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The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: trends in *Loligo* spp. abundance in the northeast Atlantic

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Since the early 1990s, *Loligo forbesi* has apparently disappeared from much of the southern part of its former range, with catches off the Iberian Peninsula, for example, declining dramatically during the 1990s. The present paper assembles data from fishery and research cruise databases to examine the evidence for a shift in distribution and identify possible environmental correlates. Time-series of abundance of *Loligo forbesi* and *L. vulgaris* were assembled using fishery and survey data from Scotland, France, and Portugal. Based on availability of data and timing of the main fishery, data for autumn (October-December) were selected. Nine squid series and two explanatory variables (sea surface temperature and the NAO index) were analysed using dynamic factor analysis (DFA). The optimal DFA model contained two common trends and two explanatory variables. The first common trend shows an increase from 1977-1997, and a slight decrease after 1998 onwards, and is positively related to *L. vulgaris* survey abundance in Portugal and *L. forbesi* fishery abundance in Scotland – and negatively related to *L. forbesi* survey abundance in Portugal. The second trend identifies an increase from 1990-1995, followed by a decrease until 2001, and is positively related to the squid (*L. forbesi* and *L. vulgaris*) abundance series from French surveys and fisheries. SST series was significantly related to three squid abundance series: positively with abundance of small *L. forbesi* in French surveys and negatively with the abundance of small *L. forbesi* from Scottish surveys and abundance of *L. vulgaris* in Portuguese surveys. The NAO series showed no significant relationship to the original squid series. The increase in SST after 1993 and subsequent high level may thus be associated with the decrease of *Loligo* abundance in the south area (France and Portugal) and the increase in *Loligo* abundance in the north area (Scotland).

Key words*: Loligo*, fishery, abundance, common trends, dynamic factor analysis

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1. Introduction

The veined squid, *Loligo forbesi* Streenstrup, 1856, and European squid, *Loligo vulgaris* Lamarck, 1798, are two important squid fisheries resources in the north Atlantic. The most important commercial catches are taken by UK, France, Spain and Portugal (Boyle and Pierce, 1994).

The range of these two *Loligo* species in the northeast Atlantic is largely overlapping, with *L. forbesi* occurring throughout the northeast Atlantic between 20°-63°N, and *L. vulgaris* between 20°-55°N (Guerra and Rocha, 1994). However, *L. forbesi* is more abundant in the northern part of its range, while *L. vulgaris* dominates the southern part of its range.

These squid are mainly landed as by-catch of multi-species demersal trawling fisheries (Cunha et al., 1994; Guerra et al., 1994; Pierce et al., 1994a). However, directed artisanal fishing is important in Spain and Portugal and there is limited directed fishing at Rockall Bank (mainly the 1980s) and in the Moray Firth (Pierce et al., 1994a) of the UK waters.

Fishery statistics do not distinguish these two species, since they are of similar apparearance and equal value. However, landing in the Scottish waters can generally assumed to be *L. forbesi* (Pierce et al., 1994a, b), while in the Mediterranean *L. vulgaris* is practically the only species landed (Guerra et al., 1994). Annual landings of *L. forbesi* in the Scotland have ranged from 82 - 1854 tonnes in the past three decades. In France, *Loligo* is the second most important fished cephalopod, after cuttlefish. Annual landings of *Loligo* in France ranged from 3711 - 6576 tonnes during 1989-2002. Landing of *Loligo* in Portugal ranged 310-1870 tonnes annually in 1986-1997, *Octopus* being the most important fished cephalopod.

Abundance trends, movements and distribution patterns of *Loligo forbesi* in UK waters have previously been shown to be related to environmental conditions, particularly water temperature (Pierce et al., 1998; Waluda and Pierce, 1999; Bellido et al., 2001; Sims et al. 2001; Pierce and Boyle, 2003; Zuur and Pierce, 2004. Robin and Denis (1999) examined fluctuations in abundance of loliginid squid stock in the English Channel, based on fishery statistics from the UK and France ,and showed that squid cohort strength is related to water temperature, especially to winter temperature. Analyses of French commercial trawling *Loligo* LPUE per rectangle, showed that SST observed in April and July had a significant effect on squid distribution and inter-annual changes (Denis et al, 2002). However, there are fewer studies on distribution and abundance *Loligo* spp. in the southern part of their range. Trends in landings from Spanish and Portuguese *Loligo* fisheries were described by Guerra et al. (1994) and Cunha and Moreno (1994), respectively. However, an overview on abundance trends across the distribution regions of *L. forbesi* and *L. vulgaris* is still lacking.

The particular interest in larger-scale variation arises from the apparent disappearance of *Loligo forbesi* from commercial landings in Spain and Portugal during the early part of the 1990s (see Boyle and Pierce, 1994). This leads to several questions: was the decline in abundance consistent across a wide area, has the decline been sustained or has the stock recovered, has there been a concurrent rise in the abundance of *L. vulgaris*, and can these trends be related to changes in environmental conditions? Many studies have indicated changes in abundance and species composition in marine communities associated with a general warming of the northern Northeast Atlantic.

Dynamic factor analysis (DFA) is a dimension-reduction technique for processing time series. DFA can be used to model short, non-stationary time series in terms of common patterns and explanatory variables (Zuur et al., 2003a). In this study, we compile fishery and survey data of *Loligo* spp. in the northeast Atlantic from Scotland, France and Portugal to quantify abundance trends for *L. forbesi* and *L. vulgaris* in the northeast Atlantic and their relationships with marine climate.

2. Materials and methods

2.1. Squid data

The squid data used in this study included fishery and survey data from Scotland (UK), France, and Portugal. The fishery and survey data of Scotland were extracted from databases held at Fisheries Research Services Marine Laboratory. The fisheries data consist of monthly average trawler landings per unit effort (LPUE) of squid (assumed to be *Loligo forbesi*) for the two ICES subdivisions IVa (northern North Sea) and VIa (west coast of Scotland) from 1970-2000. *Loligo* is mainly a by-catch of the whitefish fishery in Scottish waters and fishing effort is assumed to be independent of squid abundance. The relatively high value of squid means discarding is minimal (Young *et al.*, In Press). Hence, we assume that LPUE is equivalent to CPUE and will be a reasonable index of abundance (Pierce and Boyle, 2003). The survey data ranged 7°25'E - 16°12'W, 48°04' - 62°08'N during 1963-2004. Surveys took place in most calendar months, with the best coverage being for February (n = 28 years), March (n = 25), August (n = 27), and November (n = 26). For comparability with the fishery data set, we extracted the *Loligo* catch data from hauls within ICES subdivision IVA and VIA for further analysis.

French *Loligo* landings data were provided by the Centre Administratif des Affaires Maritimes St Malo (CAAM) for the period of 1989-2002. Since both *Loligo* species are present in French waters and landings are not identified to species, we used the LPUE of *Loligo* spp. for further analysis. French survey data, from the EVHOE bottom trawl surveys, were extracted from a database held by the French Research Institute for Exploitation of the Sea (IFREMER). The survey was carried every year since 1987 on the eastern continental shelf of the Bay of Biscay. The survey periods were May-June in 1988 and 1991 and September-December during 1987-2003 (except 1991). Squid were identified to species level, so that CPUE was available for both *L. forbesi* and *L. vulgaris*.

Fishery and survey data from Portugal were extracted from databases held by the Instituto de Investigação das Pescas e do Mar (IPIMAR). Fishery data consisted of monthly catch and LPUE for *Loligo* spp. from 1988-1996. The survey data came from the area 10°02' - 7°16'W, 36°25' - 42°34'N from 1990-2002. Surveys took place in most months but the best coverage was for July (n = 13 years), October (n = 20), and November (n = 18). The squid were identified to the species level, so that CPUE was available for both *L. forbesi* and *L. vulgaris*.

The localities of survey catches, pooled by ICES statistical rectangle (i.e. with a spatial resolution of 1° longitude by 0.5° latitude), from the three countries are presented in Fig. 1. For the complete of data set by year in each country, we chose the autumn months (October - December) for further analysis. From the fishery data of these three countries, the autumn catch accounted for around 40% of total catch.

In a preliminary analysis of the biological data of squid, two modes were found in the mantle length (ML) composition of *L. forbesi* from the French surveys. Accordingly, the data on squid from Scottish and French surveys were separated into small-sized and large-sized components (divided at 150 mm mantle length (ML)). Small-sized *L. forbesi* are dominant in both countries, comprising 75% (by number) of the total survey catches of the species in Scotland and 70% in France. The CPUE for *L. forbesi* collected by Portuguese surveys was not divided by size due to small sample sizes. The ML frequency distribution for *L. vulgaris* was uni-modal so no division of the data was applied.

The final time series of squid CPUE or LPUE were as follows:

(1) Scottish survey, small-sized *Loligo forbesi* (Sc_Lf_S), 1977-2003;
(2) Scottish survey, large-sized *L. forbesi* (Sc_Lf_L), 1977-2003;
(3) Scottish commercial trawling *Loligo* (Sc_LPUE), 1977-2000;
(4) French survey, small-sized *L. forbesi* (Fr_Lf_S), 1987-2003;
(5) French survey, large-sized *L. forbesi* (Fr_Lf_L), 1987-2003;
(6) French survey, *L. vulgaris* (Fr_Lv), 1987-2003;
(7) French commercial trawling *Loligo* (Fr_LPUE), 1989-2002;
(8) Portuguese survey *L. forbesi* (Pt_Lf), 1990-2002;
(9) Portuguese survey *L. vulgaris* (Pt_Lv), 1990-2002;
(10) Portuguese commercial trawling *Loligo* Pt_LPUE), 1988-1996.

In addition, we had access to some shorter or incomplete time-series for survey abundance of squid (a) close to the Mediterranean (Gulf of Cádiz, Spain, 2000-2004), provided by Instituto Español de Oceanografía, and (b) in the Mediterranean (Ligurian coast, Italy, 1990-2003; from 7.6^{o} to 10^{o} N and 43.0^{o} to 44.3^{o} E). The Ligurian data arose from national trawling surveys (mainly in quarter 4) and surveys under the MEDITS project during quarters 2 and 3. These data were standardised to numbers of squid caught per 1 hour haul.

2.2. Explanatory variables

Reynolds sea surface temperature (SST) data were downloaded from the National Center for Atmospheric Research, USA (NCAR) website. The data are monthly average model results from remotely sensed data, survey temperature data, and sea ice distribution, with a spatial resolution of 1° longitude by 1° latitude (Reynolds and Smith, 1994). The data were re-sampled to the ICES statistical rectangle spatial resolution of 1° longitude by 0.5° latitude

(Wang et al., 2003). Monthly SST time series were extracted for arbitrarily selected locations off the coasts of Scotland, France and Portugal (Figure 1): 40E4 (5.5°W, 55.75°N) and 46E6 (3.5°W, 58.75°N) for Scotland, 24E5 (4.5°W, 47.75°N) and 32E2 (7.5°W, 51.75°N) for France, and 06E0 (9.5°W, 38.75°N) for Portugal. For the autumn period (October – December) the three monthly SST time series were significantly correlated. Hence we used the SST time series of October for further analysis.

In a preliminary analysis, dynamic factor analysis was applied to these five October SST time series. Results indicated that all these time series could be described by two common trends. Point 6E0 was most important to trend 1, while 40E4 was most important to trend 2. Therefore, we used the SST time series from these two points as explanatory variables for further analysis, denoting the 06E0 SST as "SST_south", and the 40E4 series as "SST_north".

Another explanatory variable used in the analysis is the winter North Atlantic Oscillation (NAO) index (Hurrel, 1995). This index is defined as the difference on the normalised sea level (atmospheric) pressures (SLPs) between Ponta Delgada (Azores) and Stykkisholmur / Reykjavik (Iceland). A higher index indicates strong westerly winds; a lower index indicates weak westerly winds. The "winter" index for a given year is the average of monthly values for (the previous) December through to February.

3. Dynamic factor analysis

Dynamic factor analysis (DFA) is a multivariate time-series analysis technique used to estimate underlying common trends in a set of time series. The dynamic factor model can be written as:

$$y_t = A \times z_t + B \times x_t + e_t \qquad (1)$$

where: $\boldsymbol{y_t}$ is a matrix containing the value of the *N* time series at time *t*,

$\boldsymbol{z_t}$ is a matrix containing the values of the *M* common trends at time *t*,

$\boldsymbol{A}$ contains the factor loadings (an $N \times M$ matrix),

$\mathbf{x}_t$ is a matrix containing values for the explanatory variables,

$\boldsymbol{B}$ contains regression parameters for each time series and each explanatory variable,

$\boldsymbol{e_t}$ are the noise components.

It is assumed that $e_t \sim N(0, \boldsymbol{R})$, where $\boldsymbol{R}$ is the error covariance matrix. The magnitude and sign of the factor loadings ($\boldsymbol{A}$) determines how these trends are related to the original time series. The regression parameters ($\boldsymbol{B}$) and their standard errors indicate the influence of the explanatory variables on the time series.

There are two options for the modelling of $\boldsymbol{R}$. One approach is to use a diagonal matrix. Another approach is to use a symmetric, non-diagonal matrix. The elements of a non-diagonal $\boldsymbol{R}$ matrix represent the information that cannot be explained by the common trends and explanatory variables.

For M time series, DFA can be applied in various forms, with N common trends ($1 \leq N < M$), with and without explanatory variables and constant parameters; models with a diagonal or non-diagonal error covariance matrix $\boldsymbol{R}$. Zuur et al. (2003a, b) suggested that the Akaike information criterion (AIC) could be used for model selection. The AIC is a function of the measure of fit (maximum likelihood) and the number of parameters (number of trends, explanatory variables and structure of matrix $\boldsymbol{R}$). In this paper, the DFA model with the smallest AIC values is taken to be the 'best' candidate model. DFA was performed using the software package Brodgar version 2.3.4. (Highland Statistics Ltd).

The available time period of the Portuguese LPUE series was too short to obtain a stable model. Therefore, we used the other nine squid abundance series for further analysis. Four types of dynamic factor analysis (DFA) models were used to estimate the underlying common trends (Table 1). Type 1 models described the nine squid abundance series using a constant, a linear combination of M common trends, and a noise term, with the assumption of normal distribution with an expectation (mean) of 0 and a diagonal error covariance matrix $\boldsymbol{R}$. Models with 1, 2 and 3 common trends are denoted as 1a, 1b and 1c respectively. Type 2 models are the same as type 1 models, but with explanatory variables (SST & NAO) added in different combinations. Type 3 and 4 models are the same as types 1 and 2 respectively, except that a positive definite, symmetric non-diagonal was assumed for the error covariance matrix.

The error covariance matrix can be used to illustrate the information that cannot be explained in the fitted model and explanatory variables. To visualise this matrix, multidimensional scaling (MDS) can be applied (Zuur et al., 2003a).

3. Results

The normalised squid CPUE and LPUE series are presented in Figure 2. The explanatory variables, SST_north, SST_south and the NAO index, are shown in Figure. 3. Although the two SST series showed somewhat different trends, the instability of a model containing both SST series as explanatory variables could reflect collinearity between them ($r = 0.48$, $N = 21$, $P < 0.05$). Therefore we used only SST_north and the NAO index in the model as explanatory variables.

The AIC value of each model is shown in Table 2. The AIC values indicated that a model with two common trends, and SST and NAO as explanatory variables, under a non-diagonal error covariance matrix, was the optimal model.

The estimated common trends are shown in Figure 4. The first common trend shows a slow increase from 1977-1987 and a more dramatic increase from 1988-1997, with a slight decrease after 1998. The factor loadings indicate the relationship between common trends and original series. Results indicate that the first common trend is important for the series Pt_Lv (which is positively related to it) and for Pt_Lf, Fr_LPUE, and Fr_Lf_S (which are negatively related to it). In other words, this trend represents a general increase in abundance of *Loligo vulgaris* in Portugal, and the general decline of *L. forbesi* in Portugal and France. Note that this first common trend is very similar to the trend identified in a model with a single trend (not illustated).

The second common trend shows a slight decrease between 1977 and 1990, an increase until 1995, followed by a decrease until 2001. This second trend is positively related to Fr_Lv, Fr_Lf_L, and Fr_LPUE and negatively related to Sc_LPUE. Thus this appears to mainly reflect a higher abundance of *Loligo vulgaris* in French waters in the mid 1990s and the lower abundance of *Loligo forbesi* in Scottish waters during the same period. The fitted curves for the optimum model are presented in Figure 5. The Portuguese commercial LPUE series (not used in the model) is also shown for comparison.

The time-series for SST was characterised by a decreasing trend during 1989-1993, and an increase in 1994-1995, following which SST remained at higher levels than in the 1980s. The estimated regression parameters and t-values for the SST and NAO series are shown in Table 3. The SST series is significantly related to three squid abundance series (see Figure 6): positively with Fr_Lf_S and negatively with Sc_Lf_S, Pt_Lv. The NAO series was weakly positively related to Sc_Lf_S, and negatively related to Pt_Lv, although neither relationship was significant (see Figure 6). Thus abundance of *Loligo forbesi* in the north of its range, and *L. vulgaris* in the south of its range, appears to be higher in years with lower autumn SST, while at the south of its range (currently effectively the English Channel), *Loligo forbesi* abundance is positively related to autumn SST.

The MDS results for the error covariance matrix are presented in Figure 7. It may be noted that the series Pt_Lf and Sc_Lf_L cluster together. Note that this plot represents features of the data that cannot be explained by the common trends and explanatory variables.

Time series for Cádiz and Genoa are presented in Figures 8 and 9 respectively. The survey abundance of *Loligo forbesi* in the Gulf of Cádiz (2000-04) has declined since 2000, while that of *L. vulgaris* was highest in 2001. Patterns for quarter 1 and quarter 4 surveys were virtually identical. These "snapshots" of trends do not obviously correspond to trends recorded elsewhere.

Survey abundance of *Loligo forbesi* off the Ligurian coast (Italy) is also difficult to interpret. Abundance in the autumn survey was high between 1993 and 1998, and low between 1999 and 2003, although the value for 1990 was also very low. However, spring and summer surveys showed increasing abundance of *L. forbesi* from 1993 to 2001.

4. Discussion

In this study, we compiled fishery and survey data from Scotland, France, and Portugal to examine abundance trends for *Loligo forbesi* and *L. vulgaris* across their range in the northeast Atlantic and their possible relationships with to environmental variables.

Small-sized *L. forbesi* (<15 cm ML) dominated catches of *L. forbesi* during autumn in both Scottish and French survey cruise, accounting for 75% and 70% (by number) of total catch, respectively. This corresponding to the main period of recruitment of *L. forbesi* in autumn as proposed by Collins et al. (1999).

Both common trends in the optimum model highlight differences between the two species, the first trend reflecting a general increase in abundance of *L. vulgaris* in the south, coupled with a general decrease in *Loligo forbesi* abundance. The second trend relates more to the north, with a peak in *L. vulgaris* abundance in the mid-1990s corresponding with of *Loligo forbesi* in Scottish waters during the same period.

Relationships of abundance series with autumn SST also suggest opposite trends. Thus abundance of *Loligo forbesi* in the north of its range, and *L. vulgaris* in the south of its range, were higher in years with lower autumn SST, while in the English Channel, *Loligo forbesi* abundance was positively related to autumn SST.

It could be suggested that the different relationships with SST shown by *L. forbesi* reflect the fact that it competes with *L. vulgaris* in the English Channel but experiences no such competition further north. This interpretation is broadly supported by life history data. In Spanish and Portuguese waters, evidence from the early 1990s suggests that both species breed during December to February (Guerra and Rocha, 1994; Moreno *et al.*, 1994). In the English Channel, data on the proportion of both species in fishery landings during 1992 to 1995suggest that the life-cycles of the two species are out of phase (Robin and Boucaud-Camou, 1995) – which could be a mechanism for reducing competition.

The idea that *Loligo forbesi* and *L. vulgaris* compete in the English Channel is supported by stock assessments carried out on cohorts 1993 to 1995 where an opposite trend in recruitment estimates was observed (Royer et al, 2002). However, in 1996 low recruitment was observed in both species and also in *Sepia officinalis* (Royer, 2002) which suggest that environmental conditions in this area can be unfavourable to all cephalopods.

Additional data from the Gulf of Cádiz and Ligurian Sea were insufficient to be included in the analysis and catch rates were low. However, they do indicate that abundance trends reported for the Atlantic may not be applicable to the Mediterranean. As noted by Anon. (2002), comparisons between Northeast Atlantic and Mediterranean cephalopod fishery production figures indicate that cephalopod landings from the ICES (Atlantic) area have increased in the last decade while Mediterranean landings have been decreasing.

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Table 1

The types of dynamic factor models used in the analysis

Type	Model	R
1	CPUE series = constant + M common trends + noise	diagonal
2	CPUE series = constant + M common trends + explanatory variables + noise	diagonal
3	CPUE series = constant + M common trends + noise	non-diagonal
4	CPUE series = constant + M common trends + explanatory variables + noise	non-diagonal

Table 2

AIC values obtained from DFA on the CPUE and LPUE time series. *M* is the number of common trends. Models are labelled following Table 1, and using a, b, and c to denote the fitting of 1, 2 and 3 common trends respectively. The best model is indicated in bold face.

Model	M	AIC	Explanatory variable
1a	1	499.344	
1b	2	487.108	
1c	3	492.622	
2a	1	510.893	SST
2b	2	581.602	SST
2c	1	504.420	NAO
2d	2	495.504	NAO
2e	3	494.660	NAO
2f	4	505.842	NAO
2g	1	495.735	SST & NAO
2h	2	491.876	SST & NAO
2i	3	498.356	SST & NAO
3a	1	482.591	
3b	2	482.003	
3c	3	494.933	
4a	1	498.107	SST
4b	1	481.446	NAO
4c	2	487.562	NAO
4d	1	415.496	SST & NAO
4e	**2**	**410.303**	**SST & NAO**
4f	3	426.711	SST & NAO

Table 3

Estimated regression parameters and *t* values for the SST and NAO series. Significant values are shown in bold face. Key: Sc_Lf_S = CPUE for small *Loligo forbesi* in Scottish surveys; Sc_Lf_L = CPUE for large *L. forbesi* in Scottish surveys; Sc_LPUE = LPUE for *Loligo* in Scottish commercial trawling; Fr_Lf_S = CPUE for small *L. forbesi* in French surveys; Fr_Lf_L = CPUE for large *L. forbesi* in French surveys; Fr_Lv = CPUE for *L. vulgaris* in French surveys; Fr_LPUE = LPUE for *Loligo* spp. in French commercial trawling; Pt_Lf = CPUE for *L. forbesi* in Portuguese surveys; Pt_Lv = CPUE for *L. vulgaris* in Portuguese surveys.

	SST		NAO	
Series	Estimate	t-value	Estimate	t-value
Sc_Lf_S	**-0.47**	**-2.62**	0.31	1.98
Sc_LF_L	0.08	0.39	0.06	0.30
Sc_LPUE	0.11	0.46	0.28	1.54
Fr_Lf_S	**0.68**	**3.51**	-0.10	-0.59
Fr_Lf_L	0.45	1.99	-0.03	-0.17
Fr_Lv	0.20	0.97	0.08	0.55
Fr_LPUE	0.10	0.33	-0.02	-0.10
Pt_Lf	-0.13	-0.38	-0.58	-2.37
Pt_Lv	**-0.78**	**-2.45**	-0.10	-0.37

Figure 1. The locations of trawling survey catches (pooled by ICES rectangle) by Scottish (pink circle), French (blue circle) and Portuguese (red circle) research vessels. All data from French and Portuguese survey cruise were used, while only data for areas IVa and VIa were used in the case of Scottish trawling surveys. The selected localities for sea surface temperature (SST) series are also presented (green circles).

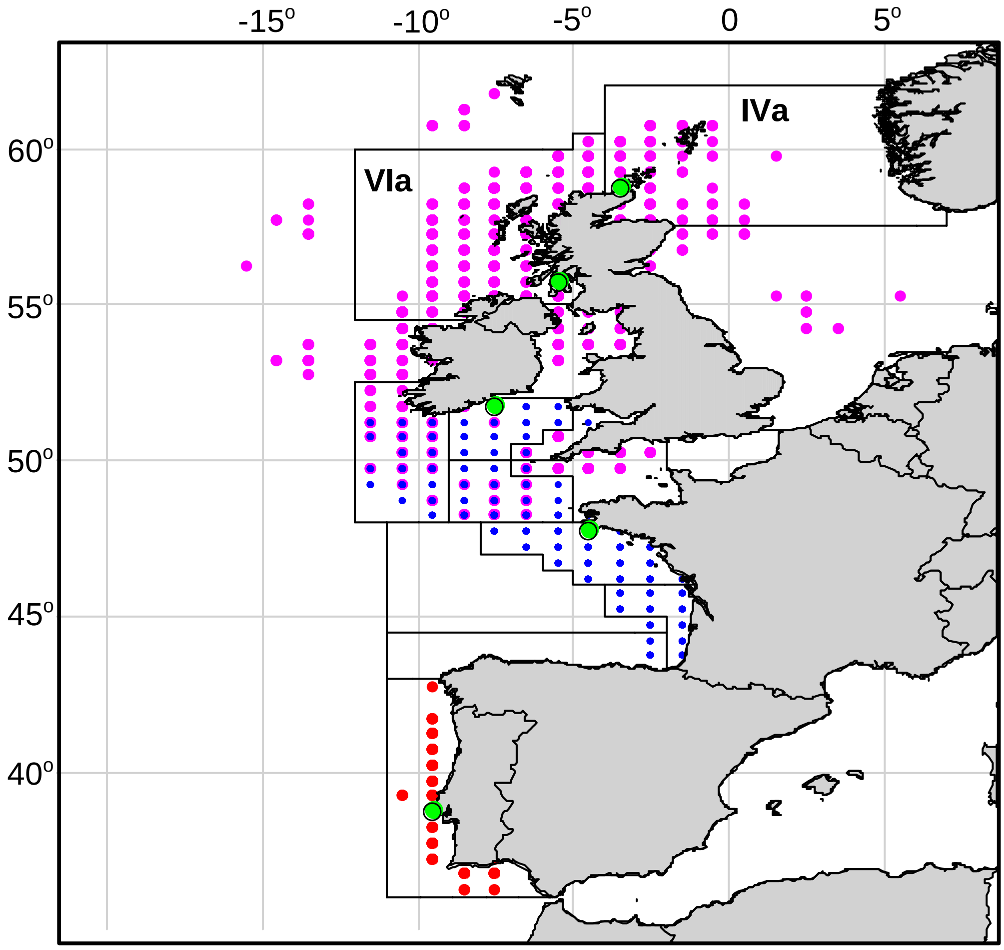

Figure 2. Standardised CPUE and LPUE time series for survey and fishery data on squid from Scotland, France and Portugal. (1. Scotland, survey, large *Loligo forbesi* CPUE; 2. Scotland, survey, small *L. forbesi* CPUE; 3. Scotland, commercial trawling *L. forbesi* LPUE; 4. France, survey, large *L. forbesi* CPUE; 5. France, survey, small *L. forbesi* CPUE; 6. France, survey, *L. vulgaris* CPUE; 7. France, commercial trawling *Loligo* spp. LPUE; 8. Portugal, survey, *L. forbesi* CPUE; 9. Portugal, survey, *L. vulgaris* CPUE; 10. Portugal, commercial trawling *Loligo* spp. LPUE).

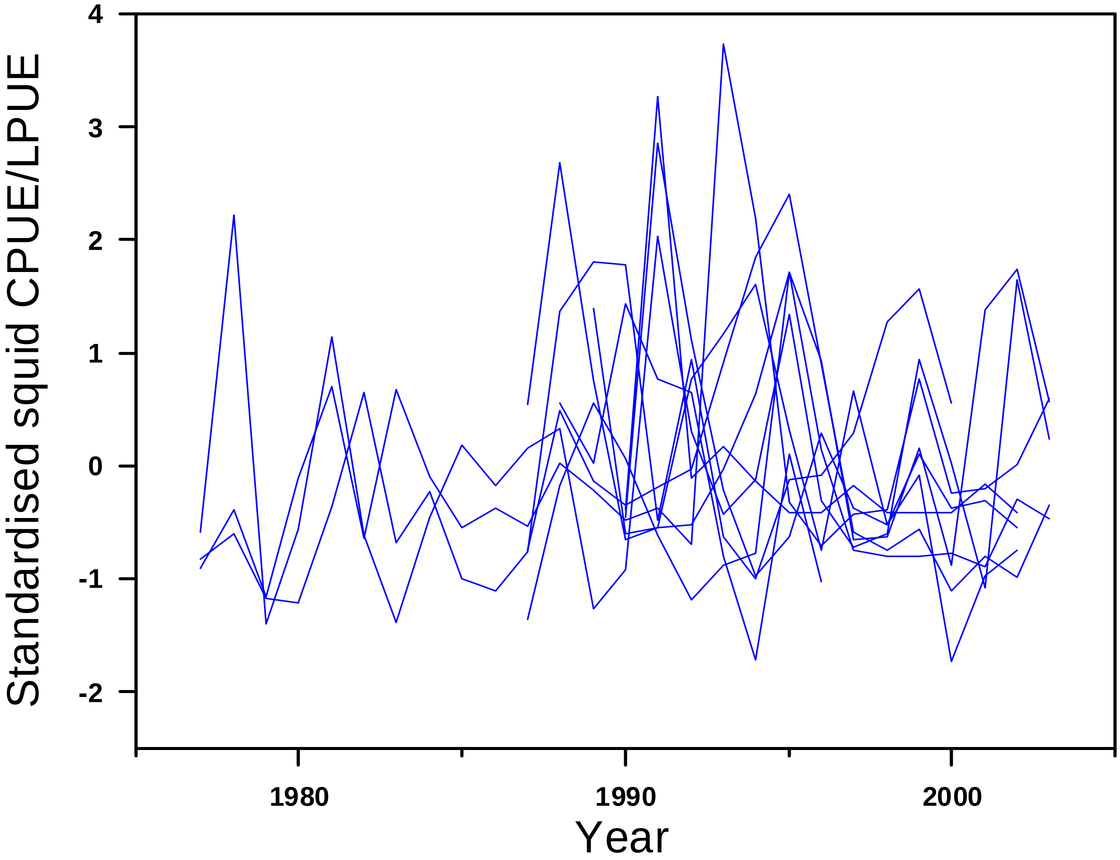

Figure 3. Standardised SST and NAO index time series. The SST data were extracted from the NCAR SST database. The “north” SST series was extracted for ICES rectangle 40E4 (5°5’W, 55°75’N), and the “south” SST series extracted from ICES rectangle 06E0 (9°5’W, 38°75’N).

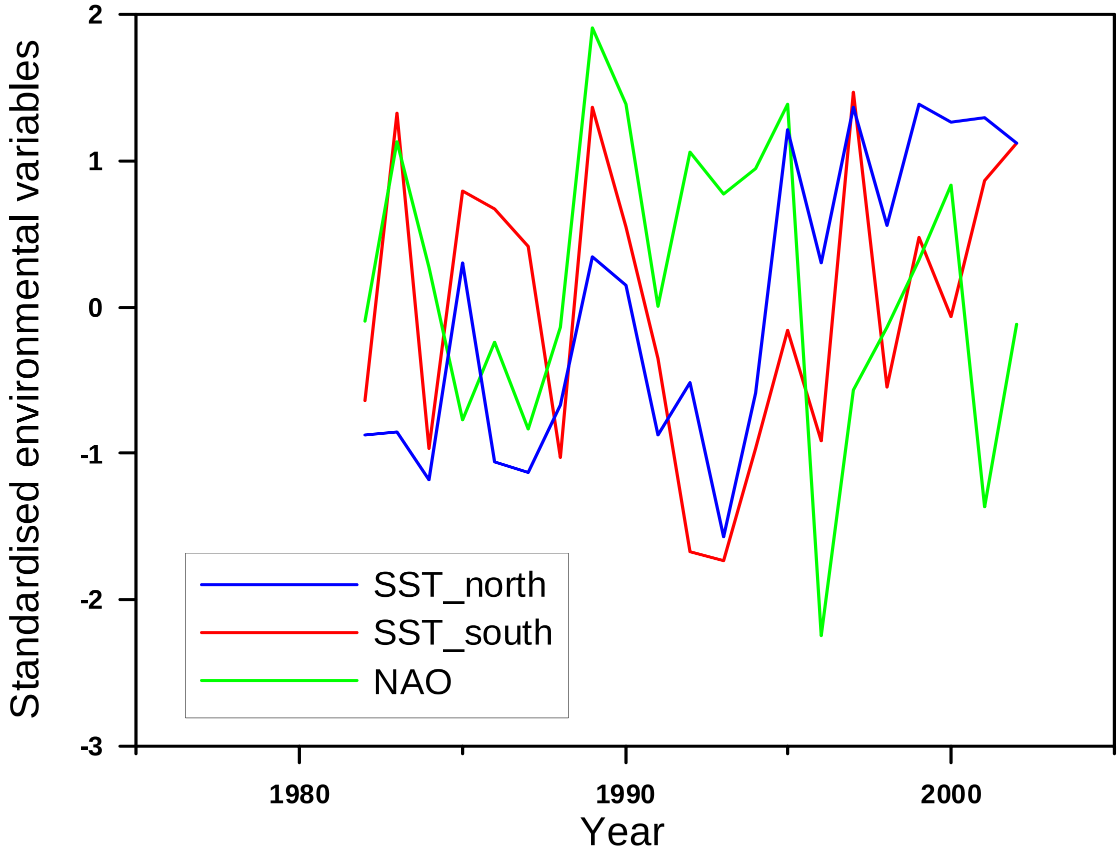

Figure 4. Results for dynamic factor analysis. The upper row of figures contains the first common trends (left), and factor loadings (right). The lower rows contain the graphs for the second common trend. Series labels are as in Table 3.

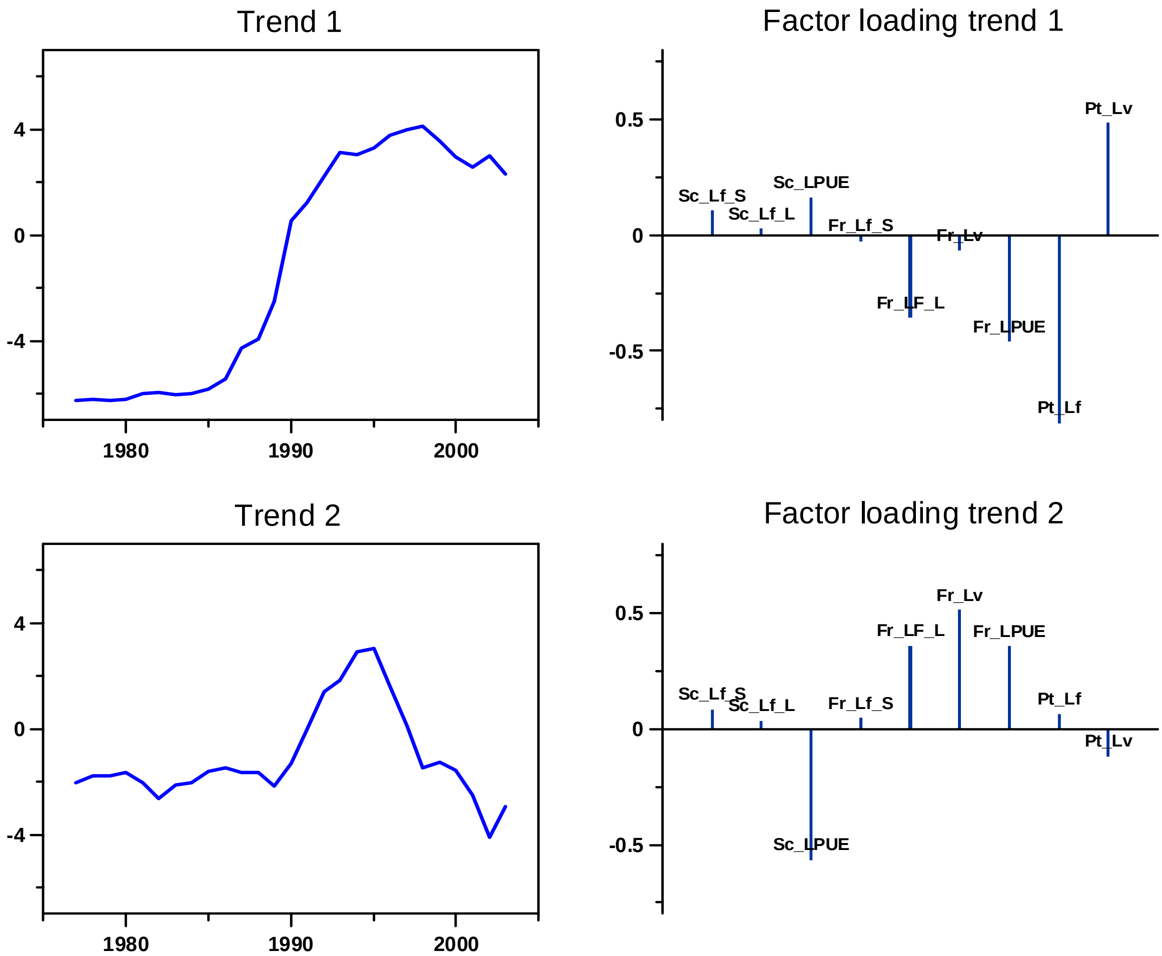

Figure 5. Fitted values (lines) and standardised observed values for CPUE and LPUE series. The labels for each graph are as in Table 3.

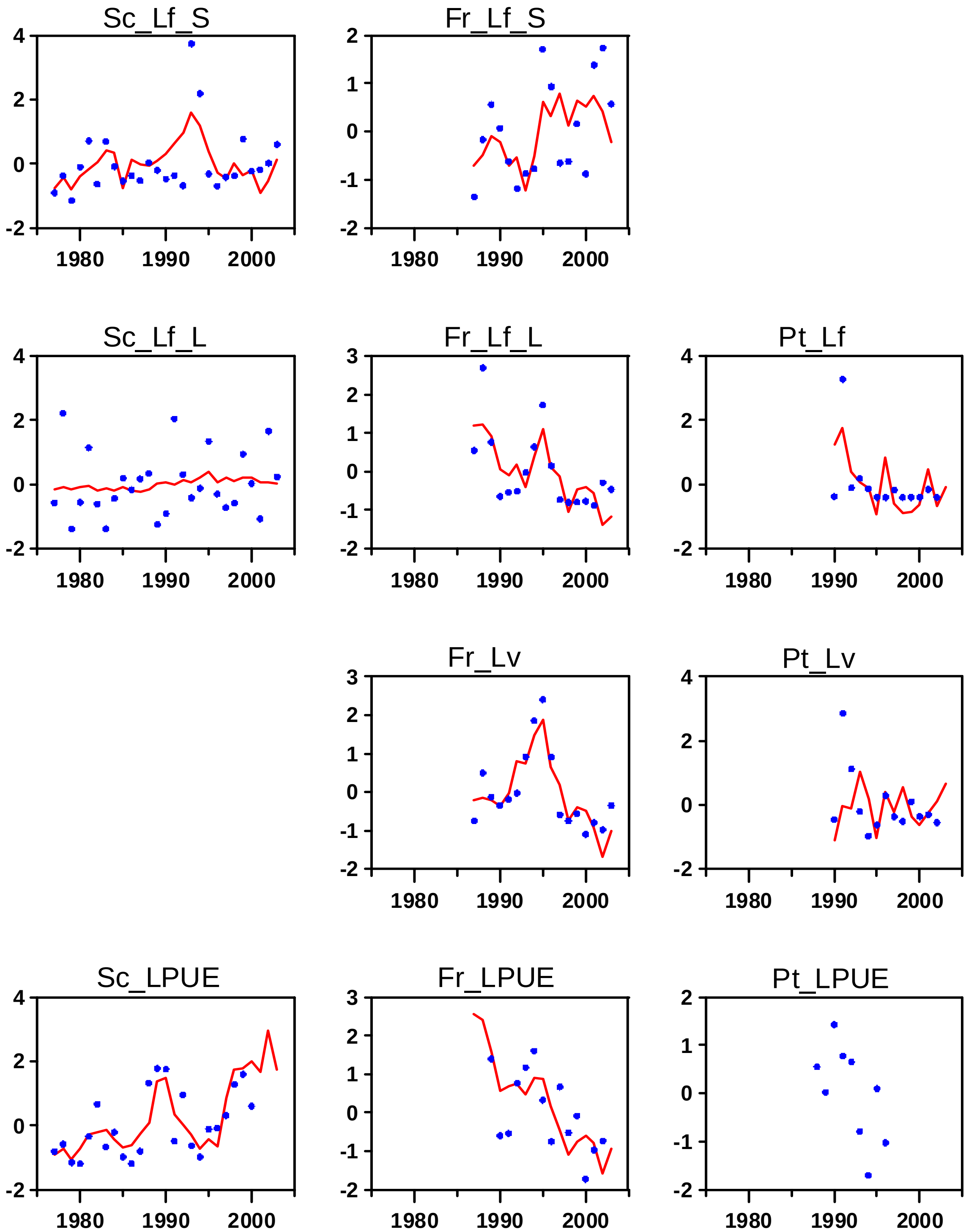

Figure 6. Selected squid time series and explanatory variables: thick blue lines represent common trends and explanatory variable series, thin black lines represent positive relationships and red lines are negative relationships between common trends and explanatory variable series and squid abundance series.

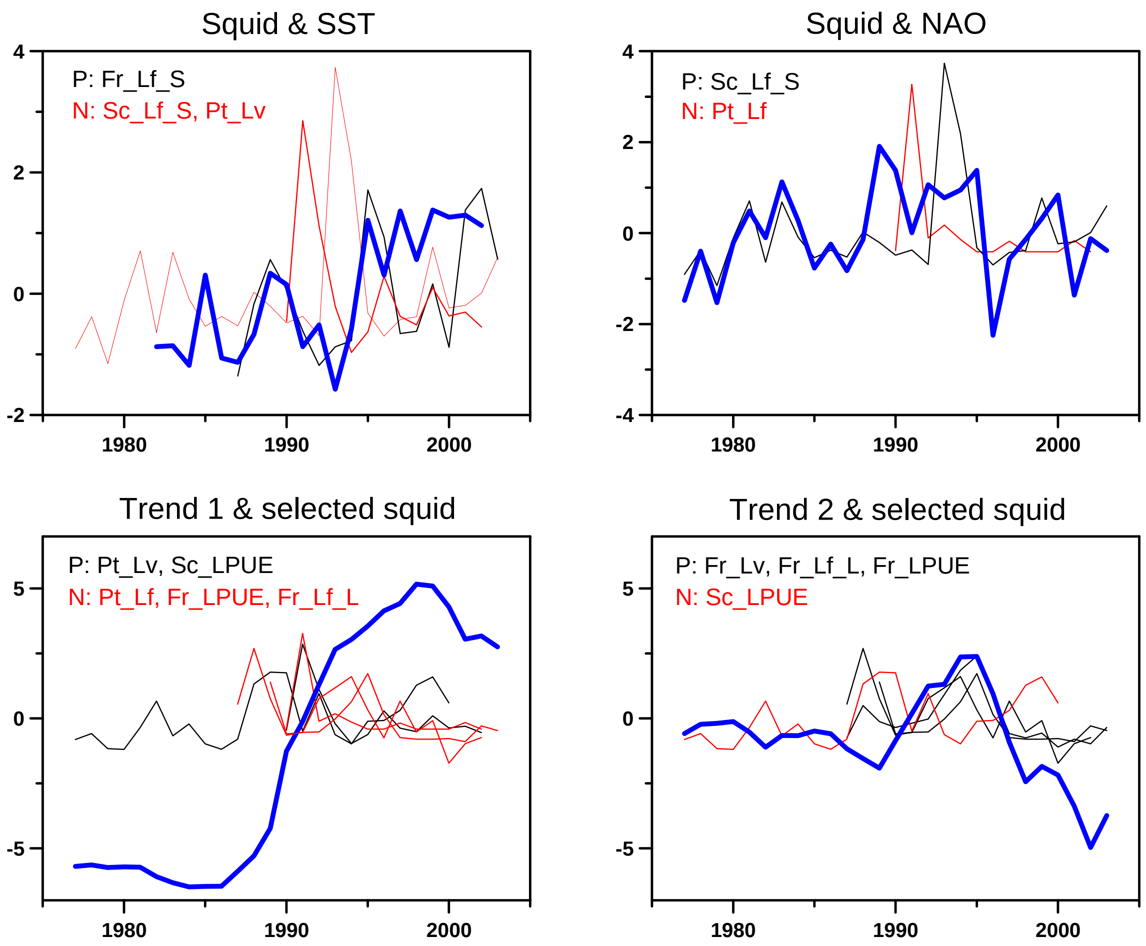

Figure 7. Multidimensional scaling plot for the error covariance matrix. (Labels are as in Table 3).

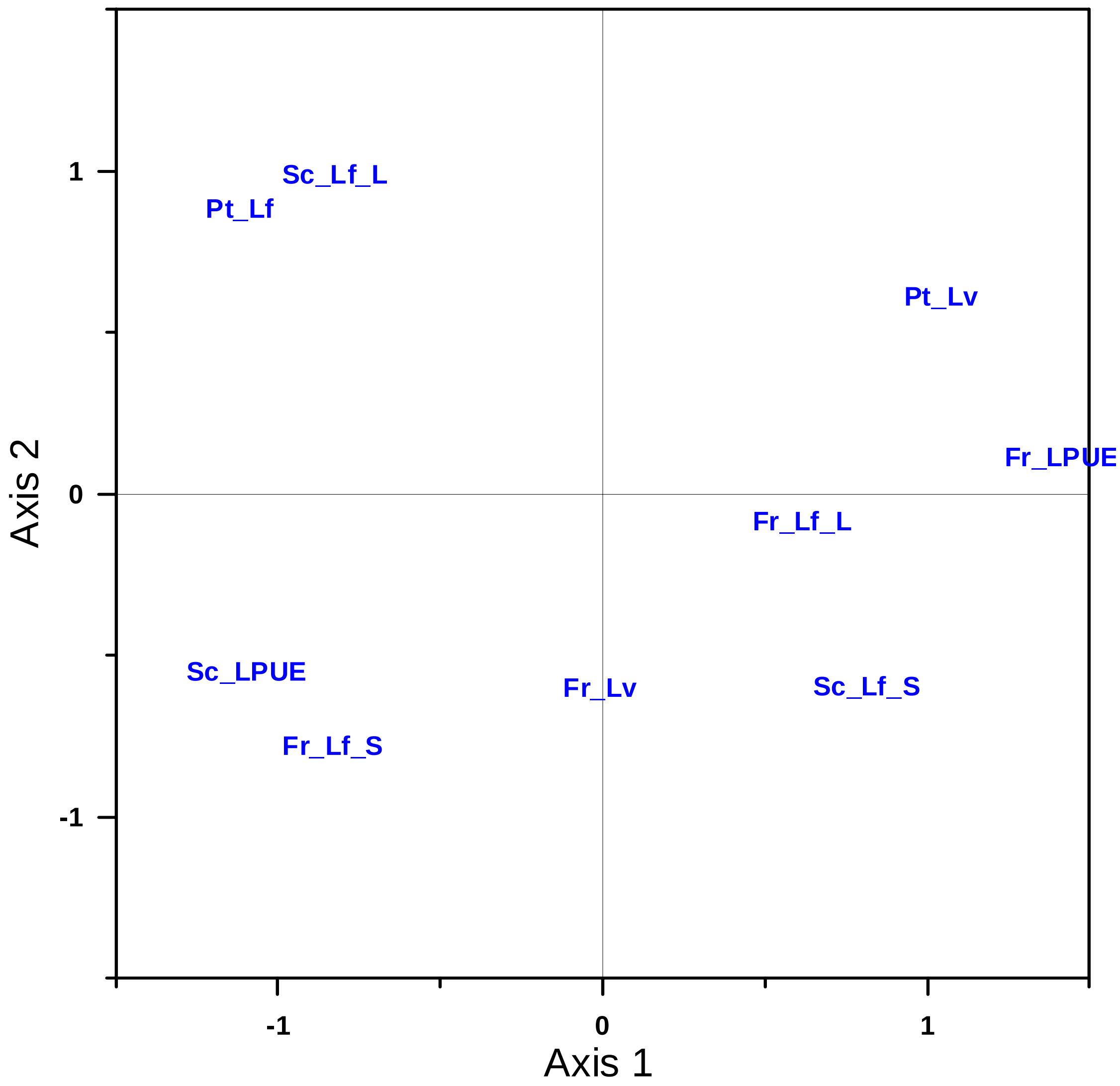

Figure 8. Trawl survey abundance of *Loligo forbesi* and *L. vulgaris* in the Gulf of Cádiz, 2000-04 during quarters 1 and 4 of the year.

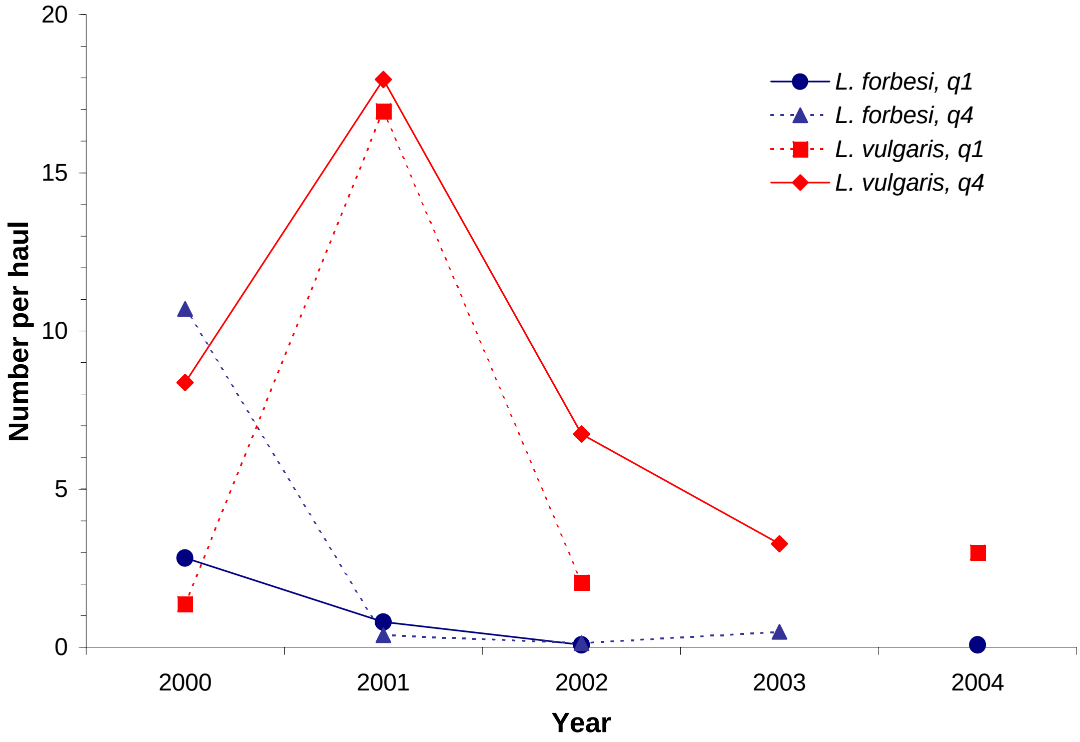

Figure 9. Trawl survey abundance of *Loligo forbesi* (squid caught per 1 hour tow) in the Ligurian Sea, Mediterranean.