea (GSA10), using a random stratified sampling design. Hauls in the range 10-200 m depth, have been considered, taking into account the limit of the red mullet vertical distribution. A commercial trawl net was used during the GRUND surveys with a stretched mesh size in the cod-end of 20 mm, except in 1994-1995 and 2003-2004 when a mesh of 40 mm was used. A standard gear (GOC 73, by P.Y. Dremiere,

IFREMER-Sete), with a 20 mm stretched mesh size in the cod-end, was instead employed throughout the MEDITS surveys. Net openings were monitored in each tow and the swept area estimated according to Pauly et al. (1983), hence data were standardised to the surface unit (mn²). GRUND and MEDITS surveys were carried out in two different key seasons for the red mullet, the former generally during October-November, when recruitment occurs, and the latter in May-July, i.e. during the spawning season.

The length frequency distribution (LFD) of each GRUND haul has been split between recruits and adults after the modal components of a pooled LFD were separated (Bhattacharya method, in Gayanilo et al., 1996) and average length for the first component (95 mm total length) was estimated. Gonad maturity stages, recorded during MEDITS surveys, helped to split the population between immature and mature individuals.

Spatial indices definitions

Centre of gravity and inertia

The spatial distribution of population can be easily summarized by tools such as centre of gravity and inertia (Bez, 1997). The centre of gravity is the mean location of the population (the mean location of an individual fish taken at random in the field) and the inertia describes the dispersion of the population around its centre of gravity (the mean square distance between such an individual fish and the centre of gravity). They are unaffected by zero values of population density and are spatial statistics (they are modified when changing the location of samples values). In the case of an irregular sampling, surfaces of influence affected to samples are used as weighted factors.

Global index of collocation

The global index of collocation looks at how two populations are geographically melted or distinct by comparing their distance between their centres of gravity and the mean distance between individuals taken at random and independently from each population (Bez and Rivoirard, 2000a). It is a spatial statistics that ranges between 0, in the extreme case where each population is concentrated on a single but different location (inertia equal to 0), and 1, when the two centres of gravity coincide.

Anisotropy

The total inertia of a population can be decomposed on its two principal axes, orthogonal to each other, explaining respectively, the maximum and the minimum parts of the overall inertia. When there is a marked difference in inertia between the two directions, anisotropy exists. The square root ratio between the maximum and the minimum of the inertia summarizes the anisotropy of the spatial distribution of the population.

Number of spatial patches

The spatial distribution of a fish population in a given area may not be homogeneous. Local aggregations of fish, i.e. spatial patches, may be present. To identify spatial patches, an algorithm has been written, based on the choice of a threshold distance: a sample is attributed to a patch according to the value observed and to the distance of its location from patches previously identified. Are retained at the end the spatial patches whose abundance

are higher than 10% of the total abundance. The summarizing index is the number of patches.

Positive area

The positive area is the area covered by fish densities strictly greater than zero. It is expressed in square nautical miles and estimated from data as the sum of the areas of influence around samples where are the fish densities strictly greater than zero.

Zero values of density make 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.

Spreading area

This index comes from the selectivity curves which have been developed in mining geostatistics to characterize probability distributions and their dispersion (Matheron, 1981). They have been used in fisheries to look at the aggregation of values when the abundance changes (Petitgas, 1998). In order to have statistics which are not affected by the zero sample values, curves have been reversed bottom up, leading to the spreading area.

Let T be the cumulated area occupied by the density values, ranked in decreasing order, Q(T) the corresponding cumulated abundance, and Q the overall abundance. The SA (expressed in square nautical miles) is then simply defined as twice the area below the curve expressing (Q-Q(T))/Q as a function of T.

Equivalent area

A transitive geostatistical approach (Matheron, 1971) can be used to describe the spatial distribution of a fish population when it includes a few large values of density, and when it is difficult to delimit a domain with homogeneous variations (Bez et al., 1995, 1997). The spatial structure is then represented by a (transitive) covariogram, a function of the distance between two locations: The equivalent area is the integral range of the relative covariogram. 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 lies between 0 and the positive area. It would be equal to the positive area if all strictly positive values of density were the same.

Microstructure index

The microstructure index (MI) 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. It measures the relative importance of the structural components at a scale smaller than the sample lag (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.

Abundance index

The total abundance of the population is: $Q = \int z(x) dx$ 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:

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

Further details on the calculation of spatial indicators and algorithms are reported in Woillez et al. (2007).

Population spatial organisation should not be considered implicit and ignore the population dynamics. Following Woillez et al. (2006), bivariate plots between spatial indices and population dynamics indices have been done. For each life stage, spatial indices were linearly regressed on the abundance and on the following recruitment. Correlations were considered as significant when P-Value was below or equal to 0.05.

Results

The estimates of the centre of gravity indicate that the mean location of red mullet recruits is rather stable across years (southernmost part of the area, Calabria western coasts), except in 2000 (fig. 1a). The inertia, which describes the dispersion of the population around its centre of gravity, appears generally low, except in 1997 and 1998 (fig. 1c; 1e), when a higher variability was estimated. Adults exhibit a different pattern, with less stable CG and higher I (figs. 1b and d), the former indicating more changes in spatial location and the latter a higher dispersion of this population life-stage. Indeed, what we learn from the GIC, that completes this approach by quantifying the observed charts, is that the centre of gravity of recruits is slightly varying from year to year (53.3%) of the year pairs >0.9, and generally above 0.8; fig. 2), except in 2000 when a different pattern was observed, whilst the GIC of adults was generally less matching in the year pairs (33.3%) of the year pairs >0.9, and generally less than 0.8; fig. 2), especially in 2000. Thus, the recruit fraction of the population is rather steadily located across space and time, conversely the pattern distribution of adults is more disperse. As a consequence, the two fractions of the red mullet population are poorly melted (GIC around 0.7 or less in 70% of the years, fig. 3), even in autumn season (survey time), when individuals are supposed to be grown-up enough to leave the inshore grounds and move offshore. The plot of the longitude (xcg) and latitude (ycg) CG time series (fig. 4) corroborates the analysis and confirms that the xcg of recruit aggregation is rather stable eastward (inshore direction) and the vcg southward, whilst the same indicators are more variable for the adult life-stage.

The mean and variability of the spatial indicators across years (fig. 5) derived from GRUND surveys stress the different spatial location of the two life stages (xcg and ycg) and the lower dispersion of the recruits (I), in addition a marked anisotropy, indicating the directionality of the inertia, exists and is slightly lower for recruits. Also the positive area is, on average, lower for recruits, indicating the occurrence of less positive density values and, hence, a reduced spatial coverage compared to the adults. Similar pattern, although characterised by a higher variability, is observed for the equivalent and spreading areas. More spatial patches are observed for adults than for recruits, indicating a higher spatial

aggregation of the latter. The microstructure is similar for both life-stages and rather high, corresponding to an irregular density surface at small scale. The spatial distribution of adults show, however, a different pattern during the spawning season (May-August, MEDITS surveys), when red mullets are more aggregated inshore and southwards, with smaller inertia and anisotropy besides fewer number of patches (fig. 6). Also the lower positive areas indicate a reduced spatial coverage, while the smaller microstructure index is a sign of a more regular density surface at small scale.

The scatter plots of the pairwise relationships highlight an absence of correlations between xcg, ycg, inertia and abundance, both for adults and recruits (fig. 7), i.e these indicators are rather stable with abundance, although inertia seems positively related with abundance for the adults, but only with a P-value=0.15. On the opposite, positive, equivalent and spreading areas are positively correlated with abundance (P-value<0.05) for recruits, while no correlations is detected for adults (fig. 7). This might indicate that juveniles tend to expand their occupied area when abundance increases, whereas adults do not show this behaviour, likely because population is already scattered on a wider area.

Among the delayed relationships (fig. 8) the lone significant (P-value<0.05) regards the microstructure index of adults (mature) and the following abundance of recruits, that decreases as the microstructure increases. This would imply that a better recruitment occurs when the spatial structure of mature is more regular. Also interesting to note is that the abundance of recruits tend to decrease, although not significantly, at the chosen level of probability (P-value<0.05), when the ycg of matures tend to be located more northwards.

Discussion and conclusion

M. barbatus is one of the most important demersal inshore fish targeted by different fishing gears along Mediterranean (Tserpes et al., 2002). Life history traits of Red mullet are characterised by an early maturation with a late spring-early summer spawning season and a discrete recruitment mode, occurring in late summer-early autumn. Aggregation of juveniles and subsequent movements towards more offshore grounds have been reported and indicated as a source of increased vulnerability of this population component to the harvest strategy (Voliani et al., 1998).

Spatial indices that have been selected allowed us to better understand and document, using quantitative metrics, the pattern of the spatial distribution of recruits and adults of the red mullet population in the investigated area. In addition, differences related to the spatial distribution and occupation depending on the reproductive phase have been highlighted.

The approach of the spatial indicators enabled us to identify the geographical zone (southwards in the study area, along the Calabria coast) where recruits of red mullet are mainly distributed and to verify that these locations are rather stable across years. This preferential geographical location might be due to the ecological characteristics of the inshore ecosystems, where sea grass meadows occur intermixed to uneven grounds in a very narrow and steep coastal zone. A further important result is that, in addition, we found a strong relationship between positive area and abundance of recruits. This outcome is in agreement with the statement of Woillez et al. (2006), who observed an expansion of the nursery areas surface in the case of good year-classes in different fish stocks, i.e. with increasing abundance and biomass, as also reported by (Abella et al., 2005) for European

hake juveniles. Similarly to recruits also spawning adults exhibit a higher level of aggregation compared to the post-spawning fish. Interesting to note is that, as for the Eastern Baltic cod (Woillez et al., 2006), also red mullet exhibits a better recruitment when matures are well structured (low microstructure index) with a smaller dispersion than on average. Sustainable exploitation of *M. barbatus* population in the Tyrrhenian sea is a concern, owing to the deterioration of the stock that has been documented in the area (Abella et al., 1999). As regards management considerations, different measures are taken in the Mediterranean, i.e. the interdiction of the fishery within the inshore waters, the mesh size of the trawl net, the minimum landing size of 11 mm, all generally regarded as suitable for a sustainable exploitation of the red mullet stocks. This consideration is based on the biological characteristics of the species whose recruitment takes place in the inshore waters (up to 30-40 m depth), where the fish remain until they grow up and migrate towards the more offshore grounds (in late summer-early autumn, Relini et al., 1999). However, the analysis based on the spatial indicators have shown that there are, furthermore, specific geographical areas where recruits are preferentially distributed with a rather remarkable stability along time. Thus, the potential benefit of complementary measures, based on the 'area closure' and aimed to the protection of recruits should be further explored.

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References

- Abella A., Belluscio A., Bertrand J., Carbonara P., Giordano D., Sbrana M., Zamboni A. (1999) - Use of MEDITS trawl survey data and commercial fleet information for the assessment of some Mediterranean demersal resources. Aquat. Living Resour., 12 (3): 155-166.
- Abella, A., Serena, F., and Ria, M. 2005. Distributional response to variations in abundance over spatial and temporal scales for juveniles of European hake (*Merluccius merluccius*) in the Western Mediterranean Sea. Fisheries Research, 71: 295-310.
- Bertrand J.A., De Sola L.G., Papaconstantinou C., Relini G., Souplet A. (2002) The general specifications of the MEDITS surveys. Sci. Mar., 66 (Suppl. 2): 9-17.
- Bez, N., Rivoirard, J., and Poulard, J-C. 1995. Approche transitive et densité de poissons. Compte-rendu des journées de Géostatistiques, 15–16 juin 1995, Fontainebleau, France. Cahier de Géostatistique, 5: 161–177.
- Bez, N., 1997. Statistiques individuelles et géostatistique transitive en écologie halieutique. Thèse Dr. En géostatistique. ENSMP, France, 276 p.
- Bez, N., and Rivoirard, J. 2000a. MS Indices of collocation between populations. In: Chekley, D.M., J.R., Hunter, L. Motos, and C.D. van der Lingen (eds). Report of a workshop on the use of Continuous Underway Fish Egg Sampler (CUFES) for mapping spawning habitat of pelagic fish. GLOBEC Report 14, 1-65.

Bez, N., and Rivoirard, J. 2000b. On the role of sea surface temperature on the spatial distribution of early stages of mackerel using inertiograms. ICES Journal of Marine Science, 57: 383–392.

Beverton R.J. 1998. Fish, fact and fantasy: a long view. Rev. Fish Biol. Fish., 8: 229-249.

- Caddy J.F. 1990. Options for the regulation of Mediterranean demersal fisheries. Natural Resources Modeling, 4: 427–475.
- Caddy J.F. 2006. Practical issues in choosing a framework for resource assessment of Mediterranean and Black Sea fisheries. Joint meeting on Stock Assessment Methodology and Workshop on Black Sea Assessments of Pelagic and Demersal Fish Stocks. Istanbul 8-10 March, Turkey. 32 pp.

http://www.icm.csic.es/rec/projectes/scsa/WS%202006%20PWGAM%20+%20Black%20 Sea/Papers/Caddy-consultation-Istanbul.doc

- Food and Agriculture Organization (FAO). 1995. The state of the world fisheries and aquaculture. FAO Fisheries Department, Rome.
- Gayanilo F.C. Jr., Sparre P., Pauly D., 1996. FAO-ICLARM Stock Assessment Tools (FISAT) User's Manual. FAO Computerized Information Series Fisheries: 1-126.
- Matheron, G. 1971. The theory of regionalized variables and its applications. Les Cahiers du Centre de Morphologie Mathématique, Fascicule 5. Ecole Nationale Supérieure des Mines de Paris, Paris. 212 pp.
- Matheron, G., 1981. La sélectivité des distributions. Note N-686. Rapport du CGMM, ENSMP, Fontainebleau, France, 45p.
- Pauly D., 1983. Algunos methods simples par la evaluacion de recursos pesqueros tropicales. FAO Documento Tecnico de Pesca, 234: 1-49.
- Petitgas P.1998. Biomass dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. ICES J. Mar. Sci., 55, 443-453.
- Relini G., Bertrand J., Zamboni A. (eds.) (1999)- Sintesi delle conoscenze sulle risorse da pesca dei fondi del Mediterraneo centrale (Italia e Corsica)-Syndem. Biol. Mar. Medit., 6 (suppl. 1): 868 pp.
- Relini G., 2000. La ricerca sulla pesca: le risorse demersali. Biol. Mar. Medit., 7 (4): 13-45.
- Spedicato M.T., Lembo G., Carbonara P., Silecchia T. (1998) Valutazione delle risorse demersali dal Fiume Garigliano a Capo Suvero. *Biol. Mar. Medit.*, 5 (3): 64-73.
- Tserpes G., Fiorentino F., Levi D., Cau A., Murenu M., Zamboni A., Papaconstantinou C. (2002) - Distribution of *Mullus barbatus* and *M. surmuletus* (Osteichthyes: Perciformes) in the Mediterranean continental shelf: implications for management. In: Abelló P., Bertrand J. A., Gil de Sola L., Papaconstantinou C., Relini G., Souplet A. (eds.), Mediterranean Marine Demersal Resources: the MEDITS International Trawl Survey (1994-1999). Sci. Mar., **66** (Suppl. 2): 39-54.
- Voliani A., Abella A., Auteri R. (1998) Some considerations on the growth performance of *Mullus barbatus*. Cah. Option Mediter., 35: 93-106.
- Walters C. J. & Maguire, J. J. (1996). Lessons for stock assessment from the Northern Cod collapse. Rev. Fish Biol. Fish., 6: 125–137
- Woillez, M., Petitgas, P., Rivoirard, J., Poulard, J.-C., and Bez, N. 2005. Indices for capturing spatial pattern and change across years of a fish population: an application on European Hake (*Merluccius merluccius*) in the Bay of Biscay. ICES CM 2005/L:16.

- Woillez, M., P. Petitgas, J. Rivoirard, J.-C. Poulard, P. Fernandes, R. ter Hofstedte, K. Korsbrekke, A. Orlowski, M.-T. Spedicato and C.-Y. Politou. 2006. Relationships between population spatial occupation and population dynamics. ICES CM 2006/O:05.
- Woillez, M., Poulard, J-C., Rivoirard, J., Petitgas, P., and Bez, N. 2007. Indices for capturing spatial patterns and their evolution in time, with application to European hake (*Merluccius merluccius*) in the Bay of Biscay ICES J. Mar. Sci., 64: 537-550.



Fig. 1 - Centre of gravity by life stage (a and b) with inertia (c) and inertia distribution by life stage and year (d) (GRUND surveys 1994-2004).

Recruits											
Year	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
2004	0.998	0.975	0.815	0.885	0.985	NA	0.235	0.961	0.975	0.994	1
2003	0.991	0.964	0.743	0.829	0.973	NA	0.096	0.939	0.927	1	
2002	0.976	0.907	0.743	0.945	0.988	NA	0.298	0.896	1		
2001	0.978	0.996	0.912	0.805	0.975	NA	0.175	1			
2000	0.282	0.160	0.173	0.619	0.545	NA	1				
1999	NA	NA	NA	NA	NA	1					
1998	0.990	0.975	0.916	0.949	1						
1997	0.889	0.812	0.691	1							
1996	0.860	0.876	1								
1995	0.986	1									
1994	1										
					Ad	ults					
Year	1994	1995	1996	1997	Adı 1998	ults 1999	2000	2001	2002	2003	2004
Year 2004	1994 0.985	1995 0.848	1996 0.951	1997 0.561	Ad 1998 0.471	ults 1999 NA	2000 0.275	2001 0.802	2002 0.828	2003 0.997	2004
Year 2004 2003	1994 0.985 0.970	1995 0.848 0.845	1996 0.951 0.949	1997 0.561 0.542	Add 1998 0.471 0.457	ults 1999 NA NA	2000 0.275 0.239	2001 0.802 0.794	2002 0.828 0.823	2003 0.997 1	2004 1
Year 2004 2003 2002	1994 0.985 0.970 0.830	1995 0.848 0.845 1	1996 0.951 0.949 0.955	1997 0.561 0.542 0.915	Adi 1998 0.471 0.457 0.787	ults 1999 NA NA NA	2000 0.275 0.239 0.705	2001 0.802 0.794 1	2002 0.828 0.823 1	2003 0.997 1	2004 1
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Year 2004 2003 2002 2001 2000 1999 1998 1997 1996 1995	1994 0.985 0.970 0.830 0.830 0.336 NA 0.495 0.588 0.951 0.849	1995 0.848 0.845 1 0.999 0.702 NA 0.782 0.908 0.964 1	1996 0.951 0.949 0.955 0.947 0.525 NA 0.646 0.771 1	1997 0.561 0.542 0.915 0.917 0.910 NA 0.938 1	Add 1998 0.471 0.457 0.787 0.787 0.787 0.998 NA 1	ults 1999 NA NA NA NA NA	2000 0.275 0.239 0.705 0.699 1	2001 0.802 0.794 1 1	2002 0.828 0.823 1	2003 0.997 1	2004

Fig 2 - Global index of collocation by life stage (adults and recruits from GRUND surveys) and year (1994-2004).



Fig 3 - Global index of collocation between life stages (adults and recruits from GRUND surveys) and along years (1994-2004).



Fig. 4 - Centre of gravity (xcg-longitude and ycg-latitude) by year (1994-2004) and life stage (adults and recruits from GRUND surveys).



Fig. 5 - Box plots of the main spatial indicators (averaged from the time series 1994-2004) by life stage (adults and recruits from GRUND surveys).



Fig. 6 - Spatial indicators related to the adult component of the population in two different seasons (late spring-early summer and autumn) and reproductive stages (spawning and post-spawning) monitored by two different trawl-surveys (MEDITS and GRUND).



Fig.7 - Pairwise relationships between the main spatial indicators and abundance by life stage (adults and recruits from GRUND surveys).



Fig. 8 - Delayed relationships between spatial indices of matures and abundance of following recruitment.