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Spatial fisheries ecology: Recent progress and future prospects

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Abstract

We review recent progresses made in the study of fish distribution and survival over space — i.e., fisheries spatial ecology. This is achieved by first surveying the most common statistical approaches and relative challenges associated with the analysis of fisheries spatial data, loosely grouped in geostatistical and regression approaches. Then we review a selected number of case-studies implementing the discussed techniques. We conclude by proposing new areas of statistical and ecological research to further our understanding of how fish distribute and survive in space. This review serves a dual purpose by emphasizing the scientific importance of studying spatial interactions to better understand the temporal dynamics of fish abundance, and by promoting the development of new analytical and ecological approaches for the analysis of spatial data. Through our survey we cover different statistical techniques, marine ecosystems and life stages. This analytical, geographic and ontogenetic variety is also purposely selected to highlight the importance of comparative and multidisciplinary studies across diverging ecological disciplines, ecosystems and life stages. Besides having a general ecological relevance this review also bears a more applied significance, owing to the increasing need for protecting renewable marine resources along with their primary habitat.

Keywords: Fish spatial ecology; GAM; Geostatistics; Spatial autocorrelation; Scaling; Zero inflation

1. Introduction

A central challenge in fisheries ecology is to understand why species abundance changes over time (Sissenwine, 1984; Cushing, 1990). Consequently, the majority of fisheries research focuses on temporal variability of fish populations. Within this context, demographic (i.e., population abundance) and environmental variables are averaged over large geographic areas, and their degree of correlation is then examined (e.g., Ciannelli et al., 2004a; MacKenzie and Köster, 2004). This time series approach continues to shed light on how density-independent (i.e., environmental) and density-dependent (i.e., demographic) variables interact to affect the dynamics of species abundance (e.g., Bjørnstad and Grenfell, 2001). However, species can experience different environmental conditions and survival rates throughout their distribution range (Kareiva,

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1990; Tilman et al., 1997; Ciannelli et al., 2007a), and these conditions usually influence the observed abundances. Moreover, it is well-established that species–environment interactions are complex, as they vary over different observational scales (Fauchald et al., 2000), and can be nonlinear (Stenseth et al., 2002; Dingsør et al., 2007) and nonadditive (Ciannelli et al., 2004a). Hence, spatial averages may misrepresent the underlying mechanisms that regulate fish survival and may veil the true underlying relationships that regulate abundance. It follows that a better understanding of how species distribute and survive over space (or more succinctly: *spatial fisheries ecology*) will ultimately lead to a better understanding of how species abundance changes over time.

Spatial fisheries ecology, besides having direct applied relevance to resource management, also bears a broad ecological significance. There is in fact an increasing emphasis on protecting marine ecosystems in their entirety (Botsford et al., 1997). This poses a scientific need to spatially characterize marine ecosystems (Dayton et al., 2000; Ciannelli et al., 2004b) and calls for a better understanding of what actually constitutes habitat quality (Sale et al., 2005; Dahlgren et al., 2006; Agostini et al., 2008-this volume).

The need to sustainably manage ocean resources has resulted in collections of long-term data on fish spatial distribution in numerous marine ecosystems. In some instances these data are available for different life stages of the same species, as managers are interested in monitoring the progression of a cohort abundance to forecast the year class strength (i.e., recruitment). The availability of spatial data in fisheries science may well exceed that of other marine and terrestrial ecological disciplines, opening up a tremendous potential for new stimulating studies on spatial ecology and resource management. However, fish distribution data are typically characterized by a number of undesirable statistical features which makes their analysis challenging. Furthermore, in marine ecology, as in other systems, different observational scales are likely to highlight different aspects of species–environment interactions (Ricklefs, 1990; Fauchald et al., 2000; Bailey et al., 2005). These complexities speak to the need of implementing and developing statistical techniques better suited to analyze fish distribution. Here, we discuss the progresses made in the analysis of fish spatial data, and highlight the associated statistical challenges. Our emphasis is on ecological interactions (i.e., the patterns and the mechanisms affecting fish abundance and survival over space).

The paper is divided in three parts. The first (Section 2), more statistically oriented, is a survey of most common approaches and relative challenges associated with the analyses of fisheries spatial data. The second part (Section 3) is a case-study implementing these techniques. We conclude (Section 4) by proposing new areas of ecological and statistical research to further our understanding of fish spatial ecology. Although we do not claim new discoveries, it is our hope that this review will have dual benefit. First, emphasizing the scientific importance of studying spatial interactions to better understand the temporal dynamics of fish abundance. Second, promoting the development of new analytical and ecological approaches for the analysis of spatial data. Through our survey we cover different statistical techniques, marine ecosystems and life stages. This analytical, geographic and ontogenetic variety is also purposely selected, to highlight the importance of comparative and multidisciplinary studies across diverging ecological disciplines, ecosystems and life stages.

2. Fish distribution: modeling approaches and analytical challenges

2.1. Modeling approaches

The statistical approaches mostly used to analyze fish spatial abundance data can be loosely grouped in two categories, according to whether the emphasis is on the relationship among neighboring observations or on the relationships among the observations and the co-located environmental variables. The first group is based on techniques initially developed for geological and mining resources (Matérn, 1986; Isaaks and Srivastava, 1989) also known as geostatistical analysis, while the second group is an extension of common regression techniques applied to spatial data (e.g., Guisan et al., 2002). Separately, the two techniques capture important ecological processes of fish distribution, namely, the neighboring effect of other fish (e.g., schooling) and of environmental forcing (e.g., water temperature). It is also important to note that both analytical techniques attempt to model the local species abundance (y_i) based on a similar underlying statistical model of the type:

$$y_i = \mu_i + e_i \qquad (1)$$

where μ is a mean effect (i.e., the known and explainable portion of the model) and e is the error (the unknown portion of the model). The geostatistical approach places greater emphasis on the error structure, while the regression approach emphasizes the mean effect.

2.1.1. Geostatistics

We first briefly survey some main concepts for characterizing the spatial dependence among a set of observations. The *variogram* provides a spatial partitioning of the sample variance (Rossi et al., 1992). Given a variable x measured at several locations identified by the subscript i, the sample or *empirical variogram* $\gamma(h)$ at a specific lag-distance h, is estimated as the semivariance among all pair of points N separated by the distance h:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} (x_i - x_{i+h})^2 \qquad (2)$$

The quantities x_i and x_{i+h} are the abundance estimates at the two sides of the distance vector (h). The empirical variogram can be standardized by dividing each estimate by the overall sample variance (s^2). An increasing semivariance estimate over increasing distances is indicative of a spatial correlation among samples. As shown in Fig. 1, both the age-0 Atlantic cod catches in the Barents Sea and the adult Pacific cod (*Gadus macrocephalus*) catches in the Bering Sea are highly correlated over space, and their respective variograms are of increasing shape.

The semivariance cannot be estimated at distances below those of the sampling scale, and even at the smallest sampling distance estimates are likely to be higher than zero due to measurements errors. As a consequence, the variograms always start at a positive value along the *Y*-axis, defined as the *nugget* (τ^2). For increasing distances among sampling stations, observations tend to be less correlated, and the semivariance will accordingly increase until the distance reaches a point where observations are uncorrelated, defined as the *sill* (σ^2). The distance at the sill is defined as the *range* (ϕ) and thus represents the smallest spatial scale at which data points are uncorrelated. The difference between the nugget and the sill, over the range, is indicative of the total sample variance (s^2) explained by spatial correlation structure of the data. Both the age-0 Atlantic cod and the Pacific adult cod have a comparable and relatively large nugget, sill and range.

Statistical models can be fit to the empirical variograms to obtain the *theoretical variogram*. Different models can be used to fit an empirical variogram.

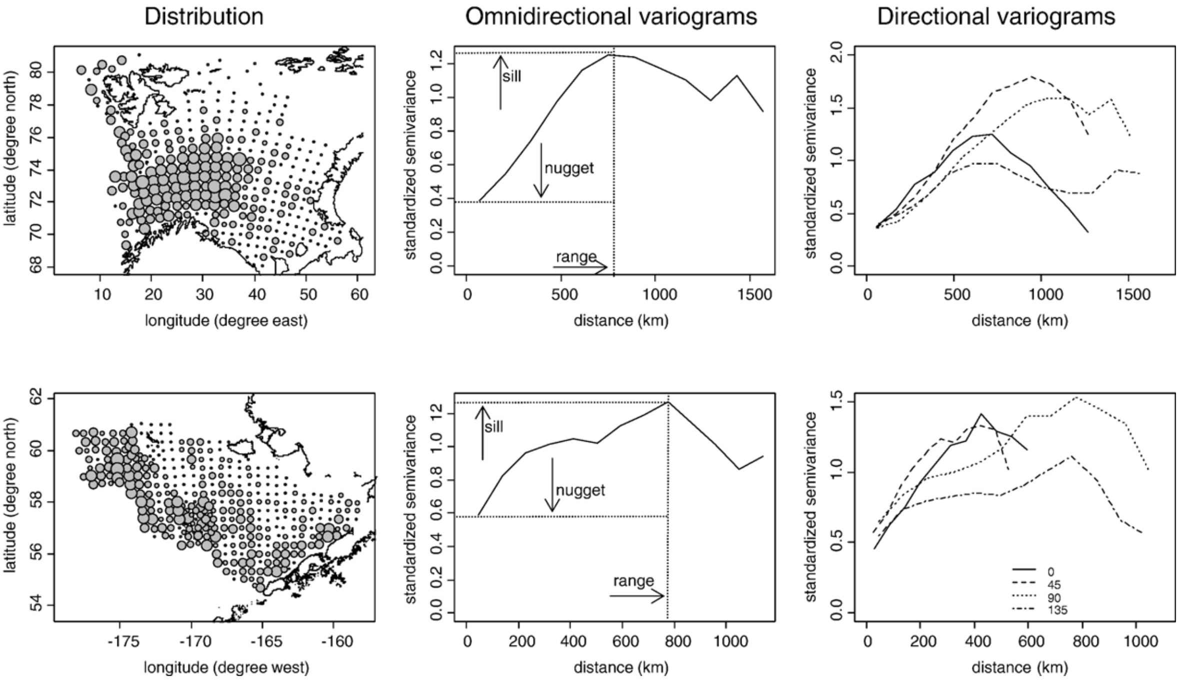

Fig. 1. Plots of spatial distributions (left column), and omnidirectional (center column) and directional variograms (right column) for Barents Sea age-0 Atlantic cod (*Gadus morhua*, top row) in 2005 and for Bering Sea adult (age-2+) Pacific cod (*Gadus macroephalus*, bottom row) in 1990. The radius of the circles in the distribution plots is proportional to the logarithmic standardized species abundance. The increasing shape of the variograms as a function of distance (km) indicates spatial autocorrelation. Also shown in the variograms are the approximate locations of the *nugget*, *sill* and *range* (see text for more explanations). The tolerance angle for the directional variogram estimates was 22.5°. Only distances with >50 pairs were included in the analysis. Both data sets show sign of *anisotropy*, being the shape of the variograms different for the different angles examined.

The most common shapes include the exponential, spherical, Gaussian, linear or more generally the Matérn class of isotropic covariograms (see Matérn, 1986; Handcock and Stein, 1993; Handcock and Wallis, 1994). The choice of theoretical variogram to be applied depends on how close a fit can be obtained between the shape of the intervening model and the residual spatial variation.

The degree of correlation between two sets of abundance estimates separated by the distance *h* can also be estimated by their spatial covariance (*C(h)*):

$$C(h) = \frac{1}{N(h)}\sum_{i=1}^{N(h)}(x_i - \overline{x})(x_{i+h} - \overline{x}) \tag{3}$$

where $\overline{x}$ is the mean of the data. The spatial covariance can be expressed in the standardized form, as a correlogram (*ρ(h)*), by dividing it for the overall data variance (s^2):

$$\rho(h) = \frac{1}{N(h)}\frac{\sum_{i=1}^{N(h)}(x_i - \overline{x})(x_{i+h} - \overline{x})}{s^2} \tag{4}$$

Correlograms are particularly useful in detecting scales of patchiness (Legendre and Fortin, 1989). Generally, for a spatial patchy pattern the autocorrelation at the shortest distance class is positive and then decreases for increasing distance. When the distance corresponds to the distance between patch and non-patch, the autocorrelation becomes negative. Thus, the first *X*-intercept of the autocorrelation function indicates the characteristic scale of a spatial structure. When the distance corresponds to the inter-patch distance, the autocorrelation becomes positive again. Thus, for a regular multi-patch field, the correlogram will oscillate between negative and positive values. This point will be further illustrated in a later application of variograms and correlograms to a patchy data system.

Variograms and correlograms can be *omnidirectional*, if the lag separating two sets of points is only a scalar or *directional* if the lag is defined by both a scalar and a direction. Directional variograms are used to inspect differences (or lack thereof) of spatial correlation over different directions — a condition known as *anisotropy* (*isotropy*). Anisotropy is clearly evident in both the age-0 Atlantic and the adult Pacific cod, as their respective variogram estimates differ according to the direction considered (Fig. 1). In the latter case, variograms in the 0° and 45° directions (with origin at the positive *x*-axis and increasing angles counterclockwise) are characterized by a sharper increase of semivariance over distance, indicating a steeper gradient of cod catches in these directions. A strong anisotropy may indicate the existence of a *trend* in the spatial data (i.e., *nonstationarity*), a condition characterized by the mean changing as a function of location and by the variance changing as a function of both distance among samples and location. A trend is apparent in the adult cod catches in the Bering Sea, as the bulk of the biomass is spread in the southeast–northwest direction (about 135°, Fig. 1). Trends in the data may reflect environmental forcing, due for example, to thermal or bathymetric gradients.

Variogram estimates can be used to model spatial data as a function of their correlation structure and of other co-located predictor variables. For example, fish abundance $Y_i (i=1,\ldots N)$, can be modeled as a function of habitat quality at that location x_i , and by other fish in surrounding locations $\mathbf{x}_j = 1,\ldots,i-1,\ldots N, j \neq i$.

$$Y_i = \mu_i + S(\mathbf{x}_i) + \varepsilon_i \tag{5}$$

where μ_i is a mean effect, x_i the observation location, $S(\mathbf{x}_i)$ is the spatial dependence term represented as a stationary Gaussian process with expected value $E[S(x)]=0$ and cov $[S(\mathbf{x}_i), S(\mathbf{x}_j)] = \sigma^2\ \rho(\mathbf{x}_i - \mathbf{x}_j)$ (σ^2 = variance; ρ = correlation coefficient) and ε are mutually independent Gaussian random variables with mean = 0, and variance = τ^2 (Diggle et al., 1998). In biological terms, μ_i the effect of habitat, is modeled as a function of co-located variables (e.g., $\mu_i = \beta_0 + \beta_1 * C_1 + \beta_1 * C_1^2$, where C_i is a covariate measured at location x_i). Note that the effect of co-located covariate is often assumed to be linear in the coefficients, even though these may have a nonlinear effect.

Geostatistical analyses have been often applied to fisheries and marine ecology data. Most of these applications focus on stock abundance and variance estimates (e.g., Fletcher and Sumner, 1999; Rivoirard et al., 2000; Petitgas, 2001; Wieland and Rivoirard, 2001; Bez, 2002). Ecological applications of geostatistical analyses have been very useful for a number of purposes, including: (a) spatial characterization of fish distribution in relation to biomass (Petitgas, 1998) or season and geographic areas (Mello and Rose, 2005), (b) patterns of spatial correlation over progressively increasing scales (Fauchald et al., 2000), (c) nested spatial structures (Maravelias et al., 1996; Fauchald et al., 2000), (d) spatial distribution of fish in relation to physical habitat (Sánchez and Gil, 2000; Agostini et al., 2008-this volume). Furthermore, geostatistical estimates of spatial dependence can be readily extended to two co-located sets of data, for example to study the correlation structure between two different species (e.g., predator and prey aggregation and distribution, Fauchald and Erikstad, 2002).

2.1.2. Regression

The second category of statistical models of spatial data that we will consider here are an extension of the common regression analyses. We focus exclusively on regression techniques which do not assume linearity. In particular, we describe the use of multiple penalized regression splines, known as Generalized Additive Model (GAM, Hastie and Tibshirani, 1990; Wood, 2004a, 2006). Given a response variable y and a set of m forcing variables x (covariates), the relationship between the two is established by:

$$y_i = \alpha + \sum_{j=1}^{m} g_j\left(x_{ji}\right) + e_i \tag{6}$$

The g_j are smooth nonparametric functions, typically natural cubic splines (Green and Silverman, 1994). The extension of GAM to two-dimensional data (e.g., latitude and longitude) is accomplished with thin-plate regression splines (Wood, 2003). In recent applications of GAM, the number of degrees of freedom for each smooth function can be simultaneously estimated by minimizing the model generalized cross-validation (GCV), a measure of the leave-one-out mean predictive square error (Green and Silverman, 1994). To guarantee that the model is identifiable, each function estimate is constrained to average to 0 over the entire data set, i.e.$\sum_{i=1}^{n} g_j\left(x_{ji}\right) = 0$, where n is the sample size. Thus, to scale the model prediction back to the level of the response variable, an intercept term (α, typically equal to the mean of y) is added to the sum of all the smooth terms. The error terms e_i are generally assumed to be independent and identically distributed with zero mean and common variance, but in very recent applications it is possible to generalize the model to allow for (spatially) correlated errors (Wood, 2004b).

There are numerous applications of GAM to marine ecology and fisheries spatial data (for a general review see: Guisan et al., 2002). These include, but are not limited to, distribution study of eggs (Fox et al., 2000; Wood and Augustin, 2002; Ciannelli et al., 2007b), tuna (Zagaglia et al., 2004), seatrout (Kupschus, 2003), crabs (Jensen et al., 2005), squids (Denis et al., 2002), flatfish (Swartzman et al., 1992; Simpson and Walsh, 2004), herring (Maravelias et al., 2000), and fish stomach contents (Stefansson and Palsson, 1997; Trenkel et al., 2005). Probably the main motive behind the proliferation of GAM applications is their versatility in modeling different functional responses between the species and the co-located environmental variables.

2.2. Analytical challenges

Spatial marine fisheries data are characterized by a number of undesirable statistical features which challenge their analysis through the currently available statistical techniques. These features are: (1) patchiness, (2) scale dependency (3) excess of zero or low counts (zero-inflated counts) and (4) spatial correlation. In addition, the many variables that locally affect fish abundance can interact among each other to affect the outcome — a feature known as nonadditivity. In this section we will discuss each of these features, the challenges they present, and the opportunities that both GAM and geostatistical tools offer in addressing them.

The spatial distribution of marine organisms is highly patchy over a range of spatial and temporal scales (Murphy et al., 1988; Fauchald et al., 2000; Fauchald and Erikstad, 2002). This spatial complexity is a result of the interplay between ecological and behavioural interactions and the physical environment of the sea (Wiens, 1989; Ricklefs, 1990; Mann and Lazier, 1991; Levin, 2000). Moreover, the various abiotic and biotic processes operate on different spatial and temporal scales (Levin, 1992). While large-scale physical properties of the ocean might limit the potential habitat of an organism, the local distribution may be determined by ecological interactions, such as competition and predation, occurring at smaller scales. Such scale-dependent spatial processes are often hierarchically interlinked so that large-scale processes sets the conditions for processes at smaller scales (Wu and Loucks, 1995). For example, large-scale heterogeneity in primary production may determine the distribution of prey. The resulting spatial pattern of the prey may form the primary focus for an aggregative response of a predator. At smaller scales the prey may try to escape predation through predator avoidance. Often, these hierarchically linked spatial processes generate nested patch mosaic hierarchies where small-scale patches are nested within patches at larger scales (Kotliar and Wiens, 1990; Fauchald et al., 2000).

A hierarchical patch mosaic structure challenges the way of doing analyses of spatial relationships and structure because the spatial pattern at a particular scale is masked by the pattern at other scales. Assume a likely scenario where two organisms (species A and B) have a positive spatial association on a large-scale and a negative spatial association on a small scale. The large-scale positive association might for example be due to similar habitat preferences or it might be a result of a predator–prey interaction where the predator aggregates in large-scale areas of high prey densities. The small-scale negative association might for example be due to intense local competition or it might be due to predator avoidance or simply local consumption of prey. In Fig. 2A we have simulated such a simple set of two-scale interactions. On a large-scale, species A and B are aggregated in the same patch while on a small scale, species B avoid species A. Plotting the density of species A against species B using a small measurement scale (the scale that matches the small-scale interaction) gives a highly zero-inflated plot with no clear relationship (Fig. 2B). Clearly, in this plot, the small-scale negative interaction is masked by the large-scale interaction and vice versa. When the measurement scale is increased, the small-scale interaction is averaged out and the positive large-scale interaction is revealed (Fig. 2C). Accordingly, to identify the large-scale interaction one has to remove the noise from smaller scales by aggregating the data. However, in order to identify the small-scale interaction one has to remove the masking effect of the large-scale process by identifying and controlling for it in the analyses. Thus, the plot of the total sample on a small spatial scale is confounded by the interactions on both scales and accordingly shows no clear relationship (Fig. 2B). However, plotting the data inside the large-scale structure (Fig. 2D) reveal the small-scale negative relationship. This simple system is hierarchically interlinked in the sense that the large-scale interaction sets the conditions for the small-scale interaction to occur. Obviously, the small-scale interaction occurs with higher intensity under high density. Thus, the spatial pattern of species B is hardly affected by the distribution of species A outside the large-scale patch while the opposite is true within the large-scale patch.

Zero inflation and spatial correlation are a direct consequence of the patchy nature of marine spatial data and result in highly right-skewed histograms (Fig. 3) and variograms with increasing shape, respectively (Fig. 1). The biological origin of both zero inflations and spatial correlation are several, including the natural tendency that fish have to school (Fréon and Misund,

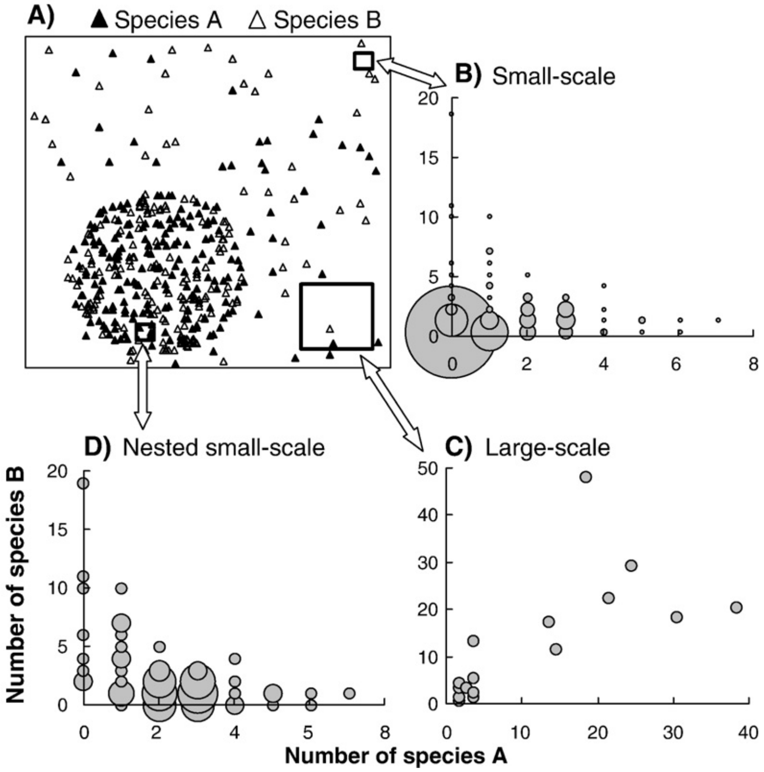

Fig. 2. A) Simulation of a spatial interaction between two species where both species are aggregated in the same large-scale area but where species B avoid species A at a small spatial scale. B), C) and D) are plots of the number of species A versus the number of species B within quadrates with sizes as indicated. The area of the circles is proportional to sample size. B) and C) are plots of the total area for small and large measurement scale (quadrate size) respectively. D) is a plot on a small measurement scale for the data *within* the large-scale patch.

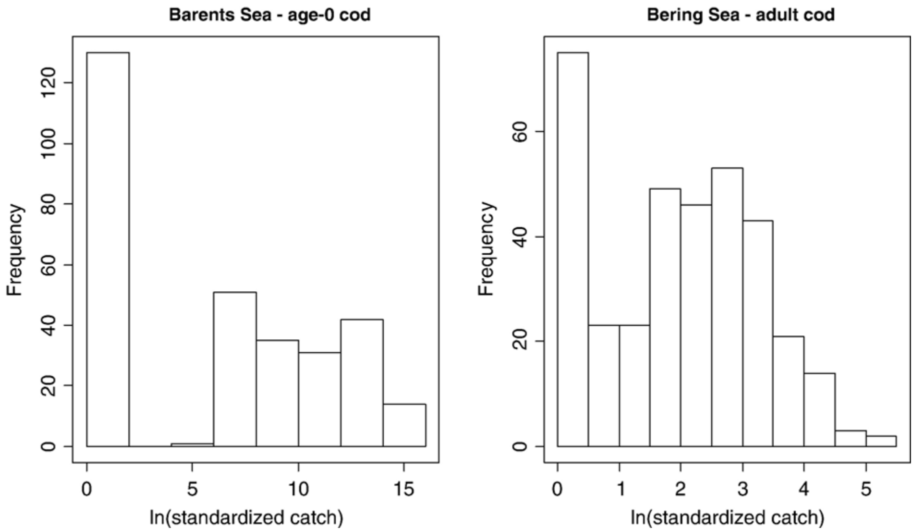

Fig. 3. Histograms of the 2005 age-0 Atlantic cod (left) and of the 1990 adult Pacific cod (right) samples. Both histograms illustrate the excess of zero samples.

1999), a similar responses to an environmental variable which is also spatially correlated (e.g., water temperature), or an aggregative response toward conspicuous topographic or hydrographic features (e.g., seamounts, canyons, fronts and eddies, e.g., Genin, 2004).

Zero inflation limits the use of GAM and geostatistical approaches. The high number of zeroes generally requires the use of non-exponential-family response distribution, e.g. mixture of zero and a Poisson distribution (Fig. 3). Some researchers have modified geostatistical approaches to deal with highly skewed data (Cressie and Hawkins, 1980; specific applications for fisheries in Maravelias et al., 1996; Mello and Rose, 2005). Cunningham and Lindenmayer (2005) reviewed current analytical approaches to model zero-inflated counts in ecological data. One simple solution is to eliminate the zero from the data and to only focus the analysis on the presence observations. While this approach may correct the skewness problem, it may also yield biologically unrealistic results, because part of the data is discarded. A second approach, the two-step approach or conditional modeling, is to first model the presence/absence using a binomial distribution, and then to model the species abundance conditional on the presence, using a truncated Poisson or negative binomial distribution (Welsh et al., 1996). Stefansson and Palsson (1997) and Fox et al. (2000), among others, used the two-step approach to model distribution of fish stomach content and fish eggs, respectively. While the two-step approach retains the information carried by the zero-counts and produces unbiased predictions, it makes inference rather complicated as there are two sets of environmental effects to consider, those from the presence/absence and those from the abundance model — often with contradictory results (Barry and Welsh, 2002). Finally, the two-step approach still heavily relies on the assumption that the observations are independent (i.e., not spatially correlated). Thus, the effective modeling of zero-inflated data is still a challenging issue in ecological statistics.

In order to effectively capture spatial relationships, the influence of spatial correlation needs to also be identified. Statistical models that do not consider autocorrelation may result in rejections of a true null hypothesis (i.e., Type I error) more often than the nominal tolerance level (Legendre et al., 2002). In fact, in highly spatially correlated data the same information is used several times, causing an unjustified increase of the sample size, and a bias in the variance estimate (Legendre, 1993). Also, regression analyses without accounting for the inherent spatial correlation may result in an excessive nonlinearity of co-located covariate effects, c.f. Wang (1998). This issue is particularly relevant to GAM techniques, where the shape of the underlying model function is *a posteriori* determined from the data. Bootstrap routines may help drawing robust inferences in the presence of spatial correlation (Stige et al., 2006), but may not necessarily solve the issue of excessive nonlinearity. In this particular case, it may be advisable to *a priori* impose an upper limit on the degrees of freedom of the smooth covariate functions.

Geostatistical models overcome these problems by explicitly accounting for the correlation effect in the spatial distribution of the examined data. This is typically done by including a spatial dependence term (Eq. (5)). However, the emphasis of geostatistical approaches on the correlation structure of the data may mask some underlying species–environment relationships that are responsible for causing the autocorrelation in first place. For example, fish may aggregate in space because of a similar response to an environmental variable which is also spatially correlated (e.g., bathymetry).

In contrast to geostatistcal techniques, GAM emphasize the mean portion of the model, therefore attempting to explain the spatial pattern of the data solely based on the effect of the examined co-located variables. However, the theoretical basis of GAM approaches reveals other inherent limitations, such as the additivity condition. Given two covariates (x_1 and x_2), their effect on the variable y is additive if the conditional mean response given x_1 and x_2 equals:

$$E(y_i|x_1,x_2) = f(x_1,x_2) = f_1(x_1) + f_2(x_2) \tag{7}$$

In words, the additivity condition implies that the effect of any particular covariate on the response variable is independent of the level of other covariates in the model. There are many instances in which such condition is not met in fisheries spatial data. For example, predation is assumed to be a size-selective process (Sogard, 1997), so that prey of different sizes distributed over different regions may have different vulnerability to the same predation pressure. Similarly, it is well-established that the physiological responses of fish to temperature change through the ontogeny (Post and Lee, 1996), so that fish of different sizes (ages) distributed in different regions may differently respond to a similar thermal regime. Lack of additivity (i.e., nonadditivity) is also common between two-dimensional (e.g., space) and unidimensional covariates. An extreme case of nonadditivity over space may take the form of a threshold response, resulting in drastic re-arrangement of fish distribution following subtle changes of forcing variables. Threshold responses are common in species distribution data (Turner, 2005), and in marine ecology may occur over contrasting climate periods (Perry et al., 2005). Similar re-arrangement of species distribution may also occur in relation to demographic variables (e.g., the average abundance of the studied species) and are known as density-dependent habitat selection (Swain and Wade, 1993; Swain, 1999; Simpson and Walsh, 2004).

The additivity condition can be in part circumvented by allowing the GAM model formulation (Eq. (6)) to change over different temporal or environmental regimes. This is readily accomplished by introducing a threshold variable which indicates the environmental regime. Specifically,

$$y_i = \sum_{j=1}^{k} g_j(x_{ji}) + e_i + \begin{cases} \alpha_1 + s_1(\varphi_i, \lambda_i) & \text{if } E_i \le r \\ \alpha_2 + s_2(\varphi_i, \lambda_i) & \text{if } E_i > r \end{cases} \tag{8}$$

The variable in E is a threshold covariate (or a set of covariates) that partitions the effect of position (specified by latitude φ and longitude λ) over a ‘low’ or a ‘high’ environmental or temporal regime. Similar thresholds can also be applied to other covariates (x) included in the regression. The threshold level (r) of the covariate E, separating the two regimes, can be chosen by minimizing the model Generalized Cross Validation (GCV) — a measure of the model predictive squared error (Green and Silverman, 1994). In the examples provided below we refer to this nonadditive model formulation as TGAM, where T stands for ‘threshold’.

3. Progresses in the analysis of fish spatial data

3.1. Ecological scales of investigations: The hierarchical approach

The hierarchical and patchy nature of fish spatial data highlights the importance of carefully disentangling the various spatial structures that operate over different spatial scales. A large-scale spatial structure will be detected by the analyses and will necessarily mask any spatial pattern at finer scales. Large-scale trends can be removed by regression analysis, stratification according to large-scale environmental features or by nested spatial analyses. This last procedure was followed in the study of Fauchald et al. (2000), where the spatial interaction between capelin (*Mallotus villosus*) and seabirds preying on capelin (murres, *Uria* spp.) was scrutinized using auto- and cross-correlation analyses (Fig. 4). First, the data were analysed on a low resolution to detect large-scale spatial patterns. Then, large-scale patches of capelin were defined by successively removing the observations with the lowest densities until the first order autocorrelation (correlation at the first distance class) for the remaining data points was less than 0.1. By applying this procedure, the remaining dataset represents the high density areas with a small (<0.1) large-scale internal autocorrelation. Nested spatial pattern within these large-scale capelin structures were then analysed by auto- and cross-correlation functions with data aggregated at a higher resolution. The same steps were performed until

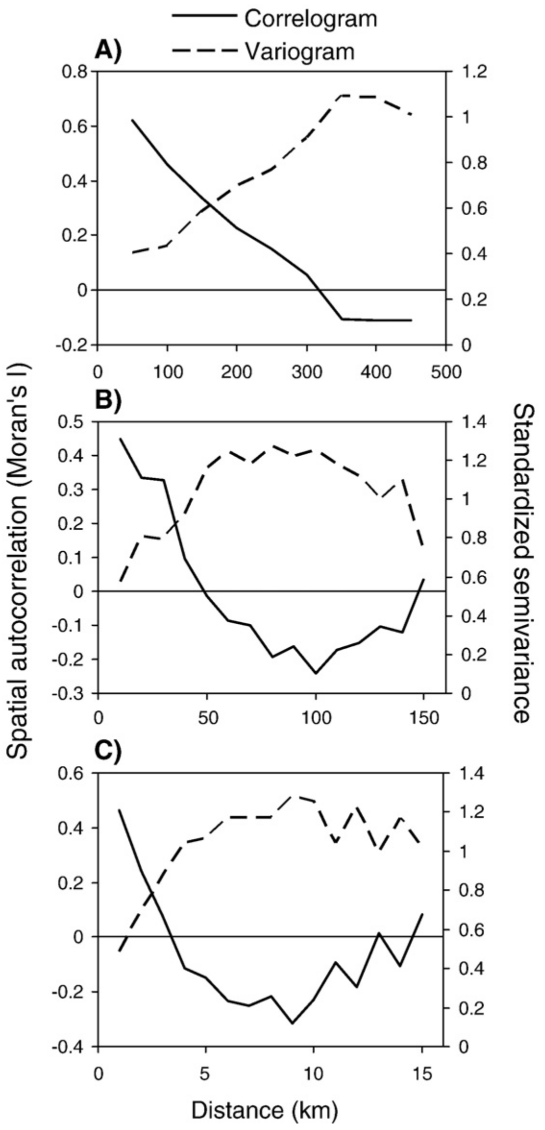

Fig. 4. Nested spatial analyses of acoustic data of capelin from the Barents Sea. Data are from Fauchald et al. (2000). Data were log(X+1)-transformed and standardized to mean equal to zero and standard deviation equal to one within each defined patch. For definition of patches see text. A) Large-scale variogram and correlogram for data aggregated within circles with a radius of 25 km. B) Medium-scale variogram and correlogram for observations within the large-scale patches. Data were aggregated within circles with a radius of 5 km. C) Small-scale variogram and correlogram for observations within the medium-scale patches. Data were aggregated within circles with a radius of 0.5 km.

the highest resolution (i.e., small scale) was reached. The so-described procedure gave the opportunity to investigate spatial pattern and interactions at three nested hierarchical levels. The correlogram and variogram estimates in Fig. 4A indicate that capelin at the largest scale were aggregated within patches with a diameter of hundreds of kilometers. Within these large-scale patches capelin were aggregated at a scale of about 50 km (Fig. 4B) and within these medium-scale patches capelin were aggregated at a scale of only a few kilometers (Fig. 4C). At the two largest scales in the patch hierarchy, murres and capelin had similar and overlapping spatial structures, while at the smallest scale the two species had similar but non-overlapping spatial structures, indicating that murres were able to follow the spatial distribution of capelin on large-scales but that capelin successfully avoided predation on a small scale. Similar scale-dependent patterns between predator and prey have also been observed for other species (e.g., Rose and Legget 1990). The characteristic schools of capelin occur at even smaller scales, suggesting the existence of at least one more level in the hierarchy. Temporal and spatial scales are tightly interlinked (Haury et al., 1978). By including time in the spatial analyses, Fauchald et al. (2000) showed that the large-scale capelin patches changed position within weeks while medium-scale patches lasted for several days.

3.2. Spatial correlation: The geostatistical approach

In order to carefully disentangle the multiple processes that drive fish distribution, it is essential to use tools that effectively capture spatial correlation structures as well as the effects of co-located variables. Not accounting for one or the other may point to erroneous relationships. The study reported in this volume by Agostini et al. (2008-this volume) illustrates the potential pitfalls of not capturing multiple processes. The authors use a geostatistical approach to examine the processes driving Pacific hake (*Merluccius productus*) distribution in the west coast of USA and Canada. Previous studies indicated that hake distribution may be affected by water temperature, with hake expanding further north during warm years. However, recent study points to the importance of poleward undercurrent as a factor affecting hake habitat quality (Agostini et al., 2006). Here we show comparisons among models with and without spatial dependence. The results show that the shape of the relationship between hake distribution and poleward current flow, one of the co-located variables included in the analysis, would be different if an autocorrelation component had not been included (Fig. 5).

3.3. Changes of distribution patterns: The threshold GAM approach

We present the main results of a recent analysis (Ciannelli et al., 2007b) implementing GAM and

TGAM techniques to model the distribution of walleye pollock egg data in Gulf of Alaska (GOA). Historically, the GOA pollock used to spawn during a two-week period at the end of March and the beginning of April in the Shelikof Strait, between Kodiak Island and the Alaska Peninsula (Kendall et al., 1996). Through the last decade however, spawning biomass in the Shelikof Strait has greatly dwindled (Dorn et al., 2004) while in other areas along the Alaska Peninsula (Dorn et al., 2004) and in coastal areas (Anderson and Piatt, 1999) pollock biomass has actually increased. Pollock eggs were also collected during these years of change in adult spawning distribution. Ciannelli et al. (2007b) analyzed the egg collections to assess whether similar changes in distribution occurred also at the egg stage.

Both a GAM (Eq. (6)) and a TGAM formulation (Eq. (8)) were applied to the analysis of the pollock egg data. The latter formulation, with year of sampling as a threshold, allowed to model patterns of egg distribution that changed over time. In addition to position, bottom depth and time of the year (expressed as Julian days) were included in the model as covariates. While the results of the egg abundance through a GAM model corroborated the existence of a high spawning activity in Shelikof Strait, the analysis also highlighted the presence of other secondary centers of egg distribution on various locations along the shelf and slope regions (Fig. 6). The results from the TGAM formulation indicated that the relative importance of the non-Shelikof spawning locations has increased over time, with a shift in distribution estimated to occur in 1989 (Fig. 6). Based on the GCV score, the TGAM formulation was superior to a GAM formulation, indicating that the change in adult spawning distribution was also followed by a change in egg distribution.

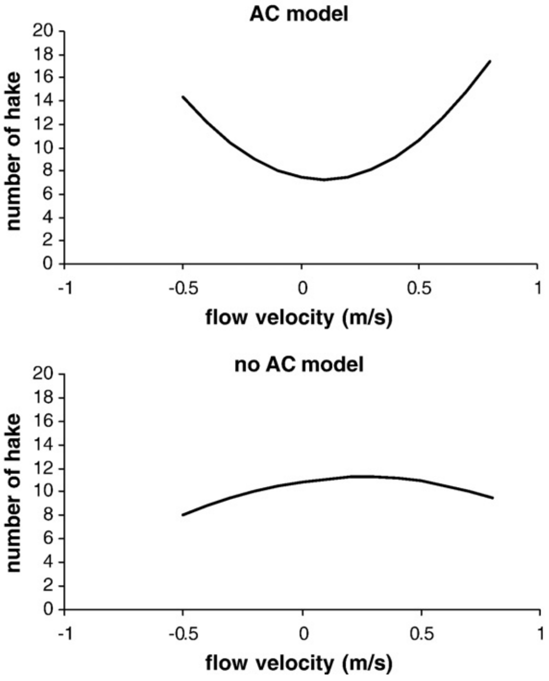

Fig. 5. Shape of the functional relationship between hake abundance and poleward current in the Northeast Pacific with (upper panel) and without the autocorrelation (AC) term (lower panel) (Agostini et al., 2008-this volume).

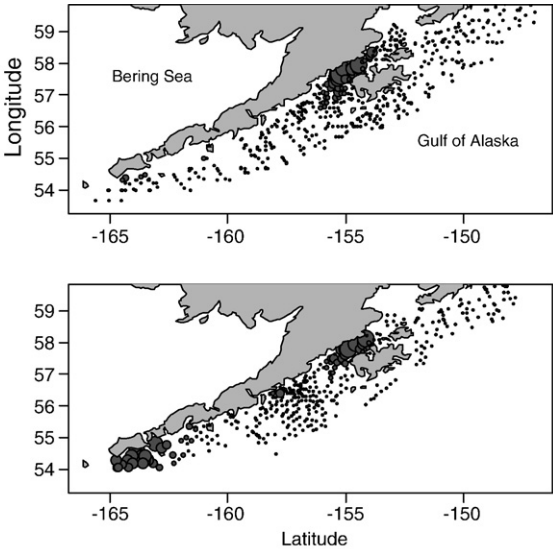

Fig. 6. Average distribution of walleye pollock (*Theragra chalcogramma*) eggs as estimated from a TGAM formulation before (top panel) and after (lower panel) 1989 — the estimated year of change in egg distribution (Ciannelli et al., 2007b).

4. Conclusions

The processes underlying the spatial distribution of fish populations can be ecologically complex, as they operate on a variety of scales, change through species ontogeny and over different environmental regimes and are often nonlinear and nonadditive. Thus, the study of fish spatial data is punctuated by a number of ecological and analytical challenges, some of which are hitherto unsolved. In the remaining part of the paper we concentrate on these unsolved challenges, and propose new ecological and statistical areas of investigation to overcome them.

Predator–prey interactions can generate spatial and temporal variability of species abundance and survival. Indeed a prerequisite of a successful capture and consumption event is that the predator and the prey spatially overlap. In marine ecology, the study of spatial overlap between predator and prey has primarily focused on contact scales (e.g., Rose and Legget, 1990; Fauchald et al., 2000; O'Driscoll et al., 2000). An example, based on simulated data, is here shown in Fig. 2. On field data, Rose and Legget (1990), studying Atlantic cod and capelin spatial association in northeast Canada, illustrated how on large spatial scales the predator and the prey are predictably and positively associated while on smaller scales the correlation disappears or becomes negative. The authors also underscore the importance of environmental variability as an important factor affecting predator–prey overlap and contact scales — an emphasis echoed in the recent work by Neuenfeldt and Beyer (2006) on cod distribution in the Baltic Sea and by Ciannelli and Bailey (2005) on cod–capelin interactions in the Bering Sea. However, studies that explicitly focus on the spatio-temporal variability of predator–prey overlap still remain rare. This is a significant knowledge gap in fisheries spatial ecology, given that predation is one of the primary mechanisms that locally affect fish abundance, particularly during juvenile stages and in forage species.

Fish–environment interactions can also generate spatial and temporal variability of species abundance and survival. Physical processes can directly influence organisms for example by impacting their physiology or by facilitating spatial processes such as migration and offering competitive advantages that may improve their survival. Physical processes can also indirectly influence organisms by forcing their distribution to specific locations characterized by certain abundances of prey, competitors or predators which ultimately directly impact their survival. Most studies focusing on the relationship between fish abundance and environmental forcing usually involve the aggregation of impacts across large spatial scales and range of ontogenetic stages. For example, climate metrics are often used to explain either fish abundance or distribution variability (e.g., Perry et al., 2005). This approach has been instrumental in detecting patterns of fish spatial dynamics over contrasting environmental regimes. However, changes in distribution can often be the result of smaller scale variability, like those associated with the physical and biological feature of the species habitat, that are not clearly identifiable through these large-scale climate indices. Some authors use small-scale spatial data to address physical mechanisms that may explain fish distribution patterns (e.g., Sánchez and Gil, 2000; Agostini et al., 2006). For example, Agostini et al. (2008-this volume) use acoustic data on distribution of hake and physical parameters to examine processes that force the distribution patterns of Pacific hake in the California Current System. They use a geostatistical approach and predict hake habitat distribution based on poleward flow and bottom depth. This approach allows them to account for both the spatial correlation between observations as well as environmental forcing.

Fish distribution and survival change over the species ontogeny — a fact that underscores the importance of monitoring a year class through its various life stages. This is particularly applicable to pre-recruitment stages (i.e., egg, larval and juvenile stages) where mechanisms of survival are well known to vary through ontogeny (Bailey, 2000; Munch et al., 2005). Spatial pattern of species distribution over different ontogenetic stages, are also indicative of the degree of genetic association and structure among putative subpopulations of the entire distribution range. In this context, the distribution of spawning individuals or egg stages deserves particular attention. Moreover, for marine commercial species, the spawning site is often the location where harvest and the assessment surveys mostly occur, placing a critical management implication on the understanding of phenology and geography of fish spawning habits. Shrinkages in fish distribution can also be an early warning that the population is loosing its genetic or social structure, and that it may be bound to a rapid decline. For example, the collapse of the northwest Atlantic cod (Newfoundland and Labrador Seas) was preceded by shrinkage of their spatial distribution (Atkinson et al., 1997; Warren, 1997). The California sardine population has also been described to significantly shrink its distribution range during low abundance periods (Lluch-Belda et al., 1989; McFarlane et al., 2002).

The investigations of these interesting ecological questions call for the development of new statistical methodologies. In our opinion priority should be given to combine geostatistical and regression techniques in a blend capable of accounting for both the underlying spatial structure of the samples and the nonlinear and nonadditive nature of habitat–species interactions. Recent mixed-effect approach (Wood, 2004b) to fitting a GAM with correlated errors provides an exciting new development. However, in our limited experience, such an approach may sometimes have problems with fitting unbalanced data with complex regression structure. Further work is needed regarding the development of (i) computationally-efficient approaches to fitting nonlinear and nonadditive models with correlated errors and zero-inflated counts, and (ii) their associated theoretical investigations (i.e., inference). The extension of the TGAM to incorporate spatially correlated errors is another interesting problem. Again it is important to develop computationally-efficient algorithms for fitting the TGAM, and to study methods for drawing inference from a TGAM. Another challenging problem is to formulate a model-based approach that includes different processes occurring simultaneously on different spatial scales. Such processes are frequently hierarchically interlinked and for the time being these complex patterns seriously limit our ability to pinpoint important ecological interactions.

The study of fisheries spatial ecology also bears more general implications such as the identification of habitat quality and the establishment of marine protected areas. Spatial ecology studies in fisheries science have primarily evolved around the link between species abundance and environmental variability (e.g., Guisan et al., 2002, and references therein). Such focus is necessary to unravel the processes that regulate species distribution, but it may be misleading when extended to the identification of species habitat quality (e.g., Dahlgren et al., 2006). Conceivably, the location where a species is present with its highest abundance may not necessarily be the location where the species experience the highest survival. Furthermore, the spatial patterns of species survival may change in relation to the background regime of the physical and biological environment (Ciannelli et al., 2007a). There is paucity of studies focusing on spatial patterns of key ecological processes affecting species demographic rates (e.g., survival). Consequently, we lack the basic knowledge to answer simple questions relevant for the management of marine resources, such as: How does population survival change over space? Where and when do species become more vulnerable to predation or to food limitation? Are spatial patterns of survival stationary? And if not, in relation to which processes do they change? The answers to these questions are essential to manage marine renewable resources in a spatial framework and would project our understanding of species habitat quality beyond the concept of species abundance.

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