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Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea. Prediction by climatic variables

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Abstract—The archives of the Station Zoologique at Villefranche-sur-Mer contain records of "years with *Pelagia noctiluca*" and "years without *Pelagia*". These records, plus additional data, indicate that over the past 200 years (1785–1985) outbursts of *Pelagia* have occurred about every 12 years. Using a forecasting model, climatic variables, notably temperature, rainfall and atmospheric pressure, appear to predict "years with *Pelagia*".

INTRODUCTION

POPULATION densities of marine planktonic species are known to fluctuate with time and place. Although at first annual variations monopolized the attention of biologists, interest currently is focused on longer term variations, generally within the context of hydrology and climatology: e.g. the Russell cycle (CUSHING and DICKSON, 1976), El Niño (QUINN *et al.*, 1978), and upwellings on the western coasts of continents (CUSHING, 1971).

We are concerned here with fluctuations in the population of the Scyphomedusa *Pelagia noctiluca* (Forsskål, 1775). *Pelagia noctiluca* can reach a diameter of 12 cm; with a carnivorous level. In contrast to the other Scyphomedusae, it completes its life-cycle without any fixed stage.

In the western Mediterranean Sea, the records of the Station Zoologique at Villefranche-sur-Mer (France), from 1898 to 1916 (GOY, 1984; MORAND and DALLOT, 1985) give evidence of the occurrence of "years with *Pelagia noctiluca*" and "years without *Pelagia*". During the years with medusae, the *Pelagia* can be so abundant that the phenomenon is referred to as a "bloom".

Many earlier authors have noted swarms of individuals, sometimes described as "a soup of medusae" (UNEP, 1984). During periods of bloom, swarms of individuals, pushed by winds and local currents, reach the coast and cause trouble to fisheries and tourism.

The sudden and local aspects of *Pelagia* infestations have led many specialists in Mediterranean marine biology (UNEP, 1984) to conclude that "presence–absence" characterizes the annual variation of this species. We used this behaviour to establish a pelagic biological series of binary nature, over a very long period. This series, dealing with one species and for more than two centuries, is a new approach to research in the

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field of plankton studies. A temporal scale of the *Pelagia* bloom phenomenon was then correlated to climatic patterns. This type of analysis can reveal major oceanic and biological fluctuations in the western Mediterranean Sea, although on a less spectacular scale.

METHODS AND RESULTS

Chronological data of Pelagia noctiluca *in the Mediterranean*

In order to deduce a chronological record of the dates of observations and sites of collections of *Pelagia*, we first extract and then analyse 55 published data sources (Table 1) as well as collections from the British Museum (Natural History), the Musée Océanographique at Monaco, the Muséum National d'Histoire Naturelle in Paris, the archives of the Station Zoologique at Villefranche-sur-Mer and from various other sources, all listed in the Appendix.

Examining Table 1, three major points appear: (1) The *Pelagia* blooms have been noted for more than 200 years. (2) The groups of "years with *Pelagia*" seem to occur with a certain pattern of regularity. (3) During the blooms that have been described with the most accuracy (1908–1913 and 1982–1985), the entire western basin of the Mediterranean Sea seemed to be invaded at once. Thus we suggest that any observation of an occurrence, however isolated, may indicate a *Pelagia* bloom in the whole western basin. [We note that the Adriatic Sea seems to have been infested only five times during the past two centuries; that is the reason that it is excluded from our analysis. Perhaps its occurrence in the Adriatic does not have the same explanation (BENOVIC *et al.*, 1987).]

In order to obtain a single valid series for the whole western basin from Table 1, any single or multiple observation is taken to define a "year with *Pelagia*". On the other hand, years without recorded observations are considered to be either "years without *Pelagia*", if they fall during periods of regular monitoring and scientific observations by the Marine Stations at Naples and Villefranche, or as missing data if no observations were recorded. To minimize this latter problem in our statistical treatment, only data for the years 1875–1986 have been used.

Periodicity in the Pelagia *series by the contingency periodogram method*

The periodicity of "years with *Pelagia*" has been studied using the contingency periodogram method (LEGENDRE *et al.*, 1981), which allows for the existence of missing data. This data treatment, carried out for the 112 years between 1875 and 1986, with 93 data points (53 occurrences, 40 known absences and 19 cases of a lack of information) shows a periodicity (significant at the $P = 0.01$ level) of about 12 years, as well as harmonics at 24, 36 and 47 years and other secondary periodicity under the level of significance (Fig. 1).

Forecasting "Pelagia-*years*" *by means of climatic variables*

The most complete long-term meteorological series obtained from the Meteorological Observatory of Genoa in Italy (FLOCCHINI *et al.*, 1983) was selected for our analysis. The method used to build the forecasting model was conceived to reduce the number of estimated parameters required. The principal component analysis, based on 112 years of observations (1875–1986), was performed on a correlation matrix of 18 meteorological variables: temperature, log rainfall and atmospheric pressure, for six pairs of successive

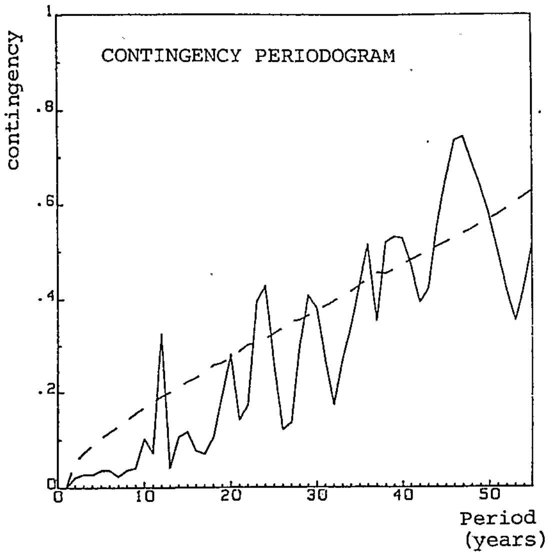

Fig. 1. Contingency periodogram calculated for the *Pelagia* series for 112 years (1875–1986), showing a periodicity of about 12 years in the western Mediterranean Sea (significant at the 1% level in broken line).

months. The first seven principal components were retained. The forecasting model was then used to attempt to correlate principal climatic components (as input) to the probability of occurrences of a "*Pelagia*-year" (as output). Three stages were needed to construct this forecasting model:

(1) A cubic polynomial distributed lag model (MALINVAUD, 1978) was used to describe the lag effects of each climatic component. This model provides a curve of various time-lag effects, which can include a combination of successive positive and negative effects. Assuming the time-lag effect curve and its first derivative both reach zero value for the (maximum lag +1) h, a climatic component C lag effect at year t can be rewritten as

$$z_{(t)} = a\left[\sum_{i=1}^{h} (i^3 - 3\,ih^2 + 2\,h^3)c_{t-i}\right] + b\left[\sum_{i=1}^{h} (h-i)^2 c_{t-i}\right], \qquad (1)$$

where h, a and b remain the only three parameters to be estimated. This specification is far better than a simple regression when values from more than 3 years are taken into account.

(2) Lag effects of several climatic components are combined and added.

(3) Finally, combined lag effects act on the probability P (t) of a "*Pelagia*-year" occurrence, by a logistic transformation characterized by a more or less marked threshold effect, controlled by an additional parameter b_0:

$$P_{(t)} = 1/1 + \mathrm{e}\left[-b_0 - \sum_{j=1}^{n} z_{j(t)}\right], \qquad (2)$$

where n climatic components are taken into account. [Z (t) is described by equation (1).]

Table 1. *Chronological data of* Pelagia noctiluca *in the western basin of the Mediterranean and the Adriatic Seas (the numbers correspond to the 55 mentions in the Appendix)*

	Balearic Is.	Algeria	Toulon	Nice	Villefranche	Monaco	Genoa	Naples	Messine	Palermo	Adriatic Sea	Mediterranean
1775	1											
1780												
1785									2			
1790												
1830								3	4			
1831												
1832												
1833												
1834												
1835												
1836												
1837												
1838												
1839				5								
1840												
1841												
1842		4							6			
1843											7	
1844												
1845												
1846												
1847												
1848												
1849								8				
1850												
1851												
1852									9			
1853									9			
1854									10			
1855												
1856												
1857												
1858												
1859												
1860												
1861												
1862												
1863												
1864												

	Balearic Is.	Algeria	Toulon	Nice	Villefranche	Monaco	Genoa	Naples	Messine	Palermo	Adriatic Sea	Mediterranean
1865												
1866												
1867												
1868												
1869												
1870								11				
1871												
1872												
1873												
1874												
1875								12				
1876				13				12			13	
1877							14	12, 15	16			
1878												
1879								17				
1880												
1881												
1882									18			
1883												4
1884												
1885						20						
1886												
1887												4
1888								21				
1889												
1890								22				
1891								23, 24				
1892												
1893												
1894												
1895											25	
1896												
1897												
1898					26							
1899					26							
1900					26							
1901					26					4		
1902					26							
1903					26					4		

1904											
1905											
1906											
1907											
1908					26					27	28
1909				29	26	30					28
1910					26					25	28
1911					26, 31					25	
1912					26						
1913										15	
1914										32	
1915									33		
1916											
1917											
1918											
1919											
1920											
1921											
1922											
1923		34									
1924		36									
1925			t								
1926											
1927					38						
1928					39						
1929											
1930											
1931											
1932											
1933											
1934											
1935	t										
1936											
1937					t						
1938					t						
1939								40			
1940											
1941								40			
1942					t						
1943					t						
1944					t						
1945		t									
1946					t						
1947					t						
1948											
1949					22						
1950											
1951											
1952											
1953											
1954											
1955											
1956											
1957			44, 45		41, 42		43	46			
1958					47		43				
1959					T48						
1960					49						
1961											
1962											
1963											
1964											
1965											
1966											
1967											
1968			50								
1969			51		52						
1970					52						
1971											
1972											
1973											
1974											
1975											
1976											
1977										53	
1978										53	
1979										53	
1980										53	
1981										53	
1982					53	53					
1983	54				53						
1984	54				53						
1985					55						

Fifty-five publications and *t* = answers to inquiries.

Parameters were estimated by fitting the model (equation 2) to the *Pelagia*-year time series (1884–1986). This includes 88 cases of known data, the 15 missing ones simply being omitted. A preliminary least-squares estimation was obtained on the linear form of equation (2) (Cox, 1972), then final optimization was realized on the logistic form using the Berndt–Hall–Hall–Hausman iterative algorithm (Gourieroux, 1984) based on log-likelihood maximization.

A step-by-step upward procedure was used to choose and progressively introduce new climatic components into the model. At each step, the more active component was retained and its particular new contribution was tested by comparing the new log-likelihood criterion with the preceding one (Anderson, 1982). The procedure was stopped when the criterion increase was not significant (at the $P < 0.05$ level). This method retained a model based on four climatic components, corresponding to 12 (4×3) parameters added to the threshold parameter b_0.

Figure 2 shows the "years with *Pelagia*" and their probability of occurrence as predicted by the model. The long-term probability fluctuations are seen to agree well with recorded observations of *Pelagia*, except for the 1935–1941 period where the model fails completely to predict the occurrence of the medusae.

The quality of the model was evaluated by the log-likelihood ratio:

$$2\ln\,(M_f/M_0),$$

where $\ln\,(M_f)$ is the log-likelihood finally obtained (= –42.2) and $\ln\,(M_0)$ the log-likelihood of the null hypothesis (= –60.6), computed as in Anderson (1982). The value obtained (=36.8) is significant at the $P < 0.001$ level in the chi-square distribution, with 12 degrees of freedom. However, we recognize that such a level of significance must be accepted with caution, because the successive data in the *Pelagia* time-series are obviously not independent.

From the 12 above-estimated parameters, the coefficients directly applied to original meteorological variables can be reconstituted, since we know the weights of these in principal components. This type of computation yields a great number of non-independent coefficients, represented by the figure for six pairs of months during the eight preceding years, for each type of climatic variable (Fig. 3). (Further details on the model will be described in a future publication.)

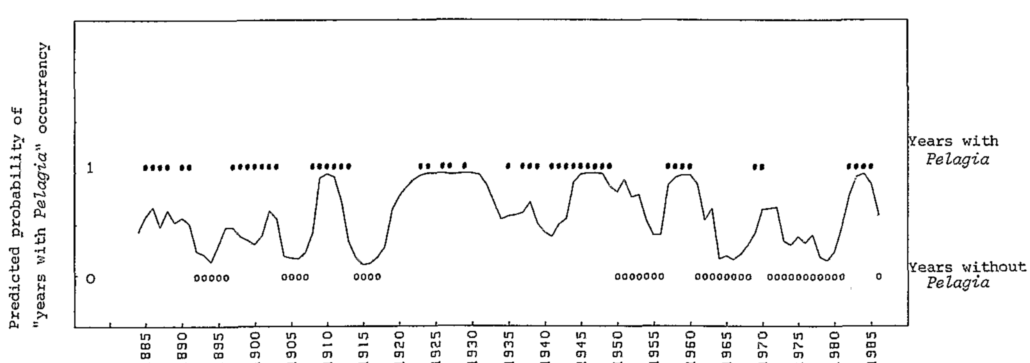

Fig. 2. *Pelagia*-years 1885–1986 (solid circles indicate years with *Pelagia*, open circles indicate years known to be without *Pelagia*) and the predicted probability of their occurrence as estimated by the model (solid line).

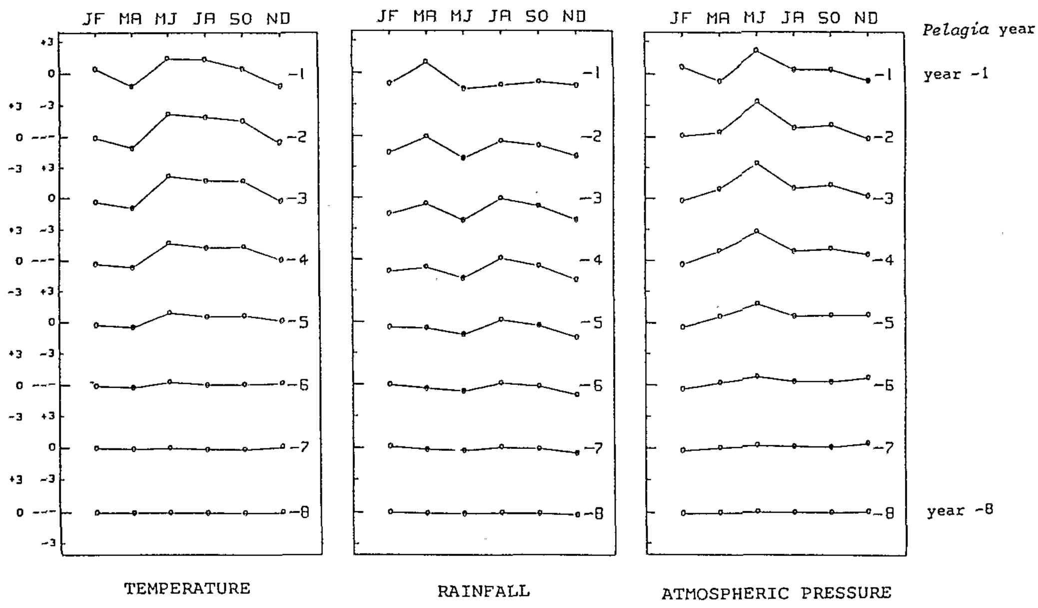

Fig. 3. Relative weight (as a percentage of the sum of the absolute values of weights in the model) applied to the different variables: temperature, rainfall and atmospheric pressure, for the eight years taken into account in the forecast, since a value of eight has been estimated for the lag parameter by the iterative fitting procedure based on log-likelihood maximization.

DISCUSSION

A basis for discussion of the model in physical terms is provided in Fig. 3. A general lack of rainfall, associated with high temperature and atmospheric pressure from May to August, appears to be the best predictor of a *Pelagia*-year occurrence. These combined anomalies can be interpreted in the Mediterranean climatic area as an excess of anticyclonic meteorological situations (high pressure), mainly during the late spring–early summer. Several different hypotheses may be drawn from this result:

(1) First, it is of some interest to note that the reproductive period of *Pelagia noctiluca* in the Mediterranean Sea corresponds to the May–November season (UNEP, 1984). Fine weather during this period no doubt has a favourable effect on reproduction, either by decreasing larval mortality caused by vertical mixing or by some unknown intermediate trophic processes such as an increase in microzooplankton production, the major food at the ephyrae larval stage.

(2) However, the lag effects estimated for a considerable period, for all three meteorological variables—temperature, rainfall and atmospheric pressure—(Fig. 3), make a very indirect link more likely, due to an impact of the climate on the western Mediterranean hydrodynamics in general. Indeed, Bethoux and Prieur (1983) showed that large-scale superficial circulation in the Mediterranean Sea is controlled by regional water inflow. Moreover, it is known that certain pelagic physical structures, such as an oceanic front, often are associated with circulation (Boucher *et al.*, 1987). Hence, a longer causal chain possibly exists, correlating climate to oceanic circulation, physical

structure, pelagic production and, finally, the appearance and maintenance of a *Pelagia* population.

This discussion, however, should not be considered as a definitive causal explanation, owing to the atmospheric nature of explicative variables and the structure of the model. Nevertheless there is a logistic transformation (which provides a realistic threshold effect) though it does not take into account the autocorrelative structure of the *Pelagia* time series and so neglects ecological stability. Unfortunately, the relatively small amount of "real" information (eight periods with *Pelagia* separated by seven periods without *Pelagia*) prevented the construction of a greater and more sophisticated model.

The above results, combined with other recent studies (Morand and Dallot, 1985; Laval *et al.*, 1989), indicate that certain major components of the Mediterranean pelagic ecosystem exhibit relatively regular pluriannual fluctuations (the appearance–extinction cycles), compared with some other species at the same trophic level, for example, herbivorous salps could alternate with appendicularians and carnivorous *P. noctiluca* with ctenophores. On a large spatial scale, the fluctuations of *P. noctiluca* could be correlated, at least partly, to certain climatic patterns. Further verification of causal events for these faunal fluctuations awaits future investigation of other inter- and pluriannual physical and biological events occurring in the Mediterranean, this supposedly well-known sea.

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APPENDIX

Chronological list of mentions of *Pelagia noctiluca* for Table 1.

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