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Species richness and environmental conditions of fish along the Norwegian Skagerrak coast

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Long-term temporal variation in the community structure of fish species richness over the period 1953–1994 along the Norwegian Skagerrak coast is analysed in relation to abiotic environmental factors (oxygen saturation, salinity and temperature respectively at the sea surface, 10 and 50 m depth). Data on the observed number of fish species derive from a long-term and ongoing beach-seine monitoring programme being conducted each autumn. Data on observed fish species richness are analysed using multivariate techniques especially designed for the coupling of environmental and biological tables (Co-inertia analysis). The correlation structure of the abiotic variables is investigated by applying the STATIS ("**S**tructuration des **T**ableaux **A** **T**rois **I**ndices de la **S**tatistique") multivariate technique. We demonstrate that environmental variables in the deeper waters are linked to the community structure of the coastal zone of the Southern Skagerrak Coast. It is suggested that this effect probably operates through the Norwegian Coastal Current (NCC) and is a proxy measure for advective processes.

Keywords: advection, biodiversity, co-inertia, macroecology, STATIS.

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Introduction

Species richness varies temporally on both regional and local spatial scales because of a multitude of processes (Lawton, 1999; Gaston, 2000; Crawley and Harral, 2001). Biodiversity and ecosystem properties has been studied extensively at the community level (Gaston, 1996) leading to the discovery of several general macroecological patterns (Brown, 1999) and the development of theoretical models to explain them (Loreau, 2000; Loreau, 2001). At local levels carefully designed experiments have provided new insight into fundamental ecosystem functioning (Tilman *et al.*, 1997). However, at larger scales, experiments cannot be undertaken in order to explain emergent patterns and a macroecological and correlative approach is required in order to study the relationships between organisms and their environment (Brown, 1995). In pattern-oriented studies, macroecological, spatio-temporal patterns are seen as a reflection of the causal relationship between species and its environment (Brown, 1995). Using data on the fish community along the Norwegian Skagerrak coast we analyse in this paper the temporal variation of species richness, attempting to demonstrate such a reflection.

Along the Norwegian Skagerrak coast temporal variation has been observed on various temporal and spatial scales. Fromentin and co-workers (1998) demonstrated short-term variability of gadoids (cod-like fish) on a fjord scale and long-term variability on a scale equal to or larger than the entire southern parts of the Norwegian Skagerrak coast. A similar spatial scale of temporal variation was documented for species richness of fish in the nursery areas within the coastal zone (Lekve *et al.*, 1999).

Specifically we aim at identifying patterns of variability and their appropriate spatial scales through the investigation of the influence of extrinsic abiotic processes on species richness of varying and known spatial scales. Finding a correspondence of processes and scale may suggest mechanisms linking physical and biological principles to emergent ecological patterns. Such analyses require that biological and abiotic factors be measured at comparable spatial and temporal scales. Few appropriate long-term data sets of natural variability of both biological and environmental variability exist which can be used for such analysis. However, we do have access to such data from the Norwegian Skagerrak coast. Since the turn of the 19th century marine fish in the coastal zone has been monitored by beach seine surveys every autumn (Solemdal, 1997; Lekve *et al.*, 1999). From 1927 these surveys were supplemented by the standardized monitoring of environmental variables (Johannessen and Dahl, 1996) and the number of stations has steadily increased since then.

Measurements of three abiotic variables, oxygen saturation, salinity and temperature respectively, are available at three different depths. In shallow depths, these variables are all known to have a direct influence on some or all of the fish species in the coastal zone (Wootton, 1990), while for the deeper waters they probably act as proxies for larger-scale processes such as basin-wide currents. Less is known, however, about abiotic influence at the community level. The investigation of such community-level effects is the overall topic of this paper.

Oxygen saturation may be seen as a proxy for the growth conditions, especially for plankton. Decreases in oxygen saturation may be due to increased oxygen consumption caused by increased eutrophication (Mann and Lazier, 1991). We thus expect that observations of low oxygen saturation in the fall are indicative of unfavourable growth conditions for several species in the nursery phase in the spring and thereby create low species richness. This effect is closely linked to the stratification of the water masses (Mann and Lazier, 1991); we expect less effect at the sea surface compared to deeper, more stable water masses.

Salinity within normal ranges probably exerts a weak direct effect on fish (Wootton, 1990). In our dataset salinity is probably an indicator of freshwater runoff and thus of nutrient supply from the land (Mann and Lazier, 1991). As several of our study sites are located within fjords the rivers supply permanent freshwater runoff. We expect, therefore, that salinity will represent a local effect on species richness in general and specifically for salinity in the upper water masses.

Temperature is known to influence the metabolism of most organisms (Wootton, 1990). High temperature creates high metabolism and subsequent high demands for food. However, high temperature also facilitates high activity, which is necessary for food search for active fish predators and high growth of algae and zooplankton, which forms the basis of the food chain. We believe the latter effect to be stronger than the former (Lekve *et al.*, 1999; Lekve *et al.*, 2002a) and thus expect that temperature will be positively related to patterns of species richness.

In order to explore the validity of these expectations, in this paper we examine possible covariability of long-term patterns of fish species richness and environmental factors (i.e. oxygen saturation, temperature and salinity at three depths) in the coastal zone along the Norwegian Skagerrak coast. We apply multivariate techniques in order to couple the spatial patterns of temporal variability of diversity and environmental factors and test the significance of these. Finally, we use the obtained covariation structure to infer spatial scales and suggest mechanisms responsible for the observed patterns.

Materials

The Norwegian Skagerrak Coast consists of skerries and medium sized fjords (Figure 1). The only major fjord is the Oslofjord (length 110 km) and this is strongly influenced by a sill at 19 m depth close to Drøbak (Figure 1) acting as a natural barrier against the replacement of the water of the inner basins. The bottom water layers in the inner Oslofjord are, as a result, replaced only every 6–8 years; Andersen *et al.*, 1970. In contrast, the outer part of the Oslofjord is characterized by extensive exchanges with the open Skagerrak waters. The south-western part of the Norwegian Skagerrak coast (called the "Southern coast" in the following) and the Oslofjord area (the Oslofjord and the areas along the entrance of the fjord) have been found to differ in several respects (see, e.g. Bjørnstad *et al.*, 1999; Lekve *et al.*, 1999).

The 69 stations used in this paper each have a time series of the observed number of fish species that runs continuously from 1953 to 1994 along the Norwegian Skagerrak coast and were selected from the large set of beach seine data collected by the Institute of Marine Research, Flødevigen research station since 1919 (Lekve *et al.*, 1999). At approximately the same time and at the same sites as the beach seine survey a sampling programme of environmental variables has been conducted since 1927. For 40 years, in our analysis 1953–1994, 27 time series (i.e. stations) of hydrographic variables run parallel with the fish species data. (For a description of the data see Johannessen and Dahl, 1996; Fromentin *et al.*, 2000 and note that we have removed a few stations that are not in the vicinity of any beach seine station.) For each station there exists data on temperature, salinity and oxygen saturation at the sea surface (0 m depth), at 10 m depth and at approximately 50 m depth (30–35 m depth were used for 3 shallow stations),

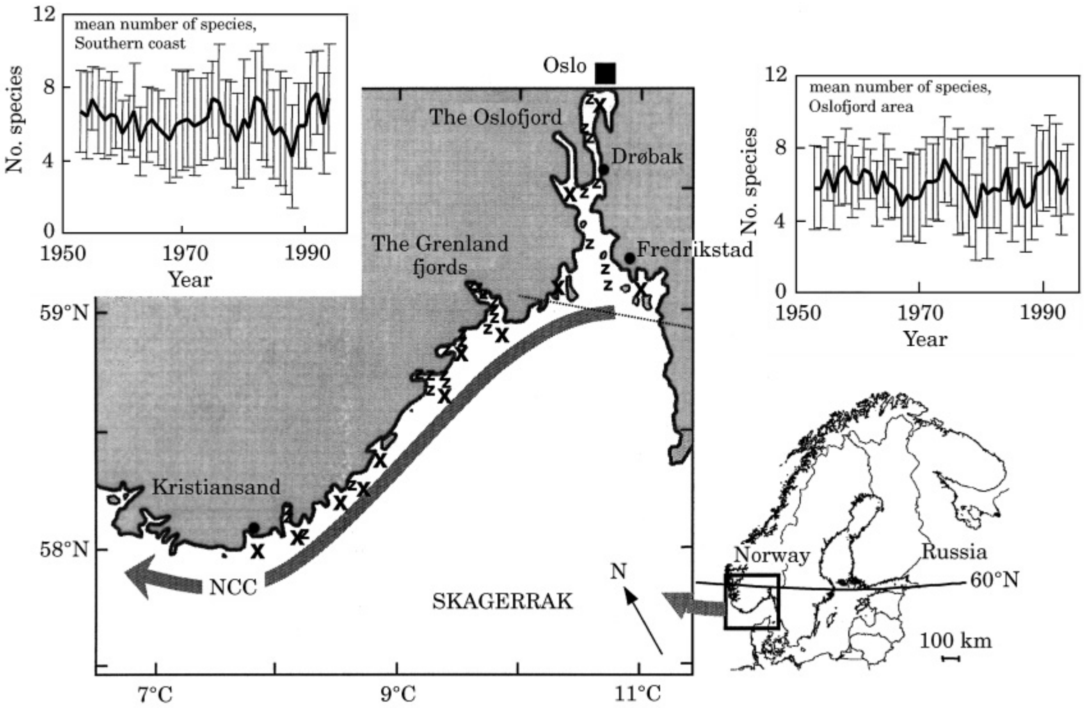

Figure 1. General location of the sampling stations along the Norwegian coast (map in the lower right corner). Coastline in detail (upper left) of the 69 stations studied. The 69 time series (stations) were obtained from an extensive research survey, the "Flødevigen data set", running from 1919 to present. Indicated with a "z" are the 27 hydrographic sampling sites used in this study, and with an "X" the approximate location of areas with beach seine monitoring. The stippled line indicates the separation between the Oslofjord area and the rest of the coast. Inset is the mean number of species for the Southern coast and the Oslofjord areas with standard deviations. The grey arrow indicates the direction of the Norwegian Coastal Current (NCC; see text).

altogether 9 environmental variables. There were 4.3%, 3.2% and 6.3% missing values in the environmental data sets for the sea surface, 10 m and 50 m depth respectively. The missing values were estimated as $z_{i,s,t}=\bar{z}_{i,\cdot,t}*r_{i,s,\cdot}+\varepsilon_{i,s}$, where:

$z_{i,s,t}$ is the value of the variable i (oxygen saturation, salinity and temperature at three depths) at stations s and year t,

$\bar{z}_{i,\cdot,t}$ is the mean value of the variable i over all stations at time t,

$r_{i,s,\cdot}$ is the relative magnitude of the variable at stations s calculated as the mean value of the variable at station s divided by the mean value of the variable over all the stations and

$\varepsilon_{i,s}$ is the noise estimated by a number drawn randomly from a normal distribution with an expected value of 0 and a standard deviation of the variable at the station over all years. This will ensure a neutral contribution of the missing data to the spatial and temporal patterns (Lekve *et al.*, 1999).

Altogether the Southern coast contains 43 stations for beach-seine hauls and 19 environmental stations while the Oslofjord area contains respectively 26 and 8 stations. Only taxonomically fish species proper (i.e. Pisces) were included in the analysis, excluding species groups and non-fish species, leaving a total of 34 fish species available for analysis (Table 1).

Analyses

In order to draw conclusions regarding any relationship between the environmental and faunistic data the structure of the data must be taken into consideration as colinearities between variables may strongly invalidate them. The variability of the environmental data is extensive (Johannessen and Dahl, 1996; Lekve *et al.*, 1999). It is thus not likely that one single pattern will emerge. Therefore, we used STATIS (Lavit *et al.*, 1994; see below) to characterize the correlation structure of the hydrographic variables. STATIS is the French abbreviation for "**S**tructuration des **T**ableaux **A** **T**rois **I**ndices de la **S**tatistique", also known as ACT; Lavit *et al.*, 1994. The STATIS multivariate technique is designed to provide insight into the ordination and grouping of several tables and was evolved to establish a framework for interpreting the relationships between environmental variables and fish species number.

Table 1. The species included in this analysis of the "Flødevigen protocol". The taxonomy according to The Integrated Taxonomic Information System (ITIS) at http://www.itis.usda.gov/itis/index.html. The fish species were sampled using beach seines each autumn since 1919.

Common name	Latin name
Fish species with numerical counts (21 species)	
Cod	*Gadus morhua* Linnaeus, 1758
Whiting	*Merlangius merlangus* (Linnaeus, 1758)
Saithe (pollock)	*Pollachius virens* (Linnaeus, 1758)
Pollack	*Pollachius pollachius* (Linnaeus, 1758)
Sea trout	*Salmo trutta* Linnaeus, 1758
Eel	*Anguilla anguilla* (Linnaeus, 1758)
Ballan wrasse	*Labrus bergylta* Ascanius, 1767
Haddock	*Melanogrammus aeglefinus* (Linnaeus, 1758)
Mackerel	*Scomber scombrus* Linnaeus, 1758
Plaice	*Pleuronectes platessa* (Linnaeus, 1758)
Lemon sole	*Microstomus kitt* (Walbaum, 1792)
Turbot	*Scophthalmus maximus* (Linnaeus, 1758)
Brill	*Scophthalmus rhombus* (Linnaeus, 1758)
Norwegian topknot	*Phrynorhombus norvegicus* (Guenther, 1862)
Common topknot	*Zeugopterus punctatus* (Bloch 1787)
Sole	*Solea vulgaris* (Quensel, 1806)
Cuckoo wrasse	*Labrus bimaculatus* (Linnaeus, 1758)
Dragonet	*Callionymus lyra* Linnaeus, 1758
Armed bullhead	*Agonus cataphractus* Linnaeus, 1758
Rock gunnel	*Pholis gunnellus* (Linnaeus, 1758)
Grey gurnard	*Eutrigla gurnardus* (Linnaeus, 1758)
Fish species with categorical counts (13 species)	
Herring	*Clupea harengus* Linnaeus, 1758
Sprat	*Sprattus sprattus* (Linnaeus, 1758)
Horse mackerel	*Trachurus trachurus* (Linnaeus, 1758)
Flounder	*Platichthys flesus* (Linnaeus, 1758)
Dab	*Limanda limanda* (Linnaeus, 1758)
Long rough dab	*Hippoglossoides platessoides* (Fabricius, 1780)
Goldsinny wrasse	*Ctenolabrus rupestris* (Linnaeus, 1758)
Corkwing wrasse	*Crenilabrus melops* (Linnaeus, 1758)
Rock cook	*Centrolabrus exoletus* (Linnaeus, 1758)
Threespine Stickleback	*Gasterosteus aculeatus* Linnaeus, 1758
Fifteenspine stickleback	*Spinachia spinachia* (Linnaeus, 1758)
Poor cod	*Trisopterus minutus* (Linnaeus, 1758)
Viviporous Eelpout	*Zoarces viviparus* Linnaeus, 1758

Lekve and co-workers (1999) found that patterns of species richness differed between the Southern coast and the Oslofjord area while Bjørnstad and co-workers (1999) also found a difference in relation to cod. In order to evaluate the separation of the geographic areas and for explanatory purposes, the fish data and each environmental variable table was subjected to Principal Component Analysis (PCA; Mardia *et al.*, 1979; Legendre and Legendre, 1998) to check for spatial patterns among the time series. Preliminary attempts to investigate covariability were undertaken by correlation analysis and Canonical Correspondence Analysis (Ter Braak, 1986; Ter Braak and Verdonschot, 1995). The spatial patterns of temporal variation of the species number time series have been reported elsewhere (Lekve *et al.*, 1999).

Structure of the environmental data: STATIS and temporal structure

The STATIS method aims at investigating multi-way data situations and comparing configurations of different data observed at the same time or at the same locations (Lavit *et al.*, 1994). In our analysis the various tables represent the different hydrographic variables. Each table consists of time series at several sites over 42 years. The STATIS method allowed us to make an overall study of these tables, thus enabling the investigation of the spatial patterns of temporal variation of our hydrographic variables.

By this method the similarity between the hydrographic variables is first quantified by the RV coefficient ("R" for correlation and "V" for vectorial), which is a multidimensional correlation coefficient equivalent to the Pearson correlation coefficient (Robert and Escoufier, 1976). Secondly, common patterns of temporal variability may be synthesized into a reference table called the "compromise". The compromise table is constructed as a linear combination of the hydrographic variables in proportion to their weights (i.e. $W=\Sigma_k \alpha_k W_k$ where α_k are the weights of the tables W_k). Within the STATIS approach the table weights are selected so as to maximize the variability of the spectral decomposition of W with the additional constraint that $\Sigma_k \alpha_k = 1$. Finally, a special RV coefficient, which measures the correlation of a given table with the compromise, may be computed (the so-called square cosine, see Chessel and Hanafi, 1996; Blanc *et al.*, 1998 for further details).

Prior to STATIS the environmental variable tables were normalized by each variable (i.e. subtracting the mean and dividing by the standard error of each variable over 1953–1994). This option was selected to eliminate the scale effect of the different variables, while retaining year-to-year variability.

Common structure of environmental and faunistic data sets: co-inertia analysis

A large array of multivariate techniques is available for analysing the structure and temporal patterns of observational data whether biological or abiotic respectively (see, e.g. Manly, 1994; Legendre and Legendre, 1998). Techniques explicitly relating environmental and biological data are, on the other hand, of a more recent date although there were some initial development in the late 60s; see Dolédec and Chessel, 1994 for a review; Ter Braak, 1986, 1995; Ter Braak and Verdonschot, 1995; Dolédec *et al.*, 1996. To relate our faunistic and environmental data sets (fish species number and hydrographic data) we used the so-called co-inertia analysis – an appropriate general multivariate technique for relating (i.e. coupling) any two kinds of data sets using any kind of standard analysis (Dolédec and Chessel, 1994). This is a robust method for treating two tables in a symmetric way (Ter Braak and Verdonschot, 1995). Co-inertia analysis is less sensitive to co-linearity, a potential shortcoming in our data, in which the number of sites (i.e. columns) is more or less close to the number of years (i.e. rows; Dolédec and Chessel, 1994; Ter Braak and Verdonschot, 1995). Basically, co-inertia analysis consists of the concurrent ordination of two tables that maximizes their covariance. It defines axes that simultaneously explain the highest possible variance in each of the two tables and describes their closest possible common structure (see Dolédec and Chessel, 1994 for further mathematical details).

We used co-inertia analysis to match each of our nine hydrographic tables containing row-centred models (i.e. each variable was centred for each year) with the table containing the time series of fish species number for the Southern coast and the Oslofjord area respectively.

We evaluated the statistical significance of the relationship (i.e. co-structure) between one hydrographic variable table and the fish species number table by a random permutation test (e.g. Kazi-Aoual *et al.*, 1995). The resulting distribution of 1000 replicated matches of the two tables, after random permutations of the years, enabled a comparison with the observed total covariance, representing the relationship between the two observed tables. The number of permutation values exceeding the observed total covariance provided the level of significance.

The co-inertia and STATIS analyses were performed with the ADE-4 statistical package (Chessel *et al.*, 1997; Thioulouse *et al.*, 1997, "Environmental Data Analysis", freely available on the internet at http://pbil.univ-lyon1.fr/ADE-4/ADE-4.html).

Results

The separation between the Southern coast and the Oslofjord area found by Lekve and co-workers (1999; see Materials) is supported by this analysis as the Oslofjord has predominantly negative scores along the first PCA axis of the species richness (Figure 2A). Except for the polluted Grenland area the stations along the southern coast display predominantly positive values. This spatial difference in the temporal patterns of species richness is confirmed through the environmental structure, as there was also a distinct difference between the Oslofjord area and the rest of the coast for some of the environmental variables (e.g. salinity at the surface and temperature at 50 m depth, Figure 2B and C). Because of this difference, and also because of earlier findings, we analysed these two areas (i.e. the "Southern coast" and the "Oslofjord area") separately in what follows.

The common structure of the environmental variables

The Southern coast

The STATIS analysis for the Southern coast demonstrated that salinity and temperature at the sea surface and oxygen saturation at 10 and 50 m depth displayed the best fit to the compromise table (squared cosines of respectively 0.41, 0.29, 0.35 and 0.41; Table 2A). Furthermore, the variables can be divided into three groups (Figure 3A) with temperature and oxygen saturation at 50 m belonging to the first group, oxygen saturation at 10 m depth as the sole member of the second group and the rest of the variables in the final group. The contribution to the compromise is rather even, with salinity at 50 m making a weak contribution (weight of 0.153). For the Southern coast the variables

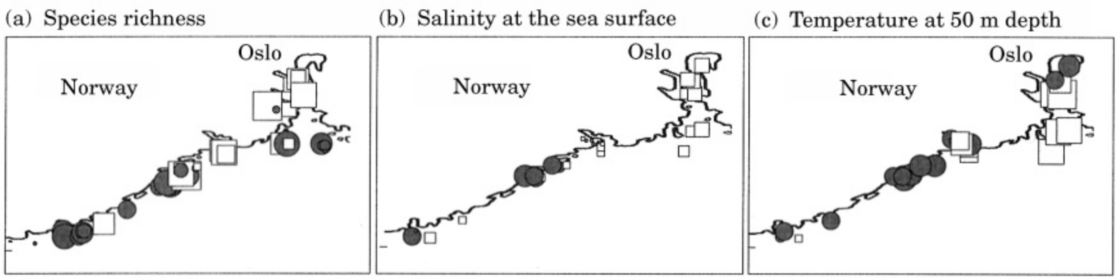

Figure 2. Exploratory PCA reflecting the spatial separation between the Oslofjord area and the Southern coast. Site scores of the first principal axis are plotted according to their geographic position along the Norwegian southern Skagerrak coast (the coastline is indicated by grey in the background, cf. Figure 1). The open squares signify negative scores whereas the grey circles represent positive values; the size of the symbols reflects the magnitude of the scores. (A) The number of species at 69 stations. (B) The salinity at the sea surface and (C) temperature at 50 m depth along the Skagerrak coast, 1953–1994.

Table 2. STATIS analysis of environmental variables 1953–1994. Description of the contribution to the compromise of the hydrographic variables for (A) the Southern coast outside the Oslofjord area and (B) the Oslofjord area 1953–1994.

Variable	Abr.	Table	(A) Southern coast Weights	Cos^2	(B) Oslofjord area Weights	Cos^2
Oxygen saturation 0 m	Ox0	1	0.264	0.092	− 0.079	0.025
Oxygen saturation 10 m	Ox10	2	0.436	0.347	0.325	0.390
Oxygen saturation 50 m	Ox50	3	0.382	0.407	0.442	0.752
Salinity 0 m	Sa0	4	0.431	0.413	0.313	0.294
Salinity 10 m	Sa10	5	0.241	0.113	0.228	0.153
Salinity 50 m	Sa50	6	0.153	0.060	0.252	0.214
Temperature 0 m	Te0	7	0.420	0.287	0.338	0.337
Temperature 10 m	Te10	8	0.227	0.085	0.399	0.529
Temperature 50 m	Te50	9	0.317	0.279	0.454	0.759

Abr.: Abbreviation for the variable. Weights: the contribution of each table to the compromise table. Cos^2: Squared cosine, indicating the fit of each table to the approximated compromise.

oxygen saturation and temperature at 50 m were strongly correlated (RV-coefficient of 0.7; Table 3A), and conclusions about them must be cross-evaluated.

The Oslofjord area

The STATIS analysis for the Oslofjord area exposed a strong reproducibility of the common structure by several variables (i.e. oxygen saturation at 10 and 50 m depth, and temperature at all three depths; squared cosines from 0.34 to 0.76; Table 2B). However, the interrelationship of the variables was rather erratic and oxygen saturation at the sea surface was totally unrelated to the other variables (Figure 3B; negative RV-coefficient values in Table 3B). All the temperature variables contributed in a similar fashion to the common structure. In the Oslofjord area, temperature and oxygen saturation at the bottom layers were strongly correlated too (RV-coefficient of 0.79 in Table 3B).

The relationship between the environmental variables and the fish species richness

The relationship between the environmental variables and the number of fish species was revealed by the co-inertia analyses of the tables in reduced space (row centred models). The tables were matched by years (each table with 42 years and respectively 26 faunistic and eight environmental stations in the Oslofjord area and 43 faunistic and 19 environmental stations along the Southern coast as the column input). The p-values found by the Monte-Carlo permutation test of the significance of the correlation between the environmental and faunistic tables are given in the top row of Table 4.

For the Southern coast, oxygen saturation at the sea surface and two deep-water values were significantly correlated with the number of fish species (oxygen saturation and temperature; Table 4; upper row). Salinity in the deep waters was not significant (p-value of 0.123; Table 4), but is displayed for comparison. From the STATIS analysis of the variables along the Southern coast it should be noted that oxygen saturation and temperature in the deep waters were strongly correlated (Table 2A and Figure 3A). These variables will be interpreted jointly below.

For the Oslofjord area, oxygen saturation and salinity – both at 10 m depth – were correlated with the number of fish species (Table 4; oxygen saturation was not

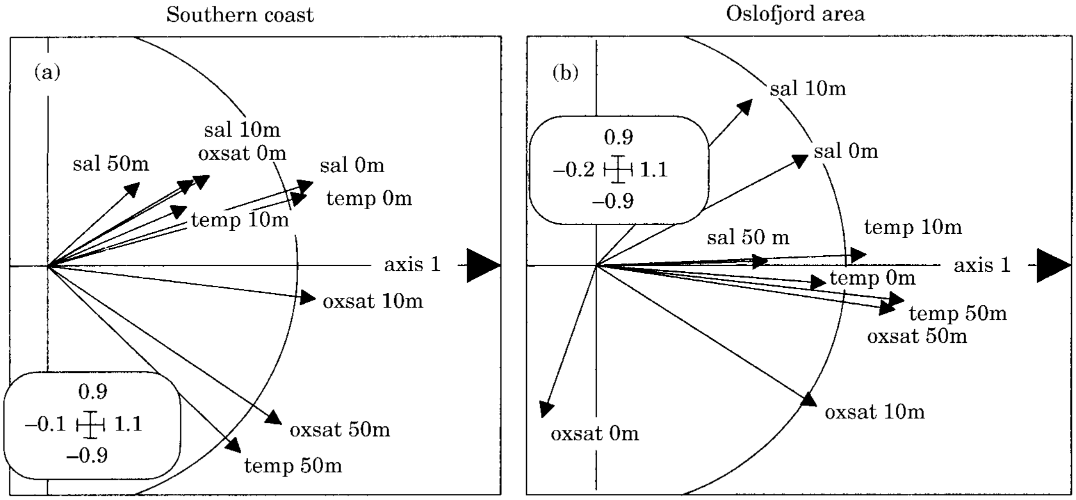

Figure 3. STATIS analysis of the environmental variables from 1953 to 1994: the eigenvectors of the RV correlation matrix. The variables that make the strongest contribution to the common structure will have the largest value when projected onto axis 1. (A) 19 stations along the Southern coast, (B) 8 stations in the Oslofjord area.

significant). In the Oslofjord area, the salinity at 10 m is not closely associated with other environmental variables (Figure 3B) and can thus be interpreted independently. Oxygen saturation was not significant (p-value of 0.100; Table 4) but is included below for comparison.

The Southern coast: fish species and oxygen saturation, temperature, and salinity in deep waters

The covariance of the number of species and oxygen saturation and temperature at 50 m depth accumulated on the first two co-inertia axes explained 59% and 60% of the variation in the data respectively (Table 4). This indicates that a large fraction of the variability of the temporal patterns is captured in the analysis. The spatial patterns appear as a spatial gradient (Figure 4A, right-hand side, shown for oxygen saturation at 50 m; negative scores for stations located in the north-east and positive scores for stations in the south-west). The species' number pattern did not show such a spatial gradient (Figure 4A, left-hand side). The common dominant temporal pattern showed a decline in both the number of species and in oxygen/temperature at 50 m in the late 1960s (Figure 5A, B). An independent and even more pronounced spatial gradient occurred in the co-inertia analysis of the number of species and salinity at 50 m (not shown; the first two axes explained 55%; Table 4). The temporal pattern was also somewhat similar (Figure 5C). However, the association between salinity and species richness was not significant (p-value of 0.123; Table 4). All the deep-water variables displayed RV-coefficients of about 0.30 and high correlation with both the first and second co-inertia axis (correlation coefficients from 0.71 to 0.81; Table 4).

The Southern coast: fish species and oxygen saturation at the sea surface

The covariance of oxygen saturation at the sea surface and the number of species accumulated on the first two axes of the co-inertia analysis explained 48.5% of the variation in the data (Table 4), indicating residual spatial variability. The spatial pattern of the covariation was not very pronounced. It seems primarily to reflect a contrast between the Grenland area and the rest of the coast (right-hand side in Figure 4B; indicated with an arrow), as both the number of species and the oxygen saturation experienced a drop in the late 1960s (Figure 5D), corresponding to a period of increased pollution load in the area (Johannessen and Dahl, 1996). Note that this temporal pattern of oxygen saturation is similar to the pattern observed in the Oslofjord (see below). The RV-coefficient of oxygen saturation at the sea surface was 0.35 and the correlation with both the first and second co-inertia axis was high (correlation coefficients of 0.73 and 0.79; Table 4).

The Oslofjord: fish species and salinity below the surface

The covariance of salinity at 10 m and the number of species accumulated on the first two axes of the co-inertia analysis explained 60% of the variation in the data (Table 4). The spatial patterns were unclear (Figure 4C). The temporal patterns were very variable with no clear long-term pattern (Figure 5E). The RV-coefficient displayed by salinity in the Oslofjord was low (only 0.15; Table 4) indicating a weak association. This weakness was confirmed by the low correlation coefficients with the first two co-inertia axes (coefficients of 0.57 and 0.59, respectively; Table 4).

Table 3. STATIS analysis of environmental variables 1953–1994. RV correlation matrix for tables of hydrographic variables along the Norwegian Skagerrak coast 1953–1994. (A) The Southern Coast outside the Oslofjord area and (B) the Oslofjord area.

	Ox0	Ox10	Ox50	Sa0	Sa10	Sa50	Te0	Te10	Te50
(A) Southern coast									
Oxygen saturation 0 m	1								
Oxygen saturation 10 m	0.24	1							
Oxygen saturation 50 m	0.04	0.42	1						
Salinity 0 m	0.40	0.40	0.12	1					
Salinity 10 m	0.09	0.07	0.11	0.25	1				
Salinity 50 m	0.08	0.11	0.17	0.04	0.25	1			
Temperature 0 m	0.22	0.28	0.18	0.54	0.25	0.14	1		
Temperature 10 m	0.05	0.24	0.06	0.14	0.14	0.12	0.25	1	
Temperature 50 m	− 0.01	0.30	0.70	0.12	0.03	− 0.16	0.17	0.01	1
(B) Oslofjord area									
Oxygen saturation 0 m	1								
Oxygen saturation 10 m	0.11	1							
Oxygen saturation 50 m	− 0.09	0.61	1						
Salinity 0 m	− 0.20	0.22	0.35	1					
Salinity 10 m	− 0.17	− 0.07	0.30	0.45	1				
Salinity 50 m	− 0.02	0.28	0.29	0.28	0.20	1			
Temperature 0 m	− 0.03	0.34	0.43	0.39	0.15	0.20	1		
Temperature 10 m	− 0.13	0.32	0.58	0.31	0.32	0.31	0.46	1	
Temperature 50 m	− 0.10	0.55	0.79	0.38	0.27	0.29	0.49	0.67	1

Abbreviations as in Table 2.

Table 4. Co-inertia analysis for the Norwegian Skagerrak coast 1953–1994. The p-value (found by 1000 permutations) gives the significance of the relationship between the tables. The correlation between the tables of fish species and the each environmental variable are given by the RV-coefficient. The correlation with the first co-inertia axis (noted Axis 1) and the second co-inertia axis (noted Axis 2) gives the correlation between the environmental variable scores and the fish species number scores. Separate ''percentage of covariation'' are explained by the first two co-inertia axes (noted % Axis 1 and % Axis 2 respectively) are given as well as the accumulated values (Accumulated %).

	Southern coast				Oslofjord area	
No. sp. with	Ox0	Ox50	Sa50	Temp50	Ox10	Sa10
p-value	0.037	<0.001	0.123	0.008	0.100	0.028
RV-coefficient	0.35	0.38	0.28	0.32	0.22	0.15
Axis 1	0.73	0.81	0.80	0.78	0.65	0.57
Axis 2	0.79	0.73	0.71	0.77	0.73	0.59
% Axis 1	26.4	39.1	43.0	35.0	48.0	31.7
% Axis 2	22.1	20.0	12.4	25.9	19.4	28.7
Accumulated %	48.5	59.1	55.4	60.9	67.4	60.4

Abbreviations as in Table 2.

The Oslofjord: fish species and oxygen below the surface
The covariance of oxygen saturation at 10 m and the number of species accumulated on the first two axes of a co-inertia analysis explained 67% of the variation in the data (Table 4). The spatial pattern were, however, not very clear (Figure 4D). The temporal pattern revealed a steady decrease in the number of species during the period and a somewhat less pronounced decrease in the oxygen saturation (Figure 5F) – a pattern similar to the pattern observed in the Grenland area (cf. Figure 5B, D). The RV-coefficient displayed by the oxygen saturation in the Oslofjord was somewhat higher than for salinity, but still low (0.22; Table 4). Also the correlation coefficients with the first two co-inertia axes were lower than those found for the Southern coast, although higher than for salinity (coefficients of 0.65 and 0.73, respectively; Table 4).

Notice that there is no spatial pattern distinguishing the inner Oslofjord area from the outer Oslofjord area – the three inner stations from the rest – neither for the fish species richness nor the hydrographic variables (Figure 4C, D). This confirms previous findings (Lekve

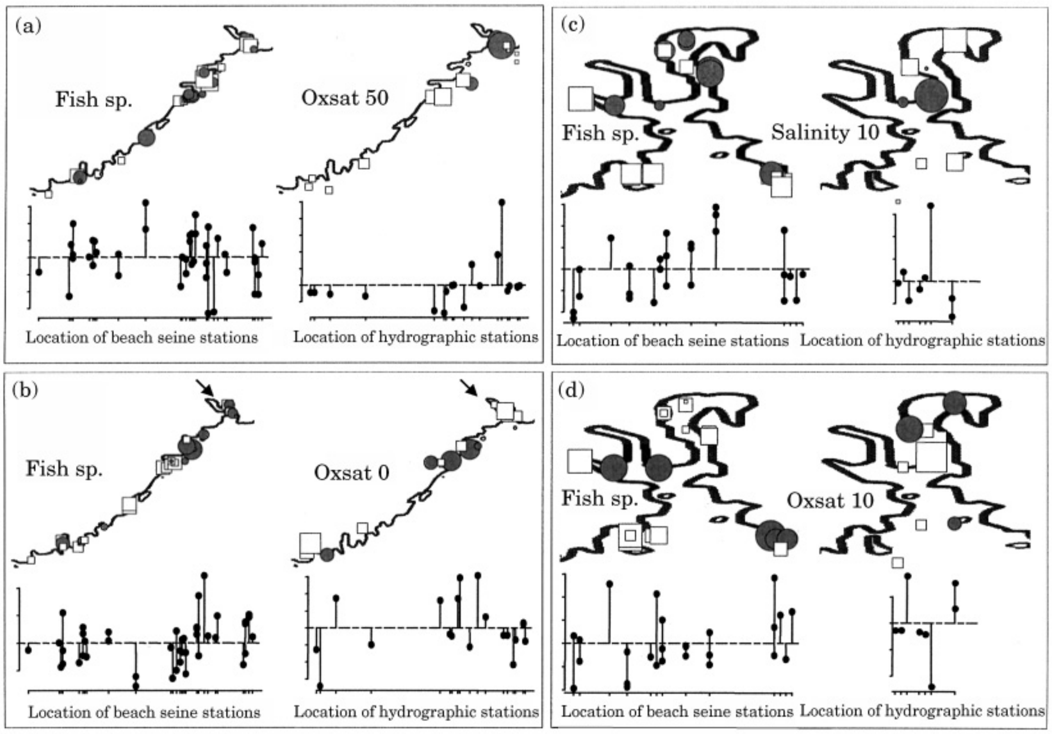

Figure 4. Co-inertia analysis results: spatial patterns. In the upper part of each panel the co-inertia axis scores are positioned in their approximate geographical position to show the spatial scores for the common temporal pattern (displayed in Figure 5). In the lower part the same scores are plotted only along their eastbound position for ease of interpretation. The coastline is indicated in grey. Note that the species axis changes for each analysis as it is re-arranged to maximize the covariance with each environmental variable. The open squares signify negative scores whereas the grey circles indicate positive values; the size of the symbols reflects the magnitude of the scores. The spatial pattern of fish number of species is drawn to the left, while the spatial patterns of the hydrographic variables are plotted to the right within each double figure. Panels (A) and (B) show spatial structure of the Southern coast, while panels (C) and (D) display the spatial structure of the Oslofjord area. Displayed are the number of fish species and (A) oxygen saturation at 50 m, (B) oxygen saturation at the sea surface – arrows indicate the Grenland area mentioned in the text, (C) salinity at 10 m and (D) oxygen saturation at 10 m in the Oslofjord area.

et al., 1999) that spatial patterns override the influence of the sill located at Drøbak (see Figure 1).

Discussion

We have demonstrated that:

(1) the diversity of fish along the Norwegian Southern Skagerrak coast is mainly related to the environmental conditions in the deeper waters and not to environmental conditions in more shallow depths. The oxygen saturation, salinity and temperature measurements in deep water show that there is a gradient from northeast to southwest along the coast;

(2) the Oslofjord seems to constitute a separate system as it is not a part of the same gradient as the rest of the coast. For the Oslofjord area variables at a lesser depth are important (i.e. salinity at 10 m depth) and no spatial structure could be found.

In the next section we discuss how these patterns may be interpreted.

Environmental factors of the Southern coast

The observed agreement between the deeper water variables and species richness may represent some proxy pattern for other processes since no reasonable hypothesis can be put forward as to how processes at 50 m depth should directly influence species richness in the coastal zone. The STATIS analyses indicated that the deep water variables are influenced by some common process as the correlation between oxygen saturation and temperature at 50 m depth is very high and the temporal patterns of all the deep water variables are similar (Figure 5A, B, C). Specifically the spatial patterns of these relationships point to a large-scale process (at least of the scale of the southern part of the Norwegian Skagerrak coast), with an "along the coast" direction. Given this combination of properties the

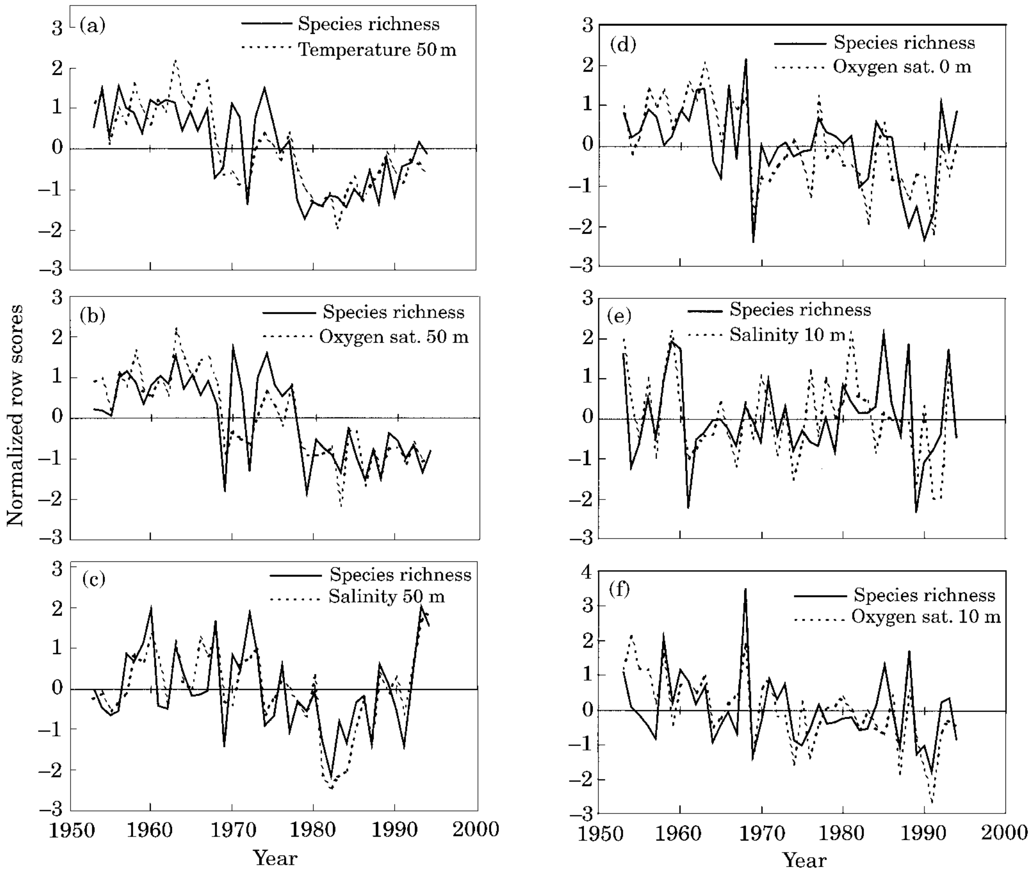

Figure 5. Co-inertia analysis: temporal patterns. For the Southern coast the number of species and (A) temperature at 50 m depth, (B) oxygen saturation at 50 m depth, (C) salinity at 50 m depth, and (D) oxygen saturation at the sea surface t. For the Oslofjord area the number of species and (E) salinity at 10 m and (F) oxygen saturation at 10 m.

Norwegian Coastal Current (NCC; see e.g. Danielssen *et al.*, 1996, 1997) is likely to be a phenomenon which might influence species richness as observed in our analyses. The NCC dominates other currents along the Skagerrak coast, flowing westward while low saline water originating in the Baltic Sea is mixed with sub-surface North Sea water of higher salinity. Consequently the NCC accumulates increasing saline content as it flows along the Norwegian coast. From our results it seems that the NCC imposes a large-scale, basic structure on the species richness while other processes (e.g. wind and temperature; Johannessen and Tveite, 1989; Johannessen *et al.*, 1995; Lekve *et al.*, 2002b) create additional variability and fine-tune the small-scale temporal patterns.

One possible explanation of how the NCC imposes a structure on the species richness involves advection processes (Kaartvedt, 1991; Roughgarden *et al.*, 1994) since these will influence the availability of food (e.g. plankton; Aksnes *et al.*, 1989; Johannessen *et al.*, 1995) and the dispersal of progeny (see e.g. Iles and Sinclair, 1982; Mann and Lazier, 1991; Ottersen and Sundby, 1995) and thus the spatial patterns of species richness. The NCC determines the main direction of advection along the Norwegian Skagerrak coast and at any area within it will be influenced by the nature of processes "upstream" (i.e. to the east).

Environmental factors of the Oslofjord area

In the Oslofjord, species richness is associated with the environmental factors at a shallower depth than in the case of the Southern coast. Furthermore there is no clear spatial pattern (Figure 4D, E) in the temporal pattern (Figure 5E, F). The observed covariability may reflect local or regional effects or both.

The variability of salinity probably does not influence the survival of fish directly (Wootton, 1990) so that is probable that the covariability of salinity and species number in the Oslofjord reflects some other properties of the water masses (e.g. nutrients in fresh-water run-off). The observed covariability in our investigation does not display any trends and so no interpretations can be made.

Hypotheses of the species richness and the scales of patterns

Numerous mechanisms have been suggested for generating patterns in species richness (Gaston, 2000; Gray, 2001). In this study we have demonstrated that abiotic factors significantly influence the patterns of the community dynamics of fish in the coastal zone. We have demonstrated, furthermore, that the basic structure of the fish species richness along the Norwegian Skagerrak coast is influenced by large-scale environmental factors such as temperature and oxygen saturation. The factors found influential in this investigation are compatible with several of the suggested mechanisms, notably the energy-productivity hypothesis (Wright, 1983). However, the sampling scheme of the available data does not provide any basis for drawing conclusions about other hypotheses of species richness patterns such as the species range or the species area approaches (see Gaston, 2000 and Gray, 2001 for reviews) nor does it permit a determination of the level of biological interactions (e.g. Loreau, 2000; Loreau, 2001).

Our suggestions about the role of the NCC in the Southern Coastal area on the one hand and those of more local factors in Oslofjord touch on the main problem area of the field of variation in biodiversity – understanding the mixing of patterns and processes at different scales (Gaston, 2000). The interplay between a large-scale process (the NCC) and small-scale processes (e.g. fresh water run-off) is one mechanism possibly responsible for the recurrently observed proportional-sampling relationship between regional species richness and local species richness (Gaston, 2000).

Conclusion

In this paper we have documented important aspects of a data set that have not been found by other approaches (e.g. correlation analysis and Canonical Correspondence Analysis; not discussed). STATIS revealed which variables were associated with each other, making apparent the importance of the Norwegian Coastal Current over much of the area.

Co-inertia analysis has been applied in several fields such as aquatic or wetland ecology (Castella and Speight, 1996; Diniz and Bini, 1996; Da Costa *et al.*, 2000), plant ecology (Bouvy *et al.*, 2000; Marby *et al.*, 2000), ecotoxicology (Devillers and Chessel, 1995), microbiology (Truu *et al.*, 1999), and molecular biology (Thioulouse and Lobry, 1995). The simultaneous interpretation of several tables of data made it possible to detect new patterns relating to the covariability of species richness and environmental factors also in the marine habitat and shows it to be a valuable tool in the investigation of the co-structure of complex environmental and biological information. We note, however, that Ghertsos *et al.* (2001) and Beaugrand *et al.* (2000) use other approaches in their own attempts at making sense of complex multidimensional data. In this study we have demonstrated that through the examination of hydrographic variables with known spatial scales, we were able to investigate community dynamics at several spatial scales, and thus demonstrate the multitude of patterns and processes (Lawton, 1999).

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References

Aksnes, D. L., Aure, J., Kaartvedt, S., Magnesen, T., and Richard, J. 1989. Significance of advection for the carrying capacities of fjord populations. Marine Ecology Progress Series, 50: 263–274.

Andersen, T., Beyer, F., and Foyn, E. 1970. Hydrography of the Oslofjord. Report on The Study Cource in chemical oceanography arranged in 1969 by ICES with support of UNESCO. ICES Cooperative Research Report, 20: 1–62.

Beaugrand, G., Ibanez, F., and Reid, P. C. 2000. Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. Marine Ecology Progress Series, 200: 93–102.

Bjørnstad, O. N., Fromentin, J.-M., Stenseth, N. C., and Gjøsæter, J. 1999. A new test for density-dependent survival: the case of coastal cod populations. Ecology, 80: 1278–1288.

Blanc, L., Chessel, D., and Dolédec, S. 1998. Etude de la stabilité temporelle des structures spatiales par Analyse d'une série de tableaux faunistiques totalement appariés. Bulletin Français de la Pêche et de la Pisciculture, 348: 1–21.

Bouvy, M., Falcao, D., Marinho, M., Pagano, M., and Moura, A. 2000. Occurrence of *Cylindrospermopsis* (Cyanobacteria) in 39 Brazilian tropical reservoirs during the 1998 drought. Aquatic Microbial Ecology, 23: 13–27.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago.

Brown, J. H. 1999. Macroecology: progress and prospect. Oikos, 87: 3–14.

Castella, E., and Speight, M. C. D. 1996. Knowledge representation using fuzzy coded variables: An example based on the use of Syrphidae (Insecta, Diptera) in the assessment of riverine wetlands. Ecological Modelling, 85: 13–25.

Chessel, D., and Hanafi, M. 1996. Analyses de la co-inertie de K nuages de points. Revue de Statistique Appliquée, 44: 35–60.

Chessel, D., Thioulouse, J., and Dolédec, S. 1997. ADE-4 on the Web. Topics documentation. ADE-4 for Windows 95. http://pbil.univ-lyon1.fr/ADE-4/.

Crawley, M. J., and Harral, J. E. 2001. Scale Dependence in Plant Biodiversity. Science, 291: 864–868.

Da Costa, K. S., Gourene, G., De Morais, L. T., and Vanden Audenaerde, D. F. E. T. 2000. Fish populations in two West-African coastal rivers facing different agricultural and hydroelectric schemes. Vie et Milieu-Life and Environment, 50: 65–77.

Danielssen, D. S., Edler, L., Fonselius, S., Hernroth, L., Ostrowski, M., Svendsen, E., and Talpsepp, L. 1997. Oceanographic variability in the Skagerrak and northern Kattegat, May–June, 1990. ICES Journal of Marine Science, 54: 753–773.

Danielssen, D. S., Svendsen, E., and Ostrowski, M. 1996. Long-term hydrographic variation in the Skagerrak based on the section Torungen-Hirtshals. ICES Journal of Marine Science, 53: 917–925.

Devillers, J., and Chessel, D. 1995. Comparison of in vivo and in vitro toxicity tests from co-inertia analysis. *In* Computer-Aided Molecular Design. Applications in Agrochemicals, Materials and Pharmaceuticals, pp. 250–266. Ed. by C. H. Reynolds, M. K. Holloway, and H. K. Cox. American Chemical Society, Washington.

Diniz, J. A. F., and Bini, L. M. 1996. Assessing the relationship between multivariate community structure and environmental variables. Marine Ecology Progress Series, 143: 303–306.

Dolédec, S., and Chessel, D. 1994. Co-inertia analysis: An alternative method for studying species-environment relationships. Freshwater Biology, 31: 277–293.

Dolédec, S., Chessel, D., Ter Braak, C. J. F., and Champely, S. 1996. Matching species traits to environmental variables: A new three-table ordination methods. Environmental and ecological statistics, 3: 143–166.

Fromentin, J.-M., Gjøsæter, J., Bjørnstad, O. N., and Stenseth, N. C. 2000. Biological processes and environmental factors regulating the dynamics of the Norwegian Skagerrak cod populations since 1919. ICES Journal of Marine Science, 57: 330–338.

Fromentin, J. M., Stenseth, N. C., Gjøsæter, J., Johannessen, T., and Planque, B. 1998. Long-term fluctuations in cod and pollack along the Norwegian Skagerrak coast. Marine Ecology Progress Series, 162: 265–278.

Gaston, K. J. 1996. Biodiversity: a biology of numbers and difference. Blackwell, Oxford.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature, 405: 220–227.

Ghertsos, K., Luczak, C., and Dauvin, J. C. 2001. Identification of global and local components of spatial structure of marine benthic communities: example from the Bay of Seine (Eastern English Channel). Journal of Sea Research, 45: 63–77.

Gray, J.S. 2001. Marine diversity: the paradigms in patterns of species richness examined. Scientia Marina, 65(Suppl. 2): 41–56.

Iles, T. D., and Sinclair, M. 1982. Atlantic herring: stock discreteness and abundance. Science, 215: 627–633.

Johannessen, A., Blom, G., Folkvord, A., and Svensen, H. 1995. The effect of local wind on the distribution of Norwegian spring spawning herring (*Clupea harengus* L.) larvae. *In* Ecology of fjords and coastal waters: proceedings of the Mare Nor Symposium on the Ecology of Fjords and Coastal Waters, Tromsø, Norway, 5–9 December, 1994, pp. 365–384. Ed. by H. R. Skjoldal, C. Hopkins, K. E. Erikstad, and H. P. Leinaas. Elsevier, Amsterdam.

Johannessen, T., and Dahl, E. 1996. Declines in oxygen concentrations along the Norwegian Skagerrak coast, 1927–1993: a signal of ecosystem changes due to eutrophication? Limnology and Oceanography, 41: 766–778.

Johannessen, T., and Tveite, S. 1989. Influence of various physical environmental factors on 0-group cod recruitment as modelled by partial least-square regression. Rapport Procès-Verbal Reunion Conseil International pour L'Exploration de la Mer, 191: 311–318.

Kaartvedt, S. 1991. Plankton as potential prey in fjords. ICES Marine Science Symposium, 192: 156–160.

Kazi-Aoual, F., Hitier, S., Sabatier, R., and Lebreton, J. D. 1995. Refined approximations to permutation tests for multivariate inference. Computational Statistics and Data Analysis, 20: 643–656.

Lavit, C., Escoufier, Y., Sabatier, R., and Traissac, P. 1994. The ACT (STATIS method). Computational Statistics and Data Analysis, 18: 97–119.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos, 84: 177–192.

Legendre, P., and Legendre, L. 1998. Numerical ecology. Elsevier, Amsterdam.

Lekve, K., Boulinier, T., Stenseth, N. C., Gjøsæter, J., Fromentin, J.-M., Hines, J. E., and Nichols, J. D. 2002a. Spatio-temporal dynamics of species richness in coastal fish communities. Proceedings of the Royal Society of London, B (in press).

Lekve, K., Ottersen, G., Stenseth, N. C., and Gjøsæter, J. 2002b. Length dynamics in juvenile coastal Skagerrak cods: effects of biotic and abiotic processes. Ecology, 83: 1676–1688.

Lekve, K., Stenseth, N. C., Gjøsæter, J., Fromentin, J. M., and Gray, J. S. 1999. Spatio-temporal patterns in diversity of a fish assemblage along the Norwegian Skagerrak coast. Marine Ecology Progress Series, 178: 17–27.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos, 91: 3–17.

Loreau, M. 2001. Microbial diversity, producer-decomposer interactions and ecosystem processes: a theoretical model. Proceedings of the Royal Society of London, B, 268: 303–309.

Manly, B. F. J. 1994. Multivariate statistical methods. A primer. Chapman & Hall, London.

Mann, K. H., and Lazier, J. R. N. 1991. Dynamics of marine ecosystems. Blackwell, Cambridge.

Marby, C., Ackerly, D., and Fritz, G. 2000. Landscape and species-level distribution of morphological and life history traits in a temperate woodland flora. Journal of Vegetative Science, 11: 213–224.

Mardia, K. V., Kent, J. T., and Bibby, J. M. 1979. Multivariate analysis. Academic Press, London.

Ottersen, G., and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography, 4: 278–292.

Robert, P., and Escoufier, Y. 1976. A unifying tool for linear multivariate statistical methods: the RV coefficient. Applied Statistics, 25: 257–265.

Roughgarden, J., Pennington, T., and Alexander, S. 1994. Dynamics of the rocky intertidal zone with remarks on generalization in ecology. Philosophical Transactions of the Royal Society of London B Biological Sciences, 343: 79–85.

Solemdal, P. 1997. The Three cavaliers: a discussion from the golden age of Norwegian marine research. *In* Early life history and recruitment in fish populations, pp. 551–566. Ed. by R. C. Chambers, and E. A. Trippel. Chapman & Hall, London.

Ter Braak, C. J. F. 1986. Canonical Correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology, 67: 1167–1179.

Ter Braak, C. J. F. 1995. Ordination. *In* Data analysis in community and landscape ecology, pp. 91–173. Ed. by R. H. G. Jongman, C. J. F. Ter Braak, and O. F. R. Van Tongeren. Cambridge University Press, Cambridge.

Ter Braak, C. J. F., and Verdonschot, P. F. M. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences, 57: 255–289.

Thioulouse, J., Chessel, D., Dolédec, S., and Olivier, J.-M. 1997. ADE-4: a multivariate analysis and graphical display software. Statistics and Computing, 7: 75–83.

Thioulouse, J., and Lobry, J. R. 1995. Co-inertia analysis of amino-acid physico-chemical properties and protein composition with the ADE package. Computer Applications in the Biosciences, 11: 321–329.

Tilman, D., Naeem, S., Knops, J., Reich, P., Siemann, E., Wedin, D., Ritchie, M., and Lawton, J. 1997. Biodiversity and ecosystem properties. Science, 278: 1866–1867.

Truu, J., Talpsep, E., Heinaru, E., Stottmeister, U., Wand, H., and Heinaru, A. 1999. Comparison of API 20NE and Biolog GN identification systems assessed by techniques of multivariate analyses. Journal of Microbial Methods, 36: 193–201.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman & Hall, London.

Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. Oikos, 41: 496–506.