

## Long-term fluctuations (1974–1999) of the salps *Thalia democratica* and *Salpa fusiformis* in the northwestern Mediterranean Sea: Relationships with hydroclimatic variability

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### Abstract

We investigated the long-term variability of the salps *Thalia democratica* and *Salpa fusiformis* during the period 1974–1999 at a coastal site in the Bay of Villefranche-sur-mer. During this period *T. democratica* varied both interannually and seasonally, whereas *S. fusiformis* showed only seasonal fluctuations. Weeks in which *T. democratica* and *S. fusiformis* populations were developing in situ (i.e., near the sampling station without advection) are defined as the informative periods. Different species-specific optima of temperature, salinity, and chlorophyll *a* concentration, as well as stability conditions of the water column, were related to informative periods for the two *Thalia* and *Salpa* species. Long-term temperature oscillations were significantly related to the interannual maxima of *T. democratica*. The link between positive anomalies of temperature and outbreaks of *T. democratica* stress the importance of primary consumers as indicators of changes occurring in the marine system.

An analysis of long-term biological series is the most useful tool for distinguishing recurrent patterns of variability from unusual changes and for investigating their relationship with hydroclimatic factors. In the Mediterranean Sea, studies of zooplankton time series available from a few coastal sites primarily concern crustacean copepods (e.g., Cataletto et al. 1995; Mazzocchi and Ribera d'Alcalá 1995; Fernandez-de Puelles et al. 2004). Except for a few works on gelatinous zooplankton time series in the Ligurian Sea (Ménard et al. 1994; Buecher et al. 1997; Licandro and Ibañez 2000), gelatinous animals are usually neglected primarily because they are often damaged by sampling with conventional nets. However, long-term fluctuations in gelatinous plankton may be relevant for the entire pelagic community. In the northeast Pacific Ocean the long-term decline of zooplankton biomass within the California Current region was linked primarily to the interannual fluctuations of tunicates (Lavaniegos and Ohman 2003). The diminution of zooplankton and

ichthyoplankton abundance observed in the North Sea during the so-called cold biological event (i.e., decreased inflows of warm Atlantic water and increased inflows of colder, deeper Norwegian water) seemed to be related to an increase in jellyfish (Lynam et al. 2004).

Salps are an important component of the pelagic food web because they are extremely efficient nonselective gelatinous filter feeders, retaining particles over a wide size range between 1–2  $\mu\text{m}$  and 1 mm (Harbison and McAlister 1979; Deibel 1985; Kremer and Madin 1992) but also smaller than 1  $\mu\text{m}$ . On an individual basis their grazing impact on autotrophic populations may be much greater than that of crustacean filter feeders or microzooplankton, with measured clearance rates varying from 82 to 444 mL individual<sup>-1</sup> day<sup>-1</sup> (Vargas and Madin 2004 and references therein). Some measurements made in the northwestern Mediterranean Sea estimated that salp populations may remove up to 74% of the total primary production (Andersen 1998). Salps vary much in abundance according to the season, tending to peak after the phytoplankton spring bloom, when they may increase very rapidly due to the alternation of asexual and sexual reproduction; each solitary asexual zooid (oozooid) releases by budding several chains of aggregate sexual zooids (blastozooids).

Zooplankton monitoring showed that in some years salps largely exceed their usual abundance, reaching very high values up to hundreds or thousands of individuals per cubic meter; such events, which are known as outbreaks, have often been observed in the Mediterranean Sea (CIESM 2001). During an outbreak, salps are the main food source for higher trophic organisms, being preyed on by both zooplankton (e.g., siphonophores, medusae, heteropods, and amphipods) and nekton (krill and mesopelagic fish) (Hamner et al. 1975; Brandt 1981; Mianzan et al. 2001). Moreover, salps produce large, resistant, and fast-sinking fecal pellets (between 1 and

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85 mm long) that significantly contribute to the downward flow of organic matter (Andersen 1998). Measurements taken in bottom sediments of the northwestern Mediterranean Sea showed that during a salps outbreak, the downward exportation of organic carbon and nitrogen largely increases (Fernex et al. 1996).

*Thalia democratica* and *Salpa fusiformis* are the dominant salps in Mediterranean coastal waters (Braconnot 1973). Ménard et al. (1994) investigated the influence of hydrometeorological factors on the probability that *T. democratica* and *S. fusiformis* reach or maintain high abundance during their annual maximum in the Bay of Villefranche-sur-mer (northwestern Mediterranean); results of the latter study, obtained by using a Markov chain model on semiquantitative abundance classes, showed that the probability of a high seasonal peak of *Thalia* and *Salpa* was positively correlated with strong winds, whereas the annual increase of temperature and the stronger stratification of the water column coincided with a lower probability of having high salp densities (Ménard et al. 1994).

In the present study temporal fluctuations of *T. democratica* and *S. fusiformis* were investigated in the Bay of Villefranche between 1974 and 1999. For the first time, quantitative data at high resolution (weekly sampling) were analyzed considering records from the “Regent net” time series, where the Regent is a more adapted sampler to quantitatively catch delicate organisms such as salps (Braconnot 1971). The aims of this study were as follows: (1) to extract the main temporal patterns of *T. democratica* and *S. fusiformis*; (2) to identify periods during which *T. democratica* and *S. fusiformis* populations were developing in situ (i.e., near the sampling station without advection) and the environmental conditions that characterized these periods; and (3) to verify whether the interannual changes in salps were related to anomalies of hydroclimatic factors.

The overall goal was to present an overview of salp temporal fluctuations in the northwestern Mediterranean Sea by updating previous findings until the end of the 1990s. During these decades relevant interannual changes of planktonic copepods and jellyfish were signaled in the area, in relation to climate variability (Molinero et al. 2005a). Thus changes in other planktonic groups could be expected.

## Methods

**Study site**—From 1974 to 1999 (with an interruption between 1978 and 1983) zooplankton was sampled at least twice a week at the entrance of the Bay of Villefranche-sur-mer (i.e., Point B, 43°41'10"N, 7°19'00"E) in a coastal area in the proximity of the Villefranche Canyon, characterized by an irregular bathymetry varying between a depth of 80 and 150 m (Fig. 1). In this area surface water circulation is driven by the Ligurian-Provençal current, which flows primarily westward. Some modifications of circulation pattern are usually observed during strong wind events: a surface water circulation toward the open sea and upwelling associated with westerly winds; accumulation of surface waters near the coast with strong easterly winds (Nival and Corre 1976).

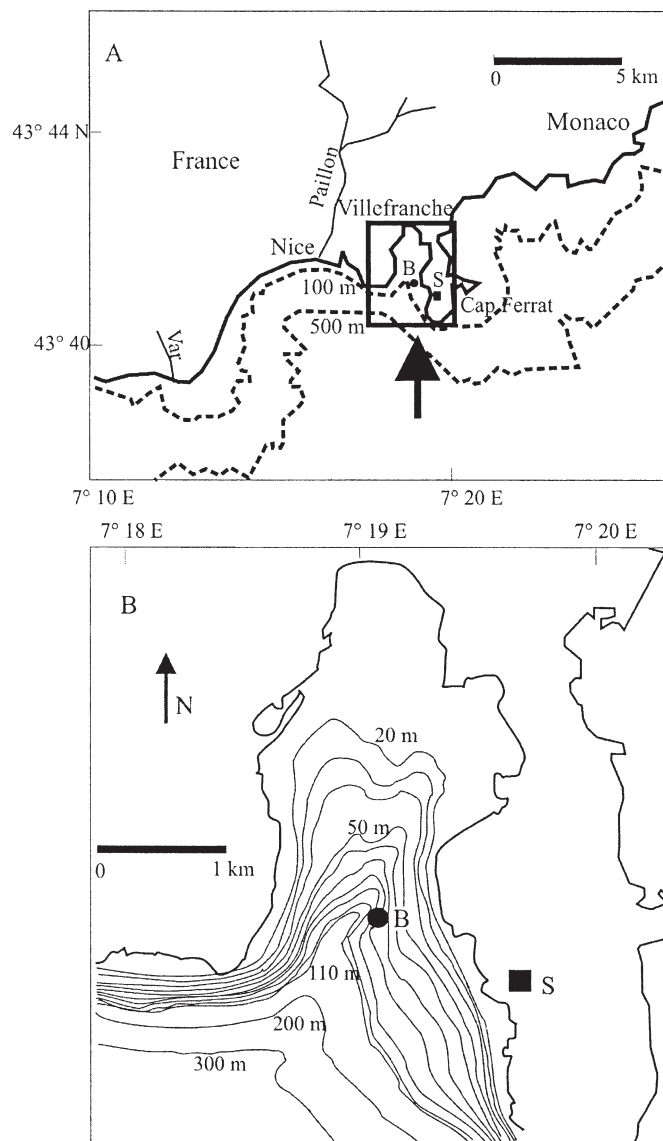


Fig. 1. (A) Map of the Ligurian coast and (B) Bay of Villefranche-sur-mer including the sampling station (Point B) and the meteorological station of Sémaphore du Cap Ferrat (Station S). Bathymetry is also indicated.

**Field sampling and counting of salps**—Sampling was performed by vertically towing a Regent net (680- $\mu$ m mesh size, mouth opening of 1 m diameter, and silk meshes) from a depth of 75 m to the surface.

The numbers of blastozooids and oozoids of *T. democratica* and *S. fusiformis* were counted in each sample or in a fraction in which at least the number of 1,000 individuals was attained. In the present study total individuals (blastozooids and oozoids) were considered.

**Environmental descriptors**—Meteorological records were registered daily at the Sémaphore du Cap Ferrat station, 800 m from the sampling site, at an altitude of 138 m. They included atmospheric pressure (in millibars), air temperature (in °C), wind direction and speed ( $\text{m s}^{-1}$ ), and total precipitation (in millimeters). Daily average light intensity

(irradiance,  $\text{J cm}^{-2}$ ) was also considered (see details in Ménard et al. 1994). Such a descriptor was not used in the analysis because it was highly correlated with air temperature (Pearson  $r = 0.8$ ).

Due to data missing between August 1991 and December 1996, atmospheric pressure and wind recorded at another station at Nice Airport (station Meteo France, 3 m above sea level) were used. Considering 999 daily observations measured at the two meteorological stations contemporaneously, we verified that the pressure records were not significantly different. On the contrary, wind speeds were different, and then missing values at Cap Ferrat were recalculated by using the following regression equation obtained from the 999 records:

$$\text{wind}_{\text{C. Ferrat}} = 0.6946 \times \text{wind}_{\text{Nice Airport}} - 0.1514 \quad (1)$$

An adjusted weekly wind stress index was calculated during the years 1976–1999 according to the method described by Ménard et al. (1994), following the equation:

$$W_{\text{stress}} = \sum_{i=1}^n V_i^2 \quad (2)$$

where  $V_i = \text{wind} > 5 \text{ m s}^{-1}$ , and  $n$  is the number of days in which  $V_i$  was recorded.

Wind direction was not considered in the analysis as the dominant patterns of winds measured in Cap Ferrat and at Station Meteo France because local variations are not always consistent.

Water temperature and salinity were measured weekly at depths of 0, 10, 20, 30, 50, and 75 m with different types of reversing thermometers and induction salinometer (see details in Etienne et al. 1991) and with a Seabird SBE 25 conductivity, temperature, depth (CTD) probe from 1991 onward.

Water density data were not considered because they are highly correlated with temperature (Pearson  $r$  between  $-0.94$  and  $-0.99$ ). No records of temperature and salinity were available from January to December 1994.

The mixed-layer (ML) depth was estimated considering waters within which the density gradient from the surface to the base of the mixing layer was  $\leq 0.05 \text{ kg m}^{-3}$ .

Between September 1991 (Week 33) and November 1999 (Week 47) total chlorophyll  $a$  (Chl  $a$ ) concentration was measured by spectrophotometry from water samples collected with Niskin bottles at depths of 0, 10, 20, 30, 50, and 75 m and filtered onto 47-mm GF/F Whatman fiber filters (for details see the observation service Rade de Villefranche Web site at <http://www.obs-vlfr.fr/Rade/>).

*Numerical analyses*—Notwithstanding the missing values, adequate methods were used to treat all the available information, rather than analyzing descriptors during a shorter period. The different steps of the numerical analyses are summarized in Fig. 2.

Step 1. Extraction of main patterns of *T. democratica* and *S. fusiformis* temporal variability: Two matrices were composed comprising the 188 (January 1974–September

1977) and 832 (January 1984–December 1999) weekly mean abundance ( $\text{ind. } 100 \text{ m}^{-3}$ )  $\log_{10}$  transformed of *T. democratica* and *S. fusiformis*.

Separately in the two periods the principal modes of variability of *T. democratica* and *S. fusiformis* were extracted by the eigen-vector filtering method (EVF; Ibañez and Etienne 1992). The EVF procedure corresponds to a principal component analysis (PCA) calculated on an autocovariance matrix based on the original time series  $X_t$  lagged with itself from 1 week to  $l$  weeks in our case, choosing  $l$  according to the autocorrelation function of  $X_t$ . The first and second axes extracted from PCA represent the main modes of variability, generally the interannual and seasonal cycles, respectively. The filtered variables,  $F_i$ , can be equally estimated by a weighted moving average (WMA) of order  $l - 1$  containing  $2(l - 1) + 1$  terms, on  $X_t$  (Ibañez and Etienne 1992). Before using EVF the  $m$  missing values in the original series ( $m = 9$  in 1974–1977 and  $m = 64$  in 1984–1999) were predicted by an iterative approach (Ibañez and Conversi 2002) that consists of replacing the  $m$  values with the main filtered axes  $F_{i_s}$  (accounting for at least 80% of the total variance) obtained by performing several iterations of EVF, the first of which occurs while retaining the missing data (Licandro et al. 2001). To stop the iterations the sum of square deviations of the predicted values at the iterations  $i$  and  $i - 1$  should be less than a fixed threshold (i.e.,  $1/1,000$ ).

$F_1$  and  $F_2$  were extracted by EVF taking  $l = 26$ , which gives a WMA of 51 successive observations. This lag was chosen considering that plankton species usually have some degree of autocorrelation at the annual scale. The gain function (Box and Jenkins 1976; Ibañez and Etienne 1992), which is the ratio between the amplitudes of the spectrum at several frequencies of the original and the smoothed time series, was utilized to detect the main acting oscillations in the filtered signal.

To identify the periodicities that primarily characterized temporal fluctuations of *T. democratica* and *S. fusiformis*, harmonic analysis (Kendall 1976; Legendre and Legendre 1998) was applied to  $F_1$  and  $F_2$  to estimate the significance of each harmonic being tested according to its associated percentage of variance (Anderson 1971).

The distributions of *T. democratica* and *S. fusiformis* abundance were compared within the 20 yr of study by using the box-and-whiskers plots on the nonzero values of abundance.

Step 2. Calculation of information associated with records of salps and identification of informative periods: In order to identify the periods during which the populations of *T. democratica* and *S. fusiformis* were developing in situ (i.e., when the biological production was causing a greater change in salp abundance than was advection), the following steps were carried out: (1) most relevant peaks and troughs (i.e., turning points;  $\text{TP}_k$  according to that described by Kendall 1976) of both salps were identified among all the 1,020 weekly observations. Peaks were retained when abundance was higher than a superior sill (50 and 25  $\text{ind. } 100 \text{ m}^{-3}$  for *T. democratica* and *S. fusiformis*, respectively), whereas troughs when abundance was lower than an inferior sill (2.7  $\text{ind. } 100 \text{ m}^{-3}$  for *T.*

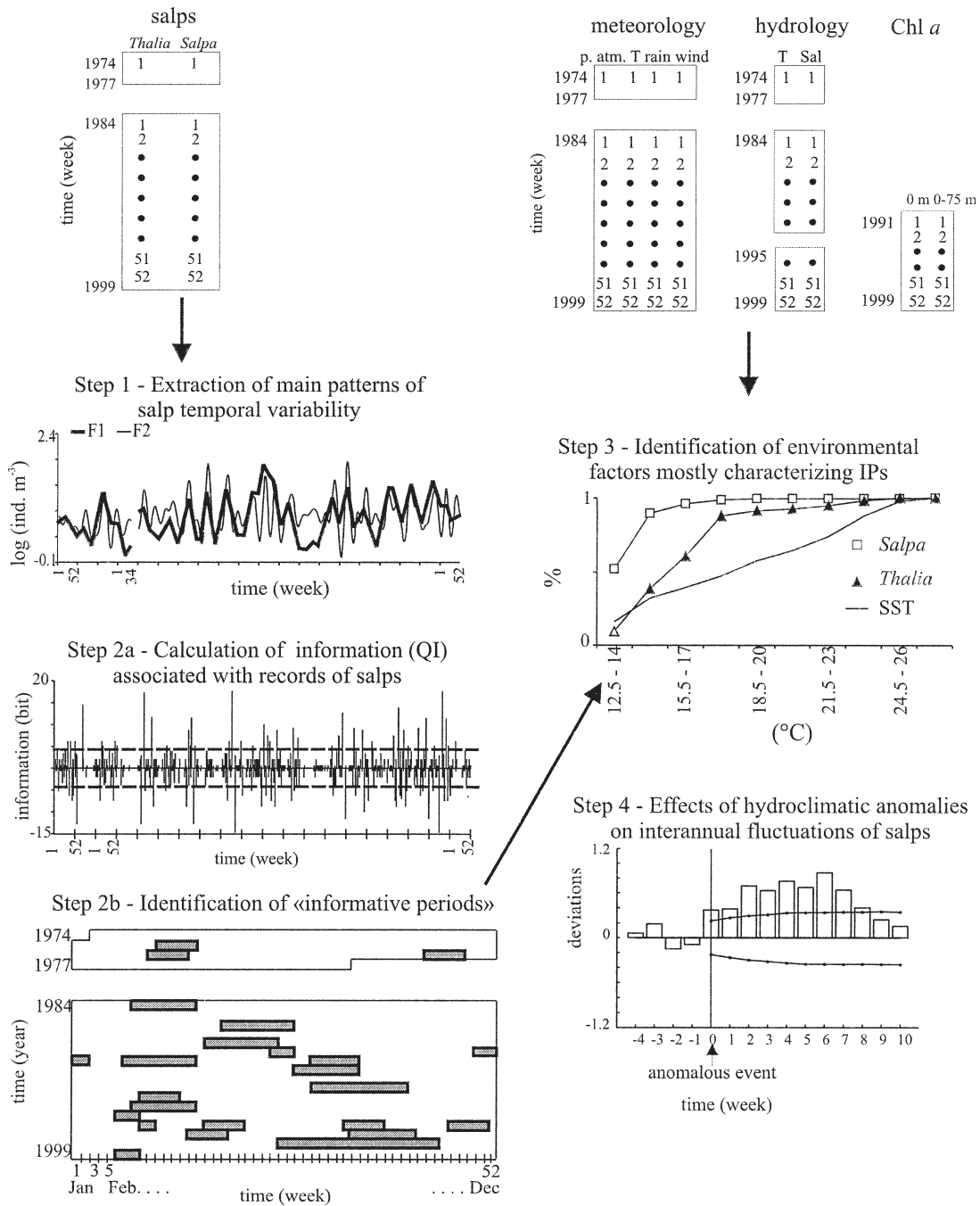


Fig. 2. Summary of the different steps and numerical procedures followed in the present study.

*democratica* and 0.8 ind. 100 m<sup>-3</sup> for *S. fusiformis*). Such superior and inferior thresholds were to the 75th and the 25th percentiles, respectively, of all nonzero records. It is worth mentioning that the greatest densities usually correspond to the peak of salp blastozoids. (2) Quantity of information (QI) associated to each TP<sub>k</sub> was calculated. This step was necessary to distinguish peaks (and troughs) characterized by high QI corresponding to a gradual local change in the salp population from TP<sub>k</sub> associated with low QI, which indicates random events (i.e., the noise [Ibañez 1982]). (3) The n-2 consecutive weeks encompassed between a trough and a following peak having significant QI were

then characterized by a gradual significant increase in salps' abundance. Such weeks (including the peaks with high QI) were thus considered as informative periods (IPs).

QI was estimated by an algorithm based on information theory (Ibañez 1982). Having at least three successive observations the probability  $p(i)$  to find a turning point at the position  $i$  between two peaks (or troughs) separated by  $n$  observations is:

$$p(i) = 2 \times \frac{1}{n_1(i-1)! \times (n_1-i)!} \quad (3)$$

where  $n_i$  = the number of  $n$  unique observations (i.e., a sequence of equal values), including the TP at the boundary.

The QI related to each turning point is derived by Shannon's formula:

$$QI = -\log_2 p(i) \quad (4)$$

According to Eqn. 3 and 4, for a given TP, QI increases as the probability  $p(i)$  of finding that TP randomly decreases. Because information has linear properties, the information of intermediate observations (i.e., the  $n - 2$  observations between a peak and a trough) can be obtained by linear interpolation.

Ibañez (1982) showed that only the TP characterized by  $QI > 4.3$  bits (information of the classical statistical test:  $-\log_2(p(0.05)) = 4.3$  bits) are significant.

Step 3. Identification of environmental factors that primarily characterized the informative periods: Considering the IPs (see Step 2) of *T. democratica* and *S. fusiformis* at the same time, the cumulative distribution of salps' abundance,  $g(t)$ , was plotted against the cumulative distribution of environmental parameters,  $f(t)$  (Perry and Smith 1993). This procedure was used to estimate the proportion of a population that occurred within a range of hydrometeorological conditions with the aim of outlining the environmental preferences (i.e., optima) of each species.

The maximum difference between  $f(t)$  and  $g(t)$  was used to assess the degree of difference between the two cumulative distributions. It can be assumed that if there is no particular association between salps and the environmental factor considered,  $g(t)$  and  $f(t)$  would be almost identical, whereas the greater their difference, the stronger is the association (Perry and Smith 1993). The null hypothesis,  $H_0$  = no particular association between  $g(t)$  and  $f(t)$ , was tested using a Monte Carlo randomization test after 10,000 permutations.

At this step all the meteorological descriptors, including temperature and salinity measurements, were considered during the entire period. Chl *a* values were taken into account for 1991–1999. Environmental values were coded in 10 classes of equal length.

Step 4. Effects of hydroclimatic anomalies on interannual fluctuations of salps: To analyze the influence of extreme environmental events on major interannual fluctuations of *T. democratica* and *S. fusiformis*, Superposed Epoch Analysis (SEA; Haurwitz and Brier 1981) was undertaken. SEA is a nonparametric statistical test that is commonly used when analyzing climatological time series (e.g., Kelly and Sear 1984; Bradley et al. 1987). In marine ecology, SEA has been used to verify the relationship between extreme environmental events and fish recruitment (Prager and Hoening 1989; Fromentin et al. 1998).

Here SEA was used to compare the abundance of salps during and after the weeks of extreme hydrometeorological events with their abundance in weeks previous to the events. To eliminate seasonal variability, standardized weekly values of descriptors were used, and these were obtained by dividing the deviation of each weekly value

from the long-term weekly mean by the long-term weekly standard deviation.

To construct the superposed epoch, first key weeks (KWs) for temperature, salinity, mixing depth (i.e., stability index), atmospheric pressure, wind stress, and rain were defined during the entire period, whereas these were defined for Chl *a* only during the years 1991–1999. Temperatures and salinities at depths of 0, 20, and 50 m were considered because they showed the greatest interannual variability (results not shown). Integrated values between depths of 0 and 75 m were also considered.

KWs were the weeks in which the highest positive or negative environmental anomalies were recorded. Anomalies were calculated for each descriptor with respect to its interannual mean  $\pm (2 \times \text{interannual standard deviation})$  obtained from standardized variables. This threshold was chosen in order to have a consistent number of KWs.

Standardized abundances of *T. democratica* and *S. fusiformis* were then arranged in a matrix  $Y$  where each  $k$  row represented a key event ( $k = 1, 2 \dots K$  total key events) and the  $q$  columns were the weekly densities before, during, and after the event. Considering that two windows of 4 weeks before and 10 weeks after the events were chosen,  $Y$  was composed of a total of 15 columns. A 10-week window after each key event was chosen as the development of salp populations in Villefranche had been observed during 2 months and more (Braconnot 1963; Ménard et al. 1994). Taking the date of each environmental extreme event as Week 0, deviations,  $D_a$ , were calculated by subtracting the 4-week average abundance of salps for the period up to but not including Week 0, to their mean weekly abundance 1, 2 ...  $t = 10$  weeks after the KW.

Then:

$$D_a = \frac{1}{K} \sum_{k=1}^K Y_{ka} - \frac{1}{BK} \sum_{k=1}^K \sum_{b=1}^B Y_{kb} \quad (5)$$

where  $a = 1, 2 \dots A$  total observations after each key event and  $b = 1, 2, \dots B$  observations before each key event.

Statistical significance of  $D_a$  was tested using a Monte Carlo technique performing 10,000 permutations to obtain the empirical distribution.

To verify whether the influence of environmental factors was the same in the different phases of the salps' seasonal cycle, SEA was also performed by separating the environmental extreme events in the following seasons: winter, December–February (Weeks 49–52 and 1–9); spring, March–May (Weeks 10–22); summer, June–August (Weeks 23–35); autumn, September–November (Weeks 36–48).

## Results

*Seasonal and interannual variability of water temperature, salinity, and chlorophyll a concentration*—In the Bay of Villefranche during 1979–1999 the annual variability of water temperature followed a typical pattern that was more pronounced at the surface (Fig. 3A), with the lowest values in February–March (monthly averages  $13.3\text{--}13.4 \pm 0.4^\circ\text{C}$  at the surface) and maximum in August ( $24.3 \pm 0.8^\circ\text{C}$ ). Salinity (Fig. 3B) was uniform throughout the water

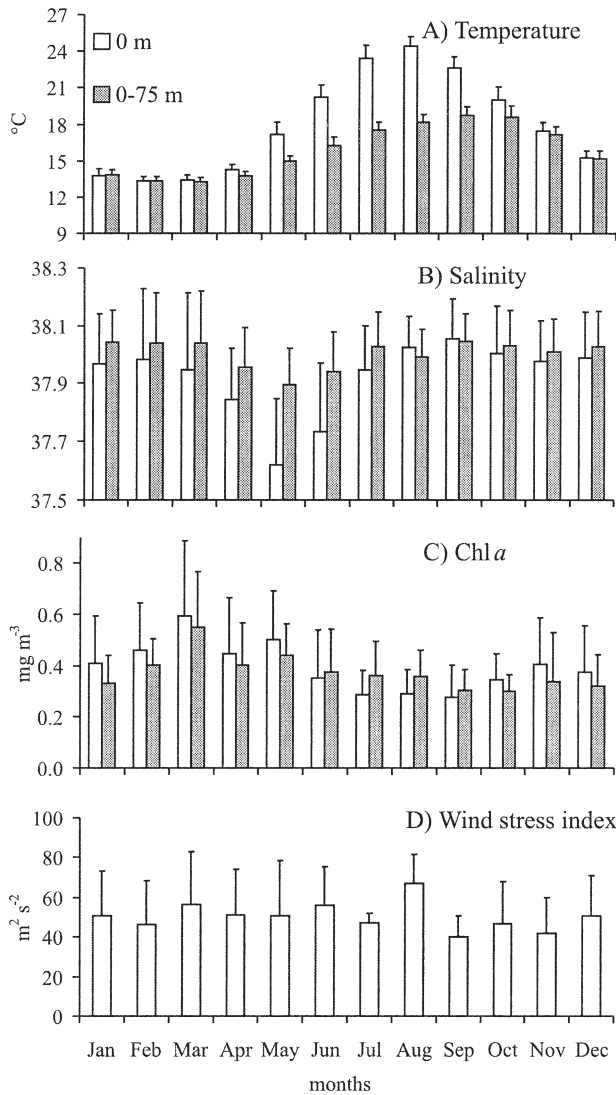


Fig. 3. Point B, 1974–1999, (1991–1999 for Chl *a*). Mean seasonal cycle of (A) temperature, (B) salinity, (C) Chl *a* concentration, and (D) wind stress index indicated by the monthly averages and standard deviations.

column during the mixing season between December and early March (monthly averages  $38.0 \pm 0.2$ ), whereas after stratification, less salty waters were recorded at the surface, reaching their lowest values in May ( $37.6 \pm 0.2$ ), which is usually the most rainy month. Highest salinity values were recorded at the surface in August and September. Similar patterns of temperature and salinity variability were observed in offshore waters (Marty et al. 2002).

Generally, Chl *a* showed maximum values in March ( $0.6 \pm 0.3 \text{ mg m}^{-3}$ ) and the lowest values at the surface in summer (Fig. 3C). A slight peak occurred in October and November. The average values during winter were  $0.41 \pm 0.19 \text{ mg m}^{-3}$  and  $0.35 \pm 0.12 \text{ mg m}^{-3}$  at the surface and in the 0–75 m layer, respectively.

Index of wind stress (Fig. 3D) reached maximum values in March ( $56.4 \pm 26.4 \text{ m}^2 \text{ s}^{-2}$ ) and August ( $66.9 \pm 14.6 \text{ m}^2 \text{ s}^{-2}$ ), whereas the lowest values were recorded

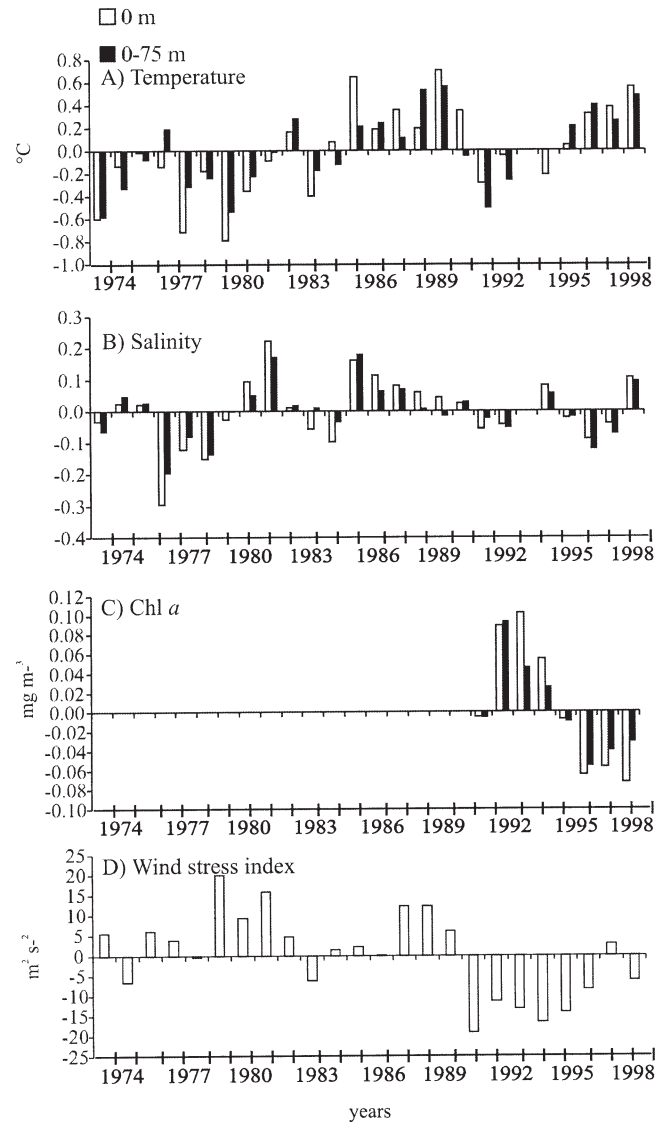


Fig. 4. Point B, 1974–1999 (1991–1999 for Chl *a*). Yearly anomalies in (A) temperature, (B) salinity, (C) Chl *a* concentration, and (D) wind stress index. Positive and negative records signify values above and below the long-term mean, respectively.

in July ( $47.0 \pm 5.0 \text{ m}^2 \text{ s}^{-2}$ ) and September ( $40.1 \pm 10.5 \text{ m}^2 \text{ s}^{-2}$ ).

The long-term variability in water temperature showed that in 1983–1991 (excluding 1984) and 1996–1999, higher temperatures were observed both at the surface and in the 0–75 m layer (Fig. 4A). The greatest positive anomalies (up to  $3.6^\circ\text{C}$ ) were observed in winter–spring 1990, whereas the lowest values were recorded in the winters of 1978 and 1980. High salinities were found in 1981–1982, 1986–1990, 1995, and 1999 (Fig. 4B), the interannual maxima values being observed in winter–early spring 1982 and 1986. The lowest salinities were recorded in springs 1977–1979. The interannual variability of Chl *a* concentration (Fig. 4C) indicated that with respect to the overall average ( $0.39 \pm 0.2$  and  $0.37 \pm 0.2$  for 0 m and 0–75 m layers, respectively) the years 1993–1995 were characterized by higher Chl *a* abundance. The overall yearly mean of wind stress index

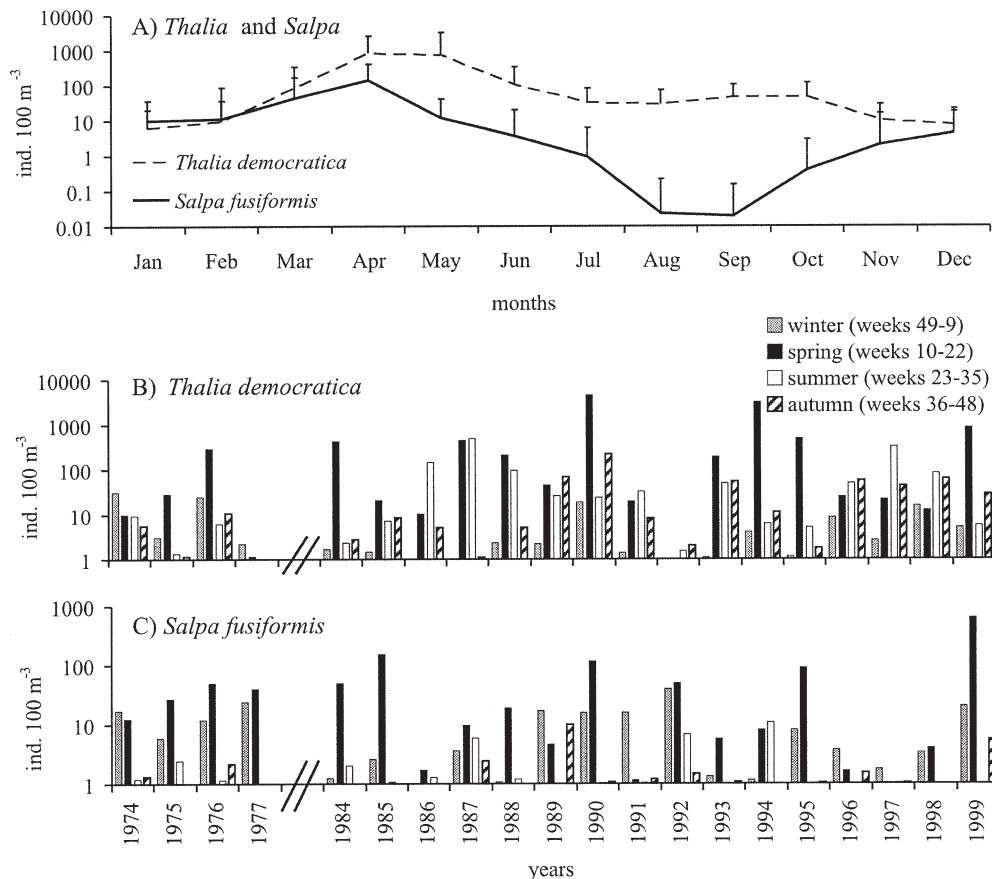


Fig. 5. Point B, 1974–1999. Interyearly monthly average (log [ind. 100 m<sup>-3</sup>]) of (A) *T. democratica* and *S. fusiformis*. Mean abundance (ind. 100 m<sup>-3</sup>) by season of (B) *T. democratica* and (C) *S. fusiformis* are also shown. Note that scales are different.

is  $49.5 \pm 10.5 \text{ m s}^{-2}$ . The highest values of wind stress characterized the years 1981–1984, 1989–1991, and 1998, whereas the greatest negative anomalies were observed in 1992–1997 (Fig. 4D).

**Temporal variability of *T. democratica* and *S. fusiformis***—In the Bay of Villefranche both *T. democratica* and *S. fusiformis* were usually more abundant in March–May (Fig. 5A), *Thalialia* being on average one order of magnitude greater than *Salpa* (the spring average, over all years, was 542 ind. 100 m<sup>-3</sup> and 33 ind. 100 m<sup>-3</sup> for *Thalialia* and *Salpa*, respectively). The period of annual maximum and the amplitude of the seasonal peak may vary greatly from one year to another (Fig. 5B,C).

*T. democratica* showed a significantly low abundance in 1974–1975, 1984, and 1995, whereas it was nearly absent in 1977 (records available until Week 35) and 1992 (Fig. 6A). High abundance (yearly median >15 ind. 100 m<sup>-3</sup>) characterized the years 1987, 1990, and 1996–1998 but only in 1987 were high densities observed for a period of several weeks (yearly 75th percentile >100 ind. 100 m<sup>-3</sup>). The greatest outbreaks of *T. democratica* were recorded in 1990 (23,313 ind. 100 m<sup>-3</sup>, weekly average) and 1994

(23,277 ind. 100 m<sup>-3</sup>, weekly average), and to a minor extent in 1999 (3,363 ind. 100 m<sup>-3</sup>, weekly average).

*S. fusiformis* was abundant during several weeks, its annual median being >15 ind. 100 m<sup>-3</sup> only in 1977 (data until Week 35), 1990, and 1999, when the greatest frequency of high densities and interannual maximum (up to 1,941 ind. 100 m<sup>-3</sup>, weekly average) were observed. A significantly lower abundance distribution was registered in 1986, 1993, and 1997 (Fig. 6B).

The filtered variables  $F_1$  and  $F_2$  represent the principal modes of variability of *T. democratica* and *S. fusiformis* between 1974 and 1999 (Fig. 7). Results of harmonic analysis on the first and second filtered variables in the period 1984–1999 (Fig. 7A; Table 1) indicate for *Thalialia* a main fluctuation of 8 yr with its harmonic of 4 yr (respectively, 22% and 19% of variance associated with  $F_1$ ), whereas the  $F_2$  represented primarily the seasonal cycle (i.e., the harmonic of 52 and 26 weeks). On the contrary, for *S. fusiformis* the annual cycle corresponds to the harmonic with the highest variance associated with both  $F_1$  and  $F_2$  (Fig. 7B; Table 1). The dominant seasonal variability of the latter species was also confirmed by the results of harmonic analysis during 1974–1977 (not shown) and by

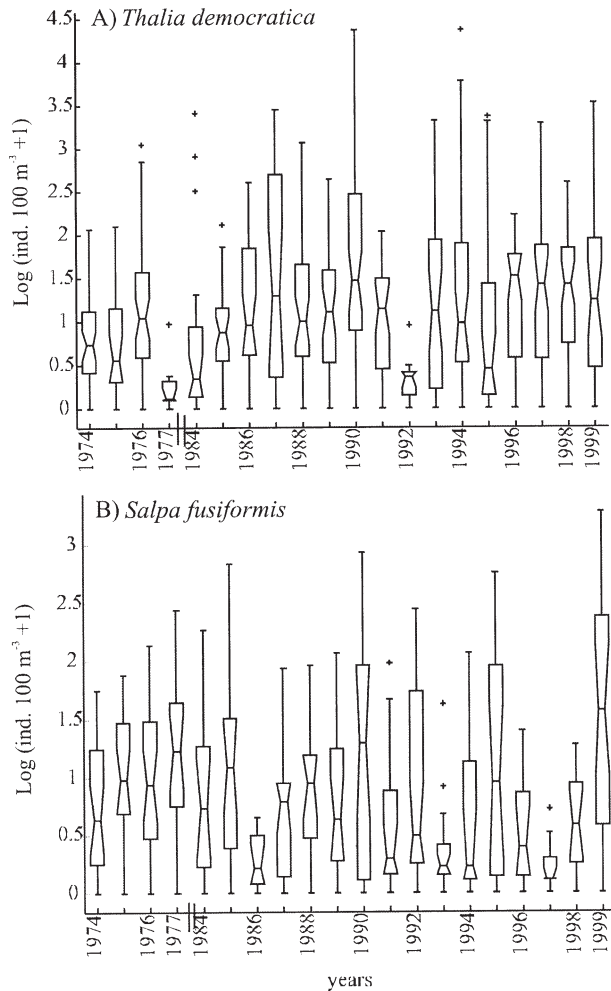


Fig. 6. Box-and-whisker plots describing the interyearly distributions of (A) *T. democratica* and (B) *S. fusiformis*. The horizontal lines across the boxes correspond to the lower quartile, median, and upper quartile values from the bottom to the top, respectively. The whiskers are lines extending from each end of the box toward maximum and minimum values. The notches in the box show the 95% confidence interval of the median. Outlier values are indicated by the cross.

the high correlation between the first two filtered variables ( $R_{F1 - F2} = 0.69$  and  $0.76$  in 1974–1977 and in 1984–1999, respectively).

**Identification of periods of *Thalia* and *Salpa* population development in situ**—Between 1974 and 1999 more turning points of *T. democratica* (170 peaks and 261 troughs; Fig. 8A) were recorded compared with those of *S. fusiformis* (95 peaks and 203 troughs; Fig. 8B).

Only a few TPs of *S. fusiformis* (14% of peaks and 8% of troughs) were associated with a significant QI (Fig. 8B), suggesting that the occurrence of such species at Point B was often related to episodic (peaks and low information) or random events (troughs and low information).

The IPs, indicating an alternation of *T. democratica* generations in situ (Fig. 9A), were generally observed between mid-March and July (Weeks 10–28), excluding 1991 when the IP was recorded after Week 28. Informative

periods of *T. democratica* often encompassed two peaks characterized by a significant QI, indicating that the population increased, slightly diminished, and then increased again. In 1976, 1990, 1993, and 1996–1998 one or more generations of population were also observed in autumn (Weeks 36–51). No informative periods were found for *Thalia* in 1974, 1977, 1985, 1987, and 1992 (Fig. 9A). Informative periods of *T. democratica* varied between a minimum of two (1996) and a maximum of nine (1991, 1993–1994, and 1998) consecutive weeks. In 1990 and 1996–1998 several generations of *Thalia* population were observed.

The *S. fusiformis* population was developing in situ in 1974, 1977, 1984–1985, 1987, 1992, 1995–1996, and 1999 (Fig. 9B). IPs of this species were observed in December to mid-May (Weeks 45–18), excluding 1987 and 1992 when they were recorded after Week 21, in late spring–summer (Fig. 9B). The informative periods of *S. fusiformis* varied between 2 (1985 and 1987) and 11 weeks (1977). Excluding 1999, no more than two informative periods were observed per year.

**Environmental optima for *T. democratica* and *S. fusiformis***—Water temperature was the only environmental factor that significantly influenced the distribution of salps during the IPs ( $p < 0.001$ ; Fig. 10A,B). *T. democratica* was found within a wide range of temperature values, but the population increase was significantly associated with temperature between  $17.0$ – $18.5^{\circ}\text{C}$  at the surface (Fig. 10A) and  $14.9$ – $15.7^{\circ}\text{C}$  when considering integrated values between depths of 0 and 75 m (Fig. 10B). On the contrary, the *S. fusiformis* increase was significantly related to sea surface temperature (SST) values of  $14$ – $15.5^{\circ}\text{C}$ , 90% of the developing population being observed with surface temperature  $\leq 15.5^{\circ}\text{C}$  (Fig. 10A) and integrated temperature  $< 14.9^{\circ}\text{C}$  (Fig. 10B).

*Thalia* and *Salpa* also showed quite complementary preferences when considering other environmental factors, despite such descriptors not being significantly related to the distributions of salps during the IPs. Thus, the development of *T. democratica* population was characterized primarily by lower salinities than *S. fusiformis* (Fig. 10C): 86% of the increasing population of *Thalia* was associated with values between 37.68 and 38.04, whereas 54% of the *Salpa* population was observed with salinity  $> 38.04$  and only 9% with values  $< 37.95$ .

The developing population of *T. democratica* was associated with higher Chl *a* concentration at the surface ( $> 0.7$  up to  $0.92 \text{ mg m}^{-3}$ ) with respect to *S. fusiformis* (Fig. 10D); almost 100% of the population of the latter species was found with Chl *a* values  $\leq 0.7 \text{ mg m}^{-3}$ .

The cumulative distribution of *T. democratica* abundance during informative periods showed a maximal slope corresponding with lower wind conditions (average speed per week,  $\leq 2.8 \text{ m s}^{-1}$ ; Fig. 10E) and more stratified waters (mixing depth,  $\leq 12 \text{ m}$ ; Fig. 10F) than *S. fusiformis*.

**Salps anomalies related to extreme events of environmental factors**—Results of SEA showed that between 1974 and 1999 the greatest positive anomalies of water temperature

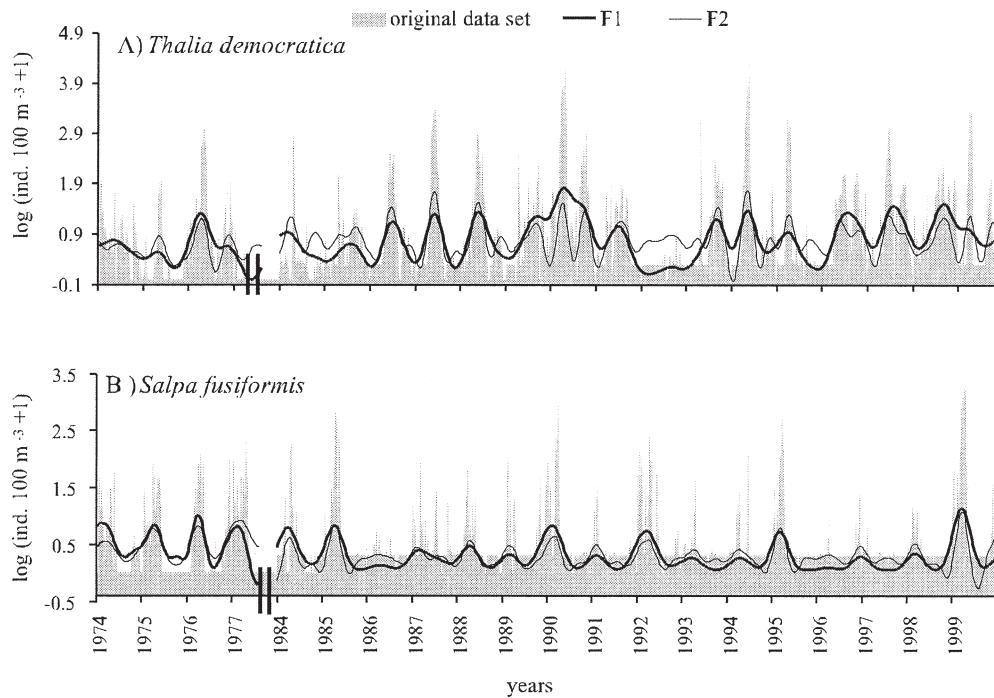


Fig. 7. Point B, 1974–1999. Log-transformed abundance and filtered variables  $F_1$  and  $F_2$  obtained by EVF for (A) *T. democratica* and (B) *S. fusiformis*.

at depths of 0, 20, and 50 m were significantly related to positive anomalies of *T. democratica* (Fig. 11A,C,E), the highest abundance being associated with temperatures close to *Thalia* optimum range (Table 2). The increase in *Thalia* reached its maximum 6 weeks after the anomaly (i.e., after the KW). When considering anomalies of temperature at depths of 50 and 20 m, a significant development of the population was already observed after 1 week and 4 weeks, respectively (Fig. 11C,E). On the contrary, negative anomalies of water temperature at depths of 0 and 20 m were significantly related to a “lower than usual” abundance of *T. democratica* recorded since the first week after the KW (Fig. 11B,D). The increment of *Thalia* in relation to extreme events of temperature changed in the different seasons. Maximum augmentation was observed after 6–9 weeks in winter and spring (Fig. 12A,B) and after only 2 weeks in summer (Fig. 12C). No significant relationship was observed in autumn (Fig. 12D).

It is worth mentioning that KWs considered in SEA included most of the weeks between January and May 1990

(Table 2), when the highest temperature anomalies at all depths were recorded and the greatest interannual maxima of *T. democratica* were observed.

The increase in *T. democratica* abundance was also significantly related to negative anomalies of salinity during spring with a lag of 1 week (Fig. 12E; Table 2) and to the highest Chl *a* concentration in summer with a lag of 5–6 weeks (Fig. 12F; Table 2).

No response to extreme events of environmental descriptors was observed for *S. fusiformis*. Only during summer were positive anomalies of *Salpa* related to the increase in water mixing with a lag of 6 weeks (results not shown).

## Discussion

This study is the first in the northwestern Mediterranean Sea and the second worldwide (after the study by Lavaniegos and Ohman 2003) concerning a long-term quantitative study of salps, whereas Ménard et al. (1994)

Table 1. Point B, 1984–1999. Results of harmonic analysis on  $F_1$  and  $F_2$  extracted by EVF on weekly abundance of *T. democratica* and *S. fusiformis*. Significant harmonics of  $F_1$  and  $F_2$  representing together  $\geq 50\%$  of the total variance are shown. Periodicities with the highest variance associated are in bold.

	$F_1$		$F_2$	
	Significant harmonics (weeks)	Associated variance (%)	Significant harmonics (weeks)	Associated variance (%)
<i>T. democratica</i>	<b>416</b> , 208, 52, 166.4	<b>22</b> , 19, 16, 12	<b>52</b> , 26, 30.8, 43.8, 27.7, 36.2	<b>21</b> , 10, 6.3, 6.2, 6.1, 5
<i>S. fusiformis</i>	<b>52</b> , 118.9, 59.4, 416, 277.3	<b>32</b> , 13, 8.9, 8.5, 7	<b>52</b> , 39.6, 59.4	<b>41</b> , 7, 6

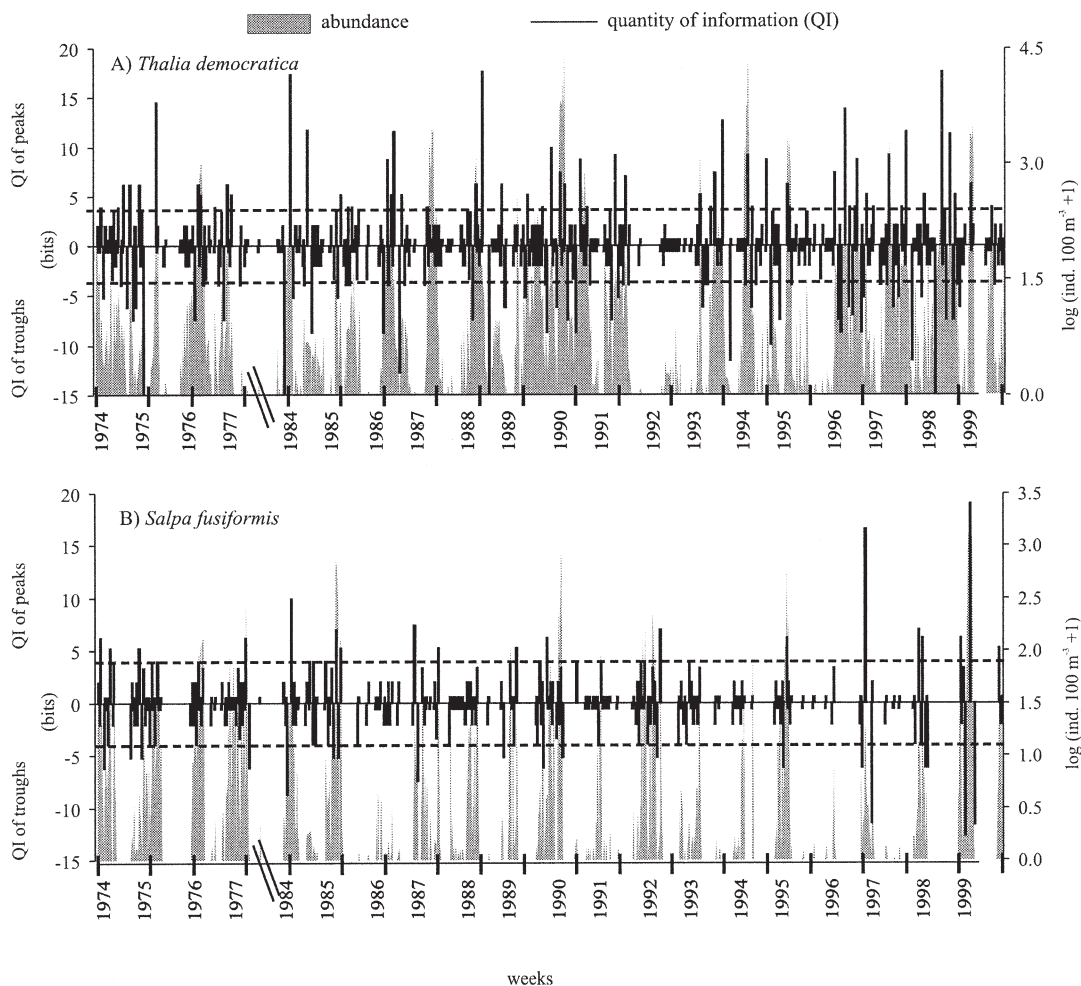


Fig. 8. Point B, 1974–1999. QI associated with weekly average abundance of (A) *T. democratica* and (B) *S. fusiformis*. Positive and negative bits indicate the quantity of information associated with peaks and troughs, respectively. Original data in gray (note scales are different). Two-tailed 5% significant levels are indicated by the dashed lines.

utilized semiquantitative abundance (i.e., class of abundance) from samples collected in the Bay of Villefranche with the Juday-Bogorov net (330- $\mu\text{m}$  mesh size, nylon net).

According to the study by Braconnot (1971), the Regent net is better adapted than the Juday-Bogorov net for catching soft-bodied organisms forming chains due to (1) a silk mesh that prevents damage to gelatinous plankton and maintains high filtration efficiency, (2) the size of the mesh, and (3) the high volume of water filtered with an estimated mean filtered volume of 60  $\text{m}^3$  per haul. The efficiency of the Regent net in quantitatively catching both solitary and aggregate forms of salps allows the data set to be utilized for studying the population dynamics of *T. democratica* and *S. fusiformis*.

Computing the QI associated with salp peaks showed that high densities of both species, particularly of *S. fusiformis* at Point B were frequently random events, probably due to lateral advection from surrounding areas. The latter hypothesis is supported by previous studies that found high abundance of both *S. fusiformis* and *T. democratica* aggregate and solitary zooids in offshore

waters scattered around a distance of 24–53 km from the coast (Braconnot 1971; Nival et al. 1990; Laval et al. 1992). In contrast, peaks associated with a significant quantity of information indicated a gradual and significant increase in salps abundance. Thus weeks after a trough and before a peak with significant QI, for us, informative periods could be considered as the periods in which the increase in salp abundance was primarily due to the development of the population in situ, rather than to advection. From 1974 to 1999 *T. democratica* and *S. fusiformis* populations were usually developing in situ in alternate years, informative periods of *S. fusiformis* generally occurring between late autumn and spring, while those of *T. democratica* occurred in late winter–early summer. The duration of informative periods was generally 2–4 weeks for both species, which considering growth rates and generation times of the two species, may correspond to a few to several generations of population, including solitary and aggregate stages (Braconnot 1963; Heron and Benham 1984; Braconnot et al. 1988). In agreement with previous observations that indicated high densities of salps occurring during several

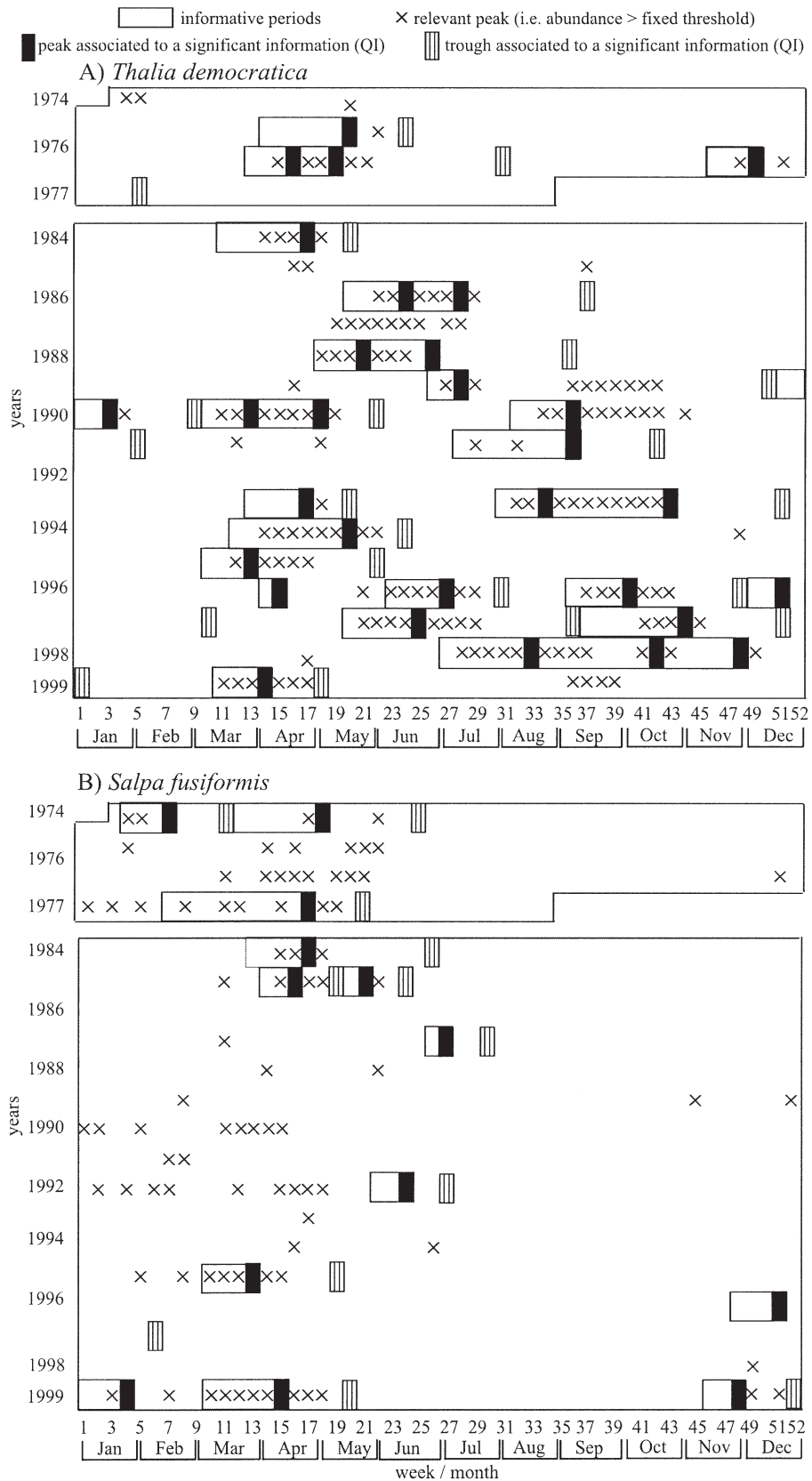


Fig. 9. Point B, 1974–1999. Informative periods (i.e., weeks during which salp populations were developing in situ) of (A) *T. democratica* and (B) *S. fusiformis*. Each IP corresponds to consecutive weeks after a trough and preceding a peak characterized by a significant quantity of information (see text for details).

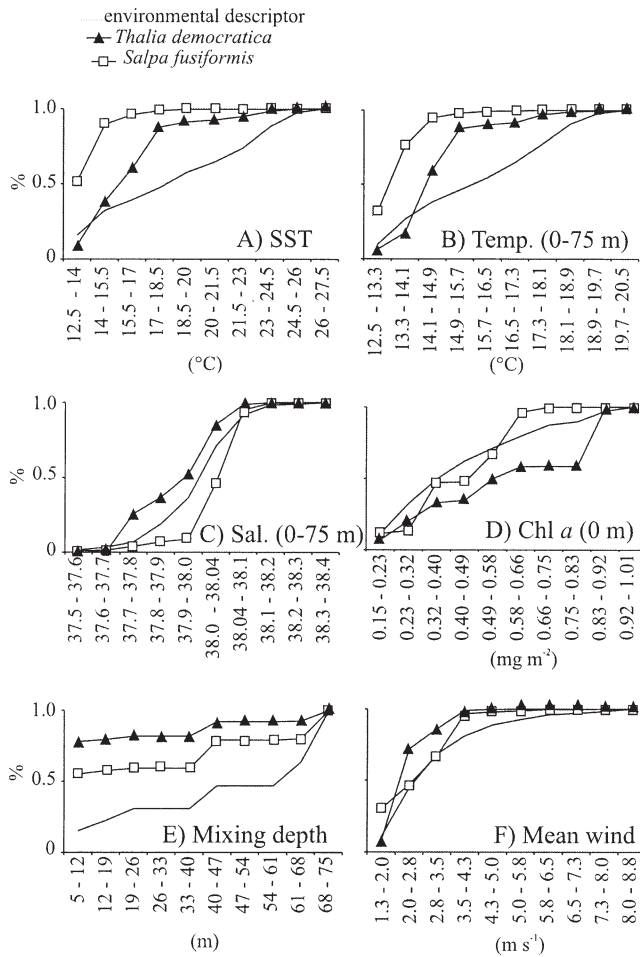


Fig. 10. Point B, 1974–1999 (1991–1999 for Chl *a*). Cumulative frequency distributions of *T. democratica* and *S. fusiformis* during informative periods (see text for details) in relation to (A) temperature at surface, (B) integrated temperature, (C) integrated salinity, (D) Chl *a* at surface, (E) mixing depth, and (F) average wind speed.

months (Berner 1967; Braconnot 1971), informative periods in some years lasted up to 9–11 consecutive weeks.

The analysis of the environmental parameters associated with the informative periods indicated that within the descriptors we considered, water temperature was the only one significantly linked with an increase in salps. Reaching a defined range of temperature, which was different for *Thalia* than it was for *Salpa*, was an important triggering mechanism for the development of their populations in situ. Temperature optima were complementary for the two species. The *T. democratica* population was associated with temperatures >15.5°C at the surface and >14.9°C when considering integrated values between depths of 0 and 75 m, while the *S. fusiformis* population was associated with lower temperatures. Such results are consistent with the known biogeography of the two salps. Although their distributions widely overlap, different thermal preferences are evident when considering that *T. democratica* is distributed in warm-temperate waters between 46°N and 40°S (Paffenhöfer et al. 1995; Esnal and Daponte 1999;

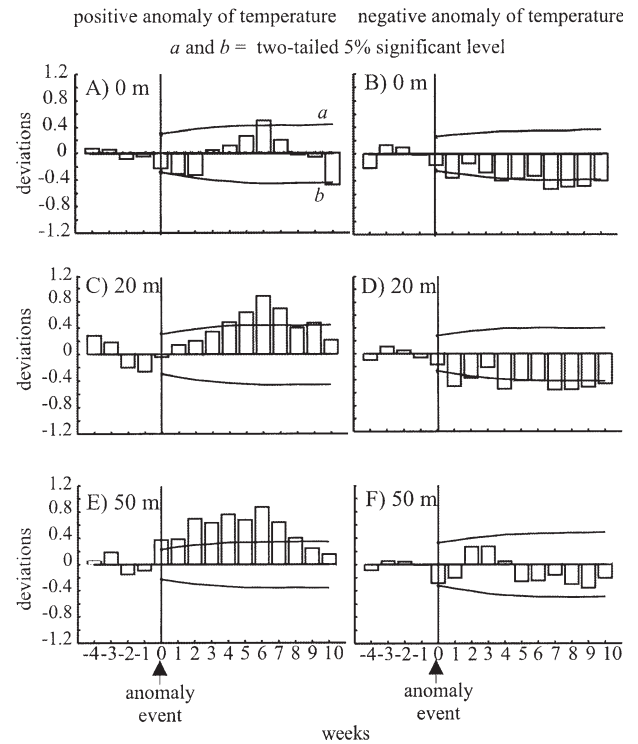


Fig. 11. Point B, 1974–1999. SEA of standardized weekly abundance (each weekly abundance was divided by the long-term [20 years] standard deviation after subtraction of the long-term weekly mean) of *T. democratica*. Deviations from the mean abundance of the previous period (i.e., 4 weeks before the event) were calculated at 1, 2 ... 10 weeks after the positive or negative anomaly event of water temperature at depths of (A and B) 0 m, (C and D) 20 m, and (E and F) 50 m. Two-tailed 5% significant levels (i.e., *a* and *b*) based on Monte Carlo simulations are indicated. Deviations >*a* and <*b* indicate respectively abundance significantly higher and lower than in the period before the anomaly.

Lavaniegos and Ohman 2003), while *S. fusiformis* is common from 65°N to 65°S (Braconnot 1963 and references therein; Esnal and Daponte 1999; Lavaniegos and Ohman 2003) and tolerates colder temperatures than other salps (Braconnot 1971). Braconnot (1971) showed that the annual peak of *T. democratica* in the Bay of Villefranche ended abruptly when a disruption of temperature increase was observed in the spring of 1960, 1963, and 1965; Berner (1957) found that in the Pacific Ocean the appearance of *T. democratica* was related only to higher temperatures. In contrast, Braconnot (1971) indicated 16.5°C SST as the upper limit of the optimum range for *S. fusiformis* in the northwestern Mediterranean Sea, higher temperatures generally coinciding with a sudden decrease in the population. This previous observation is confirmed by the present study, a value of temperature close to 16.5°C being found as the upper limit of the optimum range for *S. fusiformis*.

Although they were not significantly associated with the increase in salps, different optimum ranges of salinity, Chl *a* concentration, and stability conditions of the water column were found during the informative periods of the

Table 2. Point B, 1974–1999. Most relevant anomaly events (i.e., KEs) selected for the study. Values for temperature, salinity, and Chl *a* concentration during KE are indicated. *T. democratica* maximum abundance after each KE are also reported (in bold abundance >1,000 ind. 100 m<sup>-3</sup>). Long-term weekly median and weekly 75th percentiles are given as reference abundance.

Date (week, year)	Selected KEs				<i>T. democratica</i> abundance after KE		Weekly overall statistics	
	0–75 m	0 m	20 m	50 m	Max (ind. 100 m <sup>-3</sup> )	Week of max.	Median (ind. 100 m <sup>-3</sup> )	75 <sup>th</sup> percentile (ind. 100 m <sup>-3</sup> )
<b>Positive anomalies of water temperature (°C)</b>								
22, 1986	16.0	23.1			402	24	8	42
31, 1986	18.9			16.8	32	31	1	19
17, 1988	14.3	16.1			<b>1,150</b>	21	10	85
24, 1988	17.4			16.6	335	26	6	30
21–22, 1989	17.2–17.7			17.2–17.7	26	26	6	30
27–28, 1989	17.3–18.6			17.3–18.6	110	28	6	61
36, 1989	21.5			22.3	214	39	3	48
3–12, 1990	14.1–14.6	14.3–15.5	14.1–14.5	14.1–15.3	<b>11,063</b>	16	19	445
18–19, 1990	15.4–15.7	17.5–18.3			<b>23,313</b>	18	17	177
24, 1996	16.5	23.4			147	27	7	50
33, 1996	19.4			17.9	164	40	3	36
19, 1997	15.3			15.0	173	21	10	85
23, 25, 1997	17.5–17.6			16.2–17.0	<b>1,926</b>	25	2	32
38, 1997	20.45				87	41	7	56
10, 1998	14.8–15.3		14.8–15.3	14.9–15.1	29	3	0	1
29, 1998	18.8			16.1	397	33	3	9
34, 1999	20.08				98	38	4	54
<b>Negative anomalies of water salinities in spring</b>								
14–16, 1974	37.7–37.8	37.7	37.6–37.8	37.7–37.8	70	20	10	80
18, 1975	37.7	37.2			108	20	10	80
10–13, 1975	38.0–38.1	36.5–37.3	37.4–37.6	37.6–37.8	<b>1,106</b>	19	3	107
22, 1977	37.6	37.3	37.5		12	22	10	61
19–21, 1985	37.8	35.2–36.4			15	22	10	61
18–19, 1987	37.7			37.7	<b>1,774</b>	20	10	80
21–22, 1987	37.7			37.7	<b>2,772</b>	22	10	61
17, 1993	37.8			38.0	<b>2,081</b>	17	37	517
<b>Positive anomalies of Chl <i>a</i> in summer (mg m<sup>-3</sup>)</b>								
32, 1993				0.85	305	34	3	20
31, 35 1996				0.3–0.4	92	38	4	54
24–26 1998				0.8–0.9	397	33	3	9

two species. *T. democratica* was associated with lower salinities (<38.0) and higher surface Chl *a* concentration (>0.7 up to 1.0 mg m<sup>-3</sup>) as well as with more stratified waters and low wind conditions than *S. fusiformis*. Such differences are probably related to the different seasons in which the informative periods of the two species were recorded. In the Bay of Villefranche the weeks between December and early March (primarily associated with *S. fusiformis*) were usually characterized by mixed waters, high salinity, and low Chl *a* concentration. On the contrary, when the stratification began in late March–April (a period characterized primarily by *T. democratica*), salinity was lower and high Chl *a* values were found in relation to the spring phytoplankton bloom. However, a direct influence of the above descriptors on the dynamic of the population of *T. democratica* and *S. fusiformis* should be further verified. For instance, it could be worthwhile to compare the alternation of *T. democratica* and *S. fusiformis* with the changes in composition of the phytoplankton populations, considering that some differences in salp species-specific

retention efficiency has been hypothesized (Harbison and MacAlister 1979; Caron et al. 1989; Kremer and Madin 1992). Recent feeding experiments measuring salps retention efficiency on different taxon-specific cell sizes in situ have shown that *T. democratica* feeds with maximum efficiency on diatoms and ciliates between 20 and 50 μm (Vargas and Madin 2004). Thus it is not surprising that in the northwestern Mediterranean Sea such species achieved the highest abundance associated with the highest values of Chl *a* recorded during the spring bloom, which is usually characterized by larger cells such as diatoms (Bustillos-Guzman et al. 1995; Gómez and Gorsky 2003). In general, *T. democratica*, which has a higher clearance rate than *S. fusiformis* (Madin and Deibel 1998), is more frequent in coastal waters where the highest abundance of large diatoms is recorded whereas *S. fusiformis* is abundant in offshore oligotrophic waters usually dominated by small phytoplankton (Laval et al. 1992).

The comparison of the environmental optima for *T. democratica* and *S. fusiformis* found in the present study

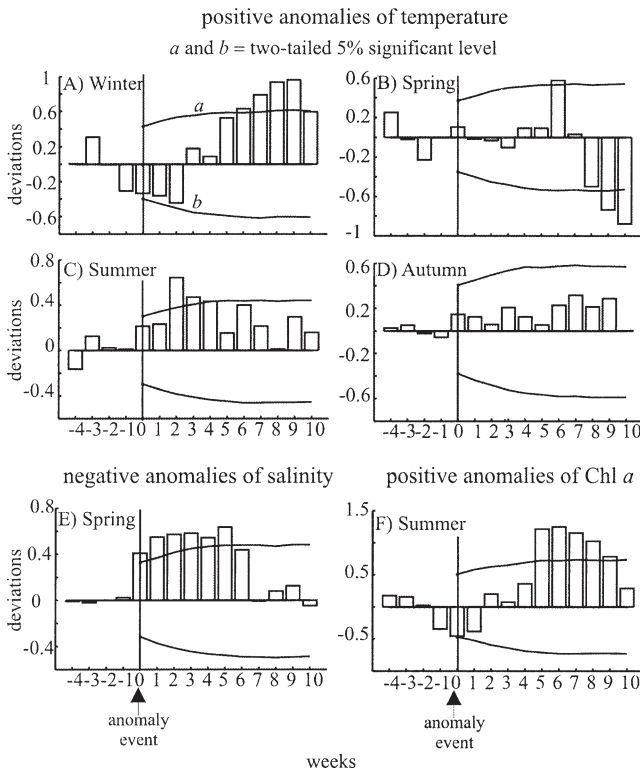


Fig. 12. Point B, 1974–1999. Superposed epoch analyses of standardized weekly abundance of *T. democratica* for (A–D) positive anomalies of water temperature in different seasons, (E) negative anomalies of water salinity in spring, and (F) positive anomalies of Chl *a* in summer. The data are expressed as deviations from abundance defined by the 4-week average for the period up to but not including the anomaly events (Week 0). See legend of Fig. 11 for further details.

with the results of Menard et al. (1994) stresses the importance of water temperature as a key factor regulating the annual peak of salps in the northwestern Mediterranean Sea. On the other hand, the significant influence of strong winds on salp abundance outlined by Menard et al. (1994) was not confirmed by our analysis. Considering that our informative periods do not include the peaks of *T. democratica* and *S. fusiformis* associated with nonsignificant information (i.e., the random events), one might think that the result of the previous study was due to the influence of strong wind primarily in relation to inputs of salps from offshore waters. In the northwestern Mediterranean Sea strong winds significantly influence the spatial distribution of salps (Ménard et al. 1994) and of plankton in general (Molinero et al. 2005b) having an opposite effect according to their direction: strong easterly winds determining the accumulation of surface water near the coast while strong westerly winds increase the offshore transport.

The long-term data set allowed us to distinguish the cycles representing a regular periodicity from the unusual changes (i.e., the “discontinuities” in the time series [Legendre and Legendre 1998]). Our analysis of the weekly abundance of *T. democratica* and *S. fusiformis* between 1974 and 1999 indicated a well-established seasonal cycle

for both species with an annual maximum generally in spring. Results of EVF and harmonic analysis in 1984–1999 showed that *T. democratica*, which was usually more abundant than *S. fusiformis*, was characterized by a significant interannual variability having a main periodicity of 8 years and a minor oscillation of 4 years. In contrast, only annual fluctuation was significant for *Salpa*.

Salps, also due to their capacity for fast development in favorable environmental conditions, sometimes reach very high abundance levels, forming big swarms that extend for several kilometers. Considering that almost no information was available until now about the effective causes related to such outbreak events (CIESM 2001), the relationship between anomalies of hydrometeorological factors and the unusual abundance of salps found by the present study may give new insights into the triggering mechanisms related to such tunicate outbreaks. In particular, results of SEA outlined the importance of water temperature anomalies in relation to the major fluctuations of *T. democratica*. During the 20 years of monitoring, negative temperature anomalies were associated with a significant decrease in the *T. democratica* population, while positive anomalies were related to the greatest abundance, including the exceptional outbreak in 1990. *T. democratica* peaked 2–9 weeks after the positive anomalies of temperature, the time lag being shorter in summer than in late winter–spring. It is worth mentioning that at a temperature of 14°C the asexual solitary oozoid of *T. democratica* needs 1 week to reach maturity and 7–9 days to release the first chain of sexual blastozoids, then releasing the second and the following chains each 2 d (Braconnot 1963). Increasing temperatures of up to around 20°C have been linked to a shortening of such a life cycle. One should then conclude that an increase in temperature within the optimum range for *T. democratica* may significantly reduce its generation time, allowing the *Thalia* population to reach very high abundance more rapidly. However, temperature anomalies could also be related to some changes in the pelagic system of which *T. democratica* may take advantage. For instance, the assemblages of phytoplankton could be different in relation to temperature oscillations. In the northwestern Mediterranean Sea periods of high temperature and low wind are usually associated with high water stratification and dominance of the small phytoplankton fraction, whereas windy years with low temperatures are characterized by stronger blooms of diatoms (Gómez and Gorsky 2003). Recently, the study of phytoplankton dynamics in both coastal and offshore waters (Gómez and Gorsky 2003; Marty et al. 2002) outlined in the northwestern Mediterranean Sea an apparent shift toward a more regeneration-dominated production system that seems to be extended to other coastal areas in the western Mediterranean (Ribera d’Alcalà et al. 2004). In this framework the high abundance of picoflagellates and nanoflagellates observed in winter–early spring 1990 and the low microphytoplankton bloom recorded in late spring the same year (Ferrier-Pagès and Rassoulzadegan 1994; Gómez and Gorsky 2003) were probably related to the high positive anomalies of temperature, up to 3.6°C, recorded throughout that period. Considering that copepods primarily feed on particles

>5  $\mu\text{m}$  (Paffenhofer 1986; Turner and Tester 1989) and that the salps can ingest particles between  $\leq 1 \mu\text{m}$  and 1 mm (Vargas and Madin 2004), one thus may argue that the high abundance of picoplankton and nanoplankton could have been efficiently utilized only by the salps. This hypothesis seems to be confirmed when considering that the total abundance of copepods in March–May 1990 was much lower than in previous years (Fernex et al. 1996).

The relevance of temperature oscillations in relation to plankton variability already has been observed in different seas. In the northeast Atlantic Ocean anomalies of water temperature related to large-scale climatic processes influenced the abundance and distribution of the dominant calanoid copepod *Calanus finmarchicus* (Fromentin and Planque 1996) as well as the diversity and the phenology of the entire planktonic community (Beaugrand et al. 2002; Edwards and Richardson 2004). Global warming was also related to the decline of krill and the contemporary increase of salps in the southern Atlantic Ocean (Atkinson et al. 2004).

In the northwestern Mediterranean Sea the changes in surface water circulation are subject to large-scale climatic forcing (Astraldi et al. 1995; Vignudelli et al. 1999). Recently, the link between the North Atlantic climate and the thermal yearly anomalies in the same area has been hypothesized (Molinero et al. 2005a). Changes in temperature were related to the jellyfish increase and the contemporary drop in density of the main copepod species being attributed to the higher predation pressure from the jellyfish observed during the late 1980s to early 1990s in the area (Molinero et al. 2005a). In this framework, the significant relationship between temperature anomalies and *T. democratica* outbreaks outlined by the present study suggests a more complex scenario, the straight decrease of copepods being possibly related to a higher competition pressure from salps. The opposite influence of temperature oscillations on crustaceans and gelatinous filter feeders that respectively decrease (Molinero et al. 2005a) and increase (present study) in relation to positive temperature anomalies point toward the different answer of taxa sharing the same trophic functional group (i.e., filter feeders) but having different life cycles (both sexual and asexual for salps, but only sexual for copepods) and feeding capacities (see previous).

The results of the present study stress the importance of taking into consideration the different biological characteristics of the main consumers at the lower levels of the pelagic food web. This is fundamental when evaluating and forecasting the dynamics of the pelagic marine system in relation to environmental changes. While an increasing importance is given to the role played by predators in controlling the primary consumers (Richardson and Schoeman 2004), the effects of competition between such consumers are completely neglected. On the contrary, the changes in dominance of crustacean versus gelatinous filter feeders may be a good indicator of the ecological status of a marine system, because such primary consumers are able to quickly respond to some environmental changes of natural or anthropogenic origin.

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