Benthic invertebrates community structure inferred from bottom trawl hauls observations and its relationships to abiotic conditions in the southern North Sea

S. Vaz, R. ter Hofstede, J. Martin, J-M Dewarumez, Y. Verin, D. Le Roy, H. Heessen, N. Daan

Benthic invertebrates caught during the French and Dutch participation in the 1st quarter IBTS (International Bottom Trawl Survey) in the southern North Sea during the years 2002-2007 were monitored as a response to growing interest in collecting additional information on the ecosystem during these fish surveys. The presence of benthic invertebrates was recorded to the lowest taxonomic level as possible. The data were explored using statistical methods adapted to community analyses showing both the structure of the assemblage with its principal indicator species (TWINSPAN, Correspondence Analysis). Diversity indices were used to further explore the differences between each previously defined sub-communities and the distribution of each type of assemblages were mapped. Correlations to environmental parameters such as depth, seabed stress, temperature and salinity were investigated (Canonical Correspondence Analysis). The relationship between the community structure and the environment was modelled (GLM) resulting into a seabed habitat map for the southern North Sea. Such study may be extended in the future, in order to obtain more detailed information on benthic invertebrate distribution and assemblages, and will prove very useful for the conservation and protection of natural marine habitats. The information obtained will help to

elaborate guidelines for the conservation and protection of natural habitats in the face of climate change and anthropogenic disturbances.

Contact author:

S. Vaz: Ifremer, Laboratoire Ressources Halieutiques, 150 quai Gambetta, BP699, 62321, Boulogne/mer, France [tel: (+33) 3 21 99 56 00, fax: (+33) 3 21 99 56 01, e-mail: svaz@ifremer.fr

Introduction

Most published studies on benthic communities are very detailed and focus on small-scale patterns of distribution and structure of coastal biota. Information on offshore benthic species and assemblages at meso-scale is often lacking and the use of scientific surveys, aiming at monitoring fish stock, as platforms enables the observation of macro-epifauna and megafauna over wide geographical areas. Such study were often realised during beam trawl groundfish surveys using a 4m-beam trawl sampling in the Atlantic continental shelf of the British Isles (sea Ellis and Rogers, 2004 for review).

In the frame of the "International Bottom Trawl Survey" program supervised by ICES, IMARES and IFREMER organise each year a scientific survey in the North Sea during the first quarter. These surveys mostly enable the production of recruitment indices for commercial fish species which are essential to the stock evaluation. Using a standardised bottom trawl, the southern part of the North Sea is systematically sampled. Providing an adequate protocol could be developed such annual survey may provide a useful mean to

regularly collect data on large-scale epi-benthic macro-invertebrate distribution collected opportunistically during trawl haul.

The aim of the current study was to describe the structure, composition and distribution of macro-epibenthic invertebrate assemblages in the southern North Sea using samples collected during such bottom trawl survey and to determine which environmental variables best explained the observed patterns in these assemblages.

MATERIALS AND METHODS

DATA collection

Demersal fish and invertebrates were collected in the Southern North Sea (ICES Divisions IVb and IVc) during bottom trawl surveys undertaken by the R.V. Trident (2002-2007) and R.V. Thalassa (2006-2007) in February. The study area was divided in rectangles of 30' of latitude and 1° longitude to enable a stratified sampling. Fishing was conducted with 36/47 GOV-trawl with chain mat and 20 mm stretched mesh cod-end. In order to achieve good bottom contact over the whole groundrope the contact of the net with the bottom was insured by changing the length of the adjustment chain between the lower leg and the bumper bobbin. The normal length of this chain is 2 metres but on rough ground it can be shortened to 1.7 metres; if the gear is fishing too light it can be lengthened to 2.2 metres (Anon. 2004). Trawling speed was 4 knots and tow duration was 30 minutes at most stations, sampling approximately 35,000 m² per tow. Depth and position were recorded during the haul.

Due to the low and very variable efficiency of bottom trawl at catching epi-benthic invertebrate, the use of truly quantitative data was pointless and presence/absence observation were preferred. All fish, cephalopods and commercial shellfish were first identified, counted,

weighed and measured. The remaining invertebrate catch was set aside and sorted. Invertebrates were identified to the lowest taxonomic level possible.

There was a need to standardise the taxonomic levels of identification both across time and countries. The number of taxons had to be reduced by aggregating some species into groups to obtain a data set with coherent level of information across countries and across the time serie.

CTD thermosalinometers were used in both cases to record the water condition in the water column close to the trawl position. Mean bottom temperatures and salinities were computed per year and quarter. Standardised anomalies were computed for each sample (eg for any given year: salinity - Mean of salinity = anomaly of salinity). higher values indicated warmer and more saline bottom conditions than average. CTD profiles generally confirmed that the temperature and salinity conditions were homogeneous throughout the water column due to shallowness, strong currents and wind and tidal mixing. Still, differences between surface and bottom salinity and temperature were computed for each sample (eg for any given position: Bottom salinity – Surface salinity = deltasal). Higher values indicated warmer or more saline conditions close to the bottom than in surface.

Bed shear stress (in Newtons per m^2) was estimated using a 2D hydrodynamic model of the north-west European shelf developed at the Proudman Oceanographic Laboratory (Aldridge and Davies, 1993). Bed shear stress is a function of the maximum predicted tidal current and reflect the friction pressure on the seabed. It often represent a good approximation of the sediment particle size which is very determined by local current. Seabed shear stress value at each location was extracted from GIS layers using spatial joining.

Data analyses

Community classification

The TWINSPAN method (Two-Way INdicator SPecies ANalysis) (Hill *et al.*, 1975, Hill 1979, Gauch and Whittaker, 1981) combines ordination and clustering and it is widely used in vegetation science to simultaneously classify species and samples. At its core, TWINSPAN is based on dividing a reciprocal averaging ordination space. The procedure was described in accessible terms by Gauch (1982, pp. 201-203). The TWNSPAN procedure was used to define different sub-communities based on the semi-quantitative data collected.

Community ordination

Correspondence Analysis (CA) is an indirect gradient analysis using a unimodal response model which is a simple approximation of the community patterns of variation. It extract axes along the main gradients in species variation and was used here to reduce to two dimensions the original presence data. This analyses also enable to project supplementary variables in the reduced space after axes extraction. Canonical Correspondance Analysis (CCA) is a constrained version of CA, in that the ordination axes are constrained to be combinations of the environmental variables. DCA was used to illustrate the species community structure relative to the TWINSPAN classification and to give hindsight to the correlation of the main variation gradients with environmental descriptors and diversity index. CCA was used in combination with Monte-Carlo permutation tests to explore the relationships between the observed epi-benthic assemblage and its environment with the help of the CANOCO software (ter Braak and Šmilauer, 2002).

DIVERSITY

Diversity indices constitute integrated community attributes and seem to be relatively unaffected by changes in species composition due to catchability variations (Wantiez, 1996).

Species richness (S or α diversity) was computed for each sample and relates to the number of species present within a specified area.

Predictive models of community habitat

The basis of virtually all species distribution modelling approaches in current use is the estimation of mean or median (central tendency) species responses to environmental factors. Generalised linear modelling (GLM) and Generalised additive modelling (GAM) fall within this family of model. GLM is a regression model less rigid than classical linear regression and may be applied to data that are not necessarily normally distributed. They enable to linearly relate a combination of predictors to the mean of the response variable through a link function. This function ensures the data transformation towards linearity and maintains the model predictions within a range of value coherent with the original data. A large set of alternative distribution families may be chosen and to each distribution type a set of corresponding link functions relate the mean of the response variable to the linear predictor (McCullagh and Nelder, 1989). This approach was chosen to model the community structure as a response of the environment.

GEOSTATISTICS AND GIS assisted MAPPING

The spatial pattern of environmental descriptors and of community structure were produced using kriging. Geostatistical analyses were performed using Genstat and the final maps were obtained using the GIS ArcMap software.

Results

In total, 547 stations were sampled (393 by IMARES 2002-2007 and 154 by IFREMER 2006-2007) and 390 epi-benthic invertebrate species were identified. In order to standardised the taxonomic level of identification both accross surveys and along time, some taxon had to be grouped into higher taxonomic level and only 131 taxon were retained in this study. The

composition of the assemblages used in this study is described in Table 1 along with species name coding used in the following analyses and the number of species grouped in each taxon.

Preliminary analyses

Exploratory analysis revealed significant differences between countries. The communities described by french experts differs from communities described by dutch experts (even if analysis was restricted to two last years). French data was made supplementary in following analyses to keep the longer time series.

Some species with rare occurrence were found to be outliers and strongly affected analyses. These (ANSEPLA, CLOPHIU, ECHUECH, OSTAEDU, SOLAEND) were made supplementary in the following analyses.

Community structure

TWINSPAN procedure was applied to the Netherlands data only (360 samples, 56 taxons) and was halted after the second division level resulting into 4 classes of species assemblages. The results are summarised in the Figure 1, giving indicator species weighting the most on each division and listing preferential species of each group. These appeared relatively well structured in space (Fig.2). The total taxon richness and mean taxon richness per trawl were computed for each class (Table 2). The groups 1 and 10 (yellow and orange) are the most diverse.

A DCA was performed and allowed to represent the community patterns of variation in the first ordination plan (Fig.3a). The first two axes reflected respectively 9.3 and 5.3% of the overall species variation. In parallel, samples were also represented in this plan and were symbolised according to the twinspan classification and formed cluster of points validating the previous classification (Fig.3b).

The structure and preferential species defined by TWINSPAN can be recognised as they tend to aggregate in the same area of the first ordination plan than the cluster of points corresponding to each class. The sample scores in the first ordination plan may be use as an approxi to the TWINSPAN classification. Both Dutch and French data (used as supplementary data in the DCA) could be pseudo-classified and a map of this newly classified data was produced (Fig.4) The total taxon richness and mean taxon richness per trawl were computed for each pseudo-class (Table 3). The group (yellow) is the most diverse.

Moreover, environmental variables and year trajectories were projected passively onto the biplot after axes extraction (Fig.5). The environmental variables available seemed strongly correlated with each other being all associated more strongly to the first axis of the DCA. The relationship between this gradient of variation in the community structure seemed mostly related to the depth, temperature and salinity anomalies and bedstress. The projection of the year trajectories revealed that there was no clear drift in the observed community structure over the last 5 years.

Community relation to the environment

A CCA was performed and enabled to test the significance of the relationship of the species community to the available environmental variables. Each variable were tested in turn and only bedstress, depth, mean bottom salinity and the anomaly of bottom temperature were found significantly related to the assemblage structure. The result of this test of each variable conditionnal effect on the community structure is detailled in Table 4.

Greater depth and warmer waters are correlated with community types 0 and 1 (higher diversity). Higher bedstress is correlated with community type 10 and 11. Interannual variation of mean bottom salinity seems to also affect the community structure (also not very visible in the plan of the first two axes).

Modelling the epibenthic community habitat

Using GLM, we tried to predict community type from significant environment and create potential map of benthic habitat types. We used the first two axes sample scores of the DCA as responses in two GLM models and the variables found significant in the CCA as explanatory variables. DCA and CCA are gradient analyses using unimodal response model. Second order polynomials of the variables may be more suitable to illustrate this type if relationship and were introduce in the models. The distribution of the sample scores on both axes being normal, the gaussian family with identity link was used. Stepwise selection of significant variables based on Akaike Information Criterion was used to reduce both models.

The final model for axis 1 sample scores (1) explained 40.7 % of the variation of the data. According to the AIC, only depth (second order), bottom temperature anomalies and mean annual bottom salinity (second order) significantly improved the model and were kept.

(1) Ax1 ~ DEPTH2 + anobtemp + MCTDBSal + MCTDBSal2

The final model for axis 2 sample scores (2) only explained 16.6% of the variation of the data. According to the AIC, only depth, bottom temperature anomalies (quadratic) and mean annual bottom salinity (quadratic) significantly improved the model and were kept.

(2) Ax2 ~ DEPTH + anobtemp + anobtemp2 + MCTDBSal + MCTDBSal2

The regression coefficients of both models are given in table 5 and described the modelled relationships to the environment.

For the evaluation of the model, Spearman correlation rank test indicated a significant (p<0.05) positive correlation of 0.65 between axis 1 sample scores in the DCA and predicted

axis 1 sample scores of the first model. It also indicated a significant (p<0.05) positive correlation of 0.40 between axis 2 sample scores in the DCA and predicted axis 2 sample scores in the second model.

Spatial prediction of the community habitat:

Maps of the environmental descriptors were obtain from existing GIS layers (depth) or by interpolating by kriging the observed bottom temperature anomalies (Figure 6).

Applying the models developed earlier these spatialised descriptors (mean annual bottom salinity was set at 34.56, which is the average value observed from 2002 to 2006)) a prediction of the community structure derived from the first DCA axes is possible. The maps of environmental descriptors were limited to the observed range of environmental conditions to avoid model extrapolation. The resulting predicted community structure are presented in Figure 7.

It is tempting at this stage to attempt to recreate the TWINSPAN pseudo-classification to obtain a predicted typology of the epibenthic community in southern North Sea. By ploting the predicting scores of axes1 and 2 with the corresponding pseudo-classification colouring, it appears far more difficult to distinguish between classes as in the original DCA (Figure 8). In particular the gradient on the second axis does not carry as much information as earlier. Still arbitrary threshold were used to produce a global typology map (Figure 9).

This predicted classification does not quite correspond to the pattern observed in Figure 4. The inability of the habitat model to account for the second axes gradient is reflected in this result. Group 1 (yellow) is not predicted and group 10 and 11 are very confused one with the other.

Discussion

The observed epi-benthic species assemblages showed a strong spatial structure that could be related to the environment, in particular depth. The habitat model was not able to distinguish the community structure corresponding to the second axis. The lesser explanatory power of the second glm model and the fact that bedstress (the only variable slightly correlated to this second axis) was rejected by the model may explain this pattern. This may highlights the importance of seabed sediment type (which particle size is often directly proportional to bedstress) as an important structuring factor of the observed species assemblages. In further studies, the sediment type may need to be added to the analyses to account for the second very structuring axis in this analyses and to better distinguish between classes.

The species observed in bottom trawl catch may only represent sessible macro-invertebrates which are likely to move about and may not be appropriate or precise enough indicators of the benthic habitat types. However, because of the large areas swept by the trawl, such observations may indicate benthic habitat on a larger scale than those usually studied using grabs. This scale may be more relevant to ecological study of fish habitat where fish species tend to use distinct habitats for resting or foraging activities and where information at grab scale is irrelevant (Hinz et al., 2006). In that respect, observations of epi-benthic macro-invertebrates made during bottom trawl survey may be used as predictors for fish distribution and preferential habitat modelling.

Moreover, these observations may become very fruitful since yearly observation may easily be made on-board scientific bottom trawl surveys, quickly accumulating data and increasing the spatial resolution to cover any area of study, here the southern North Sea. Ultimately, such observation may be use as an approximation of offshore benthic biotic habitat types at meso-scale, and may be use to monitor their quality, biodiversity and evolution in space and time.

References:

Anonymous, 2004. Manual for the international bottom trawl surveys, revision VII. The International Bottom Trawl Survey Working Group. International Council for the Exploration of the Sea.

Aldridge, J. N. and Davies, A. M., 1993. A high-resolution three-dimensional hydrodynamic tidal model of the Eastern Irish Sea. Journal of Physical Oceanography, 23 (2) : 207-224

Ellis, J.R. and Rogers, S.I., 2004. Distribution and structure of faunal assemblages and their associated physical conditions on the Atlantic continental shelf of the British Isles. ICESCM 2004/P:03 CD-ROM.

Gauch, H.G. Jr., 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, New York. pp. 298.

Gauch, H.G. Jr. and Whittaker R.H., 1981. Hierarchical classification of community data. Journal of Ecology 69: 135-152.

Hill, M.O., Bunce, R.G.H. and Shaw, M.W., 1975. Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. Journal of Ecology, 63: 597-613.

Hill, M.O., 1979. TWINSPAN : A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Section of Ecology and Systematics, Cornell University Ithaca, New York. 31 pp.

Hinz, H., Kaiser, M.J., Bergmann, M., Rogers S.I. and Armstrong, M.J., 2003. Ecological relevance of temporal stability in regional fish catches. Journal of Fish Biology 63: 1219–1234.

McCullagh, P. and Nelder, J.A., 1989. - Generalized Linear Models (2nd ed.). London : Chapman and Hall.

ter Braak, C.J.F. and Smilauer, P., 2002. CANOCO reference manual and CanoDraw for windows User's guide : Software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York. 500 pp.

Wantiez, L., 1996. Comparison of fish assemblages sampled by a shrimp trawl and a fish trawl in St. Vincent Bay, New Caledonia. Journal of the Marine Biological Association of the United Kingdom 76:759–775.

Table 1: Community composition

Phylum class sub-class order sub-order family	Taxon	Code	Nb of species regrouped	Taxon occurence
Annelida **Polychaeta**	Polychaeta	CLPOLYC	31	46
Aphroditidae	*Aphrodita aculeata*	APHRACU	1	289
Arthropoda **Arachnida**	*Arachnida*	CLARACH	1	1
Crustacea Cirripedia	*Cirripedia*	SCCIRIP	11	14
Kentrogonida *Sacculinidae*	*Sacculina carcini*	SACUCAR	1	13
Malacostraca *Squillidae*	*Rissoides desmaresti*	RISSDES	2	1
Amphipoda	*Amphipoda*	ORAMPHD	1	
Decapoda Caridea *Crangonidae*	*Crangon*	CRAG	3	272
	Pontophilus	PONP	2	3
Hippolytidae	*Eualus gaimardii*	EUALGAI	1	1
	Spirontocaris lilljeborgii	SPITLIL	2	1
Palaemonidae	*Palaemon*	PALO	4	12
	Palaemon serratus	PALOSER	2	58
Pandalidae	*Pandalus*	PANS	3	134
Processidae	*Processa*	PROC	3	22
Reptantia	*Brachyura*	IOBRACY	2	1
	Thalassinidea	IOTHALA	3	5
Atelecyclidae	*Atelecyclus rotundatus*	ATELROT	1	29
Callianassidae	*Callianassa*	CALN	1	
Cancridae	*Cancer pagurus*	CANCPAG	1	48
Corystidae	*Corystes cassivelaunus*	CORSCAS	1	142
Dromiidae	*Dromia personata*	DROMPER	1	2
Galatheidae	*Galathea*	GALA	6	12
	Munida rugosa	MUNIRUG	1	8
Geryonidae	*Geryon*	GERY	2	2
Goneplacidae	*Goneplax rhomboides*	GONERHO	1	8
Grapsidae	*Planes minutus*	PLASMIN	1	
Leucosiidae	*Ebalia*	EBAL	2	3
Lithodidae	*Lithodes maja*	LITDMAJ	1	51
Majidae	*Hyas*	HYAS	3	117
	Inachus	INAC	3	76
	Macropodia	MACR	5	127
	Maja brachydactyla	MAJABRA	2	38
	Majidae	FMMAJID	1	1
	Pisa armata	PISAARM	1	4
Nephropidae	*Homarus gammarus*	HOMAGAM	1	10
	Nephrops Norvegicus	NEPHNOR	1	30
Paguridae	*Paguridae*	FMPAGUR	6	17
	Pagurus bernhardus	PAGUBER	1	395
	Pagurus prideaux	PAGUPRI	2	108
	Pagurus pubescens	PAGUPUB	1	55
Panopeidae	*Dyspanopeus sayi*	DYSPSAY	1	
Pilumnidae	*Pilumnus hirtellus*	PILUHIR	1	29
Pirimelidae	*Pirimela denticulata*	PIRIDEN	1	
Porcellanidae	*Pisidia longicornis*	PISILON	1	33
Portunidae	*Liocarcinus depurator*	LIOCDEP	2	199
	Liocarcinus holsatus	LIOCHOL	2	424
	Necora puber	NECOPUB	2	87
	Portunidae	FMPORTU	12	55
Thiidae	*Thia scutellata*	THIASCU	2	2
Xanthidae	*Xantho pilipes*	XANTPIL	1	1
Isopoda	*Isopoda*	ORISOPD	4	8
Mysidacea *Mysidae*	*Mysis*	MYSS	1	
Bryozoa	*Bryozoa*	MBBRYOZ	7	14
Alcyonidiidae	*Alcyonidium*	ALCD	3	73
Flustridae	*Flustridae*	FMFLUST	4	206
Chordata	*Amphioxus lanceolatus*	AMPXLAN	1	1
Ascidiacea	*Ascidiacea*	CLASCID	17	121
Cnidaria	*Cnidaria*	MBCNIDA	1	
Anthozoa	*Anthozoa*	CLANTHO	1	143
Hexacorallia	*Hexacorallia*	SCHEXAC	1	
Actiniaria	*Actiniaria*	ORACTIN	14	108
Scleractinia	*Scleractinia*	ORSCLER	2	1
Zoantharia	*Epizoanthus*	EPZA	2	17

Phylum class sub-class / order sub-order family	Taxon	Code	Nb of species regrouped	Taxon occurence
Octocorallia	Alcyonium	ALCY	3	215
	Octocorallia	SCOTOCO	3	7
Hydrozoa	Hydrozoa	CLHYDRZ	19	175
Echinodermata Asteroidea	Asteroidea	CLASTER	5	3
	Stichastrella rosea	CLASTER	1	3
Asteriidae	Asterias rubens	ASTIRUB	1	528
Asterinidae	Anseropoda placenta	ANSEPLA	1	17
Astropectinidae	Astropecten irregularis irr.	ASTPIRR	3	206
Echinasteridae	Henricia	HENR	3	42
Goniasteridae	Hippasteria phrygiana	HIPAPHR	1	21
Luidiidae	Luidia	LUID	3	47
Poraniidae	Porania pulvillus pul.	PORAPUL	2	2
Solasteridae	Crossaster papposus	CROSPAP	1	59
	Solaster endeca	SOLAEND	1	4
Crinoidea	Antedon bifida	ANTDBIF	1	
Echinoidea	Echinoidea	CLECHIN	15	338
Holothurioidea	Holothurioidea	CLHOLOT	3	2
Cucumariidae	Thyone	THYO	2	3
Ophiuroidea	Ophiuroidea	CLOPHIU	8	6
Ophiurida	Ophiurida	OROPHIU	3	3
Ophiotrichidae	Ophiothrix fragilis	OPHOFRA	2	89
Ophiuridae	Ophiura albida	OPHUALB	1	84
	Ophiura ophiura	OPHUOPH	1	207
Echiura	Echiurus echiurus	ECHUECH	1	1
Mollusca Bivalvia	Bivalvia	CLBIVAL	11	1
Anomiidae	Anomiidae	FMANOMI	4	8
Arcticidae	Arctica islandica	ARTCISL	1	
Astartidae	Astarte sulcata	ASTASUL	1	1
Cardiidae	Cardiidae	FMCARDI	4	18
Cuspidariidae	Cuspidaria cuspidata	CUSPCUS	1	
Mactridae	Mactridae	FMMACTR	8	8
Mytilidae	Modiolus	MODI	2	28
	Musculus	MUSC	2	1
	Mytilus edulis	MYTIEDU	1	5

Phylum class sub-class / order sub-order family	Taxon	Code	Nb of species regrouped	Taxon occurence
	Mytilus galloprovincialis	MYTIGAL	1	5
Nuculidae	Nucula	NUCU	2	2
Ostreidae	Ostrea edulis	OSTAEDU	1	2
Pectinidae	Pectinidae	FMPECTI	7	158
Pharidae	Ensis	ENSI	3	7
Pholadidae	Barnea	BARN	2	1
Psammobiidae	Gari fervensis	GARIFER	1	
Semelidae	Abra	ABRA	2	
Tellinidae	Tellinidae	FMTELLI	2	1
Veneridae	Tapes rhomboides	TAPERHO	2	4
	Veneridae	FMVENER	9	9
Cephalopoda	Cephalopoda	CLCEPHA	1	
Sepiidae	Sepia officinalis	SEPIOFF	1	81
Sepiolidae	Sepiolidae	FMSEPIO	4	48
Octopoda Octopodidae	Eledone cirrhosa	ELEDCIR	1	4
Teuthoidea Loliginidae	Alloteuthis	ALLO	2	170
	Loligo	LOLI	3	130
Ommastrephidae	Todaropsis eblanae	TODIEBL	1	12
Gastropoda	Gastropoda	CLGASTE	1	
Opisthobranchia	Opisthobranchia	SCPISTO	15	56
Prosobranchia	Prosobranchia	SCPROSO	11	26
Buccinidae	Buccinum undatum	BUCCUND	1	232
	Colus	COLU	4	50
Calyptraeidae	Crepidula fornicata	CREPFOR	1	30
Nassariidae	Nassarius reticulatus	NASSRET	2	9
Naticidae	Naticidae	FMNATIC	5	24
Archaeogastropoda Vetigastropoda Trochidae	Calliostoma	CALS	3	14
	Gibbula	GIBB	2	
Scaphopoda	Scaphopoda	CLSCAPH	2	1
Nemertina	Nemertina	MBNEMRT	3	3
Platyhelminthes	Platyhelminthes	MBPLATY	1	
Porifera	Porifera	MBPORIF	23	149
Sipuncula Sipunculidae	Sipunculidae	FMSIPUN	2	

Table 2 :Taxonomique richness (IBTS-NL only)

class	Total taxon richness	Mean taxon richness in trawl
0	41	9.3
1	53	14.8
10	42	9.9
11	37	6.5

Table 3 : Taxonomique richness

Pseudo-class	Total taxon richness	Mean taxon richness in trawl
0	68	11.7
1	100	17.9
10	65	10
11	55	8.4

Table 4 Conditional Effects summary

Variable	Var.N	LambdaA	P	F
bedstre	19	0.16	0.002	15.48
DEPTH	12	0.11	0.002	11.07
MCTDBSal	16	0.03	0.002	2.54
anobtemp	15	0.02	0.002	2.29
MCTDBTem	13	0.01	0.174	1.17
anobsal	18	0.01	0.310	1.05
deltatem	14	0.01	0.620	0.87
deltasal	17	0.01	0.418	0.84

Table 5 : Regression coefficient for the two GLM models

Regression coef.	Axis 1	Axis 2
Intercept	-1.9E+03	9.1E+02
DEPTH		-4.6E-03
DEPTH2	-1.9E-04	
anobtemp	-1.4E-01	6.6E-02
anobtemp2		2.8E-02
MCTDBSal	1.1E+02	-5.2E+01
MCTDBSal2	-1.6E+00	7.5E-01

FIGURES
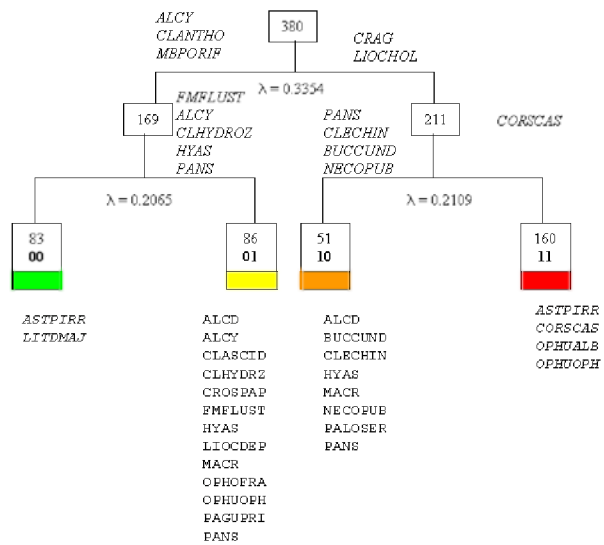
Figure 1 TWINSPAN classification of epibenthic invertebrates of Southern North Sea (NL data only).
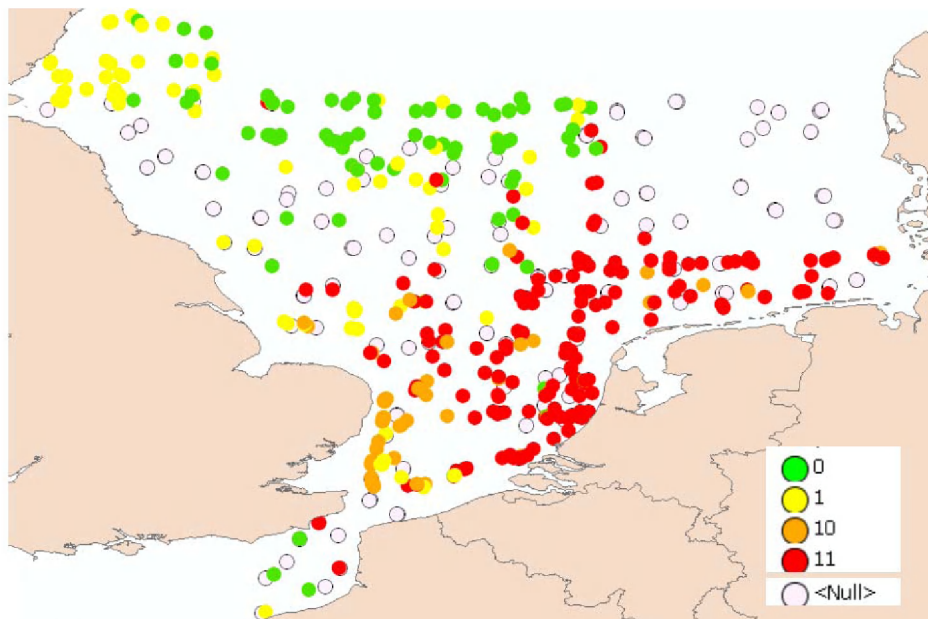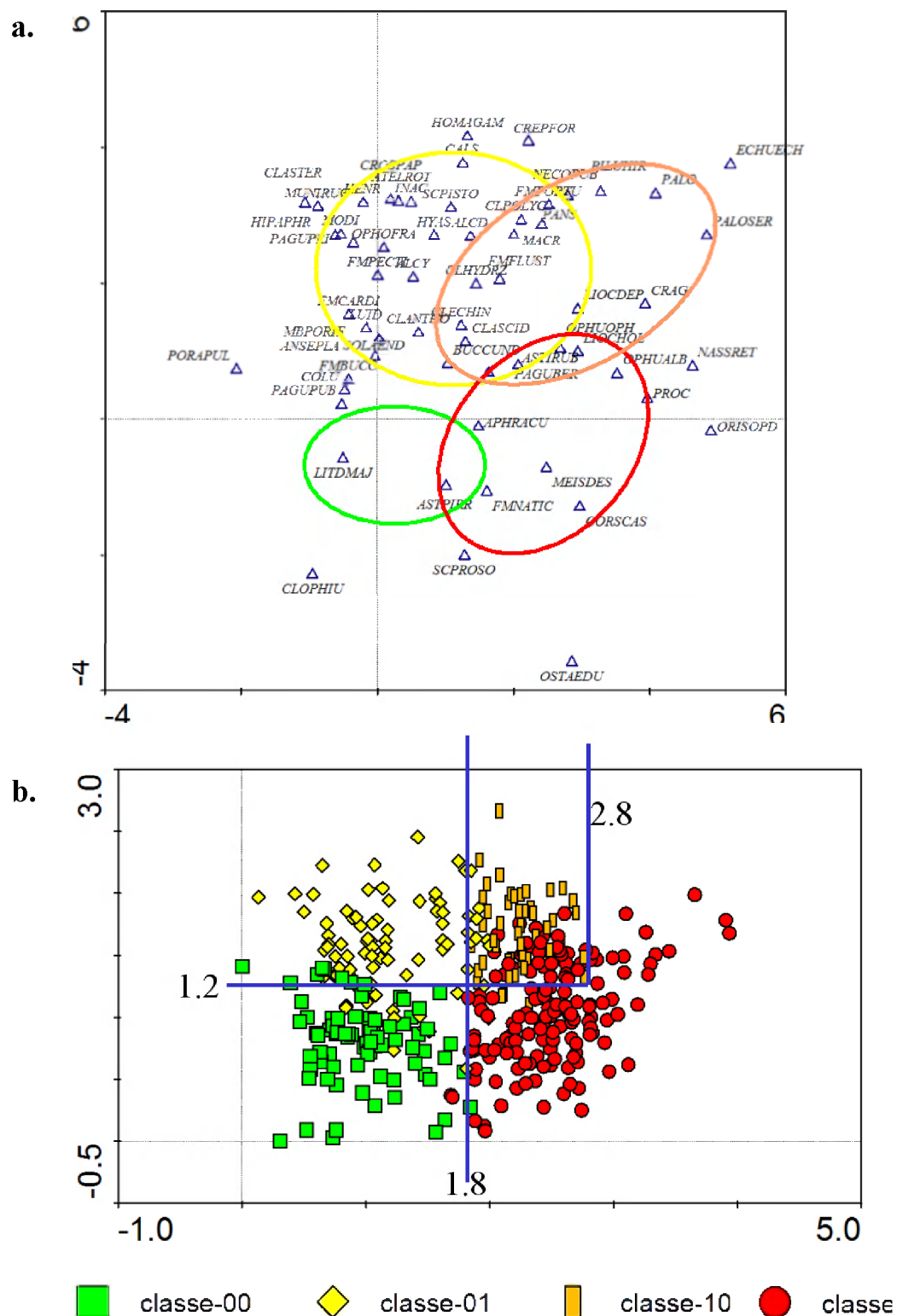

Figure 2 Map of TWINSPAN classified data

Figure 3 DCA biplot on species presence (NL data, FR data supplementary) illustrating the first ordination plan (a) DCA on species presence (NL data, FR data supplementary), preferential species of each TWINSPAN class can be recognised. (b) biplot reflecting the relative position of each observation and their TWINSPAN class.
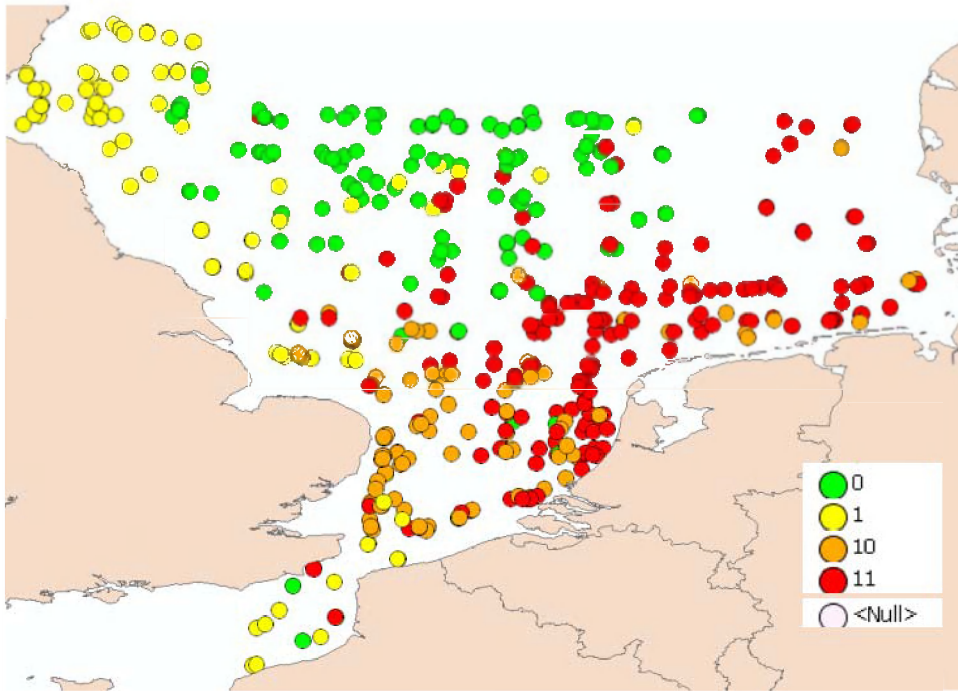
Figure 4: Map of all data pseudo-classifed from DCA sample scores.
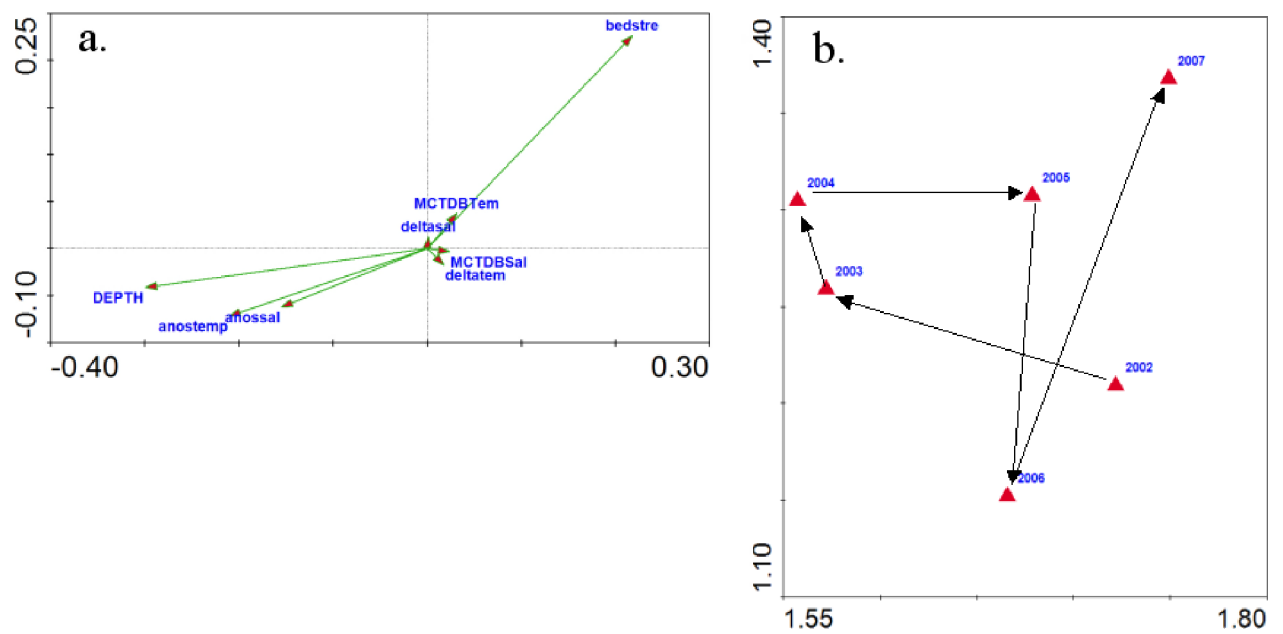
Figure 5: Passive projection of environmental variables (a) and year trajectories (b) in the first DCA plan.
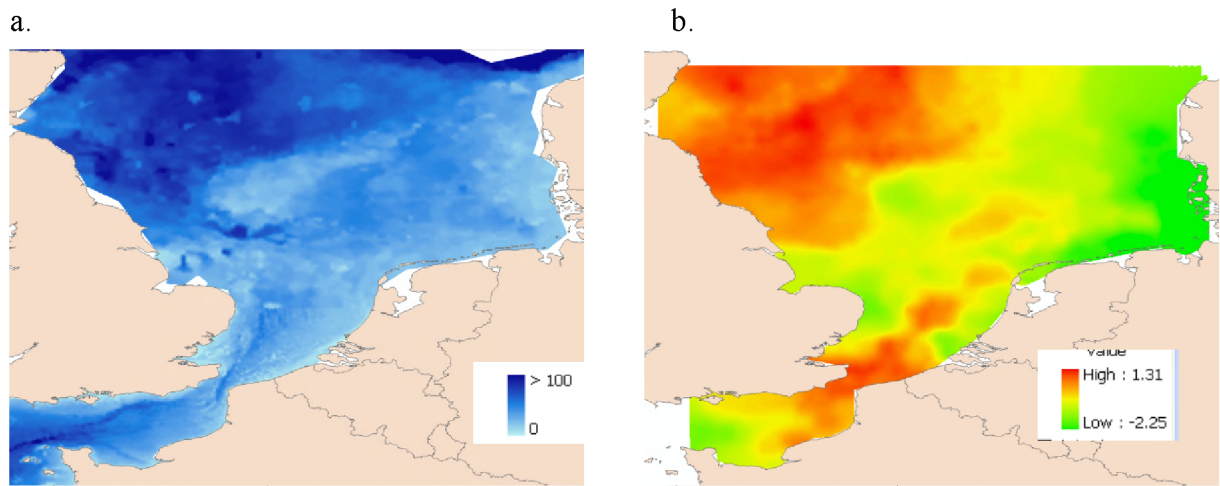
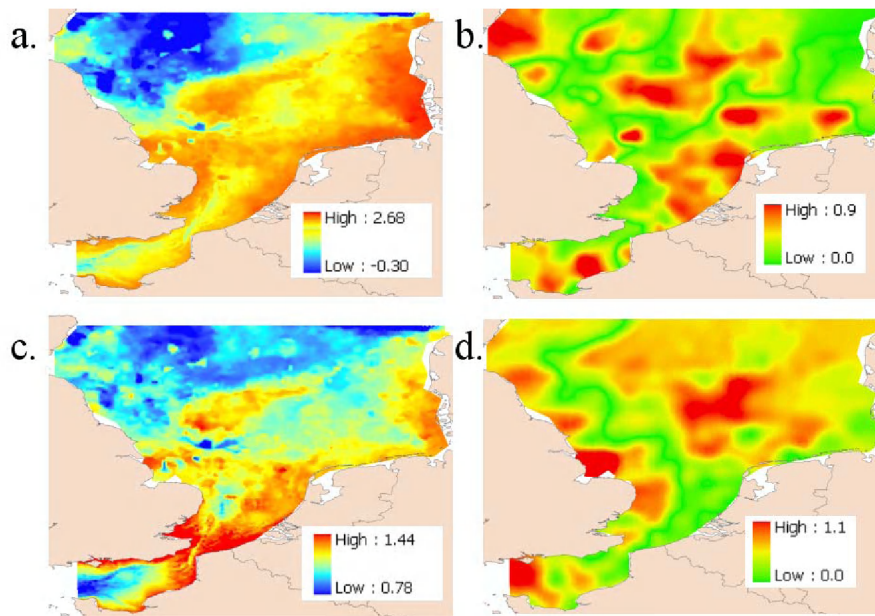Figure 6. Maps of (a) depth (m) and (b) bottom temperature anomalies.

Figure 7. Maps of predicted axis 1 sample scores (a) and interpolated absolute deviation from original scores (b) and of predicted axis 2 sample scores (c) and interpolated absolute deviation from original scores (d)
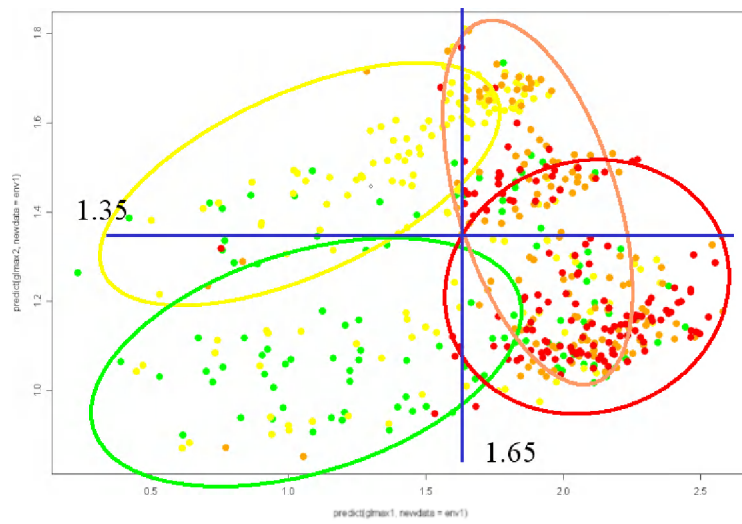
Figure 8 Plot of predicted axes 1 and 2 sample scores and associated TWINSPAN pseudo-classes.
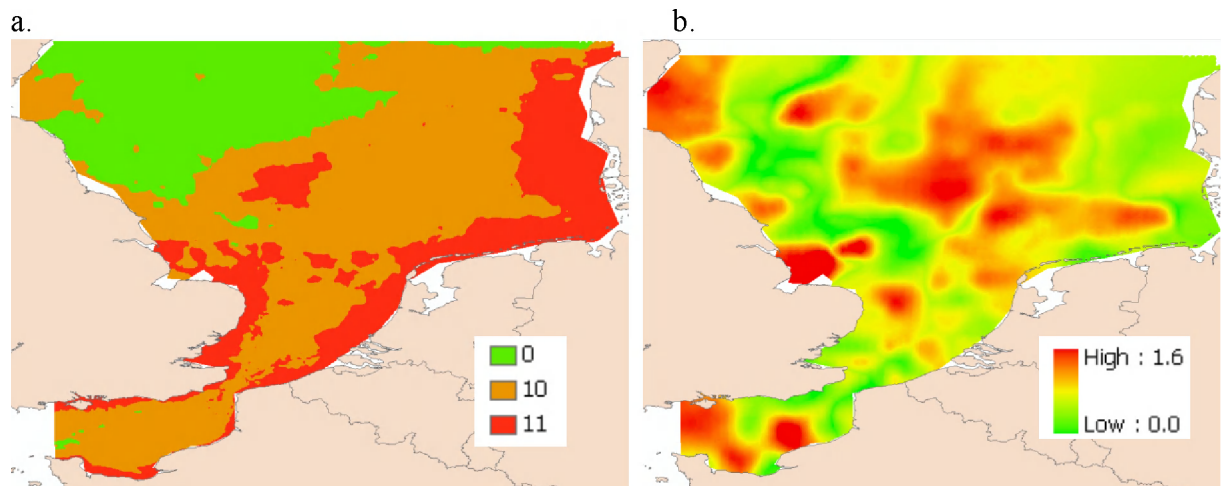

Figure 9. Maps of predicted TWINSPAN classification (a) and interpolated sum of absolute deviation from original scores (b)