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Variation and temporal patterns in the composition of the surface ichthyoplankton in the southern Bay of Biscay (W. Atlantic)

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ABSTRACT

From September 2000 to December 2006, surface plankton samples were collected on a monthly basis, from a station located in the southern Bay of Biscay (43°37N; 1°43W France), near the deep Capbreton canyon. In this paper, the results for the ichthyoplankton assemblage are presented. Among the 62 taxa recorded, only 35 were present in the larval stage whilst only 10 were represented by their eggs. Taxa represented by both stages (eggs+larvae; $N=17$) had the highest abundance. The presence in the surface plankton assemblage of species, at either or both stage, is interpreted within the context of the bathymetric distribution of species. The maxima in abundance and diversity occurred in February–March, for eggs, and May–June, for larvae. This 3-month time-lag between the stages is proposed to be related to the timing of egg spawning and larval recruitment to the pelagic environment. Mean egg abundances (82.4 ± 29.8 eggs/10 m^2) were 10-fold higher than the larval abundances (7.1 ± 1.8 larvae/10 m^2). Despite pronounced monthly variability, no statistically significant decrease in either egg or larvae abundance was observed during this 6-year study period. Compared with previous published studies, this study shows that the peak in ichthyoplankton diversity occurred two months earlier. In addition, the spawning period occurred over the whole year, even during autumn and winter. Using ordination techniques, the annual sequence appearance of taxa are described at the study site: Gadiforms, Ammodytidae and Pleuronectiforms were present during the winter whilst Sparidae, Blennidae, Labridae and Gobiidae, formed the summer group. Only three species, European anchovy *Engraulis encrasicolus*, European pilchard *Sardina pilchardus* and Atlantic horse mackerel *Trachurus trachurus* were recorded throughout the year.

1. Introduction

Ichthyoplankton in the Bay of Biscay (SW Atlantic) is well-documented, although most published studies encompass only a few, especially commercially important, species such as the European hake, European anchovy, European pilchard and Atlantic horse mackerel or Atlantic mackerel (Sola et al., 1990; Motos et al., 1996; Alvarez et al., 2001; Coombs et al., 2001, 2004 and Planque et al., 2007). Some studies have described the entire species assemblage, but sampling was restricted to an annual cycle, or sparsely distributed in time (Suau and Vives, 1979; Dicenta, 1984; Acevedo et al, 2002; Ibaibarriaga et al., 2007). Other studies from the Galician (Ferreiro and Labarta, 1988) or Cantabrian coasts (Valencia et al., 1988), have sampled over 2 or 3 years only.

The objective of the present study in the Bay of Biscay was to describe seasonal and inter-annual variation in species diversity, as well as species abundance for the whole surface ichthyoplankton assemblage on a long-term basis (>10 years). The sampling strategy was based upon monthly collection to strengthen the temporal dimension of the long-term pattern. Data collection was restricted to horizontal surface samples, at a single station. This study is part of a larger research programme, on the whole at the zooplankton community (Elbée (d') and Castel, 1991; Elbée (d') and Prouzet, 2001) and the seabird and mammal communities (Hémery et al., 2002; Castège et al., 2004) of the southern Bay of Biscay. These studies together are aimed at quantifying the impacts of global oceano-climatic changes (Hays et al., 2005; Poulard and Blanchard, 2005 and Costello et al., 2006).

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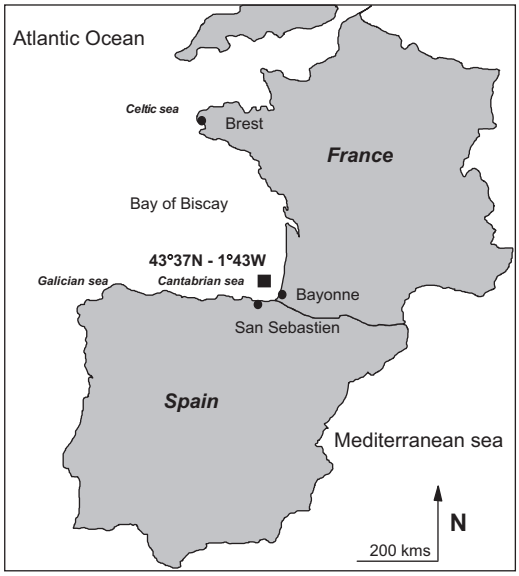

Fig. 1. Location of the sampling station (dark square) in the southern Bay of Biscay.

2. Study site

The sampling location for plankton was located in the southern Bay of Biscay (43°37N; 1°43W), on the southern border of a deep oceanic canyon (the so-called Gouf of Capbreton) (Fig. 1). Selection of this sampling site was based on logistical (practical) and biological reasons; at 20 km of the coast (the city of Bayonne) it was close enough to minimize travel costs, but remote enough to minimize anthropic and continental influences. Water depth at the sampling site was around 540 m. The planktonic community at this site is highly diversified and well-balanced between surface and deep influences (Elbée (d'), 1993, 2001).

3. Material and methods

Plankton was sampled at the same time of day (ca 0900–1000 a.m.), using a WP2-type tronconic net with 200 μm mesh size, from the vessel "*Haize Hegoa*" (30 m length), from the Douanes Françaises and the Affaires Maritimes (Coast Guard ship). Horizontal hauls were collected at 1 m below the surface and the net was towed at a speed of 0.5 m s^{-1}. The volume of water filtered through the net was estimated with a General Oceanics flowmeter. Plankton was preserved in 5% seawater formalin and then stored for further analysis. Samples were sorted in the laboratory, under a WILD M10 stereomicroscope provided with epi- and dia-scopique light. When concentrations (especially for eggs) were high, sub-sampling was carried out, using a Motoda box.

Identification of taxonomic units (TUs) was carried out using specialized literature and reference textbooks (Marinaro, 1971; Russel, 1976; Fahay, 1983; Halbeisen, 1988; Aboussouan, 1990; Olivar and Fortuño, 1991; Ré, 1996; Munk and Nielsen, 2005 and Richards, 2006), and from the following websites: http://www.larvalbase.org/; and http://access.afsc.noaa.gov/ichthyo/index.cfm. An original database of eggs and oil globule diameters, for ca 200 fish species, developed by one of the authors (J. d'E) at the LAPHY laboratory, was also used. Confirmation of the identification of some doubtful eggs/larvae was facilitated greatly by information on the presence/absence of adult fish, derived from annual bottom trawl surveys EVHOE and carried out by IFREMER over the area (Souissi et al., 2001; http://www.ifremer.fr/drvlorient/programmes/posterevhoe.htm).

Abundances were expressed as number of individuals per m^3. The total abundance for each TU was calculated, by summing the monthly abundances estimated during the study ($n = 57$ months). The relative abundance was defined as the ratio between total abundance of each TU, over the total abundance of all TUs collected.

4. Statistical analysis

Statistical analysis of the data was undertaken using StatBox v. 6.0® and SAS® (SAS Institute, V. 8) softwares. Time-series were analysed using the method of moving averages, with a window width equal to two and plotted accordingly (Spiegel, 1983). Sampling fluctuations around the mean were described by their standard error $SE = SD \div \sqrt{n}$(with SD: standard deviation and n: sample size). Correspondence analysis was performed on a contingency table of the 62 taxa (whatever their life cycle stage) and 12 months i.e. over the whole of the study period. Occurrence frequency was incremented each time a new taxon was found in the sample. Mean monthly frequencies ("MONTH'), as well as unidentified taxa ("INDETE"), were treated as supplementary elements in the analysis. Both the correlation analyses between time and the variation in the means of eggs or larval abundance means and correlation between variation in eggs and larval abundance means were performed using the non-parametric Kendall test, with the CORR procedure of SAS.

5. Results

5.1. Plankton sampling

Between October 2000 and December 2006, 57 plankton samples were collected (Table 1). The average annual sampling frequency was high (mean: 9.16 months/12) and relatively stable (coefficient of variation: 0.13), with a maximum of 11 months in 2006 and a minimum of 2 months in 2000. In contrast, the sampling frequency for the different months of the year was rather variable (3–7; mean: 4.17; CV = 0.22).

5.2. Taxon richness

A total of 62 TUs (eggs and larvae combined) were collected, over the 6 years of the study (Fig. 2). The increase in occurrence of

Table 1
Sampling effort (monthly and annual frequency) at the single station (43°37N; 1°43W) during the study period (October 2000–December 2006).

	2000	2001	2002	2003	2004	2005	2006	Total
January			11	20		39	47	4
February		3	12	21	30		48	5
March			13	22	31	40	49	5
April				23	32	41	50	4
May		4	14	24	33		51	5
June		5	15	25			52	4
July		6	16	26	34		53	5
August		7			35	42		3
September		8	17	27	36	43	54	6
October	1			28		44	55	4
November		9	18		37	45	56	5
December	2	10	19	29	38	46	57	7
Total	2	8	9	10	9	8	11	57

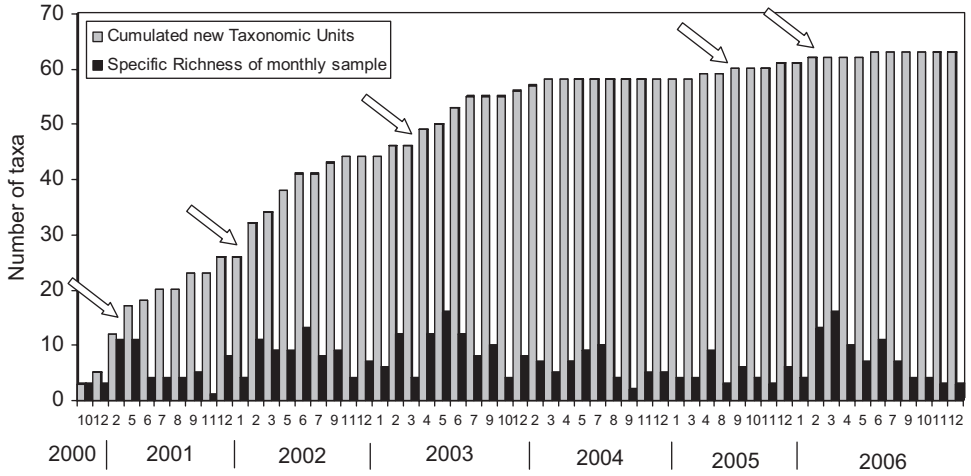

Fig. 2. Increase in total ichthyoplankton taxon richness (expressed by the cumulative curve of new taxonomic units, TUs; grey bars) during the study period (2000–2006). Specific richness of each sample ($n = 57$) is indicated by black bars. Arrows indicate maximal specific richness periods occurring especially in spring corresponding to the occurence of new taxa.

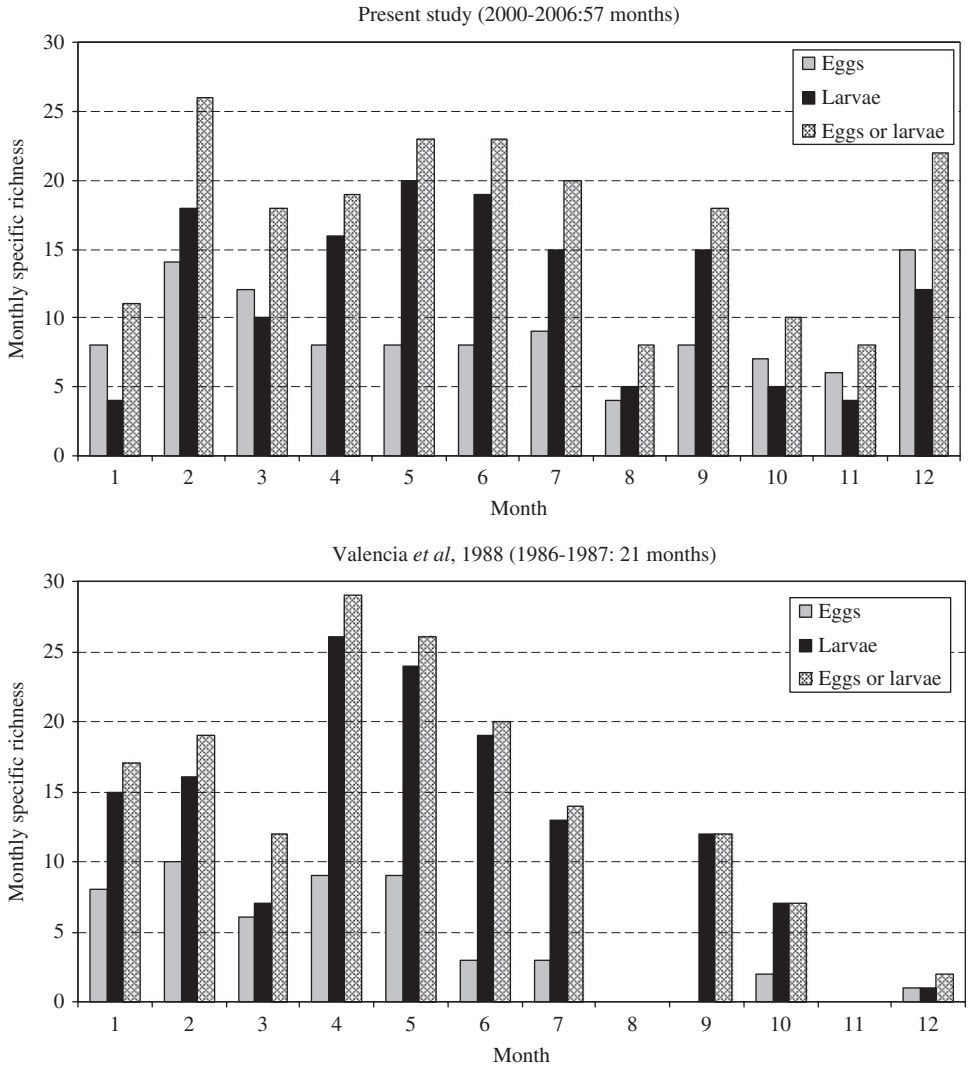

Fig. 3. Monthly change in cumulative specific richness for eggs (grey bar), larvae (black bar) and both stages. Upper figure: present study, 57 monthly samples between 2000 and 2006. Lower figure: study by Valencia et al., (1988); 21 monthly samples over 1986–1987.

new TUs was high during the first 3 years of the study (ca. 15 TUs year^{-1}), then decreased to around 2 TUs year^{-1}.

Monthly variation in species richness (Fig. 3) differed, according to the stage of the annual cycle: diversity of the egg stage peaked in winter (especially December and February), whilst the larval diversity increased regularly from March, to a peak in May. Combined taxon diversity peaked around February, i.e. between winter and spring: overall taxon diversity was lowest during the summer.

5.3. Representation and relative abundances of eggs and larvae

The 62 TUs were classified into four groups (Table 2): Group I (15 TUs) species represented only by their larvae, with demersal eggs generally fixed on benthos; Group II (20 TUs) species with pelagic eggs never found in planktonic samples and, thus, represented only by larvae; Group III (17 TUs) species whose eggs and larvae are both pelagic and present in the surface plankton samples and Group IV (10 TUs) species only present in the plankton samples as eggs.

Among the 53 TUs found as larvae, only 14 had a relative abundance of greater than 1% (Fig. 4). *Engraulis encrasicolus*, *Sardina pilchardus*, *Parablennius gattorugine*, *Diplodus vulgaris* and *Spondyliosoma cantharus* were the dominant TUs, in decreasing order of abundance, totalling more than 80% of the total abundance. Among the 28 TUs found as egg stages, only five species showed relative abundances $>1\%$: *S. pilchardus*, *E. encrasicolus*, *Trachurus trachurus*, *Scomber scombrus* and *Mugil cephalus*, in decreasing order of abundance.

5.4. Ichthyoplankton abundance and temporal variation

Abundance maxima for eggs were centred around February–March, generally preceding the maxima for larvae, which were centred around May–June (Fig. 5). The best statistical correlations, between egg abundances and larvae abundances, were obtained when a 3-month time-lag was applied (Tau = +0.265, $p = 0.016$). Over an annual cycle, the maximal abundance of eggs was followed, 3 months later, by the maximum abundance of larvae; thus was despite the taxonomic units not matching exactly. In 2003 and 2005, the abundances of eggs and larvae were lower than during the other years of the study period. The mean for the whole time-series was 10-fold higher for egg data compared to larval data (82.4 ± 29.8 eggs/10 m^3 vs 7.1 ± 1.8 larvae/10 m^3).

Monthly variations in egg abundance were high (1–1000 times; maximum of 1273 ind/10 m^3, in February 2001) (Fig. 6). Monthly variations in larvae abundance were lower (1–100 times; maximum of 73 ind/10 m^3 in June 2002). Combining data over a number of years has enabled the identification of monthly patterns in egg and larval abundances. Egg numbers reached rapidly a maximum mean of 427 eggs/10 m^3, in February, then slowly declined, until August. The pattern for larvae was slightly different with the maximum mean observed later in June (29 larvae/10 m^3), followed by a quick decline until August; this is when individual number for both stages remained low.

Data-pooled over months demonstrated similar inter-annual patterns in egg and larval abundances (Fig. 7). High mean abundances were found during the years 2001, 2002, 2004 and 2006, whilst 2003 and 2005 displayed lower values. With only two samples, the minimal values for 2000 should be considered with caution. There was no significant correlation between years and the inter-annual variation in eggs and larval abundance means ((Tau $= -0.143$, $p = 0.652$ for eggs and Tau = +0.238, $p = 0.453$ for larvae) .

Table 2
List of the 62 ichthyoplankton taxonomic units identified during the survey (2000–2006) sorted by alphabetical code order within the four functional groups according to the presence or absence of the two developmental stages egg and larvae.

Group	Code	Taxonomic units (TUs)
I (15)	AMOTOB	*Ammodytes tobianus*
	CORGAL	*Coryphoblennius galerita*
	CTERUP	*Ctenolabrus rupestris*
	CYCLUM	*Cyclopterus lumpus*
	GOBNIG	*Gobius niger*
	GYMSEM	*Gymnammodytes semisquamatus*
	LABBER	*Labrus bergylta*
	LABRID	*Labridae sp.*
	LIPARI	*Liparidae sp.*
	LIPPHO	*Lipophrys pholis*
	PARGAT	*Parablennius gattorugine*
	POMMIN	*Pomatoschistus minutus*
	SPOCAN	*Spondyliosoma cantharus*
	SYMMEL	*Symphodus melops*
	SYNGNA	*Syngnathidae sp.*
II (20)	BOOBOO	*Boops boops*
	CALLYR	*Callionymus lyra*
	CEPMAC	*Cepola macrophthalma*
	DICCUN	*Dicologoglossa cuneata*
	DIPSAR	*Diplodus sargus*
	DIPVUL	*Diplodus vulgaris*
	GADARG	*Gadiculus argenteus*
	GAIVIS	*Gaidropsarus viscayensis*
	LIMLIM	*Limanda limanda*
	LITMOR	*Lithognathus mormyrus*
	LOPPIS	*Lophius piscatorius*
	MICPOU	*Micromesistius poutassou*
	OBLMEL	*Oblada melanura*
	PAGACA	*Pagellus acarne*
	PAGBOG	*Pagellus bogaraveo*
	PAGPAG	*Pagrus pagrus*
	PHYBLE	*Phycis blennoides*
	POLPOL	*Pollachius pollachius*
	SPARID	*Sparidae sp.*
	TRIMUN	*Trisopterus minutus*
III (17)	ARNOGL	*Arnoglossus sp.*
	CILMUS	*Ciliata mustela*
	DICLAB	*Dicentrarchus labrax*
	ECHVIP	*Echiichthys vipera*
	ENCCIM	*Enchelyopus cimbrus*
	ENGENC	*Engraulis encrasicolus*
	EUTGUR	*Eutrigla gurnardus*
	MERMER	*Merlangius merlangius*
	MUGCEP	*Mugil cephalus*
	MULSUR	*Mullus surmuletus*
	SARPIL	*Sardina pilchardus*
	SCOMAX	*Scophthalmus maximus*
	SCOSCO	*Scomber scombrus*
	TRADRA	*Trachinus draco*
	TRATRA	*Trachurus trachurus*
	TRIGLI	*Triglidae sp.*
	TRILUS	*Trisopterus luscus*
IV (10)	BUGLUT	*Buglossidium luteum*
	CAPAPE	*Capros aper*
	GADIDA	*Gadidae sp.*
	LEPWIF	*Lepidorhombus wiffiagonis*
	LOTIDA	*Lotidae sp.*
	MAUMUE	*Maurolicus muelleri*
	MICVAR	*Microchirus variegatus*
	MOLMAC	*Molva macrophthalma*
	SCOPEN	*Scorpenidae sp.*
	SPRSPR	*Sprattus sprattus*

(See the text for more details). Unidentified eggs and larvae "INDETE" are separated. Number in brackets indicate group size.

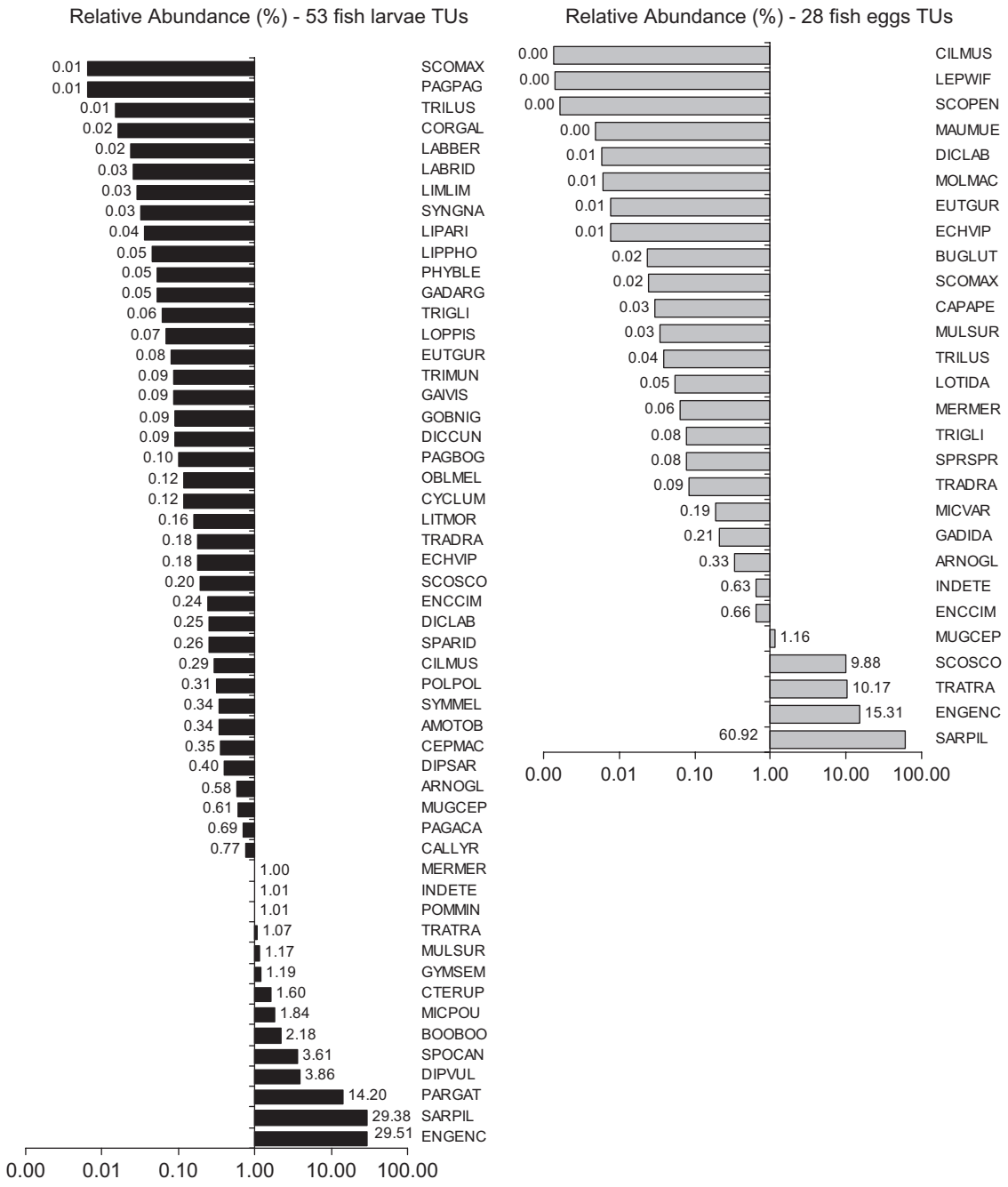

Fig. 4. Relative abundances expressed as percentage of the total cumulative abundance during the period 2000–2006 for the ichthyoplankton taxonomic units (larvae; $N = 53$; eggs, $N = 28$). (*See* Table 2 *for taxonomic units* (*TUs*) *codes*). Unidentified eggs or larvae are included as INDETE. Horizontal axis is a log scale.

5.5. Annual cycle of species present in surface waters (Fig. 8)

On the main correspondence analysis biplot, months were arranged in a circular manner. Many Gadiformes, Ammodytidae and Pleuronectiformes were associated mostly with the winter months. In summer, the species number in the plankton increased and was represented mainly by Sparidae, Blennidae, some Labridae and Gobiidae. Other Labridae species (*Labrus bergylta*, Labridae sp.), together with *Pagellus acarne*, *Capros aper* and *M. cephalus* occurred later in the year; they peaked in abundance in autumn. The central position on the biplot of the three species *T. trachurus*, *S. pilchardus* et *Dicentrarchus labrax*, close to "MONTH" and "Indete" centroids, was best described by their permanent presence all-year long.

6. Discussion

Our 6-year-long study has revealed that the ichthyoplankton assemblage in the Bay of Biscay comprised 62 taxa present as eggs, larval, or both egg and larval stages. The increase in the total specific richness during the first three years could be explained in terms of the sampling design, which was restricted to a single sampling site at the surface. The value obtained ($S = 62$ TUs) is similar to that ($S = 64$ TUs) obtained by Ferreiro and Labarta (1988), during their 3-year long study (1980–1983) off the Galician coast of Spain. Also, for the continental shelf of the Cantabric coast of Spain, Valencia et al. (1988) found similar values (59 TUs), whereas Suau and Vives (1979) and Dicenta (1984) recorded lower values (38 and 45 TUs, respectively); these

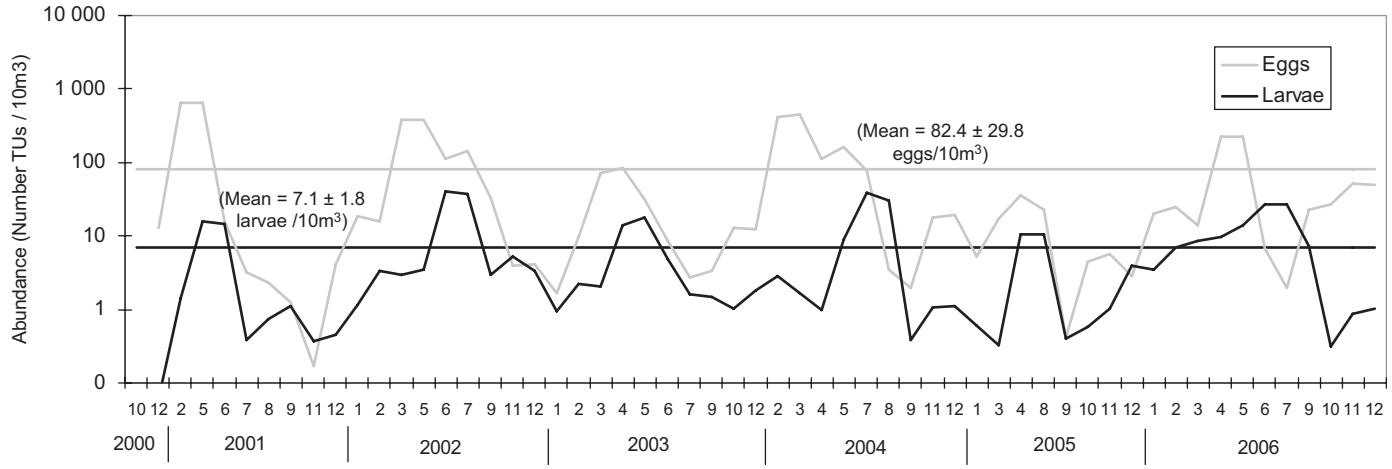

Fig. 5. Variation of moving averages (window width = 2) of monthly total ichthyoplankton abundances as shown by eggs (grey bars) and larvae (black bars) during the study period (2000–2006).

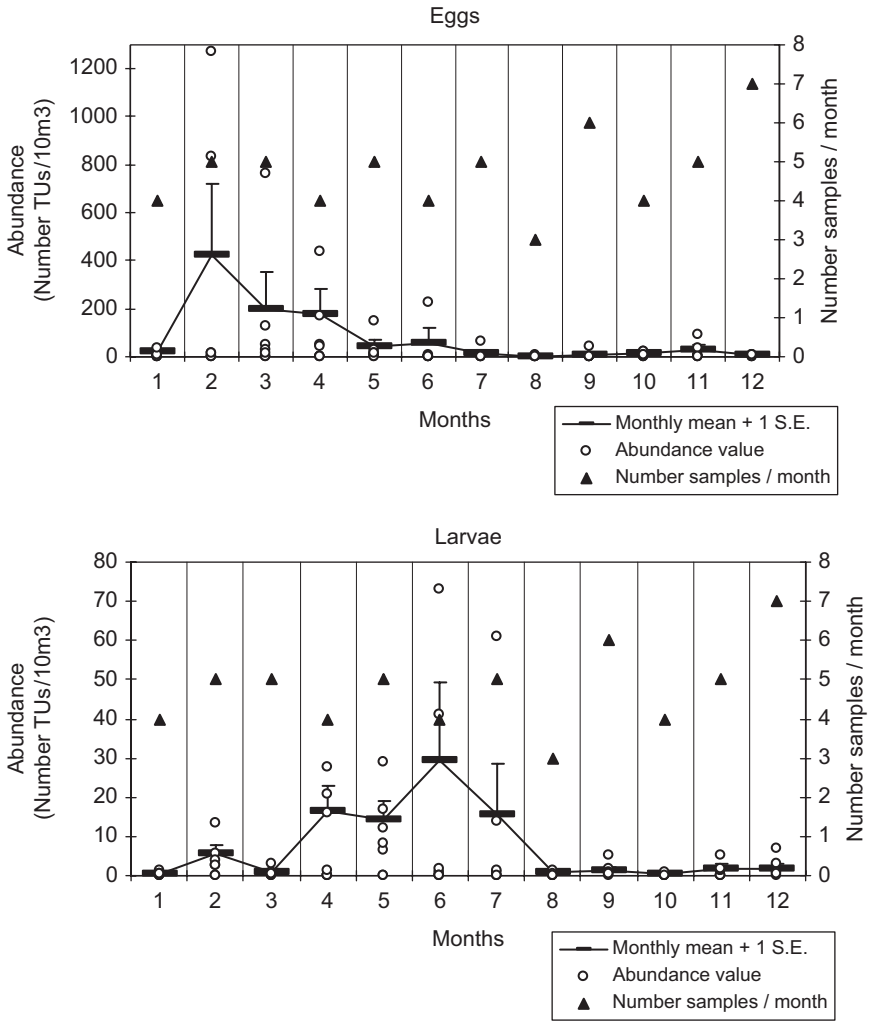

Fig. 6. Monthly variation in eggs and larval abundance means (error bars indicate+1 S.E.) during the study period (2000–2006).

may have been due to the fact that these latter studies were restricted to a single year. We consider that our estimate of ichthyoplankton diversity for the southern Bay of Biscay may increase further, with a continuation of the research programme. Despite the narrow proximity of the sampling station to the canyon of Capbreton, only a very small proportion of mesopelagic species (e.g.: *Myctophiidae*, *Sternoptychidae*, *Paralepidae* and *Stomiidae*) were recorded in this study. This pattern is in contrast to the results of other studies, that used a different sampling protocol of oblique hauls (Valencia et al., 1988; Acevedo et al., 2002; Dransfeld et al., 2000). Indeed, only eggs of *Maurolicus muelleri* were caught, whose larvae have a subsurface vertical

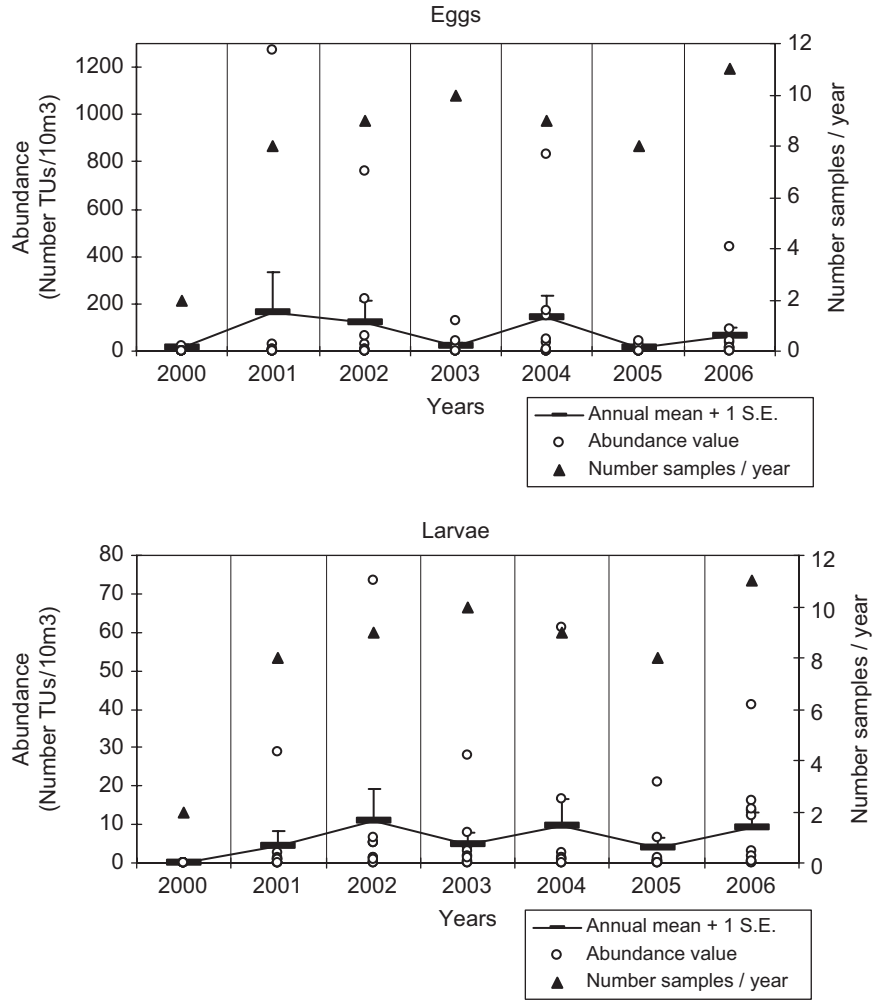

Fig. 7. Inter-annual variation in eggs and larval abundance means (error bars indicate+1 S.E.) during the study period (2000–2006).

distribution (Halliday et al., 2001). Spawning and larval development of other mesopelagic species occur in deeper oceanic strata, far below the subsurface study zone sampled in this study (Halliday et al., 2001; Sabatés, 2004).

Where the two life stages were combined, maximum specific richness was observed in February (upper Fig. 3), i.e. between the maxima observed for each of the separate stages (eggs and larvae), which occurred in December and May, respectively. It is noteworthy that both stages are observed throughout the year. In their 21-month study carried out on the Spanish Cantabrian coast close to our study site, Valencia et al. (1988) observed a somewhat different pattern in the annual variation of ichthyoplankton richness (lower, Fig. 3). Explanations for those patterns could be linked to changes in oceano-climatic conditions, especially the water temperature increase in winter (Beaugrand et al., 2002; Edwards & Richardson, 2004; Hays et al., 2005; Poulard and Blanchard, 2005; Costello et al., 2006).

Among the 47 TUs characterized by pelagic eggs and larvae (the other 15 have demersal eggs), 20 of them (Group II) were represented by larval stages only. It is highly likely that, for previous ichthyoplankton studies, difficulties in identifying species from the egg stage were responsible for the apparent lack of some of the species (Ferreiro and Labarta, 1988; Koutrakis et al, 2004; Ibaibarriaga et al., 2007). Also given that the abundance of eggs has been reported to be higher in surface waters, compared with deeper zones (Motos and Coombs, 2000; Coombs et al., 2001, 2004; Motos et al., 2004; Munk and Nielsen, 2005), this may enhance species numbers sampled in our study. Moreover, the observed increase in abundance of larvae with depth by the same authors (see above) may explain why ca 10 species (Group IV) have only been recorded as eggs, but whose larvae are easy to identify at any stage e.g. *Microchirus variegatus*, *Sprattus sprattus*, *Buglossidium luteum* and *Maurolicus muelleri*. Eventually, the presence of the two stages in the surface layers sampled could describe a slowdown in the bathymetric movement of successive larval stages, migrating to deeper zones.

The observed abundance estimates for eggs and larvae are within the published levels in the same geographic area (Suau and Vives, 1979; Dicenta, 1984; Ferreiro and Labarta, 1988; Valencia et al., 1988; Coombs et al., 2004; Motos et al., 2004; Ibaibarriaga et al., 2007). However, those values prove to be highly variable, mostly because the horizontal and vertical distribution of ichthyoplankton assemblage is driven by hydro-climatic, hydrological and biophysical factors (Sanchez and Gil, 1999; Coombs et al., 2001, 2004; Bakun, 2006; Petitgas et al., 2006a, b; Planque et al., 2007.

The observed 4-month time-lag (Fig. 6), between the maximal values of mean egg and larvae abundances was possibly over-estimated, as values for the months of February and June for both stages were derived from a unique elevated value (1273 ind./m^3 vs 73 ind./m^3). Analysis of moving averages (Fig. 5) revealed a 3-month time-lag, which probably is more representative of the

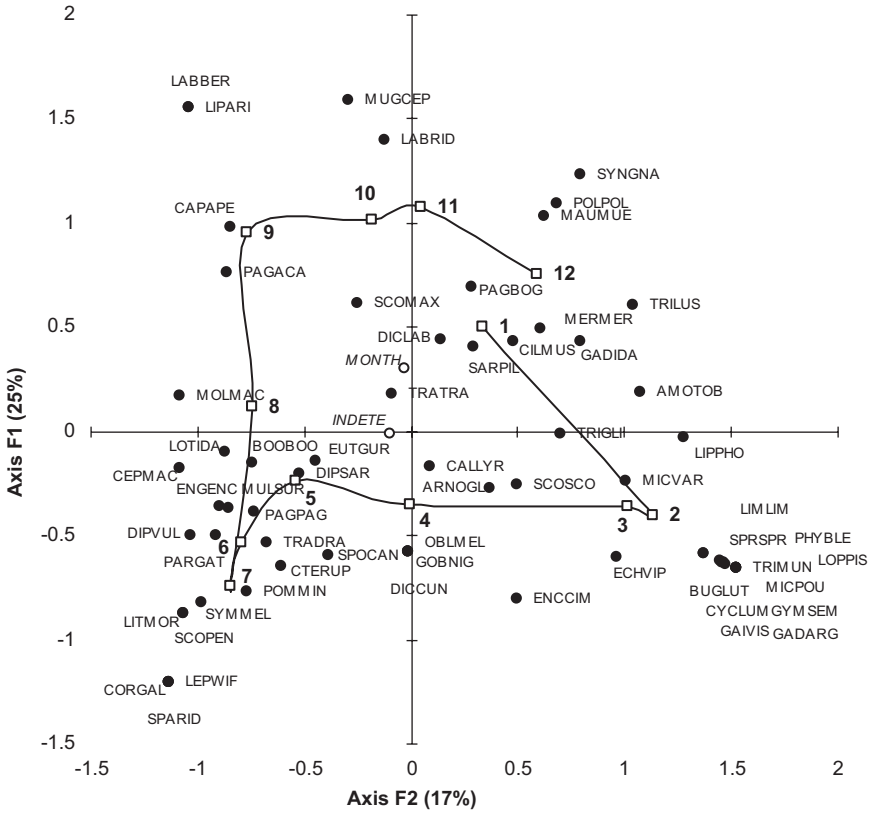

Fig. 8. Monthly biplot of the 62 taxonomic units (black dots) with first and second correspondence analysis axis. Monthly frequencies "MONTH" and unidentified taxa "INDETE" (white dots) are integrated as supplementary individuals (*see text for details*).

true situation. This interpretation is supported by the fact that the maximum abundances were synchronous with the maxima in specific richness, occurring in February–March for eggs and May–June for larvae.

Our study further confirms the dominance of *Sardina pilchardus*, *Engraulis encrasicolus* and, to a lesser extent, *S. scombrus* and *T. trachurus* in the ichthyoplankton assemblages; this has been reported already for the Bay of Biscay (Suau and Vives, 1979; Dicenta, 1984; Coombs et al., 2001, 2004; Motos et al., 2004; Ibaibarriaga et al., 2007), for the Mediterranean Sea (Palomera, 1992; Koutrakis et al., 2004; Zarrad et al., 2006) as well as at higher latitudes in the Celtic Sea (Acevedo et al., 2002) and the Irish Sea (Dransfeld et al., 2000). Of course, such dominance should not hide the important specific richness highlighted also in the present study. Many species from families of no commercial value are also caught regularly in surface ichthyoplankton samples, especially at the larval stage. Another strength of our study was to emphasize the well-structured species succession, during the course of the year. A few species are perennial, whilst most of them are temporary residents of the plankton. The replacement of species during the temporal succession process, as described here, is very similar to the pattern reported for the nearshore waters off the Spanish coast by Valencia et al. (1988). Above all, it should be emphasized that, even if the ichthyoplankton is only a small part of the whole mesoplankton, it is almost one of the most diverse communities (Elbée (d') and Castel, 1991; Poulet et al., 1996; Elbée (d') and Prouzet, 2001).

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