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Temporal fluctuations of doliolid abundance in the bay of Villefranche-sur-Mer (Northwestern Mediterranean Sea) from 1967 to 1990

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ABSTRACT

This study describes the temporal fluctuations of doliolid populations sampled in the Bay of Villefranche-sur-Mer (Northwestern Mediterranean Sea) from 1967 to 1990. The abundance level of doliolids (strongly dominated by *Doliolum nationalis* and *Dolioletta gegenbauri* phorozoids) was estimated weekly according to Frontier's (1969) ordinal scale. Population abundance shows important interannual variations. The series displays a clear upward trend from the late 1960s to the early 1980s; thereafter, the abundances remain at a high and steady level. Five annual patterns of abundance level changes are identified, using cluster analysis. The influence of hydrological and meteorological conditions on doliolid abundance is tested using a Markov regression model for ordinal ecological time series (Ménard *et al.*, 1993). A reduction of salinity in the warm surface water due to the establishment of a halocline during early summer or autumn creates the main hydroclimatic conditions favourable to the development of the populations in question. These conditions mainly occur during the oligotrophic period of the year, when the regenerated production system is the governing process.

RÉSUMÉ

Fluctuations temporelles des populations de doliolies de la baie de
Villefranche-sur-Mer (Méditerranée) de 1967 à 1990

Nous analysons les fluctuations d'abondance des populations de doliolies échantillonnées dans la baie de Villefranche-sur-Mer (Méditerranée occidentale) de 1967 à 1990. Les doliolies ont été dénombrées chaque semaine de façon semi-quantitative, en utilisant des classes d'abondance (Frontier, 1969). Une classification sur la série permet d'identifier cinq groupes d'années. L'influence de variables hydrologiques et météorologiques est ensuite évaluée à l'aide d'un modèle stochastique de type markovien, élaboré pour des séries d'observations ordinales et dépendantes (Ménard *et al.*, 1993). Les doliolies apparaissent clairement liées aux eaux chaudes dessalées en surface, typiques des conditions du début de l'été ou de l'automne. Elles sont abondantes durant la partie de l'année la plus oligotrophe, lorsque le régime de production régénérée est dominant.

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INTRODUCTION

Doliolids are gelatinous filter feeder microphages that are very common in coastal and offshore plankton communities of all parts of the world ocean. *Doliolum nationalis*, Borgert, 1894, *Dolioletta gegenbauri*, Uljanin, 1884, and – to a lesser extent – *Doliolina mülleri*, Krohn, 1852, are the main species observed in the Bay of Villefranche (Braconnot, 1963, 1967, Braconnot and Dallot, 1995); the same species inhabit the Northeastern Atlantic (Hunt, 1968). They are characterized as oceanic species (Barnes, 1961; Colebrook *et al.*, 1961; Colebrook, 1964; Hunt, 1968), although they can occur above the continental shelves. Due to their high rates of asexual reproduction, doliolid populations have one of the fastest growth rates among pluricellular organisms (Braconnot, 1970; Deibel, 1982a), forming spectacular swarms which have been frequently observed above the continental shelves of the world ocean (Braconnot, 1970; Deibel, 1985; Pomeroy *et al.*, 1987; Paffenhöfer *et al.*, 1987, 1991). Doliolids are generalist suspension-feeders, using a pharyngeal mucous net, to catch efficiently autotrophic and heterotrophic organisms of the microbial subsystem over a large range of size, from 0.2 μm to more than 100 μm (Deibel 1982b, Crocker *et al.*, 1991, Tebeau and Madin, 1994). Thus, they are among the few planktonic invertebrates that are able to take advantage of increasing bacterial biomass and small-sized autotrophic species. Nevertheless, field studies designed to corroborate these experimental results are few in number, and somewhat difficult to interpret. If intense bacterial or nanoplanktonic biomass development creates favourable conditions for doliolid population increase, then increasingly dense doliolid swarms will become rapidly able to deplete their food standing stock, resulting in an apparently inverse spatial correlation between the doliolids and their food (Deibel, 1985; Pomeroy *et al.*, 1987; Paffenhöfer *et al.*, 1995). As doliolids efficiently harvest ultraplanktonic organisms involved in the microbial loop, they lengthen the turnover time of biogenic carbon in the ocean (Fortier *et al.*, 1994). Furthermore, they produce faecal pellets that are responsible for a fast downward transfer of organic matter in the marine ecosystem (Michaels and Silver, 1988; Deibel, 1990). A thorough knowledge of the hydroclimatic conditions favourable to developing and sustaining large populations of doliolids may help to enhance our ability to predict the effects of future climate-induced changes on the pelagic ecosystem structure and function.

Despite the importance of doliolids in marine ecosystems, pluriannual records of these species are scanty. First results came from the Continuous Plankton Recorder Survey (Hunt, 1968) and the CalCOFI programme (Berner, 1967) and permitted description of the seasonal variability and spatial pattern of doliolid population distribution in the North Atlantic, North Sea and California Current regions. In the Mediterranean, Baranovic *et al.* (1992) studied overall Thaliacea abundance in the coastal waters of the Adriatic Sea over a period of 23 years (1960-1982), but did not distinguish doliolids from salps. Recent works on pluriannual variations in the Mediterranean zooplankton

community structure have focused on copepods and do not even mention doliolids (Cataletto *et al.*, 1995; Mazzochi and Ribera d'Alcalà, 1995).

Our main purpose here is to describe a pluriannual doliolid time series recorded in the Bay of Villefranche (Northwestern Mediterranean Sea) from 1967 to 1990. We considered the statistical relationship between some hydrological and meteorological changes and observed doliolid abundance fluctuations, using a markov regression model suitable for autocorrelated data (Ménard *et al.*, 1993). The same model has previously been used to study the abundance of the salps *Thalia democratica* Forsskål, 1775 and *Salpa fusiformis* Cuvier, 1804, using the same monitoring data set (Ménard *et al.*, 1994). The results permit the identification of hydroclimatic processes that modulate the population dynamics in the Bay of Villefranche. In this oligotrophic area, regenerated production through the microbial loop plays a critical role during the period of occurrence of doliolid populations. Interannual variations are also discussed in the general context of climate change.

MATERIALS AND METHODS

Sampling and experimental time series

The sampling site (station B) is a permanent monitoring station located at the southern entrance of the Bay of Villefranche-sur-Mer (Northwestern Mediterranean Sea), with a maximum depth of 80 m. Plankton was sampled twice every working day from November 1966 to December 1990 at Station B by vertically towing a Juday-Bogorov net (50 cm diameter, 330 mm mesh size) from a depth of 75 m to the surface. The mean filtered volume of sea water was about 10 m³ per haul. Samples from the same week were pooled, thus yielding a series of weekly data. Doliolid abundance was directly determined semi-quantitatively (Table 1) according to the scale of abundance classes of Frontier (1969). The sampling scheme has already been discussed (Ménard *et al.*, 1994): both pooling the samples weekly and using an ordinal class scale are adequate to minimize the effect of spatial and temporal patchiness. We did not discriminate between different species or different zooid stages, and hereafter apply the generic term 'doliolid' to every *Doliolum* (*sensu lato*) spp. zooid.

Table 1

Definition of abundance scale according to Frontier (1969) and abundance classes used in the Markov model.

Number of zooids per haul (in near 10 m ³ of sea water)	Frontier's scale	Abundance classes
0	0	1
1 to 3	1	2
4 to 17	2	3
18 to 80	3	4
80 to 350	4	5
> 350	5	5

Sea-water temperature, salinity and computed density at depths of 0, 10, 20, 30, 50 and 75 m were recorded weekly during the same period at Station B (Etienne *et al.*, 1991). Because of irregular time spacing within weeks and missing values, the data were smoothed by taking averages over two weeks. We computed the differences between sea-water density excess at 50 m and 10 m, at 30 m and 10 m, as indices of the vertical stability of the water column. Weekly means of air temperature (°C) and of light irradiance at sea level ($\text{J}\cdot\text{cm}^{-2}$) were computed from daily records from the Cap Ferrat and Nice airport meteorological stations, respectively. These stations are close to the Bay of Villefranche. The wind energy at sea-surface level is a complex function of wind velocity. As daily meteorological records of the Cap Ferrat station do not specify the duration of windy events, a weekly index of mean wind stress was computed as the sum of the daily velocities squared. We considered days with mean velocity over a threshold of $6 \text{ m}\cdot\text{s}^{-1}$ (mean wind index considering all directions), since velocities lower than these values are not expected to have a significant effect on the surface layer.

Data analysis

Different methods of data analysis were used to characterize the temporal variations of doliolid abundance and test the influence of hydroclimatic variables.

The long-term trend of the doliolid time series was computed by Eigen Vector Filtering, EVF (Colebrook, 1978; Ibanez and Etienne, 1992). Missing values (159 in a total of 1096 weekly values) were interpolated using the method of Zagoruiko and Yolkina (1982). The autocorrelation function of the time series was estimated using Spearman's rank correlation coefficient (Conover, 1980).

Patterns of change within years were obtained by Q-mode cluster analysis of the years considered as objects, the 52 weeks being chosen as descriptors. We used a hierarchical flexible clustering method (Lance and Williams, 1967) on a Bray & Curtis distance matrix between years. Groups of years were identified from the dendrogram considering a segmentation level at a distance equal to 0.6. A mean annual pattern was then computed for each group of years. Ménard *et al.* (1993, 1994) give a detailed account of the Markov regression model used here. Such an approach is specifically designed to take into account the peculiar quality of the doliolid time series: *i.e.* ordinal, autocorrelated and strongly seasonal data. Furthermore, it permits evaluation of the influence of exogenous environmental covariates (hydrological and meteorological variables).

The model is written in terms of the cumulative probability function of the doliolid abundance process (the probability that at time t the population abundance should be less or equal to some ordinal value). We choose the logistic form of McCullagh's generalized linear model for ordered categorical outcomes (McCullagh, 1980). The corresponding linear predictor includes previous doliolid abundance states (according to the order of the process, see below), and the covariate values taken previously.

Recalling that the ordinal scale for doliolid abundance has five categories, we represent doliolid abundance on week t by the vector $y_t = (y_{t1}, \dots, y_{t4})^T$, where y_{tj} is 1 if the j^{th} category of abundance is observed, and 0 otherwise; and we let x_t denote an environmental variable on the same week. For $j = 1, \dots, 4$, let

$$\gamma_{tj} = \sum_{k=1}^j \Pr(y_{tk} = 1 | y_{t-1}, x_{t-1})$$

be the conditional cumulative probability of the doliolid abundance process. Following McCullagh (1980), the model is defined by

$$\gamma_{tj} = \exp(\lambda_{tj} + y_{t-1}^T \beta_t + x_{t-1} \alpha_t) / \{1 + \exp(\lambda_{tj} + y_{t-1}^T \beta_t + x_{t-1} \alpha_t)\}$$

where $\alpha_t, \beta_t^T = (\beta_{t1}, \dots, \beta_{t4})$ and $\lambda_{t1} < \lambda_{t2} < \lambda_{t3} < \lambda_{t4}$ are unknown parameters. The parameters are estimated by maximum likelihood method.

The order of a Markov process corresponds to the number of previous states (*i.e.* former weeks) that significantly influence the outcome. Zero order corresponds to stochastic independence between successive observations. If the dependence is on the most recent prior abundance only, the process is of order 1 (such as the former equations), and so on for greater order values. The order of the process was first assessed by fitting progressively nested models in a stepwise approach. At each step, we computed a likelihood ratio statistic. Under the null hypothesis of no effect, this ratio is asymptotically χ^2 distributed with a number of degrees of freedom equal to the number of parameters just added to the last fitted model. The last significant model at the 0.05 probability level gives the order of the process.

The influence of each environmental covariate was similarly tested after the order of the doliolid abundance process was identified. Only the former value of the covariate, say at the previous week, is considered, in order to permit a causal interpretation. The word "influence" refers to the improvement of the fit of the model. When a significant effect was found, we computed the transition probability values within the observed range of variation of the corresponding environmental variable. A transition probability is the probability that the doliolid population reaches a particular abundance class, taking into account the former abundances (according to the order of the process) and the value of the environmental covariate taken at the preceding week. Computed transition probabilities permit estimation of the effect size of the environmental variable and its ecological significance.

To account for seasonal effects in the data, we assume that the unknown parameters to be estimated are periodic functions of time, with a period of one year. These functions may be specified in a number of ways. The saturated specification allows a specific value for each week. To limit the number of parameters to be estimated from the data, we assume piecewise homogeneity over subannual periods (Ménard *et al.*, 1995), based on the seasonality of doliolid abundance. We focus only on the

period from week 25 (beginning of summer) to week 51 (end of autumn), because it corresponds to the possible development of high concentrations of doliolid populations and to the maximum range of the abundance classes. All subsequent analyses were thus performed within this subannual period, assuming the parameters of the model to be time-independent.

RESULTS

Overview of the doliolid time series

Doliolid abundance is low in the Bay of Villefranche. Throughout the series (from November 1966 to December 1990), doliolids were caught in 63% of the samples. More than 50% of the weekly pooled samples contained less than 0.4 individuals.m⁻³ of filtered sea water. Maximum values were observed in 0.5% of the weeks, corresponding to about 300 zooids.m⁻³.

Both annual and interannual patterns of observed doliolid abundance are presented in Figure 1. Doliolids are more abundant during the second half of the year, showing a high year-to-year variability with respect to week number, intensity and duration of the periods of blooms (class 3 and above). Highest concentrations of doliolids are observed in

summer and autumn, whereas winter and spring are periods of infrequent presence or low abundance of the population. In 1968, 1969 and 1970, doliolids were rare. In contrast, abundance was high throughout the year in 1976. The pattern of the data suggests that high numbers of doliolids may have become more frequent, and more conspicuous since 1980, and may occur earlier in the year.

The interannual trend of the series corresponds to the third axis of an EVF analysis (Fig. 2), accounting for 11% of the total variance. The first two axes of this analysis correspond to seasonal components, also demonstrated below. The trend shows a slow increase before 1980, and large fluctuations and a quasi-stability at the higher level in subsequent years.

Annual patterns

Cluster analysis permitted identification of five different groups of years (Fig. 3). The mean annual pattern of each group is presented in Figure 4. The first two groups (years 1968 to 1970) are characterized by infrequent occurrence and low abundance. The third group (1967, the mid-1970s, 1983 and 1990) includes years with sustained medium-level abundance throughout the weeks of the year. No particular peak of high concentrations is observed, and seasonality remains weak. The fourth group (1977-1981 and 1985-1986

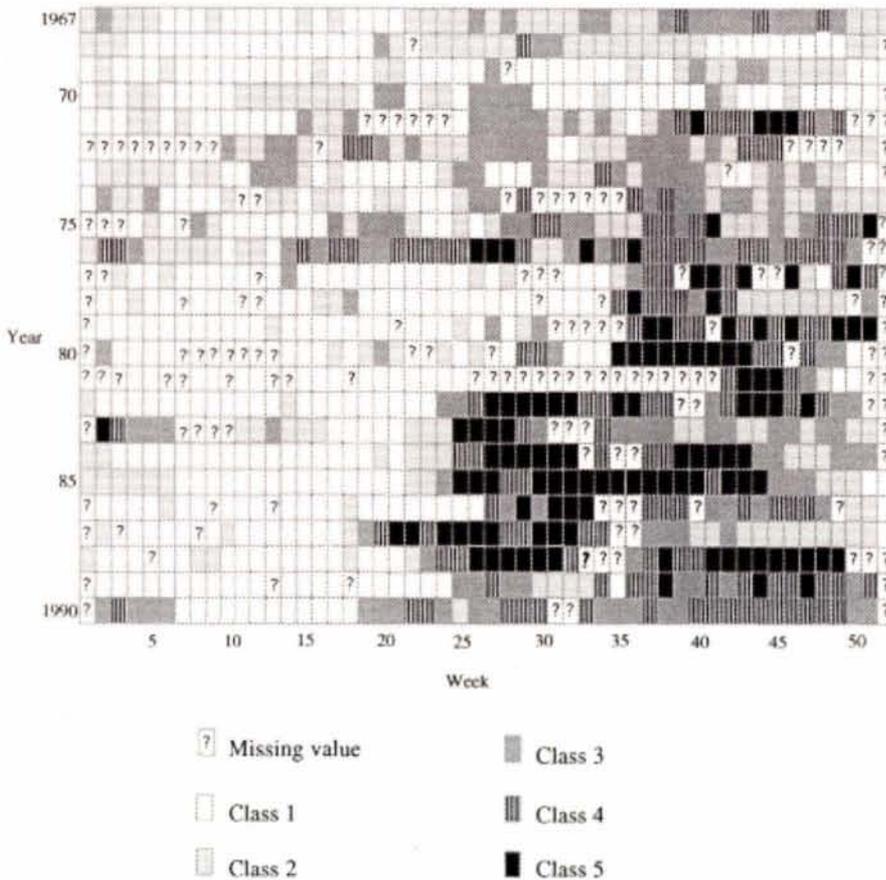


Figure 1

Weekly recordings of abundance classes (Table 1) of doliolids (columns) from 1967 to 1990 (rows).

Doliolids

Figure 2

Frontier's abundance-class series and long-term trend extracted from EVF (bold line). The straight line corresponds to the mean of the series.

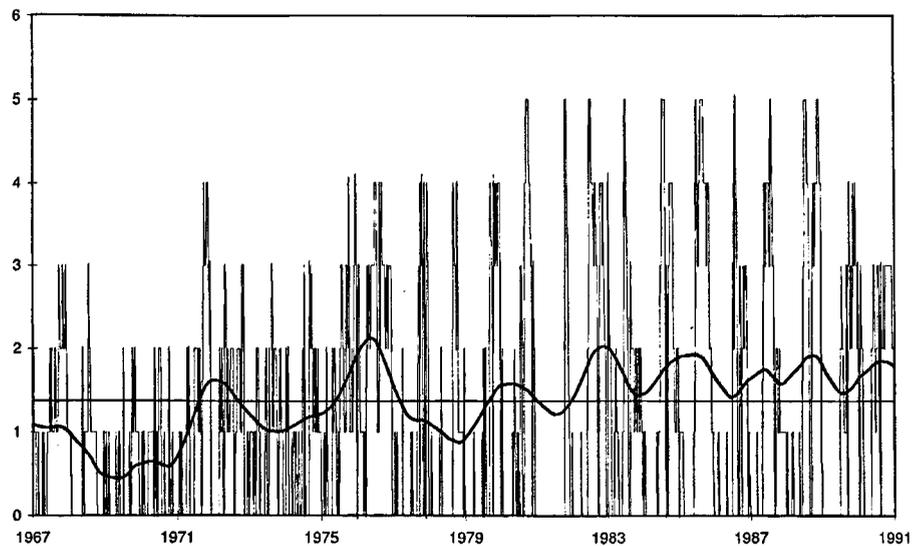
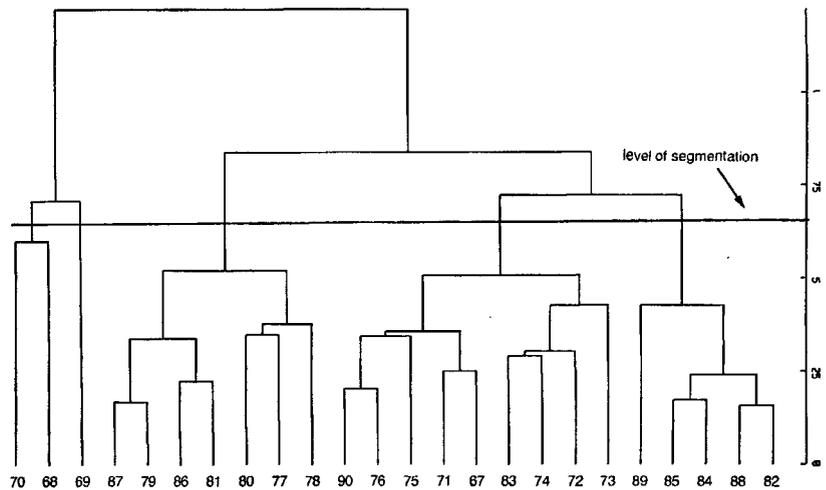


Figure 3

Dendrogram of the hierarchical flexible clustering on a matrix of Bray and Curtis distances among years. A segmentation at the level of 0.6 has been considered.



periods) is typical of the seasonal temporal fluctuations of doliolid abundance in this region (Braconnot, 1963): very low abundance during winter and spring, an increase during summer and a maximum abundance in autumn. The last identified group includes most of the 1980s. As with the fourth group, very low abundances are observed during the beginning of the year, but high abundance classes occur as early as July, and may last up to two months, September and October being characterized by slowly decreasing abundance levels.

Stochastic modelling

The rank autocorrelation function of the doliolid series reflects its periodic non-stationarity, with a period of 52 weeks (Fig. 5). Therefore, we have to determine the order of the doliolid abundance process. We tested the significance of models of order 1 versus the independence model, and order 2 versus order 1 models. Models were

also fitted separately to the 1967-1979 and to the 1980-1990 data: high abundance levels of doliolids became more frequent and more pronounced after 1979, as shown by a significant Kolmogorov-Smirnov two-sample test ($D_{max} = 0.289$, with an associated probability of 0.007). Table 2 shows that models of order 1 are clearly significantly better than independence models, but that order 2 models are not significant. Thus, knowledge of

Table 2

Significance levels (likelihood ratio test) for nested models M0 (independence model), M1 (order 1 model) and M2 (order 2 model) fitted to the complete series (67-90), to the 67-79 data and to the 80-90 data.

	67-90	67-79	80-90
M1 versus M0	p<0.001	p<0.001	p<0.001
M2 versus M1	NS	NS	NS

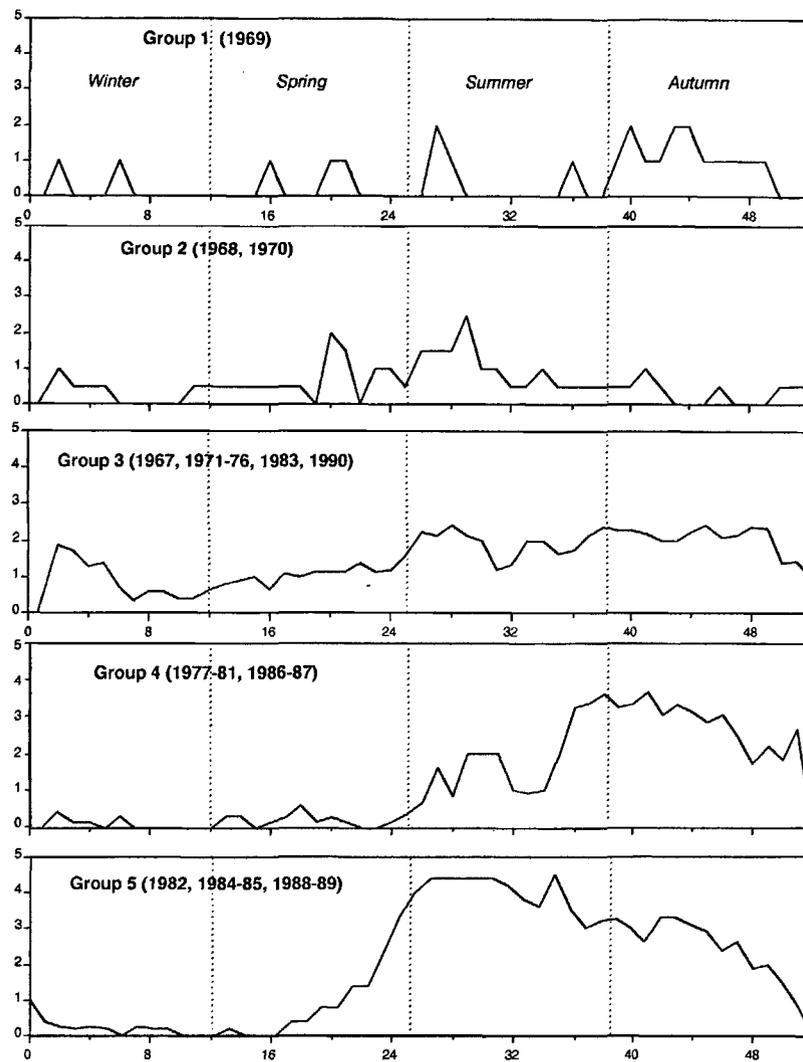


Figure 4

Mean annual patterns of the five groups of years identified by cluster analysis. X axis: weeks, Y axis: doliolid abundance in Frontier's scale.

the abundance of the two previous weeks adds no more information than did knowledge of the abundance of the preceding week. Furthermore, two separate order 1 models fitted to the 1967-1979 and 1980-1990 data significantly improve the likelihood of the data (likelihood ratio test, $p < 0.01$). This is due to a difference in the abundance process before year 1980 and after.

The influence of environmental covariates (hydrological and meteorological variables) was assessed on a one-by-one basis, using models of order 1. Models were fitted either to the whole time series, or to the 1967-1979, or 1980-1990 data. Table 3 presents the variables detected as significant. Significance levels and the sign of the coefficient of the environmental covariate estimated by the model are shown. Symbol '+' means that the higher the value taken by the significant covariates, the higher the probability of observing a high abundance state. Conversely, '-' means that the higher the value taken by the significant covariates, the lower the probability of observing a high abundance state.

Most of the significant covariates are detected by the model fitted to the 1980-1990 data. Only surface salinity and

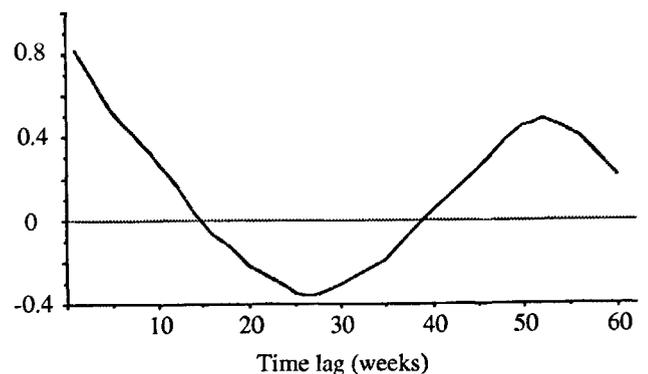


Figure 5

Spearman rank autocorrelation function computed from the ordinal time series of doliolid abundance.

index of mean wind have significant influence on the 1967-1979 period. Estimated coefficients of sea-surface temperature, density, stability index of the water column, air temperature and irradiance are positive, although coefficients of sea temperature at 75 m, salinity, and

Table 3

Hydrological and meteorological covariates detected as influential by the model M1. Sign of the parameter (see text) and significance level (in brackets) of the likelihood ratio test.

Periods	1967-90	1967-79	1980-90
Hydrological covariates			
Temperature 0 m	NS	NS	+ (*)
Temperature 75 m	NS	NS	- (*)
Salinity 0 m	- (*)	- (*)	- (*)
Salinity 10 m	NS	NS	- (*)
Salinity 20 m	NS	NS	- (*)
Density 75 m	NS	NS	+ (*)
Stability D50-D10	+ (*)	NS	+ (*)
Stability D30-D10	NS	NS	+ (*)
Meteorological covariates			
Air temperature	+ (*)	NS	+ (*)
Irradiance	+ (*)	NS	+ (**)
Mean wind velocity	- (*)	- (**)	NS

NS: non significant, * $p < 0.05$, ** $p < 0.01$.

mean wind intensity are negative. To illustrate the manner in which significant covariates influence the occurrence of high doliolid concentrations, we have computed several transition probabilities as functions of salinity and air temperature. Probabilities were computed from the parameter estimates in the corresponding models, with covariates varying within their observed range. For example, $P_{3,\geq 3}(z)$ is the probability of transition from abundance class 3 at time $t-1$ to class 3 or above at time t , when the value taken by the covariate is z at time $t-1$. This transition probability corresponds to the probability of sustained high concentrations of doliolids. Figure 6 illustrates the influence of sea-surface salinity and salinity at 20 m: high values of salinity lead to lower transition probabilities $P_{3,\geq 3}(z)$ of remaining in a high abundance class (3 or above). At greater depths, the range of observed variations in salinity is narrower, but the rate of change of the transition probability as a function of the variable is higher. Figure 7 presents the effects of air temperature: increasing air temperature values lead to increases in probabilities of initiating high doliolid concentrations ($P_{1,\geq 3}(z)$, $P_{2,\geq 3}(z)$) and in probabilities of lengthening their durations ($P_{3,\geq 3}(z)$, $P_{4,\geq 4}(z)$).

DISCUSSION

To tackle properly the ecological significance of our results concerning the statistical influence of environmental variables on doliolid abundance, we first discuss some characteristics of the doliolid populations in the Bay of Villefranche and their seasonal distribution.

Doliolid populations

The regular presence and high abundance of *Doliolitta gegenbauri* within the Bay of Villefranche is linked to the oceanic character of its plankton fauna. Doliolids

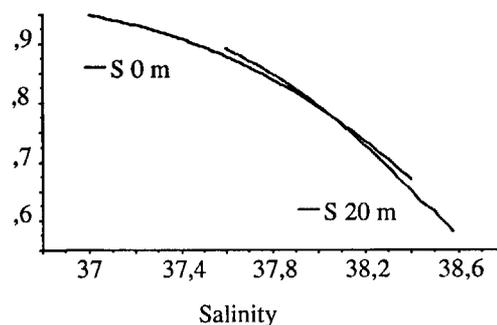
Probability $P_{3,\geq 3}$ 

Figure 6

Influence of salinity at sea surface and 20 m depth on transition probability $P_{3,\geq 3}(z)$ of remaining in high doliolid abundance.

Probability

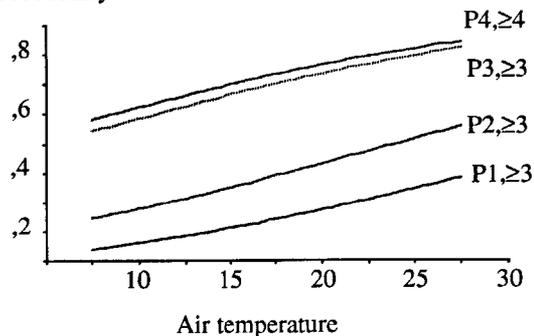


Figure 7

Influence of air temperature ($^{\circ}\text{C}$) on transition probability $P_{1,\geq 3}(z)$ and $P_{2,\geq 3}(z)$ of initiating high concentrations of doliolids, and on $P_{3,\geq 3}(z)$ and $P_{4,\geq 4}(z)$ remaining in high doliolid abundance.

are abundant offshore in the Liguro-Provenal current (Tregouboff, 1965; Boucher *et al.*, 1987), but very rare in the central zone of the Ligurian Sea. *Doliolum nationalis* has a more coastal distribution than *D. gegenbauri*, and develops intense swarms in zones influenced by fresh-water input, such as estuaries: *i.e.* Loire and Gironde in the Bay of Biscay (Beaudouin, 1971a, 1971b, 1972), Gulf of Lions influenced by Rhône river in the Mediterranean Sea (Braconnot and Casanova, 1967). These authors have shown that these peculiar ecological conditions lead to the development of a particular sexual stage (gonophorozoid), whereas, normally, asexual reproduction of the phorozoids gives rise to blooms (named the "short cycle" by Braconnot, 1967). Doliolids are epipelagic species. For example, in Southeastern Florida, Paffenhöfer *et al.* (1991) found doliolids in the upper part of the water column, with concentration in the thermocline or near the bottom in shallow water. In the Bay of Villefranche, the zooids are epipelagic organisms also, located mainly above the thermocline (Braconnot, pers. comm.). A large proportion of them must have been caught in our hauls from sea surface to 75 m, except during early winter when the thermocline dips below one hundred metres. Thus, the abundance levels we have recorded, usually many orders of magnitude less than the values commonly observed in the Atlantic, must be considered as typical of the oligotrophic Mediterranean Sea.

Seasonal distribution of doliolids

Except in particular years, doliolids appear to be characteristic organisms of the second half of the year in the Bay of Villefranche, maximum abundance values being observed in the warm months. A strong seasonality of population abundance, similar to that observed in the Bay of Villefranche, was recorded in the Northeastern Atlantic (Colebrook, 1964; Hunt, 1968). In the southwestern part of the British Isles, *D. gegenbauri* may be present from May to September. Plankton recorder pluriannual averages published in the *Annales biologiques* series show maximum values in July (*see, for example, Robinson, 1976*). In some years, maximum abundance was recorded in October and November (Harper, 1976). In her extensive survey of the plankton fauna of the Bay of Biscay during 1964, Beaudouin (1971a) observed *D. gegenbauri* mainly in spring, and blooms of *D. nationalis* in summer and autumn. A different seasonal distribution was recorded off Southeastern North America (*see the review of Paffenhöfer et al., 1995*), with a period of frequent occurrence and swarming from mid-winter to summer. This situation may be linked to peculiar hydrodynamical conditions such as frontal eddies, Gulf Stream intrusions and upwelling systems above the continental shelf (Deibel, 1985). A similar condition was recorded off Western Africa, where doliolid populations are driven by coastal upwelling (Binet, 1976). All these kinds of dynamic structure are able to increase primary production level and to alter seston composition.

Characteristics of environmental variables in the Bay of Villefranche

Environmental variables introduced in the model are classified in three different groups:

- The first group corresponds to the seasonal air-ocean thermal exchange, essentially during the period of negative thermal flux. It includes irradiance, air temperature, sea-surface temperature and stability of the water column. Sea-water density is inversely correlated with temperature.
- The second group represents the salinity fluctuations of the water column related to fresh-water input.
- The third group characterizes high-to-low atmospheric pressure oscillations and (inversely related) wind velocity.

Correlations within groups are very strong ($0.72 < r < 0.98$), whereas groups of variables are quite uncorrelated. For example, sea-surface temperature is not significantly correlated with surface salinity ($r = 0.02$). Correlations of these variables with wind stress index are low (0.13 and 0.07, respectively).

Meaning of significant environmental variables on the doliolid abundance process

The influence of the environmental covariates on the transition probabilities is restricted to the second half-year (from weeks 25 to 51 only) in our statistical analysis. During the first half-year, large changes in salinity, temperature and vertical stratification of the water column

may occur, when the doliolid population level remains low and steady. Then, to take into account the whole year data series depresses the statistical significance of the tests. Furthermore, our data processing choice is not very effective in quantifying the short-term effects (from hours to days) of isolated transient occurrences, such as gales or other extreme meteorological events.

Seasonal thermal exchange

The sign of the regression coefficients of the significant covariates that belong to the first group (air temperature, irradiance, sea-surface temperature and stability indices at different depth) is consistent with bloom occurrence, particularly frequent in July and August, when these environmental covariates are maximum, and later in the year, when covariate values decrease. The adverse significant effect of sea-water temperature at 75 m depth is probably a spurious correlation effect, due to delayed sub-superficial water warming, mainly during November and December.

The conditions which are typical from summer to autumn and which are favourable to doliolid populations are the most oligotrophic ones of the year (Nival, 1971). The regenerated production system is then involved (Sournia, 1973) through the microbial loop. During these periods, doliolids may dominate the zooplankton biomass. In the crustacean fauna, *Penilia avirostris* (Cladocera) is dominant over copepods, which are usually very scarce (Fernex *et al.*, in press). The frequently-reported (Deibel, 1985, Paffenhöfer *et al.*, 1995 for more references) exclusion of crustacean zooplankton during doliolid blooms is obviously related to low export potential of the microbial ecosystem.

Low-salinity events

The significant adverse effect of salinity underscores the changes induced in the upper-layer ecosystem by seasonal swellings of coastal rivers and water runoff mainly due to storms. The occurrence of halocline formation is generally associated with the annual doliolid population rise in early summer, and with the last new developments in late autumn. In fact, the link between perceptible halocline formation and doliolid abundance increase is generally striking. In 1992 (a year not included in the present study), the population increase of *D. gegenbauri* occurred late in May (weeks 18 to 21) (Braconnot, pers. comm.), just after a period of haline stratification (weeks 17 to 20). Similar episodes occurred in June, September, October and early December, and were closely followed by an increase in abundance of either or both *D. gegenbauri* and *D. nationalis*. The phytoplankton pigment signatures of the main algal groups was analysed at the same station during the same year (Bustillos-Guzmán *et al.*, 1995). Increases in chlorophyll concentration and changes in algal composition occurred during the low-salinity events. Algal composition and the related zooplankton community structure may deserve a careful re-examination, but this lies outside the scope of the present work. We merely note that both diatom and cyanobacteria biomass have increased in the less-saline upper layer. Furthermore, during the stratified

period and doliolid blooms, small-sized nanoflagellates and prochlorophytes were abundant. These results corroborate the ability of doliolids to harvest the smallest organisms involved in the microbial loop.

Wind effects

The increasing abundance of Thaliacea (Paffenhöfer and Lee, 1987; Ménard *et al.*, 1994) and of Appendicularia (Taggart and Frank, 1987) observed in coastal zones has been interpreted as a result of wind-driven shoreward advection of water. Here, high wind velocities have a negative effect on doliolid abundance in the Bay of Villefranche. Wind-induced turbulence in the upper layer of the sea inhibits the stratification of the water column and makes for a pumping effect on nutrients through the thermocline (Klein and Coste, 1984). Such conditions lead to a shift towards a new production system with diatom population increase, as seen with wind-induced coastal upwellings in the Bay of Villefranche (Bustillos-Guzmán *et al.*, 1995). On the other hand, turbulence appears to weakly influence the microbial ecosystem; it enhances copepod grazing, which is efficient on diatoms, and should give advantage to the classical food chain over the microbial ecosystem rule (Kiorboe, 1993).

Interannual variations

The interannual variations of doliolid abundance may be explained by climatic and hydrological changes. Air-temperature and wind-regime records from Cap Ferrat show large interannual changes (Fromentin and Ibanez, 1994). Air-temperature during the July-August period increases by more than 1.5°C between 1980 and 1991. The sea-water temperature in the Bay of Villefranche changes

accordingly. During the 1980-1990 period, characterized by higher doliolid abundance, sea-water temperature was between 0.73°C (20 m depth) and 0.40°C (75 m depth) higher in mean than during the 1967-1980 period (these differences are statistically significant). The same phenomenon was also recorded in the Bay of Naples (Mazzochi and Ribera d'Alcalà, 1995). Nevertheless, no significant changes in stability indices were observed, due no doubt to the counterbalancing effect of increasing mean salinity values (0.10 psu, highly significant) on sea-water density at all depths of the water column. However, as regards the effect of the interannual salinity trend, doliolid abundance is to some extent influenced by events of low salinity. Such events, usually lasting several weeks, still occur during the 1980-1990 period. Another very dramatic change appeared in the wind regime. A 50% regular decrease trend in the yearly number of windy days was observed from the late 1960s to the early 1990s. The special years of low doliolid abundance and flat seasonal cycle are also among the most windy years (1968-1971).

In conclusion, the time series of doliolid abundance illustrates just one among the various effects of the changing climate on the pelagic ecosystem structure (Cushing and Dickson, 1976; Jossi and Goulet, 1993; Fromentin and Planque, 1996). The processes currently working in the Northwestern Mediterranean Sea clearly favour the microbial loop-based ecosystem, known to be inefficient to support fish production (Mann, 1993).

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