

## Long-term variability and environmental preferences of calyphorophoran siphonophores in the Bay of Villefranche (north-western Mediterranean)

P. Licandro<sup>a,\*</sup>, S. Souissi<sup>b</sup>, F. Ibanez<sup>c</sup>, C. Carré<sup>c</sup>

<sup>a</sup> Sir Alister Hardy Foundation for Ocean Science (SAHFOS), The Laboratory, Citadel Hill, The Hoe, Plymouth PL1 2PB, United Kingdom

<sup>b</sup> CNRS UMR 8187 LOG, Université Lille 1 Sciences et Technologies - Station Marine - 28 Avenue Foch, 62930 Wimereux, France

<sup>c</sup> Laboratoire d'Océanographie de Villefranche (LOV), Station Zoologique, BP 28, 06234 Villefranche-sur-mer, France

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### ABSTRACT

Long-term variability of the main calyphorophoran siphonophores was investigated between 1974 and 1999 in a coastal station in the north-western Mediterranean. The data were collected at weekly frequency using a macroplankton net (680 µm mesh size) adapted to quantitatively sample delicate gelatinous plankton. A 3-year collection (1967–1969) of siphonophores from offshore waters using the same methodology showed that the patterns of variability observed inshore were representative of siphonophores' changes at a regional scale. The aims of the study were: (i) to investigate the patterns of variability that characterised the dominant calyphorophoran species and assemblages; (ii) to identify the environmental optima that were associated with a significant increase in the dominant siphonophore species and (iii) to verify the influence of hydroclimatic variability on long-term changes of siphonophores. Our results showed that during nearly 3 decades the standing stock of calyphorophoran siphonophores did not show any significant change, with the annual maximum usually recorded in spring as a result of high densities of the dominant species *Lensia subtilis*, *Muggiaea kochi* and *Muggiaea atlantica*. Nevertheless, major changes in community composition occurred within the calyphorophoran population. Since the middle 1980s, *M. kochi*, once the most dominant species, started to decrease allowing other species, the congeneric *M. atlantica* and *Chelophyes appendiculata*, to increasingly dominate in spring and summer–autumn, respectively. The comparison of environmental and biotic long-term trends suggests that the decrease of *M. kochi* was triggered by hydrological changes that occurred in the north-western Mediterranean under the forcing of large-scale climate oscillations. Salinity, water stratification and water temperature were the main hydroclimatic factors associated with a significant increase of siphonophores, different species showing different environmental preferences.

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### 1. Introduction

Siphonophores are amongst the most abundant carnivores in the marine system (Mackie et al., 1987 and references therein; Mapstone, 2009). They are colonial organisms generally composed of two (as in the order Calyphoridae) or more swimming nectophores and a stem of several metres length completely covered by cormidia that after maturation are released as monogastric sexual colonies (i.e. the eudoxids). Each eudoxid (or cormidium) carries one or more reproductive gonophores and a gastrozoid to which is attached a tentacle, usually armoured with nematocysts, which is used to attract and capture the prey (Mackie et al., 1987; Mapstone, 2009).

Because of their colonial morphology, siphonophores may rapidly become dominant under favourable conditions as they are able to release hundreds of eudoxids, each one producing a new colony.

Swarms of siphonophores can have a significant predatory impact on the abundance of other planktonic organisms including small fish (Mackie et al., 1987; Purcell, 1997) and cause massive mortalities of farmed fish (Greve, 1994; Båmstedt et al., 1998). Calyphorophoran siphonophores eat primarily small copepods, but also other plankton including ostracods, molluscs, chaetognaths and larvae of euphausiids and fish (Mapstone, 2009 and references therein). In turn, they are prey of bigger coelenterates, ctenophores, heteropods and of several fish species (Mapstone, 2009).

Even though siphonophores are common worldwide (Alvarino, 1971; Pugh, 1999), they have often been poorly studied mainly because their fragile body is easily broken by traditional sampling nets. The development of video systems adapted to monitor gelatinous plankton in situ has instead demonstrated that siphonophores may represent a significant fraction of the plankton (Mackie et al., 1987; Silguero and Robinson, 2000; Stemmann et al., 2008).

In the Mediterranean the distribution and diversity of siphonophores was first discussed by Bigelow and Sears (1937),

\* Corresponding author. Tel.: +44 (0)1752 633133; fax: +44 (0)1752 600015.

E-mail address: [prli@sahfos.ac.uk](mailto:prli@sahfos.ac.uk) (P. Licandro).

and subsequently investigated in coastal and offshore waters in the western Mediterranean (Ianora and Scotto di Carlo, 1981; Dallot et al., 1988; Madin, 1991 and reference therein; Mills et al., 1996; Licandro and Ibanez, 2000; Daly Yahia et al., 2003), Adriatic Sea (Gamulin and Kršinic, 1993a,b; Batistic et al., 2004, 2007; Milos and Malej, 2005) and in the eastern Mediterranean (Lakkis and Zeidane, 1997; Zakaria, 2004). In the Bay of Villefranche (north-western Mediterranean), gelatinous plankton have been monitored since the end of the 19th century with the intent of identifying the great variety of jellyfish, including meso- and bathypelagic species, regularly found in coastal waters as a result of advection from the nearby Liguro-Provençal frontal region (Goy et al., 1989). In the early 1960s Braconnot and colleagues developed a sampling net, the 'Regent net', suitable for quantitatively collecting delicate gelatinous plankton (Braconnot, 1971). This type of net has been used since the early 1970s to collect plankton every week at the coastal station Point B.

Previous studies have investigated the seasonal and multi-decadal variability of some dominant siphonophores in the Bay of Villefranche: the calyphorans *Chelophyes appendiculata* and *Abulopsis tetragona* (Buecher, 1999; Molinero et al., 2008a,b) and the annual cycle of *Muggiaea atlantica* and *Muggiaea kochi* (Dowidar, 1992).

The present study analyses for the first time all the 'Regent-net' siphonophore records collected between 1974 and 1999 (with an interruption between 1978 and 1983). This data set represents the only long-term quantitative data set on siphonophores in the Mediterranean. The aims of the study are to (i) investigate the temporal variability that characterised the main species and assemblages of calyphorans siphonophores during the 19 years of observations, (ii) identify the environmental optima associated with the highest densities of dominant siphonophores, and (iii) verify the relationship between long-term variability in the abundance of siphonophores and hydroclimatic changes. Interannual fluctuations of the siphonophore population offshore the Bay of Villefranche were also studied during a 3-year period, in order to verify whether the patterns observed inshore were representative of siphonophores' changes at a wider spatial scale. Several recent studies have found that the Mediterranean is a region strongly affected by climate fluctuations (Bethoux et al., 1999; Vignudelli et al., 1999), and linked hydroclimatic changes to the increasing abundance of jellyfish (Purcell, 1997; Molinero et al., 2008a,b). Although some of these studies have included in their analysis some siphonophore species (Molinero et al., 2008a,b), it is still unclear whether or not the overall siphonophore standing stock and the structure of the community have significantly changed over the last few decades.

## 2. Material and methods

### 2.1. Time series

Calyphorans siphonophores were collected weekly in the Bay of Villefranche in coastal waters at 'Point B' (43°41'N, 7°19'E, 80 m depth) from 1974 to 1999 (with an interruption in 1978–1983) (Fig. 1). Each sample corresponded to one vertical tow collected by a Regent net (680  $\mu$ m mesh size) from 75 m to the surface. The same net and sampling frequency were used to collect siphonophores in offshore waters at 'Point A' (43°39'N, 07°17'E) between 1967 and 1969 (Fig. 1). This station was situated 2 miles offshore near the Villefranche Canyon (800 m depth) (see Braconnot et al., 1966 for details). Siphonophore abundance only takes into account the anterior nectophores (asexual stage) of the most common calyphorans siphonophore species, excluding *Hippopodius hippopus* for which all the nectophores were counted.

Meteorological variables such as atmospheric pressure (millibars), air temperature ( $^{\circ}$ C), wind direction and speed ( $\text{m s}^{-1}$ ), total precipitation (mm) and daily irradiance ( $\text{J cm}^{-2}$ ) were registered daily at the Semaphore du Cap Ferrat station, 800 m from Point B, at an altitude of 138 m (Station S, Fig. 1).

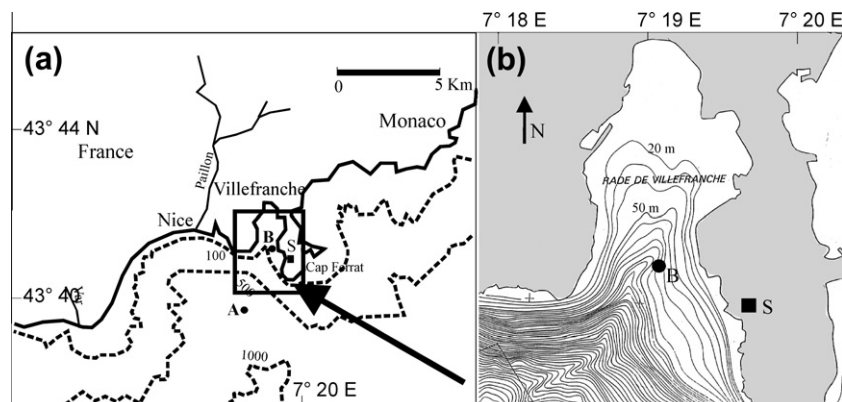
Water temperature ( $^{\circ}$ C) and salinity (psu) were measured weekly at 0, 10, 20, 30, 50 and 75 m depth, with different types of reversing thermometers and an induction salinometer, or with a Seabird SBE 25 conductivity, temperature, depth (CTD) probe from 1991 onwards. No temperature and salinity records were available from January to December 1994. More information about the area of study and about the Point B monitoring programme are given in Licandro et al. (2006).

Irradiance and water density data were not included in the analysis because they were highly correlated respectively with air temperature ( $r=0.8$ ) and sea-water temperature ( $r$  between 0.94 and 0.99).

### 2.2. Numerical analyses

#### 2.2.1. Long-term variability of siphonophore species

The main patterns of variability represented by the filtered variables  $F_1$  and  $F_2$  were extracted from siphonophore data in the periods January 1974–September 1977 (175 weekly observations) and November 1983–December 1999 (783 weekly observations) using the eigenvector filtering method adapted to time series with missing values (EVF, Ibanez and Conversi, 2002), following the procedure explained in Licandro et al. (2006). The EVF corresponds to a principal component analysis (PCA) calculated on an autocovariance matrix based on the original time series  $X_t$  lagged with itself



**Fig. 1.** (a) Map of the area of study including the offshore (Point A) and inshore (Point B) sampling stations. The meteorological station of Sémaphore du Cap Ferrat (Station S) is also shown. (b) Detailed map of the Bay of Villefranche including the Point B and Station S.

from 1 week to  $n$  weeks, choosing  $n$  according to the autocorrelation function of  $X_t$ . The first ( $F_1$ )1'1' and second ( $F_2$ ) axes extracted from the PCA represent the main modes of variability of the original series, generally the interannual and seasonal cycles, respectively.

Harmonic analysis was performed on the  $F_1$  and  $F_2$  to identify the main periodicities characterising the temporal variation of each siphonophore species and of the total siphonophore standing stock.

### 2.2.2. Long-term variability of siphonophore assemblages

The main siphonophore assemblages characterising the different periods of the time series were identified by a multivariate mapping technique based on Bayesian probabilities (Souissi et al., 2001). Following Anneville et al. (2002) the mapping was performed using the following steps:

- (1) Initially, weekly abundance of the main siphonophore species (i.e. *M. kochi*, *M. atlantica*, *Lensia subtilis*, *Lensia conoidea*, *C. appendiculata* and *A. tetragona*) were split in a  $Y$  matrix composed by 958 rows (i.e. the weekly observations in 1974–1999)  $\times$  6 columns (i.e. the species). To match the multi-normality of the data requested by the computation of Bayesian probabilities, a PCA was applied to the  $Y^{0.055}$  transformed matrix. Three principal components accounting for 77% of the total variance were then retained in a  $Y'$  matrix (958 observations  $\times$  3 PCA scores) after verification of their multi-normality by the Dagnelie method (Legendre and Legendre, 1998; Souissi et al., 2001).
- (2) Q-mode clustering based on the Euclidian distance (flexible linkage with beta of 0.25) was applied to  $Y'$ . The main periods (i.e.  $G_j$  = groups of weeks, with  $j = 1$  to  $k$ ) were identified at different cut-off levels (Fig. 1\_Supplementary material).

Conditional probabilities that each observation  $Y'_i$  belongs to a group  $G_j$ , i.e.  $P(Y'_i \in G_j)$ , were calculated for each cut-off level. Depending on the composition in each observation  $Y'_i$  its conditional probability to be a member of  $G_j$  (one element of the partition called  $j$ -model) is expressed by the Bayes' relationship :

$$P(Y_i \in G_j) = \frac{p_j |\Sigma_j|^{-1/2} \exp(-d_j^2(i)/2)}{\sum_{k \in C} p_k |\Sigma_k|^{-1/2} \exp(-d_k^2(i)/2)}$$

where  $p_j$  is an a priori probability of the  $j$ -model, i.e. the proportion of the  $n$  observations in a cluster  $G_j$  to the total observations:

$$p_j = \frac{n_j^G}{\sum_{k \in C} n_k^G}$$

and  $d_j^2(i)$  is the generalised Mahalanobis distance between  $G_j$  and  $Y'_i$ :

$$d_j^2(i) = (Y_i - m_j^G)' \sum_j^{-1} (X_i - m_j^G)$$

where  $m_j^G$  is the centroid of the group and  $\sum_j$  is a pooled variance-covariance matrix used instead of the normal dispersion matrix  $\Sigma$  when computing  $d_2$ .

- (3) The observations were reallocated to a different  $G_j$  group when the maximum value of the conditional probability of a sample was obtained for another cluster.
- (4) A map of the isoprobabilities was produced for each cut-off level of the hierarchical classification (Fig. 1\_Supplementary material). The third cut-off was arbitrarily chosen as the final partition and the different periods  $G_j$  were then mapped (Fig. 1\_Supplementary material and Fig. 6).

The most indicative species in each  $G_j$  period were identified by the IndVal method index (Legendre and Legendre, 1998). The IndVal Index is the product of two values independently calculated multiplied by 100. One value, the specificity ( $A_{ij}$ ), accounts for the species abundance in a defined group of weeks:

$$A_{ij} = \frac{Nsp_{ij}}{Nsp_{+j}}$$

where  $Nsp_{ij}$  is the mean abundance of the species  $i$  in the weeks of the period  $G_j$  and  $Nsp_{+j}$  is the sum of the mean abundance of the species  $i$  in all the periods.

The other value, the fidelity ( $B_{ij}$ ), accounts for the recurrent presence of the species in the period  $G_j$ :

$$B_{ij} = \frac{Nobs_{ij}}{Nobs_{+j}}$$

where  $Nobs_{ij}$  is the number of observations in the period  $G_j$  where the taxon  $i$  is present and  $Nobs_{+j}$  is the total number of observations.

### 2.2.3. Influence of the environment on siphonophores' variability

**2.2.3.1. Environmental preferences of siphonophores.** The hydrographic and meteorological factors that could be associated with a significant increase of siphonophores were identified by using the methodology proposed by Perry and Smith (1993) and similarly used in Buecher et al. (1997) and in Licandro et al. (2006). The aim was to define environmental optima for each siphonophore species, pointing out which factors significantly affected the changes of its abundance recurrently observed at Point B.

The Perry and Smith method is based on the pair-wise comparison of the cumulative distribution of siphonophore abundance ( $g_i(t)$ ) and the cumulative distribution of an environmental parameter ( $f_i(t)$ ), where the null hypothesis to test ( $H_0$ ) is that no particular association exists between the two. When the maximum difference between  $g_i(t)$  and  $f_i(t)$  is close to zero, i.e. when the two distributions are almost identical, the  $H_0$  can be accepted, otherwise  $H_0$  is rejected and the association between the environmental factor and the siphonophore species is considered significant at a level that is established using a Monte Carlo randomization test with 10,000 permutations.

### 2.2.3.2. Long-term trends of siphonophores in relation to hydroclimatic changes.

The major trends of hydroclimatic descriptors ( $F_1$ s) were extracted by the EVF and compared by cross-correlation to the  $F_1$  of those siphonophore taxa that showed a significant long-term variability. This was done to investigate a possible influence of hydroclimatic fluctuations on long-term changes of siphonophores. The cross-correlation was performed on 1040 weekly values (988 for hydrological factors because of the missing values in 1994), with a maximum lag of 100 weeks. The cross-correlations

**Table 1**

Average abundance (ind. 100 m<sup>-3</sup>  $\pm$  standard deviation) of the main calyphorophoran siphonophores recorded in different periods offshore (Point A) and inshore (Point B) the Bay of Villefranche-sur-mer.

Taxon	Point A	Point B	
	1967–1969	1974–1976	1985–1999
<i>Muggiaea kochi</i>	52.3 $\pm$ 61.1	167.3 $\pm$ 84.2	25.1 $\pm$ 34.7
<i>Muggiaea atlantica</i>	–	5.1 $\pm$ 7.6	93.5 $\pm$ 80
<i>Lensia subtilis</i>	44.5 $\pm$ 32.7	45.4 $\pm$ 20.4	66.4 $\pm$ 29.7
<i>Chelophyes appendiculata</i>	2.2 $\pm$ 0.9	7.7 $\pm$ 5.1	10.4 $\pm$ 4.9
<i>Abylopsis tetragona</i>	0.5 $\pm$ 0.4	2.3 $\pm$ 0.9	3.9 $\pm$ 4.6
<i>Eudoxoides spiralis</i>	0.8 $\pm$ 0.6	1.4 $\pm$ 0.9	1.6 $\pm$ 1.5
<i>Lensia conoidea</i>	1.6 $\pm$ 1.6	1.1 $\pm$ 0.5	5.3 $\pm$ 5.8
<i>Hippopodius hippopus</i>	0.1 $\pm$ 0.1	0.3 $\pm$ 0.3	0.1 $\pm$ 0.1
<i>Lensia meteori</i>	1.0 $\pm$ 0.6	0.2 $\pm$ 0.2	2.3 $\pm$ 2.2
Total main calyphorophorans	103.0 $\pm$ 93.1	230.9 $\pm$ 94.6	206.8 $\pm$ 103.8

were tested for significance by a Monte Carlo randomization test with 10,000 permutations.

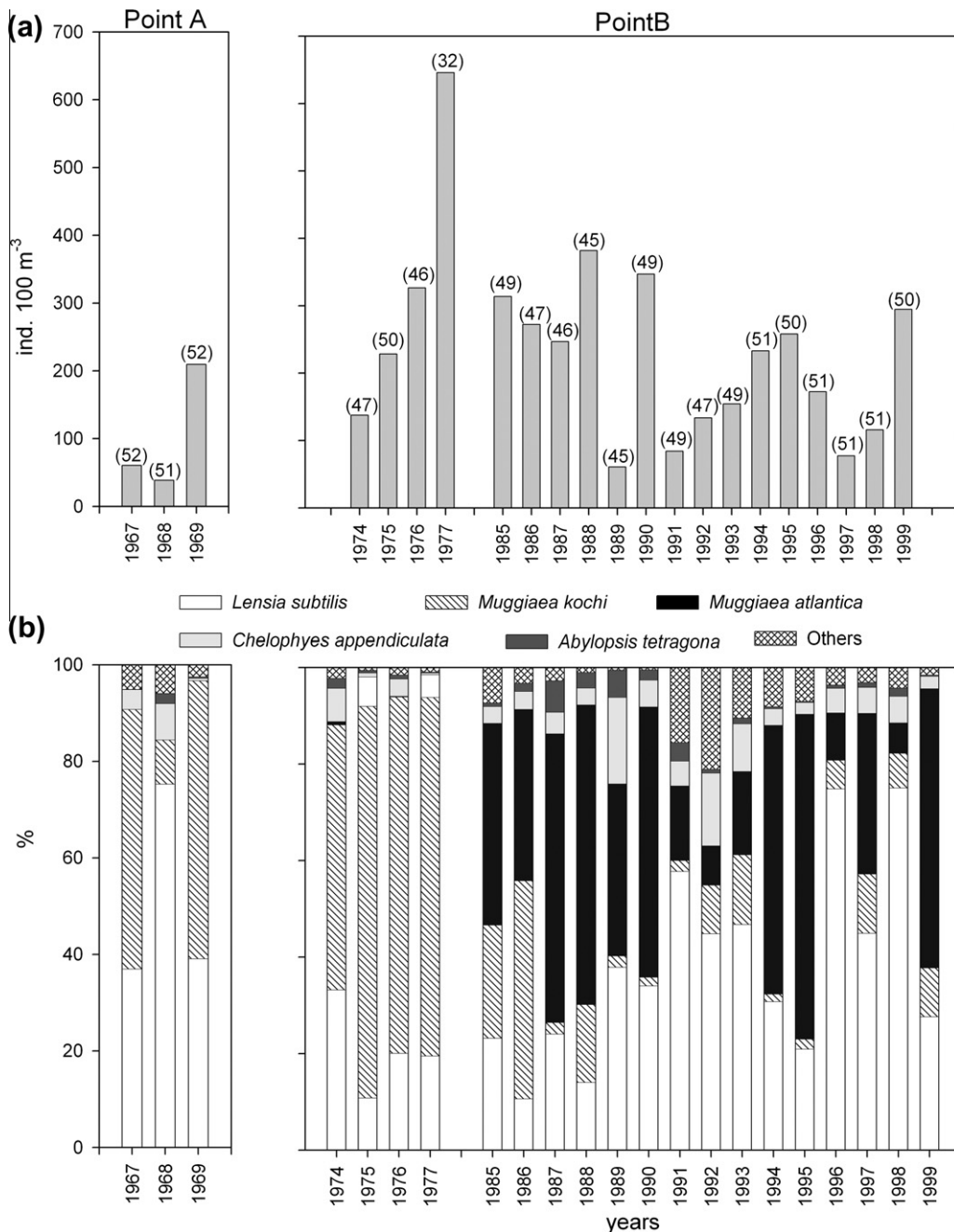
### 3. Results

#### 3.1. Long-term variability of siphonophore species and populations inshore and offshore the Bay of Villefranche

Calycophoran siphonophores showed similar patterns of temporal variability inshore and offshore the Bay of Villefranche, with the highest densities being generally recorded in more coastal waters (Table 1). At Point A (offshore station) from 1967 to 1969 total calycophorans densities averaged between 39 and 210 ind.  $100\text{ m}^{-3}\text{ yr}^{-1}$  (Fig. 2a). *Lensia subtilis* and *M. kochi* were the most

abundant species, accounting together for >80% of total calycophorans (Fig. 2b). The highest densities of those species were recorded in summer (i.e. weeks 22–31 in 1967–1968) or in spring (i.e. weeks 13–23 in 1969), and corresponded to the annual maxima of the siphonophore population (Fig. 3a). *Lensia conoidea*, *C. appendiculata*, *A. tetragona*, *Lensia meteori*, *Eudoxoides spiralis* and *H. hippopus* were also found at Point A, with annual peaks at different times of the year (data not shown).

At Point B (inshore station), the abundance of calycophoran siphonophores during 1974–1999 varied between 61 and 382 ind.  $100\text{ m}^{-3}\text{ yr}^{-1}$  (Fig. 2a), with peaks up to 2795 ind.  $100\text{ m}^{-3}\text{ week}^{-1}$  usually occurring in late spring–summer (i.e. weeks 10–25, Fig. 3b) as a result of the annual maxima of the three dominant species *L. subtilis*, *M. kochi* and *M. atlantica* and of *L.*



**Fig. 2.** (a) Yearly averages (ind.  $100\text{ m}^{-3}$ ) and standard deviations of total calycophoran siphonophores recorded at the offshore (Point A) and inshore (Point B) sampling stations between 1967 and 1999. The number of weeks sampled per year is indicated on the top of each bar. (b) Relative contribution (%) of the main calycophoran species to the total calycophoran siphonophore population.



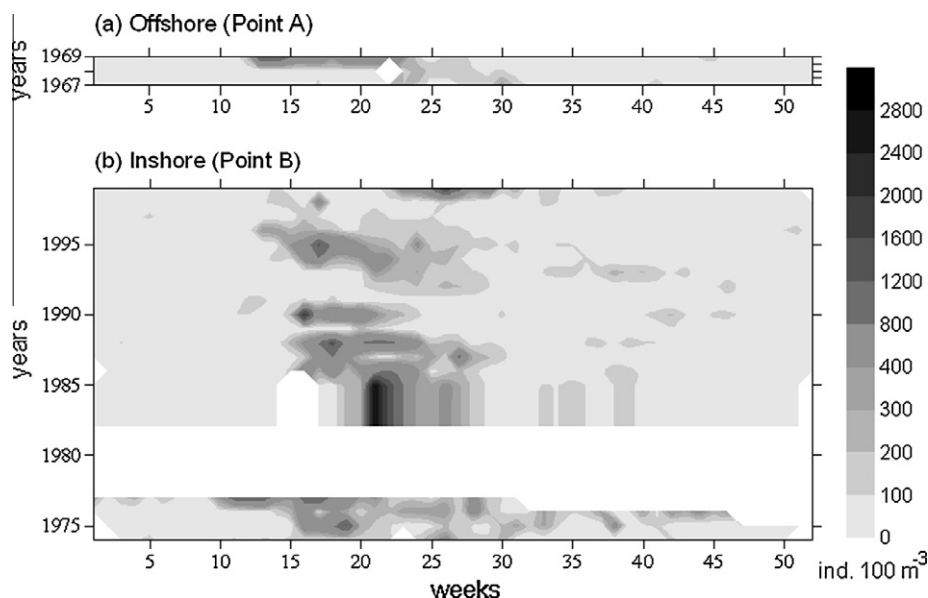


Fig. 3. Villefranche-sur-mer. Weekly abundance (ind.  $100\text{ m}^{-3}$ ) of main calycophoran siphonophores collected (a) offshore (Point A) and (b) inshore (Point B).

*conoidea* (Fig. 4a–d). High abundance of siphonophores was also found in August–November 1974–1977 (Fig. 3b) due to high densities of *M. kochi* (data not shown). *Abylopsis tetragona* and *C. appendiculata* usually peaked in summer (weeks 27–31) and summer–autumn (weeks 23–43), respectively (Fig. 4e and f). Other calycophorans (i.e. *L. meteori*, *E. spiralis*, *L. campanella*, *H. hippopus* and *Sulculeolaria quadrivalvis*) were sometimes found in low abundance at different times of the year (Fig. 4g–m).

The analysis of the filtered variables  $F_1$  and  $F_2$ , which represent the principal modes of siphonophore variability, indicated that during 1984–1999 the seasonal cycle was the predominant mode of fluctuation driving the changes in total calycophorans and of *M. atlantica*, *C. appendiculata* and *L. conoidea* (Fig. 5 and Table 2). *Lensia subtilis* mainly varied following a 3-years cycle (23% of variance associated with  $F_1$ , Fig. 5d and Table 2), while *A. tetragona* and *M. kochi* (Fig. 5b and c) showed a significant long-term decline (24% and 38% of variance associated to the  $\alpha$  period, Table 2).

### 3.2. Temporal mapping of siphonophore assemblages

During 1974–1999, four main periods could be identified characterised by different siphonophore assemblages (Fig. 6). These were: winter and summer from 1987–onwards (G1); spring from 1984 to 1999 (G2); autumn–early winter and spring–early summer in 1975, 1977 and 1985–1986 (G3); winter and late summer–early autumn in 1974–1977, including spring 1974 and 1976 (G4).

The first period identified through ordination, which corresponded to the first cut-off of the cluster of observations, was the late winter–spring season in 1987–1999 (group A1 in Fig. 1\_Supplementary material). This period was then split in two at the second cut-off, when weeks characterised by the maximum abundance of siphonophores during the spring (i.e. period G2) were separated from the weeks prior to the maximum (i.e. period G1) (Fig. 1\_Supplementary material and Fig. 6). The third cut-off separated the periods G3 and G4 (Fig. 1\_Supplementary material and Fig. 6).

The most characteristic species of the different siphonophore assemblages, based on the IndVal classification (Table 3), were: *C. appendiculata* in G1; *M. atlantica*, *L. conoidea* and *L. subtilis* in G2; *M. kochi* and *A. tetragona* in G3; *M. kochi* in G4. Very high IndVal coefficients were obtained for *M. atlantica* and *L. conoidea* in G2 due to their extremely high abundance (i.e. high specificity) during that

period. *Muggiaea kochi* characterised both G3 and G4, with higher abundance and greater IndVal in G4.

The most important changes of siphonophore in the Bay of Villefranche assemblages were caused by the progressive decrease of weeks characterised by high abundance of *M. kochi* (see changes of G4 in Fig. 6) and the corresponding increase and persistence of weeks with high abundance of *C. appendiculata* and *M. atlantica* (see changes of G1 and G2 in Fig. 6).

### 3.3. Environmental factors related to siphonophore species and assemblages

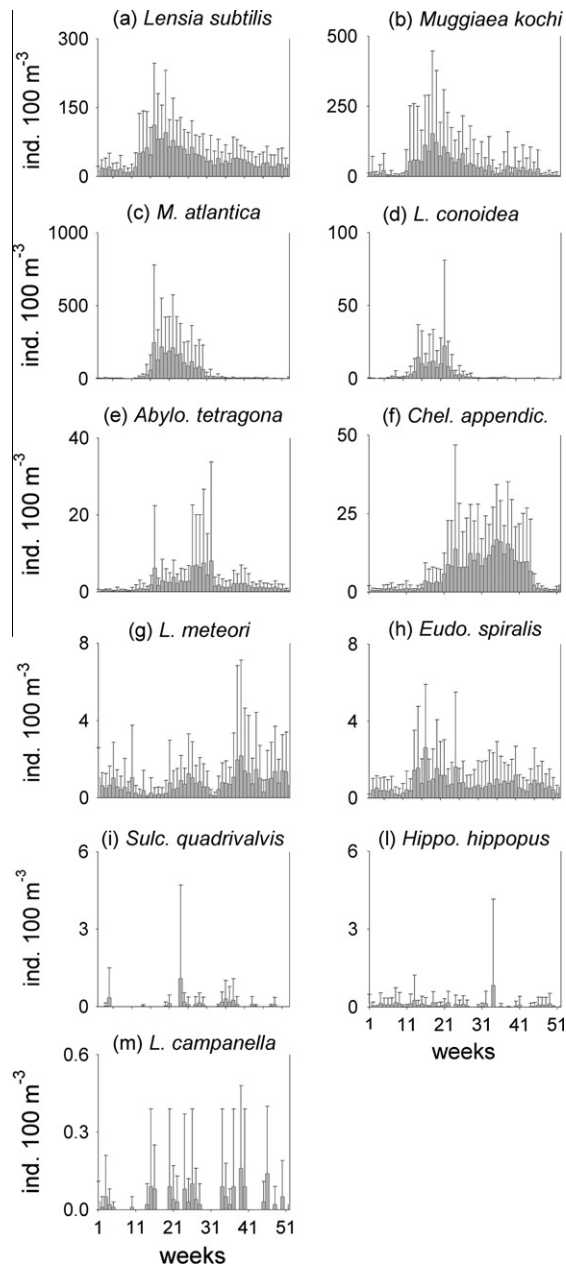
Different environmental conditions characterised periods G1–G4. The weeks in G1 were characterised by high salinities throughout the water column, while the lowest salinities were recorded during G2 (Fig. 7a and b).

G3 grouped together the warmest weeks, in which the highest values of air and water temperature were recorded (Fig. 7c and d). Strong winds were recorded in the weeks of G4 (Fig. 7e). Both G2 and G3 were characterised by a highly stratified water column (Fig. 7f). In G1 and G4 the air temperature was significantly lower than in the other two periods (not shown).

Different environmental factors were associated with a significant increase in the abundance of siphonophores. In general, the highest abundances of siphonophores were significantly associated with a well stratified water column (Table 4) and calm wind conditions, well below the yearly average (Table 4, Fig. 2a\_Supplementary material).

Water temperature significantly influenced the abundance of *C. appendiculata*, *L. conoidea* and *M. kochi*, with thermal preferences that varied between 14–14.8 °C and 15.3–16.2 °C for *C. appendiculata* and *M. kochi*, respectively (Table 4, Fig. 8a and b). Considering the typical annual variability of atmospheric pressure in Villefranche (Fig. 2b\_Supplementary material), stable weather and stratified waters were associated with peaks of *M. kochi* (Table 4, Fig. 8c), while low pressure conditions coincided with the highest abundance of *L. conoidea* (Table 4).

Among all the measured hydrographic and meteorological descriptors, salinity appears to be the main environmental factor that significantly influenced the abundance of the dominant siphonophores in the Bay of Villefranche (Table 4, Fig. 8d–f). Different values of surface salinity corresponded to the greatest abun-



**Fig. 4.** Point B, 1974–1999. Interannual weekly average abundance of (a) *L. subtilis*, (b) *M. kochi*, (c) *M. atlantica*, (d) *L. conoidea*, (e) *A. tetragona*, (f) *C. appendiculata*, (g) *L. meteori*, (h) *E. spiralis*, (i) *S. quadrivalvis*, (l) *H. hippopus*, (m) *L. campanella*. Interannual weekly standard deviations are also shown.

dance of different siphonophore species. In particular, *C. appendiculata* and *A. tetragona* significantly increased with relatively high salinities at the surface and in the whole water column (i.e. values > 37.9 psu). In contrast, high abundances of *M. kochi* were associated with relatively low salinities (i.e. values < 37.9 psu).

The comparison of the main modes of variability ( $F_1$ s) extracted from hydrographic, meteorological and biological descriptors suggest a link between fluctuations of salinity and long-term changes of some siphonophore species. In particular, the decreasing trend in the abundance of *M. kochi* (Fig. 5b) was negatively correlated with the main trend of surface salinity at a zero time lag ( $p < 0.001$ ) (Fig. 9a and b). On the other hand, no significant correlation was found between the long-term decrease or increase of siphonophore species and other hydroclimatic factors considered here.

#### 4. Discussion

This study shows that the siphonophore standing stock in coastal waters of the north-western Mediterranean (i.e. Point B time series) did not show any significant change between the middle 1970s to the late 1990s, although the annual maxima, which usually occurred in late spring–summer, were sometimes very different from 1 year to the next.

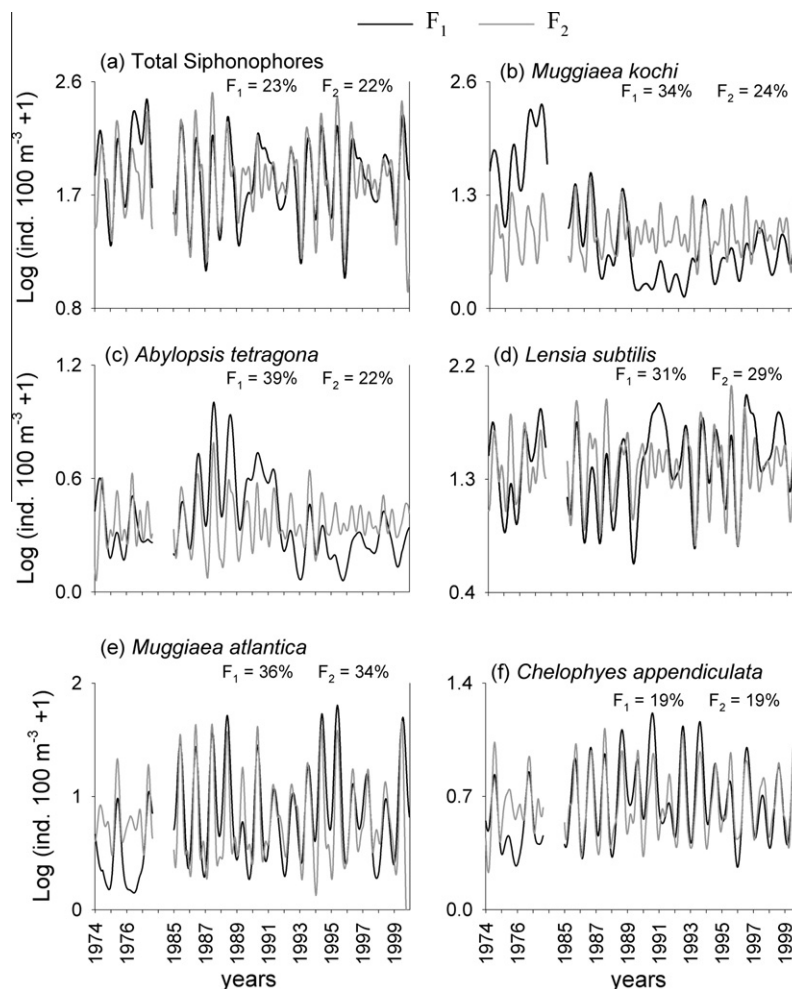
The analysis of a 3-year data series collected in the late 1960s at a sampling station two miles off the coast (i.e. Point A time series) showed that the patterns of variability were similar at both inshore and offshore locations. A wide-ranging cyclonic circulation flows westward along the Ligurian and Provençal coasts toward the Strait of Gibraltar, linking the surface layer of the entire north-western Mediterranean sector from Italy to Spain. Consequently, the Point B time series is likely a good descriptor of the long-term changes in the abundance of siphonophores at the scale of the north-western Mediterranean region.

Quantitative comparison of anterior nectophores sampled by mesozooplankton nets (mouth diameter about 0.50–1 m and 200–300  $\mu$ m mesh size) in the western Mediterranean (Dallot et al., 1988; Licandro and Ibanez, 2000) and in the southern Tyrrhenian Sea (Ianora and Scotto di Carlo, 1981) reported densities one order of magnitude lower than in the present study. This difference is confirmed when comparing records of siphonophores collected in parallel at Point B with a Regent net (present study) and with a Juday–Bogorov net (mouth diameter of 0.50 m and 330  $\mu$ m mesh size) (Buecher, 1999; Molinero et al., 2008b); as already pointed out by Patrìti (1964), small nets appear unsuitable for quantitative sampling of siphonophores.

Overall the patterns of variability identified by different studies are consistent, regardless of the net used. Our study is in agreement with previous findings that have reported a seasonal maximum in siphonophore abundance in the spring (Ianora and Scotto di Carlo, 1981; Gili et al., 1987; Gamulin and Kršinić, 1993b; Lakkis and Zeidane, 1997; Licandro and Ibanez, 2000; Batistic et al., 2007; Fernandez de Puellas et al., 2007). In the Bay of Villefranche, high abundances of calyphorans, mainly *M. kochi*, were also recorded in the summer and autumn during the late 1970s. While a secondary autumn peak of siphonophores seemed to be a common pattern in different coastal regions of the western and eastern Mediterranean (Ianora and Scotto di Carlo, 1981; Gili et al., 1987, 1988; Batistic et al., 2007), this has been recorded in the Ligurian Sea only occasionally since the middle 1980s (Licandro and Ibanez, 2000 and present study), possibly as a consequence of the decline in the abundance of *M. kochi* which had started at that time.

*Lensia subtilis*, *M. kochi*, and more recently *M. atlantica*, constituted the bulk of the calyphoran community in the Bay of Villefranche, accounting for the annual maxima of the population. The first two species are common throughout the Mediterranean, with seasonal peaks usually in late winter–spring for *L. subtilis* and in spring and late summer–autumn for *M. kochi* (Patrìti, 1964; Ianora and Scotto di Carlo, 1981; Gili et al., 1987, 1988; Gamulin and Kršinić, 1993b; Licandro and Ibanez, 2000; Batistic et al., 2007). *Muggiaea atlantica* is widespread in the western and eastern Mediterranean (Bouillon et al., 2004 and references therein), while only recently has it been recorded in the Adriatic Sea (Kršinić and Njire, 2001; Milos and Malej, 2005; Batistic et al., 2007).

*Lensia conoidea*, *C. appendiculata* and *A. tetragona* were also abundant in the Bay of Villefranche. Those taxa, as well as other species that were regularly found in relatively low numbers at the Point B (i.e. *L. meteori*, *E. spiralis*, *H. hippopus*, *L. campanella* and *S. quadrivalvis*), are common in the Mediterranean and tend to be more concen-



**Fig. 5.** Point B, 1974–1999. Filtered variables  $F_1$  and  $F_2$  (log-transformed data) extracted by the Eigen-Vector Filtering (EVF) for (a) Total siphonophores; (b) *M. kochi*; (c) *A. tetragona*; (d) *L. subtilis*; (e) *M. atlantica*; (f) *C. appendiculata*.

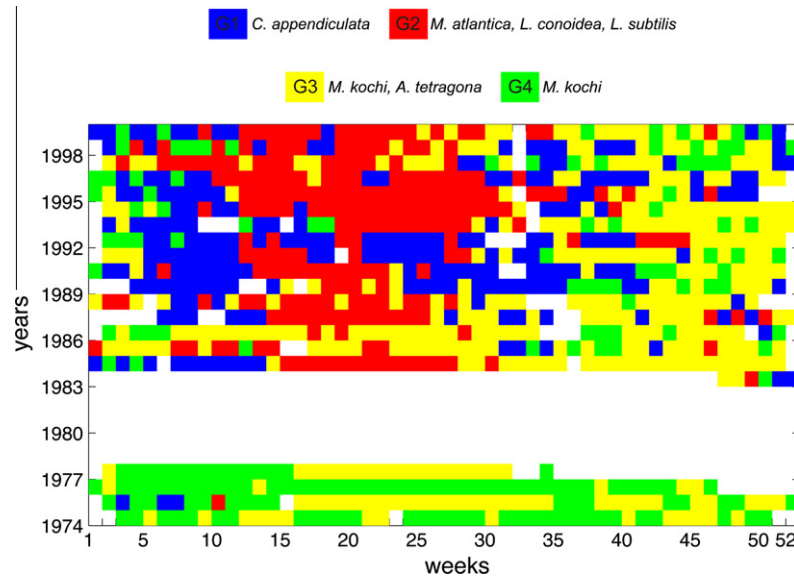
**Table 2**  
Point B: 1984–1999. Results of harmonic analysis on  $F_1$  and  $F_2$  extracted by EVF on weekly abundance of total siphonophores and of main calycophoran species. Significant harmonics and percent of variance associated with each  $F_1$  and  $F_2$  are indicated.  $\alpha$  represents the variability associated with the general trend of the series. Periodicities having maximum variance are in bold.

	$F_1$		$F_2$	
	Significant harmonics (weeks)	Harmonics associated variance (%)	Significant harmonics (weeks)	Harmonics associated variance (%)
Total siphonophores	<b>52</b> , 26, 46, 43	<b>30</b> , 11, 8, 6	<b>52</b> , 260, $\alpha$ , 46	<b>35</b> , 9, 6, 4, 5, 8
<i>Abylopsis tetragona</i>	$\alpha$ , 390, 52	<b>38</b> , 10, 7	<b>52</b> , 49, 46, 29, 28	<b>16</b> , 13, 10, 8, 6
<i>Muggiaea kochi</i>	$\alpha$ , 390, 56, 195	<b>24</b> , 16, 8, 7	<b>49</b> , 52, 26, 46, 56, 43	<b>13</b> , 10, 9, 8, 7, 6, 5
<i>Lensia meteori</i>	$\alpha$ , 87, 78	<b>32</b> , 10, 3, 9, 7	<b>41</b> , 39, 52, 30, 33, 57	<b>15</b> , 12, 9, 8, 7, 6
<i>Eudoxoides spiralis</i>	$\alpha$ , 156, 260	<b>19</b> , 18, 15	<b>41</b> , 49, 43, 33	<b>17</b> , 14, 11, 9
<i>Lensia subtilis</i>	<b>156</b> , 52, 97	<b>23</b> , 18, 12	<b>52</b> , 46, 35, 34	<b>23</b> , 14, 9, 6
<i>Muggiaea atlantica</i>	<b>52</b> , 26, 43, 37, 49	<b>27</b> , 10, 7, 6, 5, 7	<b>52</b> , 260, $\alpha$ , 130	<b>30</b> , 10, 5, 8, 5, 7, 5
<i>Chelophyes appendiculata</i>	<b>52</b> , $\alpha$ , 97	<b>39</b> , 11, 10	<b>52</b> , 29	<b>50</b> , 7
<i>Lensia conoidea</i>	<b>52</b> , 390, 130, 260, 87	<b>19</b> , 12, 10, 7, 6	<b>52</b> , 26, 46, 37, 29, 33, 24	<b>17</b> , 13, 7, 4, 4, 3, 9, 3, 9

trated in open waters where they undergo extensive vertical migrations between epipelagic and mesopelagic layers (Bouillon et al., 2004 and references therein). The high abundance of *L. conoidea*, *C. appendiculata* and *A. tetragona* in the study area is likely related to the steep bathymetry of the region, characterised by the presence of deep canyons a few miles off the coast, where patches of those species have been observed in sub-superficial waters (Laval et al., 1989; Andersen et al., 1992). Overall, all the siphonophores found in the Bay of Villefranche are cosmopolitan species that are distributed across the Atlantic, Pacific and Indian oceans with the

exception of *M. kochi*, which is typically restricted to warm and temperate regions of those oceans (Alvarino, 1971; Pugh, 1999; Bouillon et al., 2004).

Although the siphonophore standing stock was stable over time, major changes in community composition occurred within the calycophoran population around the middle 1980s, a period in which the whole north-western Mediterranean was characterised by significant hydroclimatic variability under the forcing of the North Atlantic Oscillation (NAO) (Fromentin and Ibanez, 1994; Vignudelli et al., 1999; Molinero et al., 2005). In particular, a greater



**Fig. 6.** Point B, 1974–1999. Final map of the main periods (G1–G4) characterised by different siphonophore assemblages. The most characteristic species in each period as identified by the IndVal index (see Table 3) are also indicated.

**Table 3**

Point B: 1974–1999. Siphonophore taxa that characterise the four periods identified by the temporal mapping (Fig. 6). IndVal = Indicator Value Index;  $A_{ij}$  = specificity;  $B_{ij}$  = fidelity. The greatest IndVal per taxon are indicated in bold.

Taxon	IndVal (%)	$A_{ij}$	$B_{ij}$
G1			
<i>Chelophyes appendiculata</i>	<b>33</b>	0.34	0.9
G2			
<i>Muggiaea atlantica</i>	<b>81</b>	0.83	1.0
<i>Lensia conoidea</i>	<b>61</b>	0.72	0.8
<i>Lensia subtilis</i>	<b>39</b>	0.41	1.0
G3			
<i>Muggiaea kochi</i>	39	0.39	1.0
<i>Abylopsis tetragona</i>	<b>28</b>	0.34	0.8
G4			
<i>Muggiaea kochi</i>	<b>44</b>	0.44	1.0

inflow of relatively warm and less saline Tyrrhenian waters was recorded through the Corsica Channel into the Ligurian Sea in those years of negative NAO conditions (Vignudelli et al., 1999). The relatively low salinities recorded in Villefranche between the late 1970s and late 1980s would be then well-matched with such hydrological features, while the higher salinities recorded since the early 1990s would confirm that the circulation regime was returning to its usual pattern.

The high water temperature and enhanced stratification associated with the peculiar circulation pattern of the 1980s were related to changes in the composition and abundance of phytoplankton (Gomez and Gorsky, 2003) and to higher densities of gelatinous plankton including salps and jellyfish such as the siphonophores *A. tetragona* and *C. appendiculata* (Buecher, 1999; Ménard et al., 1994; Licandro et al., 2006; Molinero et al., 2008a,b).

Our study, which provides updated information based on weekly records of siphonophores, shows that the increase of *A. tetragona* previously reported (Molinero et al., 2008b) was mainly limited to the 1980s, because the abundance of this species decreased again after the early 1990s. On the other hand, the higher annual mean abundance of *C. appendiculata* reported in recent years (Molinero et al., 2008b), was mainly due to a more persistent seasonal maximum rather than to an increasing trend in abundance.

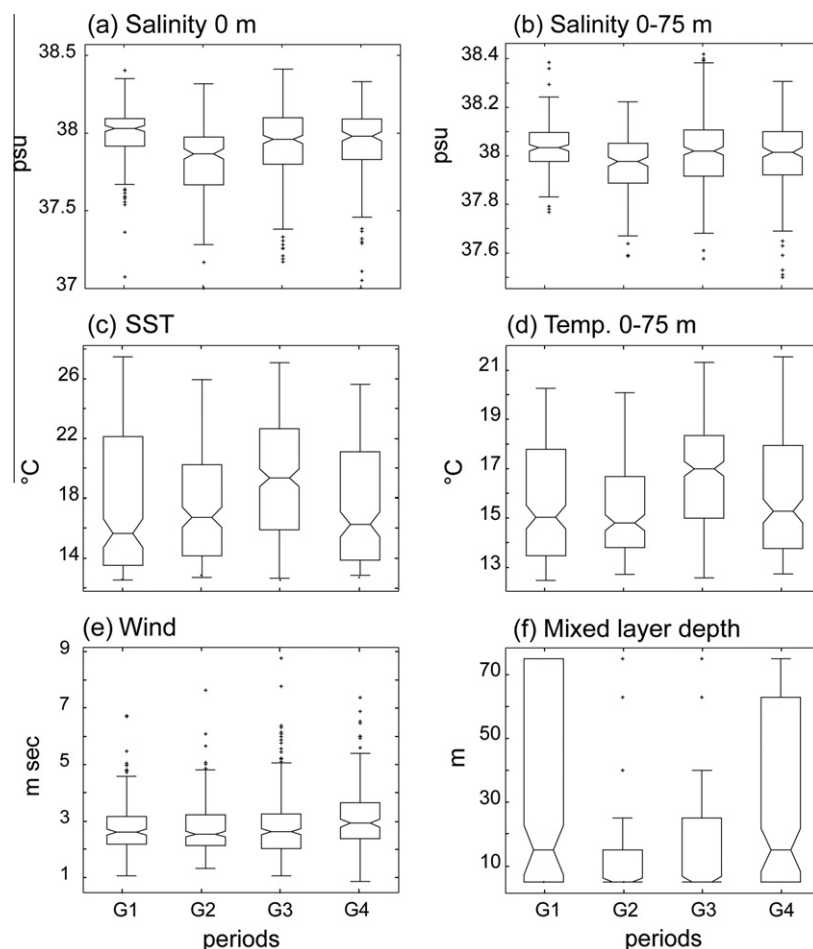
The decrease of the dominant *M. kochi*, which along the north-western Mediterranean coast reached densities of up to 2000 ind.  $100\text{ m}^{-3}\text{ week}^{-1}$  (Palma, 1985; Riera et al., 1986; present study), was probably the most dramatic change observed within the siphonophore community in recent decades. *Muggiaea kochi* numbers dropped tenfold on average since the early-middle 1980s, while the congeneric *M. atlantica* and *C. appendiculata* became increasingly dominant in spring and summer–autumn, respectively (Gili et al., 1988; present study). We hypothesise that as a result of the hydrological changes which have occurred in the 1980s, greater numbers of *M. atlantica* were advected along the Ligurian coast allowing this species to progressively become established and to dominate the siphonophore community during spring (Gili et al., 1987; Licandro and Ibanez, 2000; present study). Consequently the significant relationship between an increase in salinity and the decline of *M. kochi* identified here may reflect the decrease of that species following the hydrological anomaly. A direct cause–effect of salinity on *M. kochi* seems less likely considering that this species is usually dominant in the relatively high saline waters of the southern Mediterranean (Lakkis and Zeidane, 1997; Zakaria, 2004).

Previous studies have noted the alternation in the occurrence and dominance of *M. atlantica* and *M. kochi* in coastal regions of the English Channel (Russell, 1934) and of the north-western Mediterranean (Gili et al., 1988 and references therein). The reasons for this have not been clarified yet, mainly because the biology of these two calycophorans is still poorly known. Carré and Carré (1991) described the life cycle of *M. kochi* at different temperatures but a similar study is not yet available for *M. atlantica*.

*Muggiaea atlantica* is considered one of the most abundant siphonophores in different coastal systems, with densities that may reach up to 30–50 ind.  $\text{m}^{-3}$  in very productive regions (e.g. Toyokawa and Terazaki, 1994; Thibault-Botha et al., 2004) and swarms up to 500 ind.  $\text{m}^{-3}$  during outbreak events (Greve, 1994; Kršinić and Njire, 2001). The progressive expansion of the distribution of *M. atlantica* into some regions of the Mediterranean (i.e. the Adriatic Sea, Batistic et al., 2007 and references therein) suggests that this species is able to exploit favourable environmental conditions more efficiently than other siphonophores.

The identification of species' environmental preferences may provide useful indications about the influence of the environment on siphonophore population dynamics and may help to address





**Fig. 7.** Point B, 1974–1999. Box and whisker plots of different environmental descriptors characterising the periods G1–G4 obtained by multivariate mapping based on Bayesian probabilities (see Fig. 6). (a) Surface salinity; (b) salinity integrated in the 0–75 m water column; (c) surface temperature; (d) temperature integrated in the 0–75 m water column; (e) wind average speed; (f) mixed layer depth.

**Table 4**  
Environmental preferences (i.e. optima) of the main siphonophore species obtained from analysis of environmental records measured in the different periods, G1–G4. Asterisks indicate optima that are significantly associated with an increase of the species.

Taxon	SST (°C)	Temp. 0–75 m (°C)	Sal. 0 m (psu)	Sal. 0–75 m (psu)	Mixed layer depth (m)	Air temp. (°C)	P. atm. (millibar)	Wind (m s <sup>-1</sup> )
<i>Lensia subtilis</i>	12.7–14.0	13.5–14.2	37.5–37.7**	37.65–37.71	5–12	17.0–19.5	1011.5–1014.4*	2.3–2.8**
<i>Muggiaea kochi</i>	19.8–21.2	15.3–16.2***	37.4–37.8***	37.78–37.87***	5–12***	17.2–19.8	1013.9–1018.4**	1.8–2.3
<i>M. atlantica</i>	14.0–15.4	15.7–16.4	37.5–37.7**	37.78–37.84	5–12***	19.5–21.9	1014.4–1017.3	1.8–2.3
<i>Chelophyes appendiculata</i>	15.5–17.0**	14.0–14.8***	37.9–38.0*	37.95–38.01**	5–12***	14.0–16.2	1015.6–1019.2	2.2–2.8***
<i>Lensia conoidea</i>	16.7–18.0*	14.9–15.7***	37.3–37.5*	38.03–38.09	5–12**	17–19.5*	1008.7–1011.5**	2.3–2.8
<i>Abylopsis tetragona</i>	18.3–19.8	15.2–16.07	37.8–38.1*	38.08–38.17**	12–19***	17.2–19.8	1013.7–1016.9	1.8–2.6

\*  $p < 0.1$ .

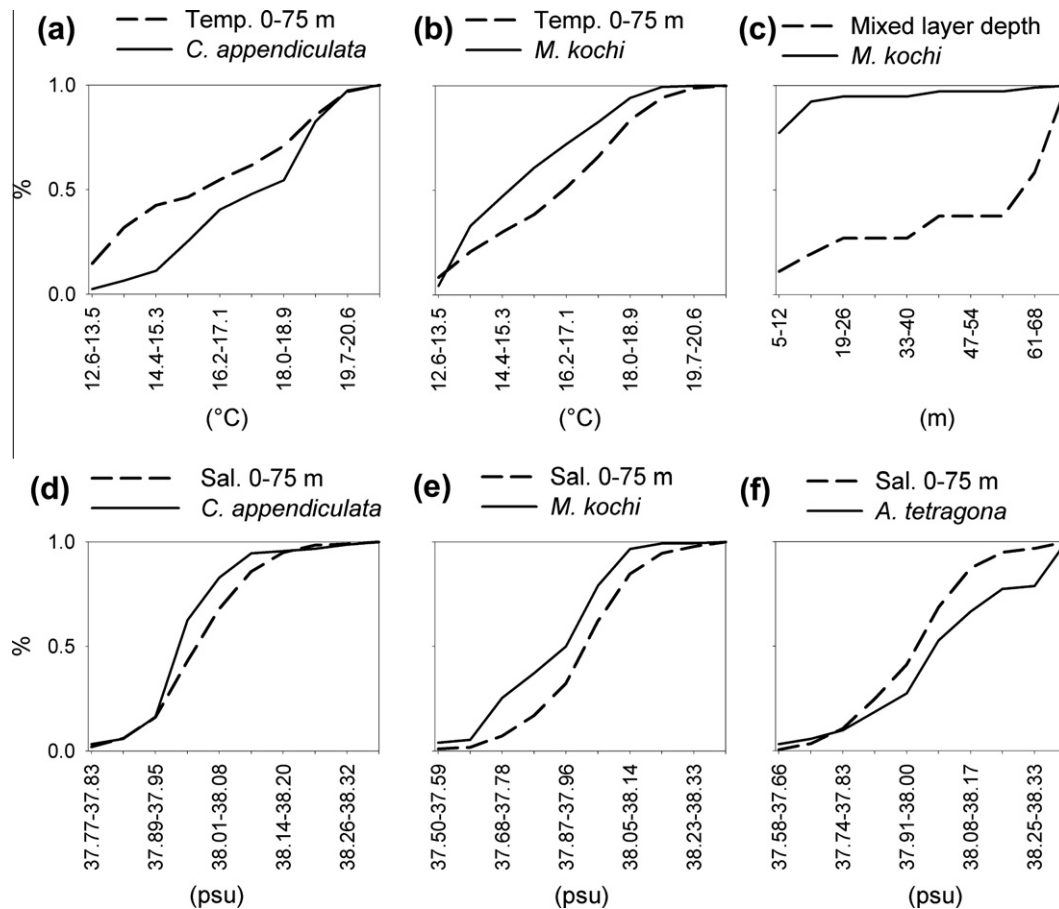
\*\*  $p < 0.01$ .

\*\*\*  $p < 0.001$ .

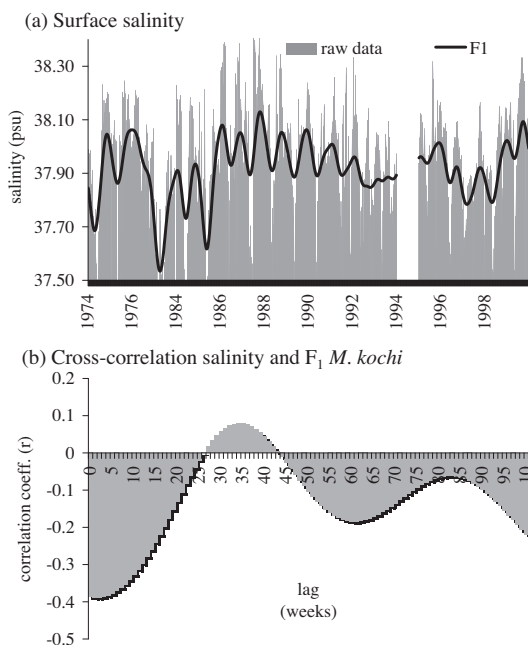
future experimental studies. In the Bay of Villefranche salinity, water stratification and water temperature were the main factors associated with a significant increase of siphonophores. Well-stratified waters and high temperatures were previously related to the occurrence and persistence of high densities of gelatinous plankton in the region (e.g. Ménard et al., 1994; Licandro et al., 2006; Molinero et al., 2008a,b). Warmer temperatures may positively affect different phases of cnidarian reproduction (i.e. strobilation period, survival of polyps and production of planulae) that can result in a very rapid increase in population abundance and survival over winter (Boero et al., 2008 and reference therein). On the other

hand, reduced turbulence and vertical mixing associated with high stability of the water column may favour the accumulation and maintenance of jellyfish swarms (Graham et al., 2001).

Thermocline and halocline as well as mesoscale features like eddies and fronts may represent a barrier for several species of siphonophores, significantly affecting the composition of the community (Mapstone, 2009). Different siphonophore assemblages have been found, for instance, on the opposite sides of upwelling regions in the south-east Atlantic (Thibault-Botha et al., 2004), south-east Pacific (Palma and Silva, 2006; Pavez et al., 2010) and in the Gulf of Mexico (Sanvicente-Añorve et al., 2007).



**Fig. 8.** Point B, 1974–1999. Cumulative frequency distributions of *C. appendiculata*, *M. kochi* and *A. tetragona* during their characteristic periods (i.e. G1–G4) in relation to temperature integrated in the 0–75 m water column (a–b), mixed layer depth (c) and salinity integrated in the 0–75 m water column (d–f).



**Fig. 9.** Point B, 1974–1999. (a) Surface salinity long-term trend ( $F_1$ ) obtained by EVF. Raw data are shown in gray. (b) Cross correlation function calculated between the  $F_1$  of surface salinity (first) and the  $F_1$  of *M. kochi* (lagged). A time lag of 0–100 weeks was considered.

Our study shows that the abundance of the most dominant calyphoran siphonophores, in particular of *M. kochi*, *C. appendiculata* and *A. tetragona*, significantly increased for different salinity optima. Abrupt changes in salinity may affect the buoyancy, reproduction and prey consumption rate of cnidarians (Mills, 1984; Ma and Purcell, 2005). The rate of osmotic acclimation of cnidarians is species-specific and varies according to their swimming behaviour (Mills, 1984). One may therefore assume that siphonophores such as *C. appendiculata* and *A. tetragona*, that are able to perform large vertical migrations crossing salinity gradients, can adapt to sudden increases in salinity better than species mainly concentrated in the epipelagic layer (e.g. *M. kochi*).

The analysis of long-term records collected in the north-western Mediterranean (present study) and in other regions worldwide (Purcell et al., 2007 and references therein) seems to suggest that salinity gradients may significantly affect the abundance of different jellyfish. Experimental studies are needed to clarify whether salinity is able to directly affect jellyfish performances, or whether it is relevant mainly as a proxy of hydrographic changes.

In recent decades a combination of hydroclimatic changes and anthropogenic impact has determined the rapid alteration of the Mediterranean marine biodiversity (Bianchi, 2007 and references therein). It is likely that changes in dominant species have occurred in different plankton groups but at present we are still unable to assess them because of the limited monitoring effort and to the poor taxonomic identification of some key plankton groups (i.e. filter-feeders and carnivorous gelatinous plankton). It is possible

that, like siphonophores, other plankton taxa have experienced significant changes in community structure while their standing stock has remained relatively unchanged. Mechanisms linking the different components of the pelagic food-web are complex and changes in dominant plankton species may alter the quality, quantity and seasonal timing of zooplankton production with a knock-on effect on top predators as fish and mammals that in the Mediterranean are already endangered as a result of anthropogenic pressures.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pocean.2011.11.004.

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