

## Interaction between marine populations and fishing activities: temporal patterns of landings of La Rochelle trawlers in the Bay of Biscay

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### Abstract

Marine populations are distributed heterogeneously in space and time because of the diversity of habitats and the requirements of species life cycles. Human exploitation of these resources also varies as a function of space, time and the type of fishing activities performed. These three factors determine fishing strategy at different levels of integration. The purpose of this study was to describe and analyse, with respect to different time scales, the relations between the modalities of resource exploitation and the biological or demographic characteristics of the species involved. These investigations relate to the more general task of acquiring the basic knowledge needed for spatialised management of fishing effort. A fleet of trawlers from La Rochelle, operating in the Bay of Biscay, was studied over a 15-year period (1979–1993), which led to the development of a reference resource exploitation scheme for these vessels. The degree of stability of this scheme over time was determined from landing profiles of the 18 most important species fished (94% of landings). An annual cycle for the species composition of landings was determined by multiple factor analysis. Two factors account for more than 55% of the inertia of the data. The first, of biological origin, is closely related to the breeding activity of species and associated migrations between the coast and the open sea. The second is spatial in nature, corresponding to the distribution and availability of resources according to a bathymetric gradient. This organisational scheme persisted over the first 13 years, but showed signs of change toward the end of the study period. Analysis of multi-year trends indicated four periods marked by sustained levels of landings per unit of effort for some species (decreasing for sole and wedge sole, or increasing for Norway lobster, striped red mullet, rays and the smallspotted catshark). These changes are attributable to restrictions on resource access imposed on the fleet (regulations and/or competition among the fishing gears for occupation of space), variations in the abundance of traditionally fished populations (hake, anglerfish) and changes in the professional behaviour of fishermen. © 2002 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

### Résumé

**Interaction ressources halieutiques et exploitation : l'organisation temporelle des apports des chalutiers de La Rochelle dans le golfe de Gascogne.** Les populations marines sont distribuées de manière hétérogène dans l'espace et dans le temps en raison de la diversité des habitats et des exigences des cycles vitaux des espèces. L'intensité de l'exploitation varie également en fonction de l'espace, du temps et des métiers pratiqués. Ces trois facteurs structurent la stratégie de pêche à ses différents niveaux d'intégration. L'objectif de cette étude est de décrire et caractériser les liens qui existent entre les modalités d'exploitation des ressources et les traits biologiques ou démographiques des espèces exploitées, à différentes échelles de temps. Il participe de la démarche plus générale qui vise à réunir la connaissance de base nécessaire à une gestion spatialisée de l'effort de pêche. Une flottille de chalutiers de La Rochelle, opérant dans le golfe de Gascogne, est examinée sur une période de 15 ans (1979–1993). Ce suivi a conduit à identifier un schéma d'exploitation de référence pour ces navires et de caractériser le degré de stabilité de ce schéma dans le temps à partir des profils de production des dix-huit espèces les plus importantes (94 % des débarquements). Un cycle annuel de la composition spécifique des productions est mis en évidence par analyse factorielle multiple. Deux facteurs expliquent plus de 55 % de l'inertie des données. Le premier d'origine biologique est fortement lié à l'activité de reproduction des espèces et aux migrations associées entre la côte et le large. La seconde composante a un caractère spatial correspondant à la distribution et à la disponibilité des ressources suivant un gradient bathymétrique. Ce schéma d'organisation subsiste au cours des treize premières années de la série mais il s'altère sur la fin de la période étudiée. L'examen des tendances pluriannuelles amène à reconnaître quatre périodes marquées par des niveaux soutenus des prises par unité d'effort de certaines

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espèces (diminution pour la sole et le céteau ou augmentation pour la langoustine, le rouget barbet, les raies et la petite roussette). Ces évolutions s'expliquent par des restrictions des conditions d'accès à la ressource imposées à la flottille (réglementation et/ou compétition pour l'occupation de l'espace entre métiers), par des fluctuations d'abondance des populations traditionnellement exploitées (merlu, baudroie) et par des changements du comportement des pêcheurs. © 2002 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

*Keywords:* Landings; Bottom trawlers; Multiple factor analysis; Seasonal variability; Bay of Biscay; Atlantic ocean

## 1. Introduction

Marine populations are distributed heterogeneously in space and time because of the diversity of habitats and the requirements of species life cycles. The degree of human exploitation of these resources also varies as a function of space, time and the type of fishing activities performed. These three factors determine fishing strategy at different levels of integration ranging from simple fishing operation (Pelletier and Ferraris, 2000) to trawler fleet scale (Bertignac, 1992). Thus, it is important, on the basis of different time-scales, to identify and define the relations between the modalities of resource exploitation, the spatial organisation of resources, and the biological and demographic characteristics of the species fished. This basic knowledge is essential to improve assessments of the populations involved and ensure long-term exploitation, particularly through spatialised management of fishing effort.

Data on resource distribution provided by scientific surveys are reliable and referenced geographically with controlled spatial resolution. The geographical scale can be considered in terms of the a priori supposed distribution of target resources. These surveys supply exhaustive knowledge about the distribution of populations at a given time, but the high cost of operations at sea generally excludes repeated sampling during the same year. On the other hand, observations obtained through commercial fishing operations are quite numerous in time, but limited spatially by the concentration of the fishing effort over some selected fishing grounds. Nonetheless, they are likely to reveal short-term changes in the accessibility and availability of fishing resources.

The use of statistical series from commercial fisheries needs to take account of the particular characteristics of this form of sampling. For example, part of the catch not in accordance with marketing standards is discarded to the sea. Moreover, technical innovations in a broad sense (changes in equipment or fishing sites, etc.) can modify the species composition of landings.

This study considered the role of the time factor on a monthly basis at the scale of the year and over a period of 15 years in the organisation of the fishery of La Rochelle trawlers on the south-eastern continental shelf of the Bay of Biscay. This multispecies approach consisted first in defining the temporal organisation of resource exploitation and its relation to the biology of the species fished and then determining the degree to which these conditions persisted.

The landings of La Rochelle trawlers fishing in the Bay of Biscay were analysed from detailed data (composition of catches by species and trip) collected by Ifremer for the national system of fishery statistics. This trawler fleet was relatively stable over time with respect to type of fishing gear used, sites fished, and the main species sought. The trawlers selected for the study were 10–24 m in length, used bottom trawls exclusively, and were at sea for 4–12 days. Fishing was conducted essentially in the Bay of Biscay (95 to 85% of fleet fishing effort between 1980 and 1990). The main modal values for the boats were 45–49 grt for the tonnage, 17–18 m for the length and 300–350 kW for engine power.

Data concerning the activity of these trawlers in the Bay of Biscay between 1979 and 1993 were considered in terms of the following points: (i) What organisation of resource exploitation can be identified on an annual scale from analysis of changes in the species composition of monthly landings per unit of effort (LPUE)? (ii) Did a common structure exist for all years? (iii) To what extent did the organisation persist over the 15-year study period?

## 2. Materials and methods

### 2.1. Data

Almost 95% of the activity of the La Rochelle trawler fleet in the Bay of Biscay concerned latitudes 44°30'–46°N, mainly between the coast and the 100 m isobath (Fig. 1). The fleet's occupation of space was characterised by the displacement of part of the fishing effort toward the open sea during the first 6 months of the year (a maximum of 20% of effort in February and March).

The fishing effort expended by each boat was defined as the product of fishing time multiplied by engine power. This method ensured some standardisation of fishing effort, allowing for possible changes in engine power (Salthaug and Godo, 2001). The localisation of fishing effort was not known with sufficiently fine spatial resolution because of the size, shape and bathymetry of the exploited area. At best, this information is available since 1986 by statistical rectangle as defined by the International Council for the Exploration of the Sea (ICES), i.e. for areas 0.5° in latitude by 1° in longitude (Fig. 1). This spatial resolution was not adapted to take into account the spatial distribution patterns of the fishing activity (Léauté, 1998) and of the species in

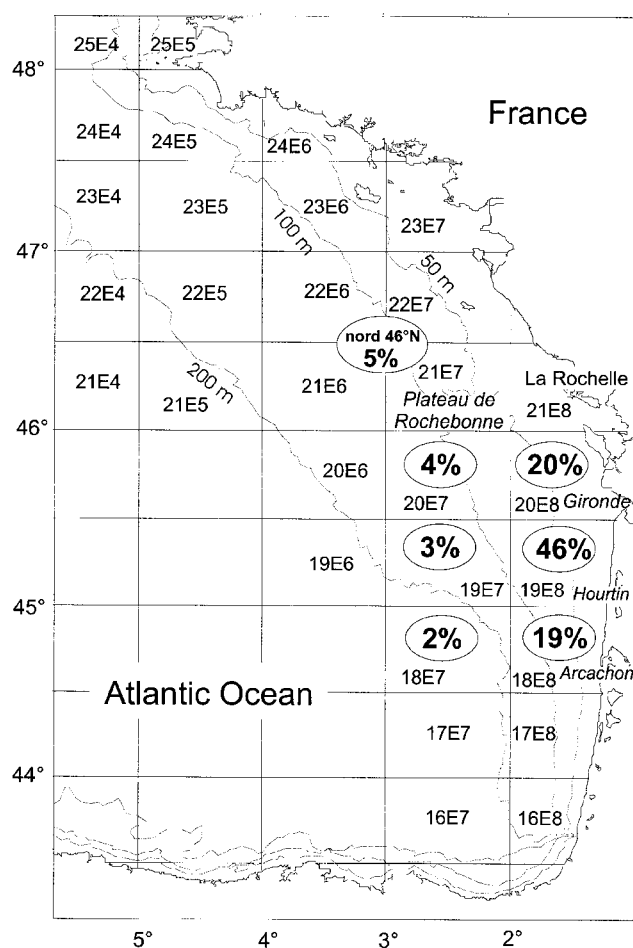


Fig. 1. Mean yearly spatial distribution of fishing effort of La Rochelle trawlers in the Bay of Biscay per ICES statistical rectangle from 1986 to 1993.

this area (Souissi et al., 2001). Therefore, the spatial distribution of fishing effort was not included in the analyses.

Landing data by species and associated fishing effort were available by trip for each boat. Data were aggregated on a monthly basis, and monthly LPUE were calculated. The LPUE were assimilated to indices of species abundance and expressed in  $\text{kg} \cdot 10^{-3} \text{h} \cdot \text{kW}^{-1}$ .

The number of species identified in the catches increased from 31 in 1979 to 69 in 1993, and the proportion not categorised decreased from 20% in 1979 to 3% in 1993. Thus, the quality of the data improved during the study period. The 18 species selected for the study were those that contributed the most to total annual landings and were identified in catches for at least 12 years. They represented on average more than 90% of the quantities landed and identified (Table 1).

On the 15-year scale studied, these 18 species can be classified into three categories depending on their contribution to landings: four main species each making more than 10% of catches, five secondary species with proportions between 2 and 10%, and nine accessory species. Annual

Table 1

List of the 18 most important species identified and selected for this study in landings of La Rochelle trawlers from 1979 to 1993

Common name	Species	Code	Mean landings (%)
Sole	<i>Solea vulgaris</i>	SOL	20.0
Bib	<i>Trisopterus luscus</i>	BIB	15.8
Cuttlefish	<i>Sepia officinalis</i>	CUT	12.7
Hake	<i>Merluccius merluccius</i>	HAK	12.0
Anglerfish	<i>Lophius</i> spp.	ANG	7.2
Squid	<i>Loligo</i> spp.	SQU	5.6
Whiting	<i>Merlangius merlangus</i>	WHI	3.2
Norway lobster	<i>Nephrops norvegicus</i>	NOR	3.2
Wedge sole	<i>Dicologlossa cuneata</i>	WED	2.8
Horse mackerel	<i>Trachurus</i> spp.	HOR	1.9
Bass	<i>Dicentrarchus labrax</i>	BAS	1.6
Striped red mullet	<i>Mullus surmuletus</i>	MUL	1.6
Red gurnard	<i>Aspitrigla cuculus</i>	GUR	1.5
Conger	<i>Conger conger</i>	CON	1.3
Small spotted catshark	<i>Scyliorhinus canicula</i>	CAT	1.1
Rays	<i>Raja</i> spp.	RAY	1.1
Pollock	<i>Pollachius pollachius</i>	POL	0.9
Mackerel	<i>Scomber scombrus</i>	MAC	0.8
Total			94.3

mean productions were greater than 200 tons for the main species, between 50 and 200 tons for the secondary species, and less than 50 tons for the accessory species.

Data collected in the area fished by the La Rochelle trawlers during the regular EVHOE groundfish surveys carried out by IFREMER in the Bay of Biscay were used as support for interpretation (Amara et al., 1998; ICES, 1997a; Souissi et al., 2001).

## 2.2. Methods

In the present study, we first intended to characterise the chronology of the changes in the species composition of monthly LPUE in order to identify a possible time scheme common to all years and to assess the persistence of this organisation during the 15-year study period.

The data set (Fig. 2) included 15 tables, each of them had 12 lines corresponding to the monthly LPUE values for the 18 species. It is a three-way (month, species and year) data set. That amounts to saying that the same variables (18 species LPUE) were measured on the same set of individuals (12 months) at 15 different occasions. To identify the common part, over years, of the yearly multispecies temporal structures requires the combined analysis of all the different tables. Although they are still little used in fishery sciences and marine ecology (Gaertner et al., 1998; Gaertner et al., 1999), multitable factorial analyses (Escofier and Pagès, 1994; Lavit et al., 1994) offer a theoretical framework suited to investigation of the reproducibility of multivariate structures.

Multiple factor analysis (MFA) (Escofier and Pagès, 1994) was used to provide a simultaneous representation of the 15 years studied. MFA is especially designed to study several groups of quantitative or qualitative variables de-

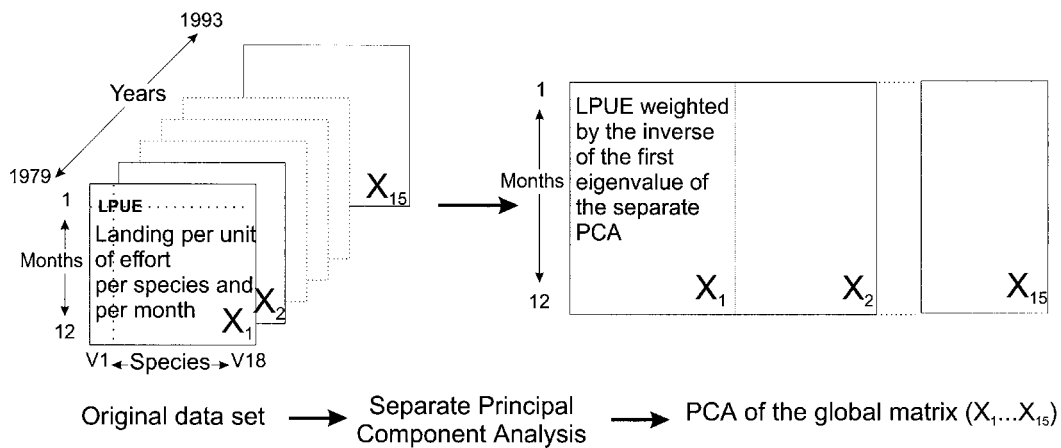


Fig. 2. Application of the multiple factor analysis (Escofier and Pagès, 1994) to the landings per unit of effort per month and per species of La Rochelle bottom trawlers over the 1979–1993 period.

fined on the same set of individuals. These groups can be composed of variables measured at different time-points (Dazy and Le Barzic, 1996).

Three different stages of analysis are emphasised. The first stage, called interstructure analysis, concerns the study of the relationships between the groups (here years) of variables (here species) from a global point of view. The second one, called the compromise analysis, concerns the study of the proximities between individuals (here months), based on the weighted means of the proximities associated with each group of variables. The third stage, named the intrastructure analysis, concerns an analytical study of the relationships among the variables and the proximities among the individuals in the different groups of variables.

The MFA first performs a separate principal component analysis (PCA) for each group of quantitative variables. Then, each group is weighted by the inverse of the first eigenvalue of its separate analysis to balance inertia between the different groups and thus balance their influences. Finally, a PCA of the entire weighted matrix is performed to study the different groups of variables in a unique reference space. The correlation between the global cloud (defined by all the variables) and the partial clouds (defined by each group) indicates whether the structure shown by each axis of the MFA is common to several groups or specific to one of them.

The landings of four of the 18 species selected (*Raja* spp. *Scyliorhinus canicula*, *Conger conger* and *Aspitrigla cuculus*) were poorly recorded at the beginning of the period. As the number of variables can differ from one table to another, they were gradually introduced into the data set from 1980 to 1982. The scatter of LPUE values was quite variable, depending on the species. Moreover, to avoid favouring one or another of the species, the data were standardised (zero mean and unit variance) within each table, thereby compensating for the hierarchical effect described above. In fact, a species defined as accessory could temporarily become a target species during certain trips.

Automatic classification techniques were used to establish a cluster distribution of the 180 months of the study and thus highlight the species profiles that characterise the exploitation activities. Hierarchical ascending classification (Legendre and Legendre, 1998) was applied to the factorial co-ordinates of the months in the space defined by MFA. The groups identified by truncating the tree diagram are consolidated by aggregation around mobile centres (Banfield and Raftery, 1992). The variables contributing most to the formation of groups were identified by the test values associated with them (Morineau, 1984). The test value corresponds to a statistical criterion, based on a test of comparison of means, which is similar to a standardised variable (zero mean and unit variance). Significance is obtained when the absolute value is  $\geq 2$ . The test value constitutes a measurement of the distance (in units of standard deviations) between the mean of the variable in a cluster and its general mean.

In a second step, the 18 series of monthly LPUE were seasonally adjusted. As most of the species showed a positive correlation between the annual LPUE means and their standard deviations, a multiplicative model was used to extract the seasonal component. The seasonal coefficients were estimated from a Buys–Ballot table (Legendre and Legendre, 1998). The seasonally adjusted LPUE were grouped in a single 180-line (months), 18-column (species) matrix, then input to a PCA (Lebart et al., 1984) to identify the multi-year trends. Fourteen active variables were considered, whereas *Raja* spp. *S. canicula*, *C. conger* and *A. cuculus* were introduced as illustrative variables. A new distribution of the 180 months was searched for by hierarchical ascending classification, using their factorial scores. Ward's criterion was used to aggregate two elements by minimising intra-cluster inertia.

In addition, the hauls performed during the EVHOE surveys in May 1988 and 1991 and during the autumn months (October and November) from 1987 to 1990 and in 1992, 1994 and 1995 were grouped by season. Eighty-eight

Table 2

Multiple factor analysis (MFA) of 18 species LPUE of La Rochelle trawlers from 1979 to 1993. Correlation coefficients between the first three factorial axes and the projection of each group of variables (years)

Years	Axes		
	1	2	3
1979	0.97	0.92	0.89
1980	0.93	0.82	0.89
1981	0.98	0.92	0.92
1982	0.96	0.88	0.96
1983	0.95	0.88	0.87
1984	0.97	0.92	0.94
1985	0.96	0.74	0.85
1986	0.95	0.96	0.89
1987	0.99	0.95	0.94
1988	0.98	0.95	0.94
1989	0.99	0.95	0.92
1990	0.96	0.94	0.89
1991	0.96	0.92	0.91
1992	0.96	0.89	0.89
1993	0.87	0.79	0.84

stations visited in the spring and 285 in the autumn south of 46°N were analysed according to bathymetry and latitude to identify seasonal changes in the distribution of species.

### 3. Results

#### 3.1. Strong seasonal organisation

The first three eigenvalues of the MFA explain 68% of the total variance of the data. The high value (13.1) recorded for the first eigenvalue shows that the first MFA factor corresponds to an important direction of inertia for each of the years. The high correlation coefficient obtained for each year (Table 2) indicates that the structuring factors expressed by the first three principal components of the MFA are common to all years. Our analysis will be limited to these three components.

##### 3.1.1. Main structuring species

The axes of the MFA summarise the main changes occurring during the year in the species composition of the landings. The correlation between the species and the axes are summarised in Table 3. The coefficients of correlation of five species with the first two axes are illustrated in Fig. 3. The first axis exhibits a main feature of the exploitation: the opposite changes observed in the species LPUE values between the autumn and winter months (species negatively correlated with the first axis) and the months from April to July (species positively correlated with this axis). The second axis distinguishes the species fished mainly in late winter and spring (*Pollachius pollachius*, *Trachurus* spp. *Scorpaenopsis scorpaenoides*, *Lophius* spp. and *Mullus surmuletus*) from those caught in summer (*Dicologlossa cuneata*). The correlation of *M. surmuletus* and *S. scombrus* with the third axis emphasizes the relatively high levels of their

Table 3

Summary of correlations between variables and the first three principal components of MFA (–: negative correlation, +: positive correlation; in brackets: number of correlated years among the 15 studied years). Three species (*Raja* spp., *S. canicula* and *A. cuculus*) are weakly correlated with these components. Distribution of the nine categories

Species	Axes		
	1	2	3
<i>D. labrax</i>	– (14)		
<i>Loligo</i> spp.	– (15)		
<i>C. conger</i>	– (10)		
<i>P. pollachius</i>	– (12)	+ (12)	
<i>S. officinalis</i>	– (14)		
<i>S. vulgaris</i>	– (11)		
<i>T. luscus</i>	– (15)		
<i>Trachurus</i> spp.	+ (10)	+ (9)	
<i>N. norvegicus</i>	+ (13)		
<i>M. merlangus</i>	+ (9)		
<i>M. merluccius</i>	+ (13)		
<i>D. cuneata</i>		– (12)	
<i>Lophius</i> spp.		+ (11)	
<i>S. scombrus</i>		+ (15)	– (12)
<i>M. surmuletus</i>		+ (8)	– (9)

LPUE during April and May. *A. cuculus* was rarely correlated with one of the three axes, while *Raja* spp. and *S. canicula* were correlated with axis 1 from 1990.

##### 3.1.2. Annual changes in the profile of fished species

Fig. 4 displays the mean positions of the months defined with respect to the whole set of species LPUE together with the projections of the 15 partial months defined with respect to each of the 15 groups of species LPUE, in MFA planes 1–2 and 1–3. The position of the month is indicative of its

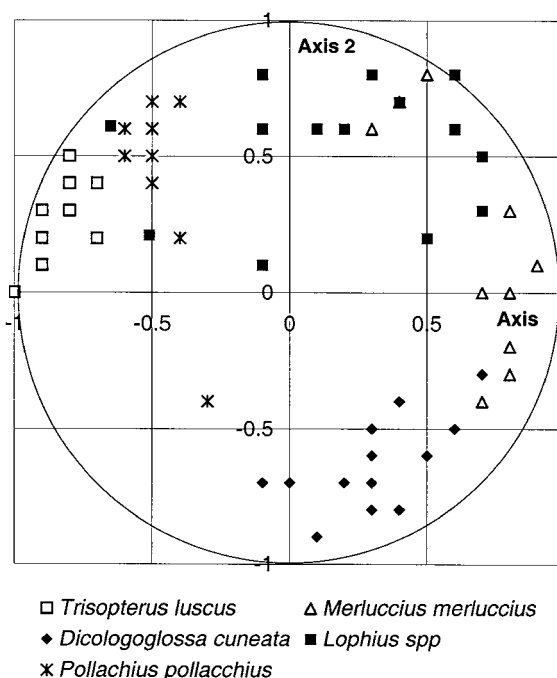


Fig. 3. Graphical display of the correlations between five species and the first two principal components of the multiple factor analysis (MFA); some points are multiple.

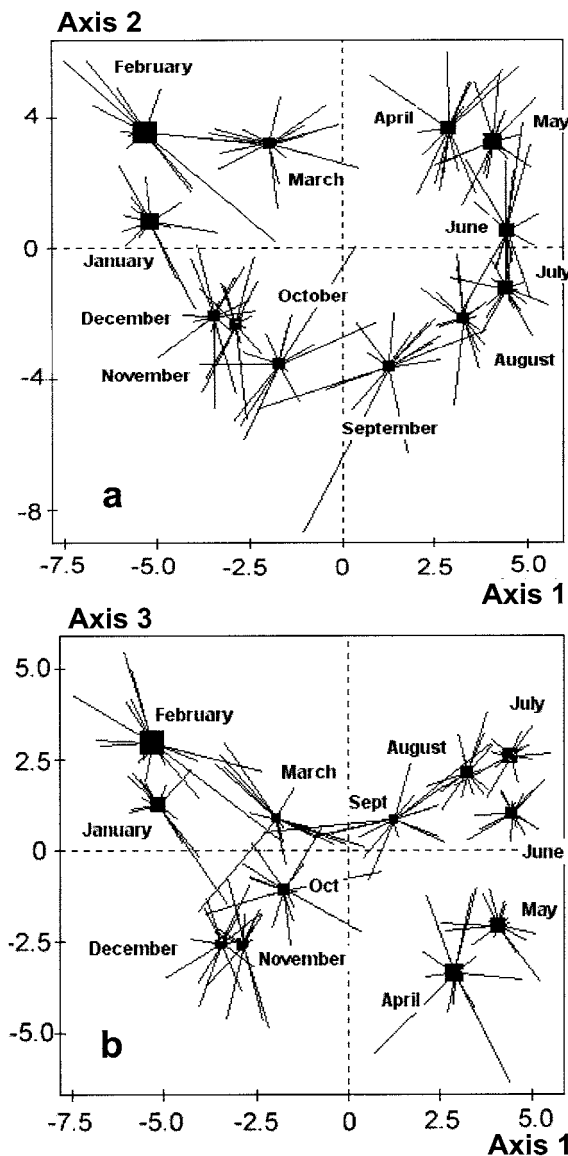


Fig. 4. Graphical display of the projections of the months: (a) in the principal multiple factor analysis (MFA) plane; (b) in the 1–3 MFA plane. Squares represent the mean (compromise) positions of the months over the studied period; they are defined with respect to the whole set of variables. Symbol size is proportional to the contribution of months to the building of axes. The associated segments of line are proportional to the distance between mean month position and each position of the 15 partial months (defined with respect to each of the 15 groups of variables).

mean species composition of the LPUE. To characterise the changes in species profiles over time, the factorial coordinates of the 180 months on the first three MFA axes (Fig. 4) were used to distribute the months into nine classes (Table 4). Twelve species contributed significantly to the construction of these classes (Fig. 5). Their mean LPUE were more often structuring factors when the means per class were lower than the general means.

Seven profile categories (A–D and F–H; Fig. 5) describe the changes in the species LPUE during the year (Table 4). The profiles dominated by *Trisopterus luscus* (A) or the pairs *T. luscus*–*Solea vulgaris* (B), *Sepia officinalis*–*Lophius*

Table 4

Distribution of the categories (A to I) of species profiles of landings per unit of effort. Nine clustering of the 180 study months were based on their factorial co-ordinate scores on the first three MFA axes

	January	February	March	April	May	June	July	August	September	October	November	December
1979	A	B	A	D	D	F	F	G	G	H	H	H
1980	A	B	C	D	D	G	G	G	G	G	H	H
1981	A	B	A	D	D	F	F	F	G	I	H	H
1982	A	B	C	D	D	F	F	F	F	H	H	H
1983	A	C	C	E	E	E	F	G	I	I	H	I
1984	A	B	C	D	E	E	F	G	G	I	I	H
1985	A	A	C	D	D	F	F	F	G	H	H	H
1986	H	B	C	D	E	F	F	G	G	I	H	H
1987	A	B	C	D	D	F	F	F	G	I	H	H
1988	A	B	C	D	E	F	F	F	I	G	H	H
1989	A	A	A	D	D	F	F	F	G	H	H	H
1990	A	B	C	D	D	E	F	G	G	I	I	I
1991	A	A	A	D	D	E	F	F	G	H	H	H
1992	H	A	C	E	E	E	F	F	I	I	I	H
1993	H	C	C	E	E	E	E	G	I	I	H	H
Dominant	A	B	C	D		F		G		H		

spp. (C) and *Merluccius merluccius*–*D. cuneata* (G) are each characteristic of a month (respectively January, February, March and September). Conversely, profiles D (*S. scombrus*–*Trachurus* spp.), F (*M. merluccius*–*Nephrops norvegicus*) and H (*S. officinalis*–*Loligo* spp.) relate respectively to April–May, June–August, and November–December.

Even though the *S. officinalis* profile (I) was quite often observed in October, its formation seems limited to years characterised by a particularly large abundance of cuttlefish. The temporal distribution of the *Lophius* spp.–*N. norvegicus* profile (E) is mainly limited to the end of the study period. The variability of the species composition around these typical profiles is measured by the trajectories of the months (Fig. 4). Thus, the not very developed trajectories of the months of January, May, July, August, November and December indicate that their species profiles differed little over years, which was not the case for February, March, April, June, September and October.

### 3.2. Persistence of the annual organisation of exploitation

The representation of the 15-year period along the first two MFA axes is shown in Fig. 6. The co-ordinate of a year on an axis indicates the extent to which the principal component is an important structuring factor for the LPUE table of the year. The intensity of this relationship is a means of comparing years. Thus, it is possible to estimate the persistence of the seasonal organisation of exploitation during the period 1979–1993.

Plane 1–2 represents 70% of the total inertia. With the exception of 1983 and 1993, all years are closely related with the first axis. Throughout the study period, fishing

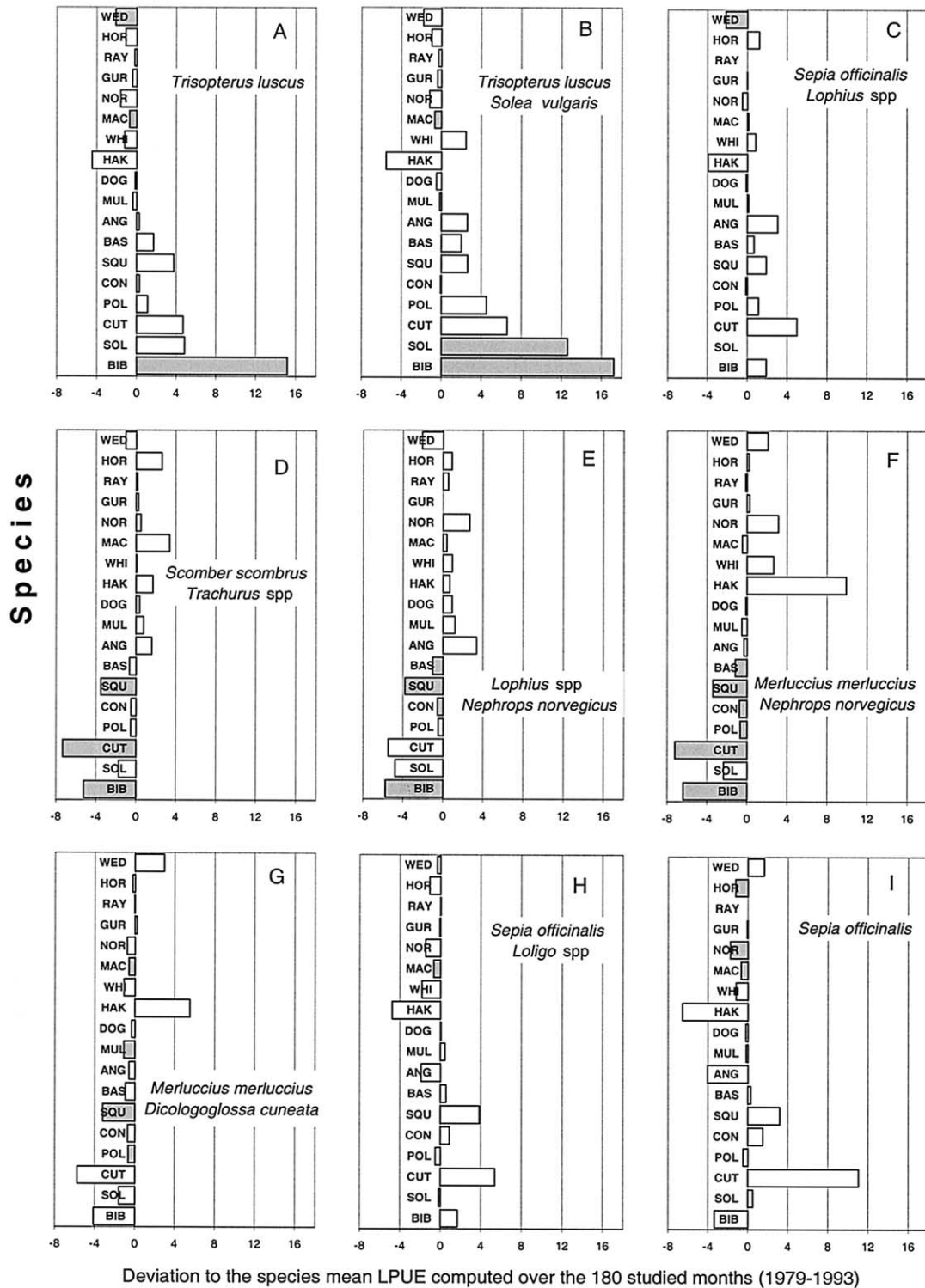


Fig. 5. Variations in the species composition of monthly landings per unit of effort (LPUE) in the nine clusters identified by ascending hierarchical classification of the 180 months, based on their factorial scores on the first three MFA axes. Each species is represented by the deviation to its LPUE mean computed over the 180 months. The 12 species showing a statistically significant test value and contributing most to the building of the nine profiles are identified by the items of the bar charts filled with grey tint.

activity as described by the monthly LPUE was thus highly determined by a change in the main species between autumn/winter and spring/early summer.

This autumn/winter and spring/early summer contrast is less strong in 1983 and 1993 when the annual cycle for the species composition of landings was disturbed (Table 4). In

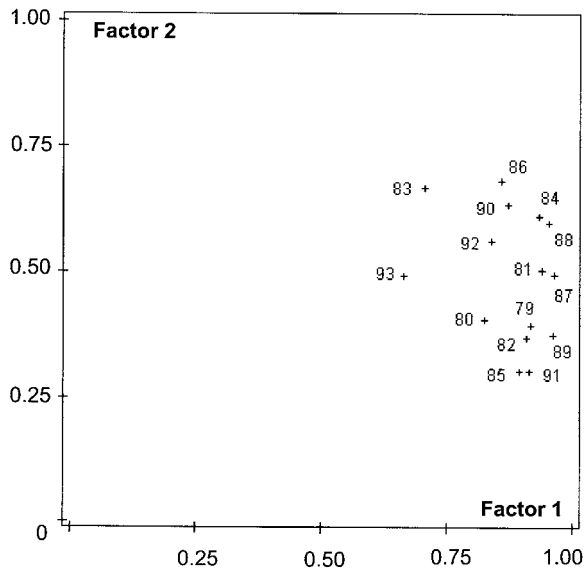


Fig. 6. Multiple factor analysis of the landings per unit of effort per month and per species of La Rochelle bottom trawlers over the 1979–1993 period. Graphical display of years in the principal MFA plane showing the relationships between the groups of variables (years) from a global point of view.

1983, the very marked B and F profiles are replaced in February, June and August by relatively flat C, E and G type profiles. This phenomenon is intensified in 1993 because of the disappearance of profiles A, B and F and the extension of the *Lophius* spp.–*N. norvegicus* profile (E). In both cases, the LPUE of *S. officinalis* are high in autumn.

The co-ordinates of the years on axis 2 are more variable, but show no temporal trends. Their distribution depends on the importance of changes in the species composition of LPUE between the first and second halves of the year. Large co-ordinates correspond to more marked contrasts.

The projection of the years on plane 1–3 (data not shown) reveals no chronological changes and highlights the years with high landings of *S. scombrus* (1984, 1986, 1987, 1988 and 1990) or *M. surmuletus* (1981), for which the LPUE were larger in April. Conversely, in 1992 and 1993, the LPUE for *S. scombrus* were very low, and the distributions for the monthly LPUE of *M. surmuletus* are atypical.

The distributions of the 15 years along the first three MFA components show no temporal trends. The years 1983 and 1993, which were clearly less related with axis 1, also have weak links with axis 3. In general, the annual organisation of exploitation persists throughout the study period.

### 3.3. Multi-year trends in landings per unit of effort

The matrix of seasonally adjusted LPUE was studied by PCA. The first two components accounted for 32% of LPUE variance, and the first five components for 63%. The first axis (Fig. 7) shows opposite LPUE trends between *Solea solea* (SOL) and *Dicologlossa cuneata* (WED) on the one hand and *N. norvegicus* (NOR), *Merlangius merlangus*

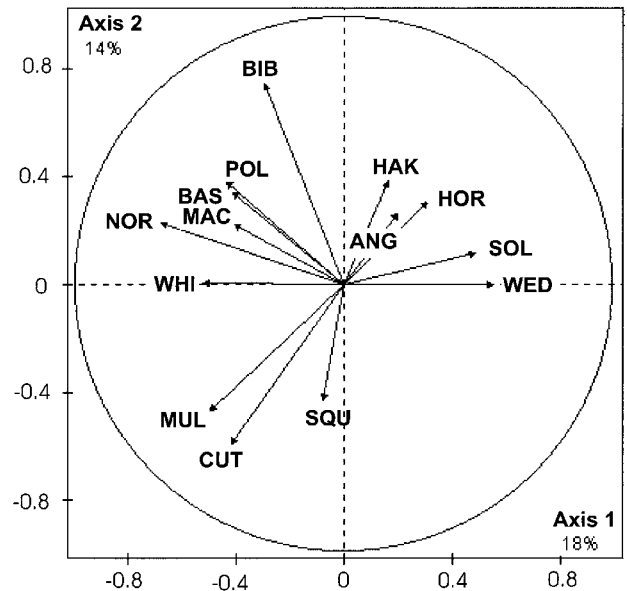


Fig. 7. Principal component analysis of the matrix of seasonally adjusted monthly landings per unit of effort (LPUE): correlation circle for the 14 active variables; species codes are listed in Table 1.

(WHI), *M. surmuletus* (MUL) on the other hand. The first component roughly divides the studied period in two groups of years, 1979–1984 and 1985–1993. On axis 2, *T. luscus* (BIB) is opposed to *M. surmuletus* (MUL) and *S. officinalis* (CUT). Three groups of months are identified by axis 2, they correspond essentially to the years 1985–1986, 1987–1991 and 1992–1993.

The clustering of months on the basis of their factorial co-ordinates led to a distribution into 4 month categories, with inter-class inertia representing 25% of total inertia. Table 5 shows the proportion of each group observed each year. Month categories 1–4 represent respectively more than 75% of the months from 1979 to 1981, 1986, 1991 and 1992–1993. Category 3 accounts for 50–60% of the months from 1987 to 1990, mainly those in the first half of the year from 1988 to 1991. In 1985, the first half of the year is in group 4 and the second half in group 2.

Fig. 8 shows the mean LPUE per species and per month category. LPUE of *S. vulgaris*, *D. cuneata* and *Trachurus* spp. tended to decrease during the studied period. Conversely, the LPUE of *N. norvegicus*, *T. luscus* tended to increase during the first half of the year from 1986 to 1991. The months composing group 2 are found essentially around 1986, and this group is characterised by the increased LPUE of seven species: *Dicentrarchus labrax*, *M. merlangus*, *M. merluccius*, *N. norvegicus*, *P. pollachius*, *S. scombrus* and *T. luscus*. Group 4 shows the highest LPUE of *S. officinalis*, *Loligo* spp. and *M. surmuletus* (Fig. 8). LPUE of other accessory species (i.e. *A. cuculus*, *S. canicula*, *C. conger* and *Raja* spp.) mainly increased from month category 2 to 3.



Table 5  
Identification of multi-year trends in LPUE: yearly ratio of the 4 month categories identified by ascending hierarchical classification of the 180 months, based on their factorial scores on the PCA axes of seasonally adjusted LPUE. Species contributing most to the building of clusters are identified in Fig. 8

Month categories	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
1	100	100	83	17	25	67		9			8			8	
2							50	83	25	17	25				
3			17	42		33			58	58	50	50	83		17
4				42	75		50	8	17	25	17	50	17	92	83

#### 4. Discussion

##### 4.1. Determinants of the annual cycle

Our analysis indicated that one feature was common to the 15 years of the study, namely that changes in the species composition of LPUE were highly structured during an annual cycle. The first principal MFA component led to a first division of the year into two long seasons, autumn/winter (October–March) and spring/summer (April–September). The second MFA component introduced a second level of division of the year, opposing the first and second halves of the year, whereas the third component designated a feature common to the months of April and May. Explanation for this temporal organisation must be searched in the ecology of the species and the spatial distribution of fishing effort during the year.

##### 4.1.1. Biological component of the catch seasonality

Table 6 compares the periods of seasonal maxima with those of reproduction for the 15 species correlated with one of the first three MFA axes. The seasonal increase of the LPUE of the first 11 species in the table is synchronous with reproduction.

*S. vulgaris*, a major species for the La Rochelle trawlers, is the only one with sizeable landings throughout the year. This species breeds from January to April (Amara et al., 1994) on the entire continental shelf. The length frequency distribution of catches by the La Rochelle trawlers showed large concentrations of big individuals at depths of 70–90 m in winter (essentially in February and March), whereas this species is fished at depths of around 50 m during the rest of the year (Guillou and Njock, 1978).

Outside breeding periods, the LPUE of *S. scombrus* and *P. pollachius* are very low. *P. pollachius* is not abundant in the Bay of Biscay, and the best catches in February occur during the breeding period when individuals congregate for spawning (Moreau, 1964).

*T. luscus*, whose LPUE are highest in winter, breeds near the coast and can then be fished on sea bottoms covered with coarse sand and gravel at depths of around 50 m. In June, after spawning, this species moves away from the coast to find shelter in hard substrates (rocks, wrecks), its preferred habitat in the open sea, where it generally escapes trawling operations (Puente, 1986).

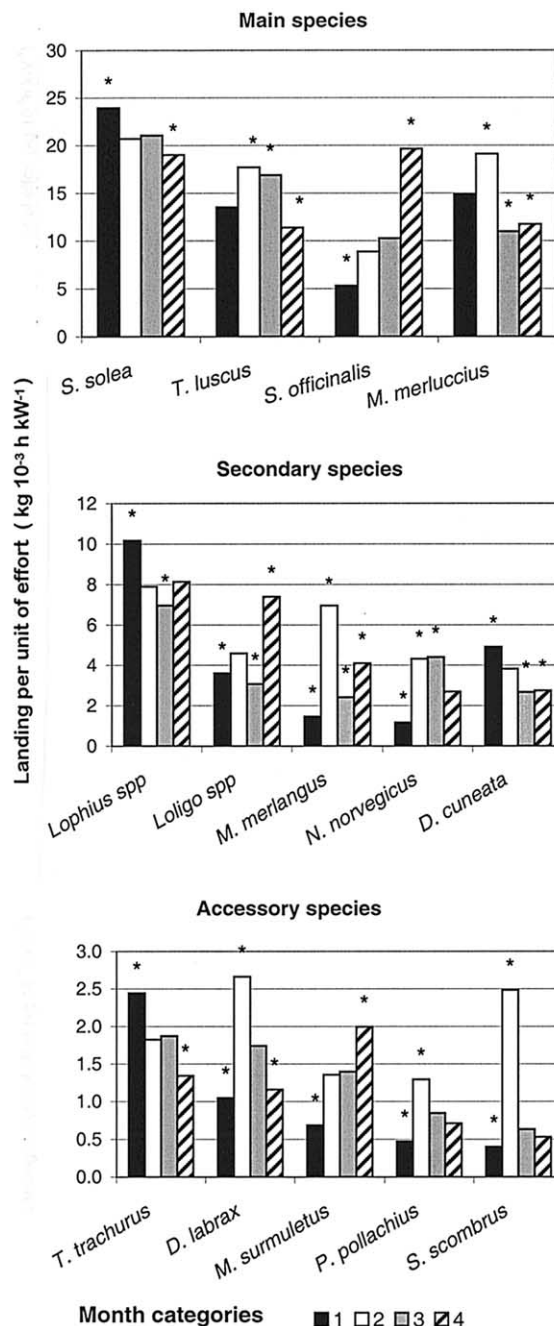


Fig. 8. Trends in landings per unit of effort (LPUE) per species exhibited through month categories. Month categories were identified by ascending hierarchical classification of the 180 months, based on their factorial scores on the PCA axes of seasonally adjusted LPUE. Species with statistically significant test values and contributing most to the building of clusters are marked with an asterisk.

Table 6

Comparison of the periods of seasonal maxima of monthly LPUE with the breeding periods of the 15 species correlated with one of the first three MFA components

Species	LPUE		Breeding		
	Seasonal maxima	Period	Spawning peak	Area	Source
<i>D. labrax</i>	December–February	February–April January–March		Brittany Spain	Boulineau, 1969 Arias, 1980
<i>D. cuneata</i>	July–October	July–September		Bay of Biscay	Forest, 1975
<i>Lophius</i> spp.	February–May	February–July		NE Atlantic	Whitehead et al., 1986
<i>M. merlangus</i>	February, June–July	February–June	February–March	south Brittany	Desbrosses, 1939
<i>M. surmuletus</i>	May	May–June		north Bay of Biscay	N'Da 1992
<i>P. pollachius</i>	February	February–March		Bay of Biscay	Dardignac, 1988
<i>S. scombrus</i>	April–May	February–July	April–May	Bay of Biscay	Johnson 1977
<i>S. vulgaris</i>	January–March	January–April	February–March	Bay of Biscay	Amara et al 1994; Guillou-Njock, 1978
<i>Trachurus</i> spp.	April–May	March–August	June–July	Bay of Biscay	Trouvery, 1978
<i>T. luscus</i>	January–February	January–May	January–March	south Bay of Biscay	Puente, 1986
<i>Loligo</i> spp.	November–February	December–April		Galicia coast	Guerra-Rocha, 1994
<i>C. conger</i>	October–January	summer			Quéro and Vayne, 1997
<i>M. merluccius</i>	June–July	January–March	February	Bay of Biscay	Sarano, 1983
<i>N. norvegicus</i>	June–July	August–November	September–October	Bay of Biscay	Fontaine and Warluzel, 1969
<i>S. officinalis</i>	October–February	March–August	April–May	Bay of Biscay	Gi Jeon, 1982

Most fish species in Bay of Biscay breed during the first half of the year. However, *D. cuneata*, which prefers warm temperate waters, is at the northern limit of its distribution area in the Bay of Biscay (Quéro et al., 1989). Thus, it breeds between July and September when water temperatures reach 13–15 °C (Forest, 1975). This species is then heavily fished by the La Rochelle trawlers.

Arcachon Bay is a spawning area for *S. officinalis*, which breeds in coastal areas (Gi Jeon, 1982). Its life cycle includes a series of seasonal migrations from the coast to the open sea and back to the coast. In late summer, individuals that have spent the summer along the coast begin to migrate offshore. In October, most of the cuttlefish have already reached the open sea where they remain throughout the winter. This migration of *S. officinalis* accounts for the seasonal changes in catches by the different fishing gears involved in its exploitation, whether inshore or in the open sea (coastal trawling, netting, potting and deep-sea trawling) in the Bay of Biscay (Donoso-Perez and Forest, 1993).

The spawning season of *N. norvegicus* (August–November) is at its peak during September and October. Shortly after spawning, females with eggs remain burrowed in the sea bottom during most of the embryonic cycle. They reappear for the hatching of larvae, which is considered to begin in February and end in June (Fontaine and Warluzel, 1969). At this time, the LPUE for Norway lobster increase markedly before decreasing again at the beginning of the next spawning season (August).

The increase in the LPUE of *M. merluccius* in June and July can be attributed to seasonal migration from the open sea to the coast after re-warming of inshore waters (Sorbe, 1972). The results with data obtained from scientific surveys between 45 and 46°N confirmed this movement concerning essentially 2-year-old fish.

Thus, for most of the species considered, there was close synchronisation between the seasonal increase of LPUE and the temporal development of reproductive activity. The migratory behaviour of hake also contributed to the seasonal increase of LPUE. The division of the year relative to this biological activity is consistent with that generated by the first MFA component, indicating that the latter is essentially of biological origin.

#### 4.1.2. Spatial component of the catch seasonality

Depth is a major spatial structuring factor of the demersal species assemblages on the Bay of Biscay eastern continental shelf (Souissi et al., 2001). Data collected during scientific surveys show that the abundance of anglerfish (*Lophius* spp.) and pollock (*P. pollachius*) increased with water depth, whereas *D. cuneata* was practically absent at depths below 50 m. Therefore, the opposition of these species relative to the second MFA component (Fig. 3) resulted from their contrary bathymetric distributions. The second MFA component can thus be interpreted as a spatial gradient (essentially from the coast toward the open sea) along which the activity of the fishing fleet took place. The displacement of a part of the fleet towards offshore areas was more marked in February and March. During the second half of the year, fishing effort was more concentrated in the shallower Hourtin sector (19E8).

The spatio-temporal nature of the third MFA component is revealed by the behaviour of *M. surmuletus*, which is correlated with it. In spring, the abundance of this species in the catches of scientific surveys increased with water depth, and the fish caught were adults (Poulard, 1989). However, most of the catches in autumn were made in coastal areas and consisted of very young individuals. Thus, the two peaks (May and November–December) of LPUE distribu-

tion of this species resulted from the exploitation of two elements of the population with different spatio-temporal distributions.

#### 4.2. Persistence of the annual cycle and fishing strategy

The accessibility of a species corresponds to a geographical component, i.e. its degree of presence on fishing sites (Laurec and Le Guen, 1981). The vulnerability depends on in situ interactions between fish and fishing gears, those are often based on species behaviour. A fish that is accessible and vulnerable is available for the 'métier' taken into consideration.

Biological requirements (species life cycles) were responsible for changes in the availability of species fished by the La Rochelle trawlers, either in terms of accessibility (most fish and molluscs) or vulnerability (e.g. the female *N. norvegicus*). Fishermen can avoid limitations on their activity by changing areas according to season (accessibility modification) or using other gear (vulnerability adaptation). In addition, fishermen must adopt an opportunistic strategy based on the possibilities offered by the resources in the area. Some trawlers leave the Bay of Biscay during summer for trips in the Irish Sea, the Celtic Sea and the Atlantic Ocean west of Ireland (Décamps and Léauté, 1988).

The distribution of years along axis 2 (Fig. 6) depends on changes in the fleet's occupation of space between the first and second halves of the year. The greater the opposition between the coast and the open sea, reinforced by the opposition *Lophius* spp.–*P. pollachius* versus *D. cuneata*, the higher the co-ordinates are for the years. This relationship is apparent from the variations in the rate of presence in sector 19E8 (Hourtin west) during the year. Thus, in 1986, overall activity was greater in 19E8, but especially higher from June to December than from January to May. However, in 1989, activity was low throughout the year, except in May and June. The displacement of the fleet along the coast–open sea gradient had a regulatory role that tended to attenuate the effect of the biological factor.

The profiles of species are generally not very marked, except for those of *T. luscus* (A) and *T. luscus*–*S. solea* (B), because of the lack of target species corresponding to a not very determined fishing strategy. Thus, the development of profiles characterised by *S. officinalis* and *M. merluccius* is concomitant with the increased accessibility resulting from the migration of these species. Moreover, sub-groups of fishermen may exist and act somewhat differently or their behaviour is more apparent some years than others. They could be responsible for the heterogeneity observed in certain years and the greater variability in certain months.

The annual cycle was partially modified in 1983 and 1993 because of the weakening of the winter/summer opposition, which is apparent in the co-ordinates for these years relative to the first component (Fig. 6). In 1993, the LPUE of *T. luscus*, *S. vulgaris* and *D. labrax* (winter species) and *M. merluccius* (a summer species) were low

(Fig. 8 and Table 5). In fact, the hake LPUE decreased strongly in summer while they stayed to their average level during the winter months (Poulard, 2001). In particular, the marked profiles of A, B and F types usually observed were replaced by rather flat profiles of H, C and E types during the first 7 months of the year (Table 4). The high LPUE of cuttlefish switched September from a summer to a winter situation. Thus, the position of 1993 along axis 1 (Fig. 6) results from the uniformity of the profiles from January to July. The distribution of fishing effort in 1993 was in no way exceptional and does not account for the situation observed. But the abundance index calculated for *T. luscus* from the EVHOE surveys was lower in 1992.

The year 1983 showed similarities with 1993. However, the uniformity of the profiles from January to July was less apparent (A and F type profiles were preserved). As in 1993, the cuttlefish profile developed early in September and was characteristic of practically all the autumn period. Species abundance showed features similar to those of 1993 (Fig. 8 and Table 5). Attempts were made to interpret these two special cases using a large scale climatic indicator like the North Atlantic Oscillation (NAO) index (Hurrell, 1995). The NAO index for 1983 was one of the three highest recorded during the period studied, involving mild winter characteristics, which agree with the weakening of the winter/summer opposition displayed by species LPUE. The NAO index for 1993 was at the fifth position when index of years 1979–1993 were ranking in a decreasing order. But this explanation failed because 1989 and 1990 years had the highest NAO index over the 1979–1993 period without special effects on the species LPUE.

#### 4.3. Multi-year trends for LPUE and exploitation modalities

The LPUE of *S. solea*, *M. merluccius* and *D. cuneata* tended to decrease over the 15-year period, while those of *S. officinalis* increased and those of *Lophius* spp. decreased before increasing appreciably in 1992 and 1993. The mean LPUE of *N. norvegicus* doubled since 1986. The LPUE of accessory species such as *S. canicula*, *M. surmuletus* and *Raja* spp. tended to increase.

Do these changes reflect variations in the abundance of the populations fished? Or do they indicate that changes occurred in the way the resources were exploited, i.e. in fleet strategy, competition between the 'métiers' with respect to sequential fisheries, etc.? The data available do not allow a thorough diagnosis, although several elements can be considered.

##### 4.3.1. Changes in abundance

The hake (*M. merluccius*) fished by the La Rochelle trawlers belongs to the North European stock, which extends geographically from the French coasts of the Bay of Biscay to Norway. The condition of this stock is assessed annually by ICES. The total biomass of the stock decreased

consistently throughout the period studied, except for a very temporary increase in 1985 (ICES, 1999). In 1993, the biomass represented only 65% of that present in 1979. The general trend in LPUE changes for the La Rochelle trawlers reflects this decrease, which resulted in the development of E type profiles to the detriment of F type (Table 4).

Two species of anglerfish are caught in the Bay of Biscay, *Lophius piscatorius* and *Lophius budegassa*, corresponding to two stocks both found on the French continental shelf of the Bay of Biscay and in the Celtic Sea, western English Channel, and the Atlantic Ocean west of Ireland. Their biomasses have been assessed since 1986 (ICES, 1999). From 1986 to 1990, the biomasses of both species as well as the LPUE of the trawlers indicated reduced abundance. Despite a continued decrease in the biomass of *L. budegassa*, good recruitment led to an increase in the stock of *L. piscatorius*, which was responsible for the marked improvement of LPUE beginning in 1991. The extension of type E profiles was favoured once again (Table 4 and Fig. 5).

*S. officinalis* is a short-lived species whose biomass is highly dependent on recruitment success. This species, which is fished by offshore trawlers in wintering areas at depths of 50–70 m is sensitive to water temperature and currents that induce spring migrations for reproduction and affect the development of juveniles (Gi Jeon, 1982). Thus, in 1983 and 1988, cuttlefish was occasionally abundant before catches began to increase in 1990. The regulatory effect of the market sometimes masked the high abundance of the species, as during the first 6 months of 1991, “an exceptional period for the cuttlefish because of weather conditions” (Le Goff, 1991). The large catches of cuttlefish prevented the maintenance of price aids since the financial resources of the producers’ organisations had been exhausted to provide market support for the sole (Front, 1992). Cuttlefish exploitation was stopped during this period, leading to a reduction of LPUE in 1991. Type I profiles, ordinarily associated with the month of October, were observed throughout the autumn of 1990. Their total absence in 1991 resulted from the interruption of fishing, whereas the decreased availability of hake favoured their exploitation in September 1992 and 1993 (Table 4 and Fig. 5).

#### 4.3.2. Modification of the conditions for resource exploitation

##### 4.3.2.1. A change in strategy

The appearance and development of the E type profile (*N. norvegicus*–*Lophius* spp.) were indicative of a change in fishing strategy. The usual fishing practices were temporarily abandoned during the year in order to search for the Norway lobster (*N. norvegicus*) further offshore. Consequently, the LPUE of anglerfish improved because of the relation between their abundance and water depth. Various events prompted and facilitated this new strategy. Changes

in the mean age of boats indicate a renewal of the fleet, especially between 1984 and 1988. This was accompanied by an increase in engine power and boat size, thereby improving fishing power. The shelf edge then became more easily accessible.

In 1986, the application of a new European Union regulation modifying the conditions for trawl-fishing of the wedge sole probably contributed also to the development of the *N. norvegicus*–*Lophius* spp. strategy. The limitation on engine power (less than 110 kW) for wedge sole fishing made many boats ineligible for this activity and available to exploit other species. Some boats shifted to Norway lobster fishing: the larger ones in Irish waters (fishing effort outside the Bay of Biscay increased) and the smaller ones on the southern slopes of the continental shelf of the Bay of Biscay. From 1986 to 1993, the activity of trawlers in the offshore areas (ICES rectangles 18 to 20E7) relatively increased, particularly in rectangles 18 and 19E7 from April to June of 1992 and 1993.

However, the exploitation of new Norway lobster grounds accounts for only part of the doubling of mean LPUE levels for *N. norvegicus* between the periods preceding or following 1984–1985. The temporary increase in the biomasses of *N. norvegicus* in the Bay of Biscay between 1985 and 1988 (ICES, 1997b) also contributed to the marked rise of LPUE.

##### 4.3.2.2. Competition between “métiers”

The fishing pattern of *S. solea* in the Bay of Biscay improved in the late 1980s because of the considerable reduction in catches of young individuals as a result of the decreased number of shrimp trawlers (ICES, 1993). This helped increase stock biomass from 1984 to 1993 (ICES, 1999), despite the increase in total international landings, which rose 2.5-fold from 1979 to 1993. However, the LPUE of *S. solea* by the La Rochelle trawlers tended to decrease throughout the study period (Fig. 8 and Table 5). At the same time, the contribution of net fishing to total French catches increased nearly 20-fold (from 3% in 1979 to 55% in 1993). As a result, competition between net fishing and La Rochelle trawl fishing for occupation of the most productive areas increased, especially in coastal sectors south of the Gironde estuary that were previously the exclusive domain of trawlers (Léauté, 1998). Catches by trawlers remained the same, while their fishing effort increased, notably because of the higher engine power of the boats. The combined effect of LPUE decreases for *S. solea* and for *T. luscus* modified the February profiles from 1991 to 1993 (transition from B to A and C types) and in January 1992 and 1993 (from A to H type).

##### 4.3.3. Changes in the behaviour of fishermen

The LPUE of *S. canicula* and *Raja* spp. tended to increase after 1984. Abundance indices calculated from data of scientific surveys showed no significant variations in the abundance of these species between 1987 and 1992. How-

ever, both were correlated with MFA axis 1 from 1990. The increase of LPUE may have been due to a change in the behaviour of fishermen concerning these species. Previously excluded from catches because of their low market value, they proved of interest to compensate for the decline in catches of traditionally valuable species, such as *M. merluccius* or *D. cuneata*. *S. canicula* and *Raja* spp. were associated with the development of the E profile (Fig. 5, Table 4).

## 5. Conclusion

Some aspects of the temporal interactions between marine living resources and their exploitation by fishing were considered in this study, notably the preponderant role of the life cycle of the species fished. The case studied was simplified, insofar as spatial interactions were intentionally ignored at first. These interactions are in fact included in the results of the analyses as a second determinant of the annual cycle described. Except for the ‘accidents’ in 1983 and 1993, the annual cycle of landings subsisted over a long period, despite the changes observed in the abundance of the populations fished and in the conditions of their exploitation. The persistence of the annual cycle provides an indirect indication of the stability of the communities undergoing exploitation. This study also emphasises the value of data derived from commercial fisheries for assessment of fishing strategy and consideration of the effects of competition between different fishing fleets. It would be useful to include the spatial component explicitly and extend the investigation to cover socio-economic variables.

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