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Long-term fluctuations of *Liriope tetraphylla* in Villefranche Bay between 1966 and 1993 compared to *Pelagia noctiluca* pullulations

Jellyfish
Liriope tetraphylla
Pelagia noctiluca
Long-term fluctuations
Mediterranean Sea

Méduse
Liriope tetraphylla
Pelagia noctiluca
Fluctuations à long terme
Mer Méditerranée

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ABSTRACT

Fluctuations in the abundance of developmental stages and adults of the medusa *Liriope tetraphylla* were monitored from 1966 to 1993 in the bay of Villefranche-sur-Mer, Northwestern Mediterranean Sea. *L. tetraphylla* exhibited large interannual variations in both mean abundance level and seasonality. Cluster analysis was applied to classify as "poor", years with medium to scarce populations evenly distributed the year; as "normal", years with a population maximum during autumn as frequently observed in the Mediterranean; and as "special", years with strong population maxima localized in spring or summer. The changing jellyfish abundance levels appeared not to be reliably linked to long-term changes in sea water temperature and salinity, even if temperature strongly affects their seasonality and generation time, which was estimated here at four to seven weeks, respectively, during warm or cold months of the year. *L. tetraphylla* interannual trends were compared to those of the large scyphozoan medusa *Pelagia noctiluca* with undecennal blooming periods (data from literature and pers. obs.). Possible links with specific composition changes in the pelagic ecosystem are discussed.

RÉSUMÉ

Fluctuations à long terme de *Liriope tetraphylla* dans la Baie de Villefranche de 1966 à 1993. Comparaison avec *Pelagia noctiluca.*

Les fluctuations d'abondance de *Liriope tetraphylla* (Cnidaria, Hydrozoa) ont été observées de 1966 à 1993, en baie de Villefranche-sur-Mer, au nord-ouest de la Méditerranée. *L. tetraphylla* montre de grandes variations interannuelles de son abondance moyenne et de ses variations saisonnières. On a utilisé une méthode de classification automatique pour grouper les années en « années pauvres » avec des populations clairsemées ou moyennes, distribuées régulièrement durant toute l'année, des « années normales » qui se caractérisent par des maxima automnaux et hivernaux, et des « années particulières » avec de forts maxima d'abondance durant le printemps et l'été. Les changements à long terme de la température et de la salinité de l'eau de mer ne correspondent pas clairement aux changements d'abondance de la méduse, même si la température affecte fortement ses variations saisonnières et la durée du développement, qui a été estimée ici entre quatre à sept semaines respectivement durant les mois chauds et froids de l'année. La tendance interannuelle de *Liriope tetraphylla* a été comparée à celle de la grande scyphoméduse *Pelagia noctiluca* (Cnidaria, Scyphozoa) qui a des périodes de pullulations undécennales (données de la littérature et observations personnelles). Les relations possibles avec des changements du peuplement de l'écosystème pélagique sont discutées.

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INTRODUCTION

Liriope tetraphylla (Chamisso and Eysenhardt, 1821) is among the best known medusae in the Mediterranean Sea. A very common epiplanktonic species found in the western and eastern Mediterranean basins (Kramp, 1924; Goy, 1968), *L. tetraphylla* is of interest because it shows direct development, without a fixed hydroid stage. Despite Metschnikoff's observations (1886) on the earliest stages of development, the total time required to reach the adult stage is unknown. In this study, we analysed the generation time during two seasons in the bay of Villefranche. Elsewhere in the Mediterranean Sea, analysis of the local population was performed over one – or two-year periods, but the abundance of different stages of development was rarely taken into account (Berhaut, 1968). We have monitored *Liriope* adult and developmental stages in Villefranche Bay during a 27-year period in order to describe the seasonal and interannual variability of abundance in relation to hydroclimatic conditions. Observations of the abundance of *Pelagia noctiluca* (Forsskål, 1775), another well-monitored Mediterranean medusa, show some blooming periods (e.g. UNEP, 1984; Goy *et al.*, 1989*a*; Morand *et al.*, 1992). Our study compared the attendance periods of these two holoplanktonic medusae.

MATERIAL AND METHODS

Area of study

In the Ligurian Sea (Northwestern Mediterranean), the bay of Villefranche-sur-Mer is a well-sheltered bay situated near Nice (Fig. 1). Hydrodynamic conditions in the bay are controlled by the Ligurian current and local winds (Gostan, 1968; Béthoux *et al.*, 1988). The current hugs the coast, enters at the surface at Cap Ferrat (in a northeasterly direction) and leaves at depth at the Cape of Nice, on the western side to the bay. At the entrance to the bay, two stations have been sampled over the last 30 years:

– Sampling station B (43 41′ 10″ N; 7 19′ 00″ E) is axially located at the entrance to the bay and has a maximum depth of 87 m. This site is not directly influenced by the incoming Ligurian current. Weekly hydrological measurements have been taken at this permanent monitoring station from 1957 up to the present time (Etienne *et al.*, 1991; pers. comm. for years 1992 and 1993).

– Sampling station S (43 40′ 95″ N; 7 19′ 47″ E) is located in the southeastern part of the bay and has a maximum depth of 40 m. The current here is usually strong, with a frequent inflow of macroplanktonic species observed in surface waters. This site is sheltered from the prevailing easterlies and has been selected for horizontal plankton tows.

Sampling

Zooplankton sampling and hydrological data measurements were performed from 1966 to 1993 at station B. Another zooplankton sample series was collected during 1963 and 1964 at both stations B and S.

The 27-year plankton series (weekly values)

Vertical plankton tows were collected from a depth of 75 m to the surface, from November 1966 to December 1993, at station B. Hauls were performed during daylight by towing a Juday-Bogorov net (mouth aperture 0.50 m, filtering length of 1.80 m and mesh of 330 m). The average volume of water filtered by the net was estimated to be 10 m^3 per haul. Organisms were preserved with 3% formalin. Samples were taken at a maximum frequency of twice daily, except during weekends. Hauls (up to 11) from the same week were pooled, yielding a series of weekly samples. A total set of 1,244 pooled samples was examined. The four developmental stages of *Liriope tetraphylla* were counted in subsamples (1/7 of each weekly sample volume). Juvenile stages were classed by changes of size, manubrium development and number and position of tentacles: stage 1 has 8 tentacles, a diameter <0.5 mm and no developed manubrium; stage 2 has 12 tentacles and a diameter <1.5mm; stage 3 has 8 tentacles and a long functional manubrium, and a diameter <5.0 mm. Adults have 8 tentacles, 4 developing gonads, and a maximum diameter of 15 mm. Figure 2 shows interannual abundance values for the totality of the four stages.

One-year plankton series (daily data)

Horizontal plankton tows at the entrance to the bay (at both stations B and S), were performed from May 1963 to May 1964. Plankton samples were collected each working day at three depths (3 m, 20 m and 50 m) using a Regent net (mouth aperture 1.0 m, length of 4.0 m, mesh size 680 m, silk fabric). The mean volume of sea water filtered during a standard haul was estimated to be 400 m^3, using flowmeter measurements. Organisms were preserved in sea water with 4% formalin. The four developmental stages

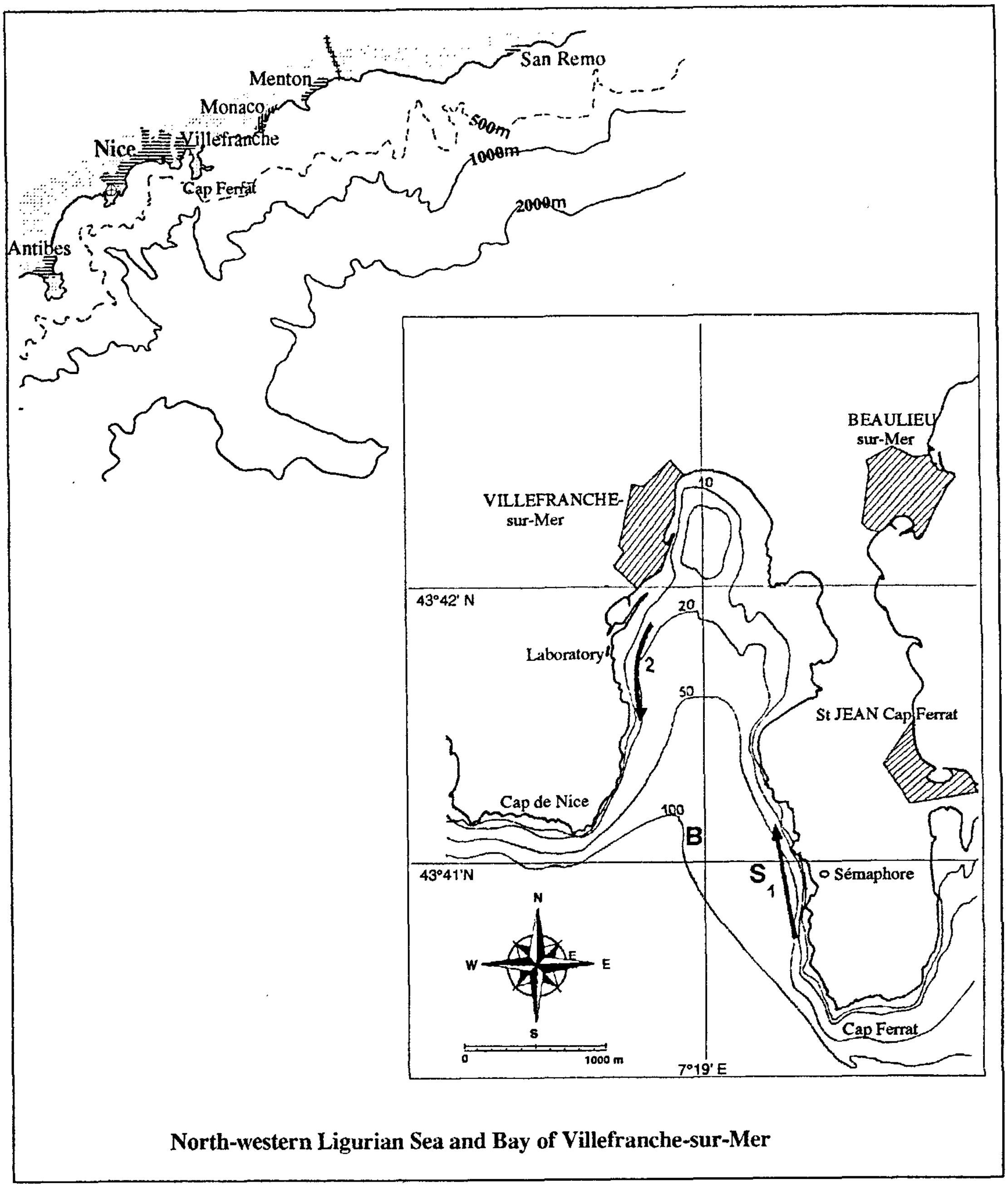


Figure 1

Northwestern Ligurian Sea and the bay of Villefranche-sur-Mer, with stations B and S. 1: Ligurian current's entrance in the bay; 2: Outflow of the current.

of *Liriope* were counted without subsampling in each of the 276 samples taken; values obtained at different depths were added together (Fig. 3).

Hydrological data

Only temperature and salinity measured at 10 and 75 m were considered here for the period of interest. Etienne *et al.* (1991) gave detailed information on hydrological methods and calculations. From 1988 to 1993, measurements were obtained by using a CTD Sea Cat profiler®.

Data analysis

Cluster analysis

We used the long time series to characterize variability in the annual abundance pattern. For each developmental stage, we logged data in abundance tables, years in rows and weeks in columns. These Buys-Ballot tables contained missing data (there was no sampling during some weeks). Missing data were interpolated by linear estimation using PCAM (principal components analysis for missing values, Bouvier, 1977). From the resulting tables, using weeks as

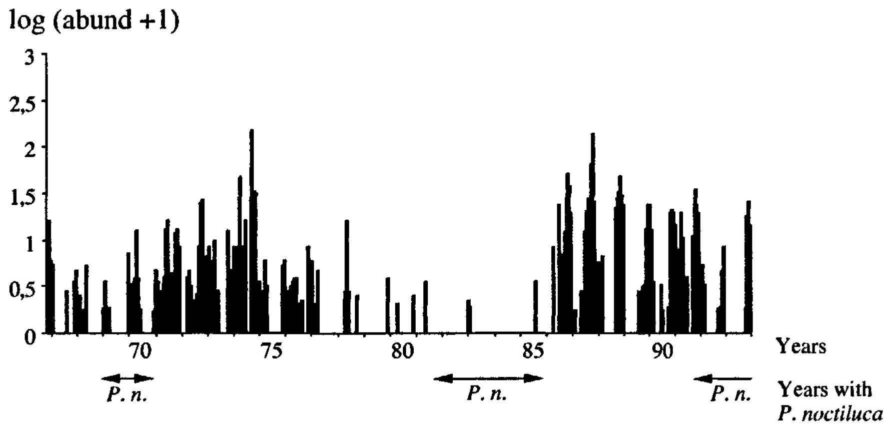


Figure 2

The 27-year series: *Weekly abundance variations of* L. tetraphylla *at station B, during November 1966 to December 1993; number of individuals per 10 m³ (Juday-Bogorov net).*

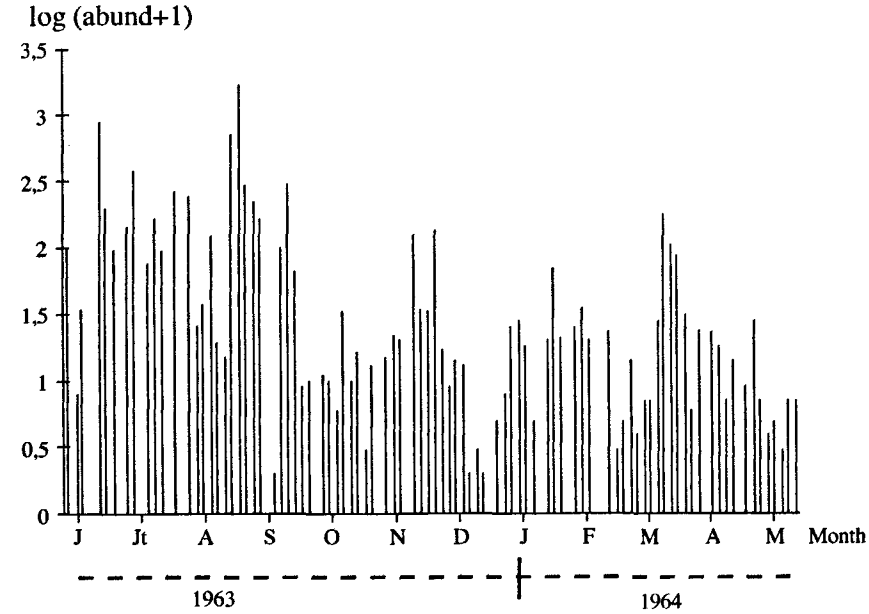


Figure 3

The one-year series: Daily abundance variations of L. tetraphylla *(sum of the four developmental stages for hauls at the three depths) at stations B and S, from June 1963 to May 1964; number of individuals per 1,200 m³ (Regent net).*

descriptors, we computed the euclidean distances between years. Years were clustered together by an agglomerative flexible sorting algorithm (Lance and Williams, 1967).

Cumulative sum of hydrological data

Temperature and salinity measurements are used to identify long-term trends in environmental conditions and to compare fluctuations of biological and hydrological series. The cumulative sum (cusum) method (Ibanez *et al.*, 1993) was applied to detect local mean changes of temperature and salinity in the long time series. In this method, a reference value, the mean of the series, is subtracted from the data. These residuals are successively cumulated. Negative residuals (data less than the mean) are represented by a decreasing slope. Positive residuals (data greater than the mean) are represented by an increasing slope. The value of the slope is proportional to the mean deviation from the overall average of the series. Sequences of data values close to the mean show null slope values. To eliminate seasonal variability of temperature, the monthly means were previously calculated and taken off to the data. The summary of the hydrological data series was compared with the general trends of medusa abundance.

Species preferences

We plotted the cumulative distribution of abundance of each *Liriope* stage (y axis) versus environmental factors (x axis) (Perry and Smith, 1993). Temperature and salinity at 10 m were chosen to represent the upper layer of the sea, where medusae were most abundant. Environmental factors were sorted in increasing rank order in such a manner that their cumulative distribution lies on the first diagonal of the graph, which then forms the reference line for *Liriope* stage cumulative distributions. Species preference was determined in the part of the graph where the slope of their cumulative abundance was maximal.

Generation time estimation

For species whose population structure is defined by cohorts, developmental time can be estimated by the duration of appearance of a particular cohort. We hypothesize that cohort development was synchronous over a large geographic range and, consequently, at a monitored station, subjected to advective process. This means that time intervals between successive peaks of abundance

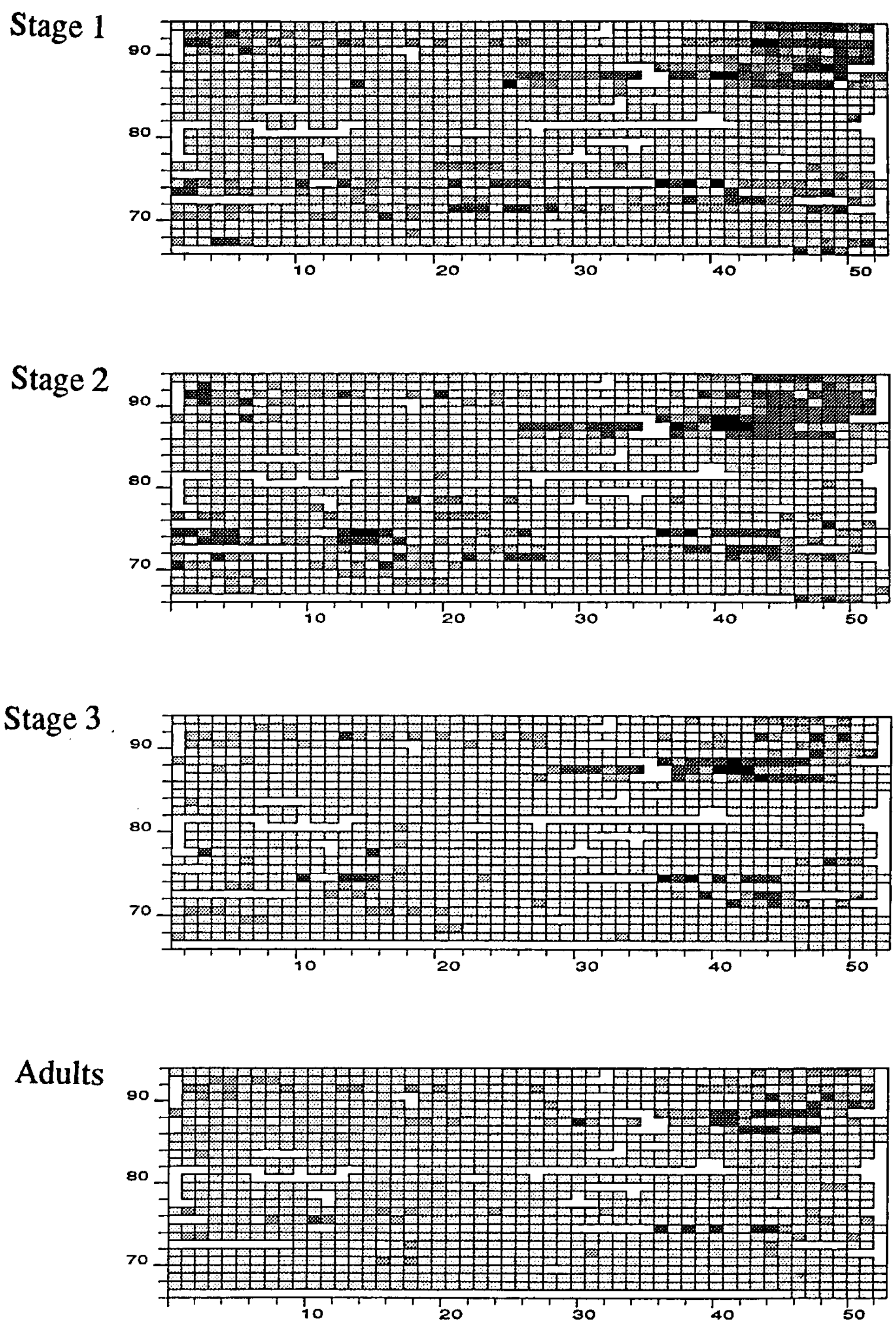


Figure 4

Weekly abundance of the four developmental stages of L. tetraphylla, *from November 1966 to December 1993. Number of individuals per 10 m^3. In the Buys-Ballot tables, years are in rows and weeks in columns. The four stages abundances are represented on a geometric scale. Different kinds of grey represent the different classes:* White: *No data;* Pale grey : *Class I: no medusae;* Grey: *Class II: from 0 to 3 ind.;* Dark grey: *Class III: from 4 to 17 ind.;* Black: *Class IV: more than 18 ind.*

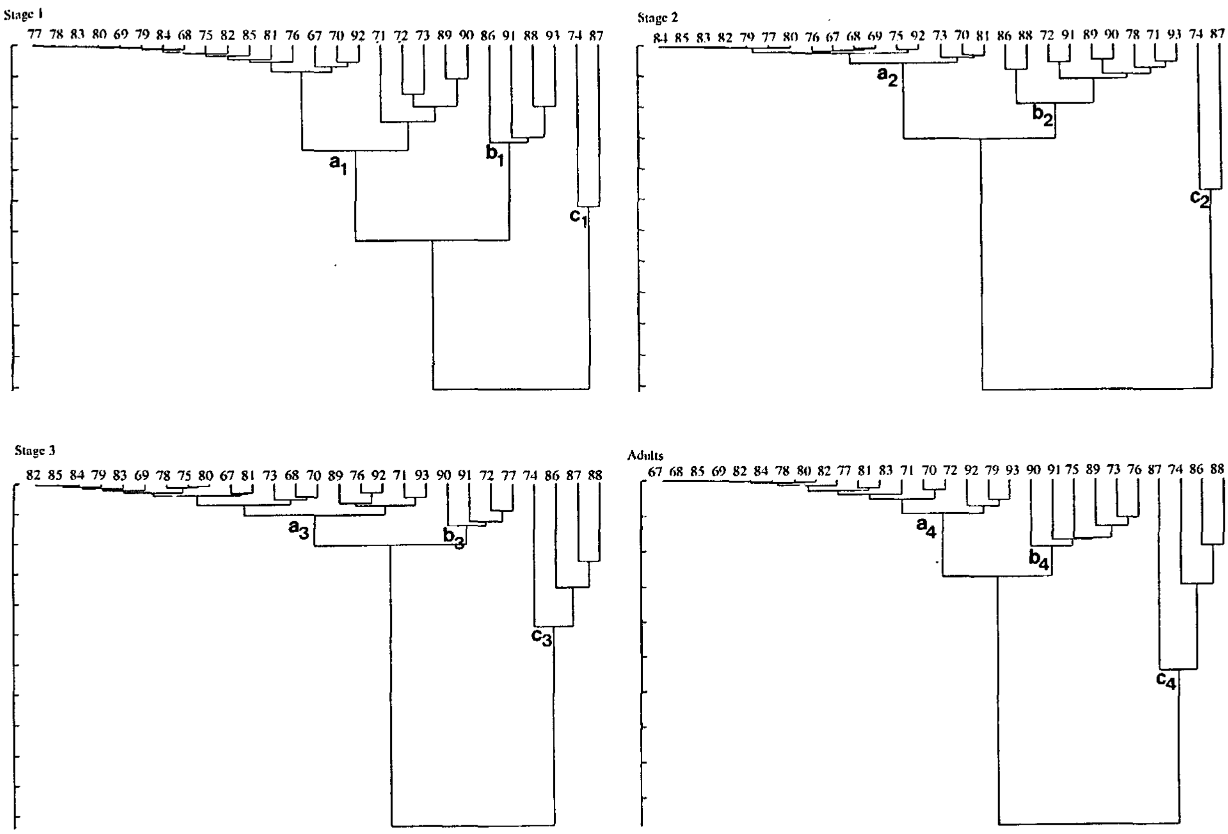


Figure 5

Dendrograms of the group of years for the four developmental stages of L. tetraphylla. **a** *(a_1 to a_4): "poor years";* **b** *(b_1 to b_4): "normal years";* **c**: *"special years": for stage 1 (c_1) and stage 2 (c_2): 1974 and 1987, for stage 3 (c_3) and adults (c_4): 1974 and 1986 to 1988.*

correspond to *in situ* generation time. We chose to study developmental stage 1 abundance periodicity, as it was the most abundant and a good indicator of *Liriope* population recruitment (for the one year 1963-1964, 70.4% of the *Liriope* population was represented by stage 1). The series was then divided into two parts, corresponding respectively to a "summer" part (June-July-August and September 1963) and a "winter" part (from December 1963 to May 1964). As the resulting series contain missing values and were too short to apply Fourier's transform accurately to identify the main periodicities of the data, we computed contingency periodograms on abundance data coded on three classes, each containing the same number of data (Legendre *et al.*, 1981; Morand, 1989). The statistically significant periods were identified at the 0.05 probability level.

RESULTS

Abundance fluctuations of *Liriope tetraphylla*

For graphical purposes (Fig. 4), abundances of the four developmental stages, during 1966 to 1993, were coded in four geometric classes (Frontier, 1969). Stages 1 and 2 were the most abundant developmental stages, adults always being scarce. Maximum abundance class IV is essentially characteristic of the last quarter of the year. During some consecutive years (1967-1969 and 1975-1985), *Liriope* were quite rare in the samples. During other years, *Liriope* were present throughout the four seasons. Maximum abundance was frequently observed during the last quarter of the year (on and after the 35th week, end of August), especially between 1986 and 1993. On some occasions, maxima were observed in late winter and early spring.

Classification of these annual patterns corresponds approximately to this visual impression. The dendrograms of each stage show two or three well-separated clusters of years, and some very dissimilar years, left unclustered (Fig. 5). We attempted to categorize clusters observed for the different stages according to their population abundance level and annual pattern of variations (Fig. 6).

The "poor years", group **a** (subgroups a_1 to a_4, indices refer to the different developmental stages) comprises years with scarce population. The seasonal pattern is flat with prevalent zeros or low abundance values randomly distributed within a year. In **a** groups, linkage dissimilarity values increased according to annual averages.

The "normal years", group **b** (subgroups b_1 to b_4) comprises years with medium abundance and more strongly seasonal populations. This group is characterized by a main population rise during autumn, for juvenile stages 1 and 2. Stage 3 and adults also have some spring medium or high values. a or b subgroups did not necessarily correspond to the same years. Discrepancies between different developmental stage cluster compositions probably reflect sampling errors, interannual variations

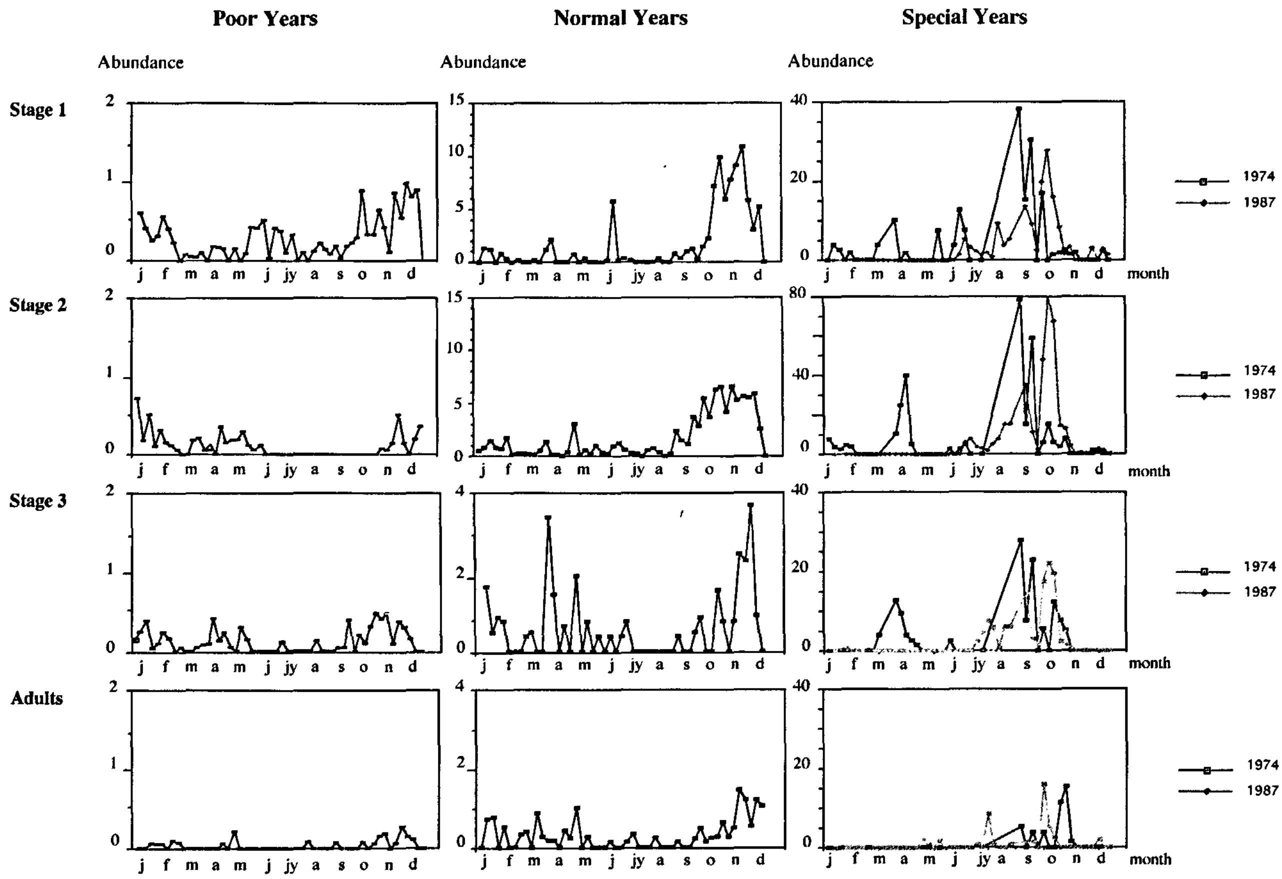


Figure 6

Abundance of the four developmental stages of L. tetraphylla *for the "poor years", the "normal years" and the "special years" (1974 and 1987) (number of individuals per 10 m^3, note the changing abundance scale).*

of abundance proportions, and in some cases advective transport of some particular medusa age classes (mainly the adults).

The "special years", group c (subgroups c_1 to c_4), were unclustered years 1974, 1986, 1987 and 1988, which were especially rich with unusual seasonal patterns.

1974: This year was characterized by an unusual secondary maximum in April. Abundance peaked at the beginning of September (no data were available in August) and included all four developmental stages; the population collapsed in October.

1987: The medusa was not observed in the bay until June. During the last six months of the year, two maxima occurred, the first in early September and the second in October. High abundance was observed for all four developmental stages.

1986 and 1988: These years are considered as special years for stage 3 and for adults. They were included within the normal years group for stages 1 and 2. Years 1986 and 1988 were characterized by large maxima restricted to October.

Cumulated abundance distribution relative to temperature and salinity in 1974 and 1987

We present the thermal and haline preference of *Liriope* during the two richest years of the long time series (1974, 1987) characterized as two "special years" by dendrogram analysis. Cumulative abundance graphs of *Liriope* as a function of rank of temperature and salinity (Fig. 7) distinguished juvenile stages from adults, for these two years and illustrated possible associations between environmental factors and *Liriope.*

In 1974, as previously shown, we observed a spring and a summer peak of abundance. Sea surface temperature ranged from 13.1 °C (21 February) to 24.2 °C (28 August). Maximum change of adult abundance occurred at temperatures higher than 15.6 °C, corresponding to the October maximum. At the same time, the upper layer of the sea was mixed after a cooling period. Increasing abundance of juvenile stages was observed over large temperature ranges including periods of the spring stratification, summer, and the autumnal mixing. Almost three-quarters of the populations of developmental stages 1 to 3 were associated with a temperature higher than 15.6 °C. Salinity at 10 m ranged from 37.4 (mid-June) to 38.1 (5 November). Juvenile stage distribution followed irregularly the diagonal line and this distribution indicates that population growth was not directly coupled with salinities variations. A very different pattern was observed for the adults, which avoided low salinity values: only 10 % of the adult population was observed at salinities lower than 38.0.

In 1987, temperatures fluctuated between 12.6 °C in mid-March and 25.4 °C on 25 August. Juveniles and adults

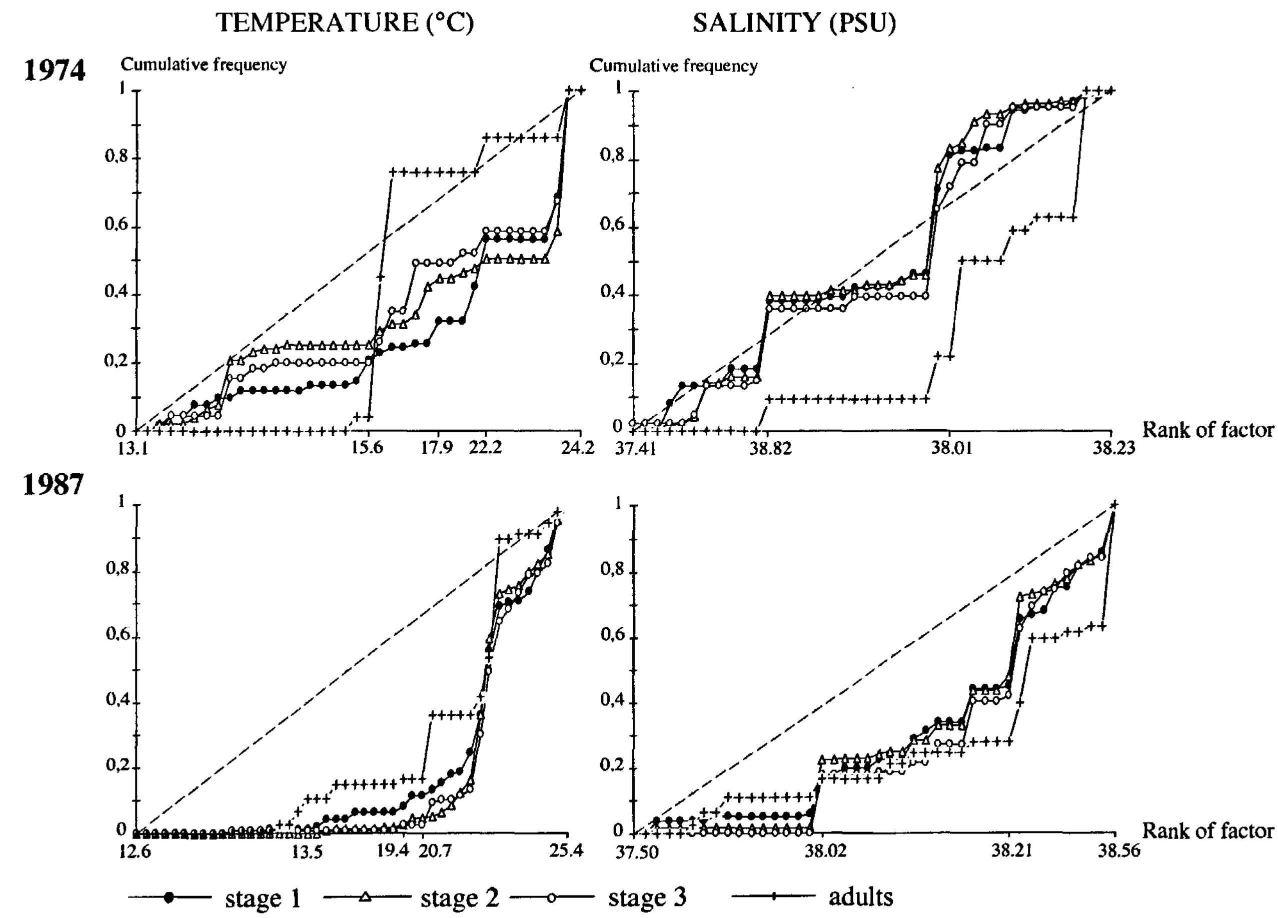


Figure 7

Cumulative frequency of the four developmental stages of L. tetraphylla *for special years in relation to temperature and salinity. Dotted line corresponds to the first diagonal.*

showed the same cumulative graph. The population was absent during the coldest weeks; a very significant increase in the population was observed at temperatures higher than 20.7 °C. The salinity range extended from 37.5 to 38.6. Several abnormally high salinity values for the Ligurian Sea were observed between July and November. No developmental stages showed a significant increase with low salinity, but major changes occurred at salinities higher than 38.2 (about 50 % of the *Liriope* population was associated with salinity higher than 38.2). All four developmental stage evolved with salinity in the same fashion.

Cumulative distribution of abundance of each developmental stage illustrates growth of the population as a function of temperature or salinity and reflectes for 1974 a specific behaviour of the adult population in relation to the other stages.

Long-term fluctuations of hydrological factors

Hydrological time series show fluctuations of temperature and salinity during the 27 years and their maxima and minima (Fig. 8 and Table 1). At 10 m, seasonality was obviously correlated with temperature in the cusum graph (Fig. 9*a*). At 75 m, temperatures were below the mean from 1969 to 1975, from 1978 to 1982 and after 1991. Higher temperatures were observed between 1989 and 1991 and between 1975 and 1978. Salinity showed a simple pattern similar at 10 m and 75 m (Fig. 9*b*). Salinity was generally lower than the overall mean between 1967 and 1980 and after 1991. Periods of high salinity were present during 1974-76 and during 1981 to 1987.

Estimation of generation time

The biology and life cycle of *Liriope* may explain the long-term fluctuations observed in the bay. Metschnikoff (1886) was the first, and the last, to describe the development during the first seven days. He observed cellular divisions which transformed the egg into stage 1. The observation of a new first developmental stage in the population characterizes a new generation. In the laboratory (during 1994 and 1995), several rearing tests of *L. tetraphylla* did not yield sufficient information on the generation time of this species.

From May 1963 to May 1964, *Liriope tetraphylla* was very highly abundant in the bay. *Liriope* was always present during this period, with a maximum from June to September, and similar densities during all the other seasons. Clearly this one-year series 1963-1964 also belongs to the "special years" heterogeneous category. Even if quantitative comparisons between Juday-Bogorov

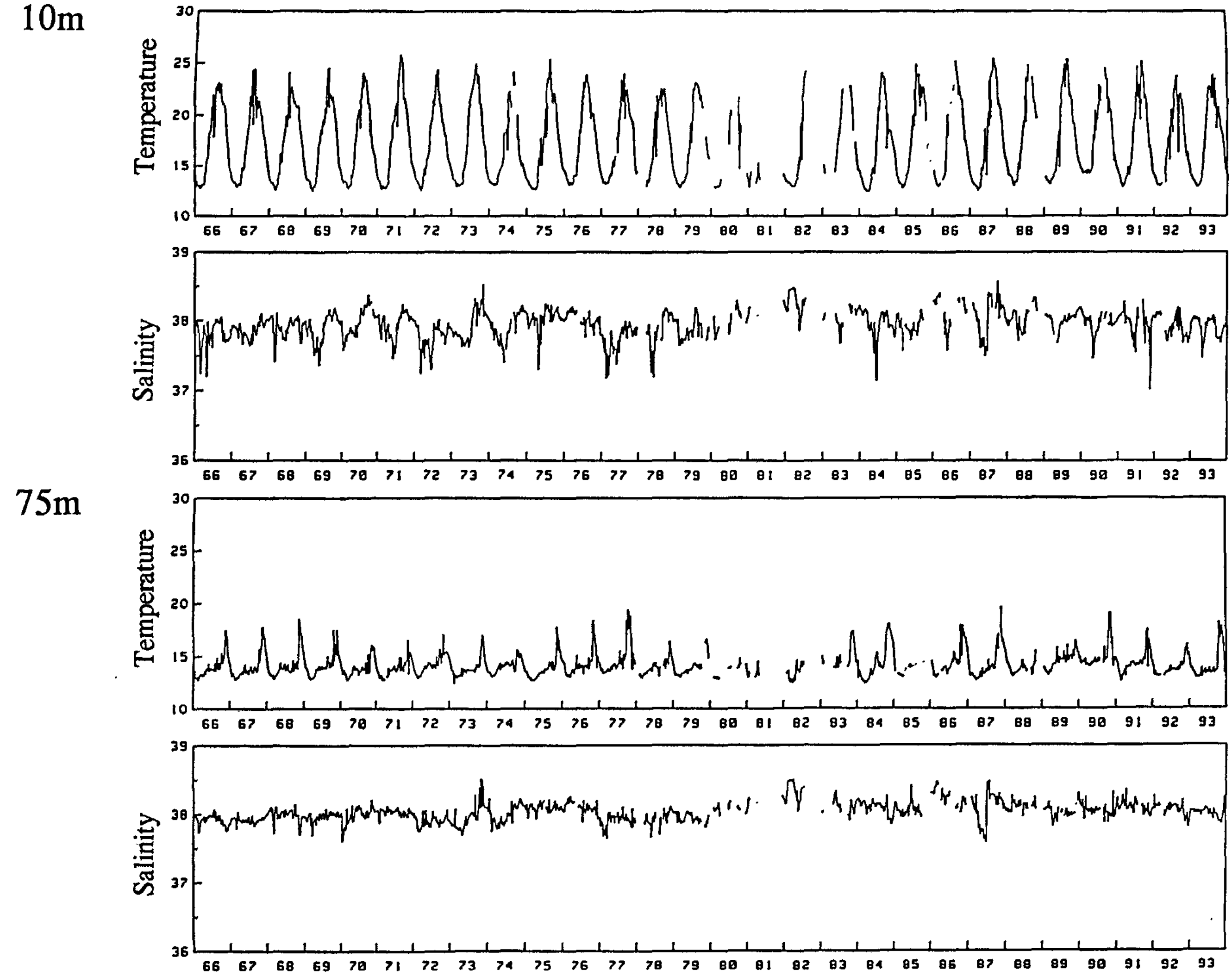


Figure 8

Weekly sea temperature (C) and salinity (PSU) at 10 m and 75 m, from 1966 to 1993.

and Regent nets may be difficult to achieve, the 1963-1964 seasonal pattern, with a strong summer maximum and similar abundance values for the three other seasons, was unique in our data. Due to the mesh size of the Regent net, the stage 1 population could have been underestimated, but a high abundance of this stage is significant. On the other hand, during this year, *L. tetraphylla* accounted for a quarter of the medusa population in the bay (Goy, 1968).

With these considerations in mind, *in situ* data of these series were examined by the contingency peridogram. In the warmest period of the year 1963 (June to September, 20-26 °C at 10 m depth) the abundance peak of stage 1 occurred with a significant period of 28 days (Fig. 10*a*). In the colder period (December 1963 to May 1964, 13-20 °C at 10 m), the significant period has a value of 44 days (Fig. 10*b*). As in the case of all marine species, in winter, growth is slower than in summer when it is accelerated. In these series, maximal abundance was observed during the warmest months.

Table 1

Minima and maxima of hydrographic data, at 10 m and 75 m, from 1966 to 1993.

	Temperature (°C)		Salinity (PSU)	
	Minimum	Maximum	Minimum	Maximum
10 m	12.45 (11.03.84)	25.77 (10.08.71)	37.02 (20.11.91)	38.58 (30.09.87)
75 m	12.41 (21.02.73)	20.04 (0.3.11.87)	37.59 (23.06.87)	38.51 (07.11.73)

DISCUSSION AND CONCLUSION

Liriope tetraphylla is a cosmopolitan and euryhaline species from temperate and subtropical waters. This jellyfish can dominate the carnivorous gelatinous zooplankton, especially in upwelling areas (Furnestin, 1959; Goy, 1973)

The "normal years" seasonal pattern in our series agrees with previous studies in different parts of the western Mediterranean. Vannucci (1966) observed maximal occurrence of *Liriope* in the bay of Naples from October to March (survey from 1959 to 1961). In the Gulf of

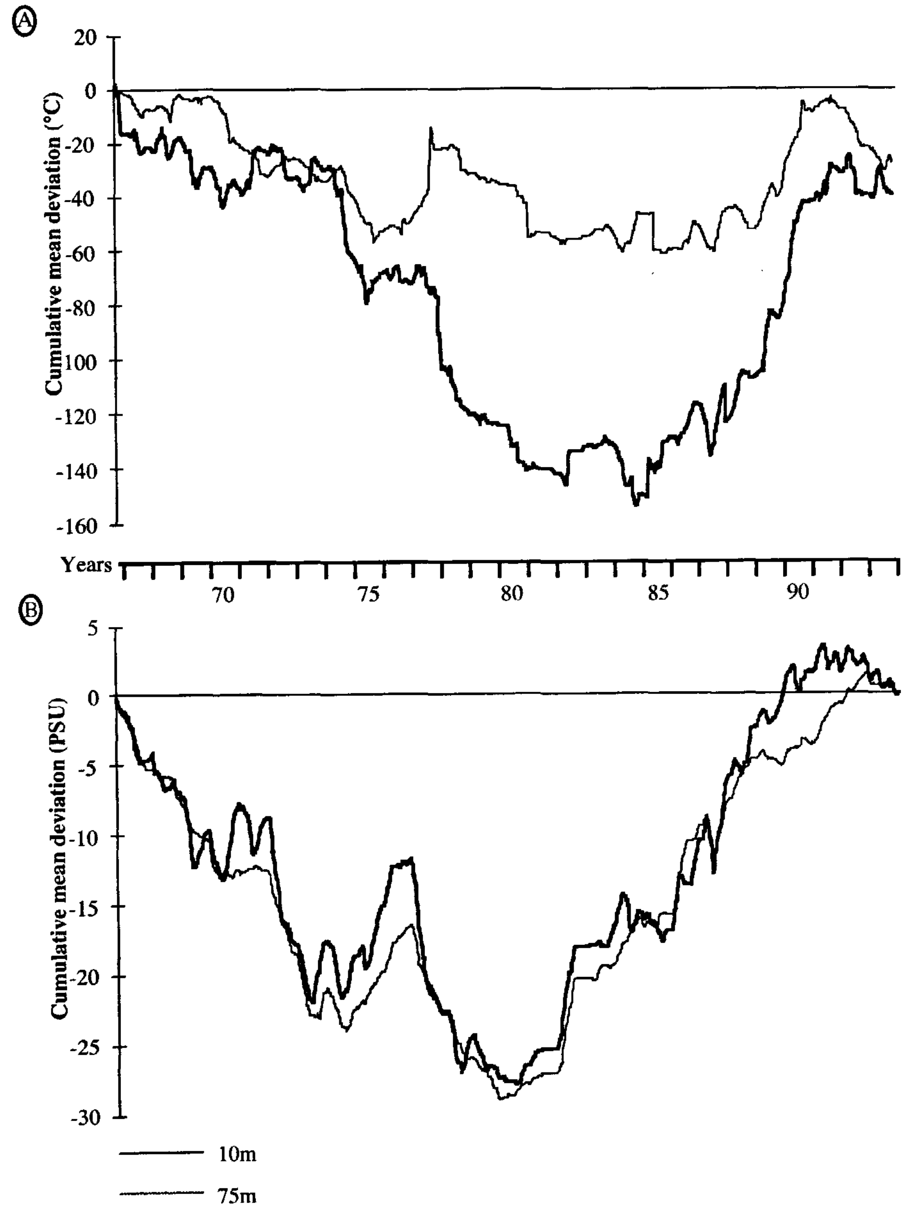


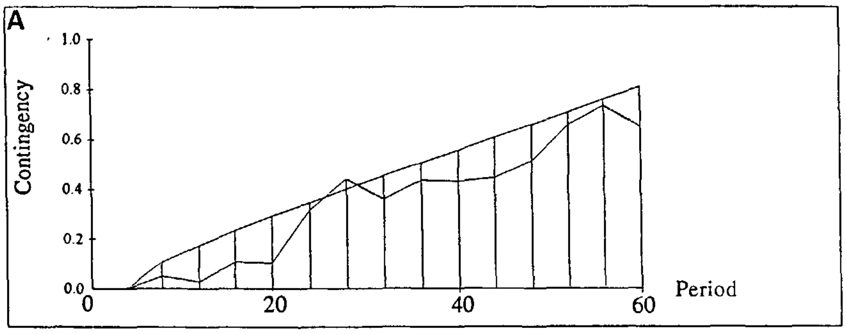
Figure 9

Cumulative sum series of weekly sea temperature (deseasonalized data; A) and salinity (B), from November 1966 to December 1993, at 10 m and 75 m.

Marseilles (Berhaut, 1968), the medusa is most abundant from October to December (years 1964-1967). In the western Mediterranean Sea, all these periods correspond to the annual cooling period. Autumn temperatures are usually between 20 °C and 15 °C and uniform from the surface to a depth of more than 50 m. As in the case of other planktonic organisms, medusae are known to be influenced by temperature and salinity (Reeve and Walter, 1972; Catalano, 1985; Larson, 1985; Morand *et al.*, 1987; Malej, 1989; Rottini Sandrini and Avian, 1989; Arai, 1992; Matsakis, 1993 and many others). However, no experimental work has been done on the metabolic and behavioural effects of these parameters on *Liriope*.

In the long-term series, direct relationships between *Liriope* population variations and hydrological parameter changes are debatable. In our area, the most important climatic events of the last 30 years were the cold winter of 1963 and the dry period during 1980-90 (Fromentin and Ibanez, 1994). During the winter of 1963, deep water formation occurred in the Northwestern Mediterranean Sea. Off Villefranche, the entire water column remains homogeneous until the beginning of surface warming in early May (Braconnot *et al.*, 1966). During this mixing event, large amounts of nutrients were found in the euphotic zone (Gostan, 1968). Planktonic production was delayed. When the temperature increased in mid-spring, new production was fueled by the large nutrient pool and may explain the high abundance of *Liriope* we observed in summer.

The dry decade 1980-1990 corresponds to high surface salinity and poor years of *Liriope* until 1986. A dramatic increase of another medusa, *Pelagia noctiluca* (Forsskäl,



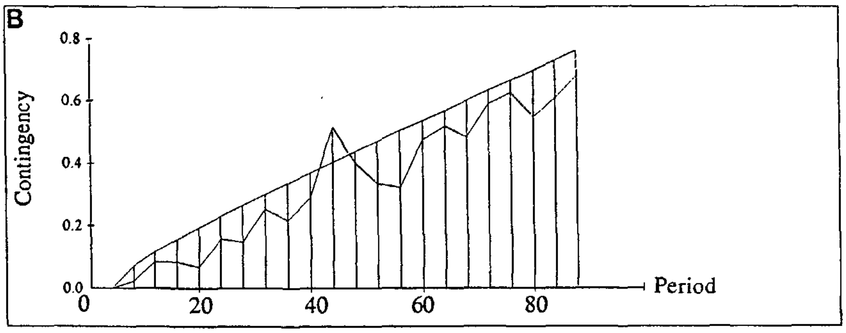


Figure 10

Contingency periodogram for stage 1 of L. tetraphylla. *A: the "summer" series (from June to September 1963). B: the "winter" series (from December 1964 to May 1964). Line which delimited hatched surface corresponds to the critical values at 5 % probability level. When the curve is above this line, calculated period is significant. Period is in days.*

1775) took place during this period (UNEP, 1984). Goy *et al.* (1989*a*) demonstrated that this holoplanktonic jellyfish exhibits near undecennal blooming periods (12 years) in the Mediterranean. Years preceding the occurrences of *Pelagia* may be characterized by special weather conditions: high atmospheric pressure and low rainfall. Therefore, periods of high abundances of the two medusae species are not coincident during our 27-year series. *Pelagia* was very abundant from 1982 to 1985, when *Liriope* was very rare. A medium-intensity bloom of *Pelagia* was observed in 1969-70, accompanied by a low *Liriope* population. A sparse and irregular population of *Pelagia* was recorded off the French Riviera in 1992-93 (pers. obs.), while at the same time *Liriope* was less abundant than the preceeding years (Fig. 2 illustrates periods of occurrence of *Pelagia* in comparison with *Liriope*). From 1963, the richest years of *Liriope* abundance always occur during *Pelagia* absences.

Both medusae are carnivorous and have a holopelagic life cycle (Metschnikoff, 1886; Delap, 1907; Morand *et al.*, 1987; Malej, 1989; Rottini Sandrini and Avian, 1989; Matsakis, 1990). *In situ* observations and experimental data do not contradict the view that, at the same size, they have similar trophic niches. Nevertheless they have very different generation times, reproductive size and maximum size (the corresponding maximum dry weights are about 1 mg for *Liriope* and 10 g for *Pelagia*). The largest *Pelagia* are able to feed on large prey (pteropods molluscs, fish larvae and krill, as we observed in the Ligurian Sea) that adult *Liriope* cannot catch at all. On the other hand, *Pelagia* could also eat medusae, for example *Liriope*. As Legovic (1987) concluded, the fluctuations of jellyfish populations could be explained by variations in food availability, standing stocks of either competitors and predators, and even direct climatic effects, such as temperature variations outside the vital range. Few data are available quantitatively to compare these various effects simultaneously for both species. Experimental work and population dynamic modelling have only been reported on *Pelagia* (Morand, 1989; Malej and Malej, 1992; Morand *et al.*, 1992).

At our present level of knowledge, the interannual pattern of succession of the two medusae species suggests a simple hypothesis. As the food requirements to enable the two species to reach maturity differ greatly, considering their different sizes, we could suppose that developing populations of the large predator *Pelagia* occur only during periods of strong and sustained secondary production accumulating biomass in the food web in large-sized prey species. Morand *et al.* (1992) showed that prey standing stocks are a critically limiting factor for *Pelagia* ephyrae which grow during five months in spring and summer. The much smaller *Liriope* may develop during periods of normal productivity, which may not be sufficient to sustain a population of *Pelagia*. As we have shown, in the absence of *Pelagia*, *Liriope* seasonality and population levels seem positively influenced by environmental conditions favourable to increases in coastal planktonic production. *Pelagia*, with its longer generation time, may not be able to benefit from transient coastal production events. In the Ligurian Sea, developmental stages appear to be localized in more permanently productive frontal zones (Boucher *et al.*, 1987).

During *Pelagia* blooms, *Liriope* populations may be reduced by direct trophic competition and predation. Evidence of competitive exclusion during *Pelagia* pullulations was documented by Morand and Dallot (1985) and Goy *et al.* (1989*b*) for other macroplanktonic predators observed in the Villefranche Bay during the years 1898-1915. The ctenophore *Leucothea multicornis* develops during *Pelagia*'s inter-bloom period. The siphonophore *Hippopodius hippopus* and trachymedusa *Geryonia proboscidalis* are both depressed during pullulations of *Pelagia*. These effects are more pronounced in summer and autumn, when *Pelagia* occurrence is maximum in coastal waters.

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