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CLIMATE AND MEDITERRANEAN JELLYFISH: ASSESSING THE EFFECT OF TEMPERATURE REGIMES ON JELLYFISH OUTBREAK DYNAMICS

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ABSTRACT

We analyzed a 27-year time series of gelatinous carnivorous zooplankton occurrence to assess the effect of different temperature regimes on abundance. The relationship between temperature and population size of gelatinous carnivores is discontinuous and no statistical relationship was found for low temperature regimes. However, prolonged exposure to high temperatures did alter population outbreak dynamics. In particular, high temperatures and strong water column stratification were related significantly to the development of massive populations of gelatinous carnivores. These results underline the importance of gelatinous carnivorous zooplankton as ecological indicators of ecosystem change in the Mediterranean Sea.

Key words: climate change, Mediterranean Sea, temperature regime, gelatinous carnivorous zooplankton, outbreaks

CLIMA E MEDUSE MEDITERRANEE: VALUTAZIONE DEGLI EFFETTI DEI REGIMI DI TEMPERATURA SULLA DINAMICA DI ESPLOSIONE DELLE MEDUSE

SINTESI

Gli autori hanno analizzato una serie di 27 anni di segnalazioni di zooplancton gelatinoso carnivoro al fine di accertare l'effetto di differenti regimi di temperatura sull'abbondanza. La relazione fra la temperatura e la grandezza della popolazione dei carnivori gelatinosi è discontinua e non è stata riscontrata alcuna significatività statistica per regimi di bassa temperatura. In ogni caso, esposizioni prolungate ad alte temperature hanno alterato la dinamica di esplosione della popolazione. In particolare, alte temperature ed una forte stratificazione della colonna d'acqua sono state significativamente relazionate allo sviluppo massiccio delle popolazioni dei carnivori gelatinosi. Questi risultati sottolineano l'importanza dello zooplancton gelatinoso carnivoro quale indicatore ecologico di cambiamenti nell'ecosistema del mare Mediterraneo.

Parole chiave: cambiamenti climatici, mare Mediterraneo, regime di temperatura, zooplancton gelatinoso carnivoro, esplosioni

INTRODUCTION

Synergies between ecosystem degradation, overexploitation and climate change may drastically alter ecosystem dynamics as well as the resources and services they provide. Understanding how these factors interact to affect marine populations is a challenge for global ecology. In recent years, outbreaks of gelatinous carnivores have been documented in many coastal areas worldwide (Mills, 2001; Purcell, 2005). Although the occurrence of this phenomenon is a common feature of their population dynamics, the apparently enhanced recent increase in frequency and intensity of gelatinous carnivore blooms has warned scientists on the possible consequences (CIESM, 2001). Proliferations of gelatinous carnivore populations have a wide range of ecological implications, including alteration of entire plankton assemblages through both top-down and bottom-up effects (Pitt *et al.*, 2007; West *et al.*, 2009a, b). Their massive blooms also hamper fishing activities by clogging and bursting trawl nets (Graham *et al.*, 2003; Xiang *et al.*, 2005). They impact tourists through beach closures (Richardson *et al.*, 2009, and references therein), and their contact may cause allergic and toxic reactions in bathers (Burnett, 2009). The reported recurrent massive proliferations of gelatinous plankton during the last decade may alter the entire ecosystem dynamics (Hay, 2006).

There is also growing evidence that inter-annual and long term climate changes affect plankton communities and marine ecosystem (Hays *et al.*, 2005). The Mediterranean basin is affected by both subtropical and North Atlantic climates (Reddaway & Bigg, 1996) and it reflects secular trends of Northern Hemisphere temperature (Bethoux *et al.*, 1990). Quantifying the impact of climate regime changes on marine populations is needed to implement sound ecosystem management policies.

Here we evaluate a 27-year record of gelatinous zooplankton abundance in relation to temperature and demonstrate that high water temperature and size of gelatinous carnivore populations are related.

METHODS

Physical data. Averaged monthly data of sea surface temperature (SST) from 45˚ to 41˚ N, and from 0˚ to 20˚ E were used as a proxy of climate forcing. The dataset used was from the National Center for Environmental Prediction- National Center for Atmospheric Research (NCEP–NCAR) gridded reanalysis during the period 1950–2000 (Kalnay *et al.*, 1996). In addition, weekly water temperature records in the northern Ligurian Sea at 1, 20, 50, and 75 m depth, were used to investigate the long term variability of water column stratification.

Biological data. Data analyzed cover the years 1967 to 1993. Throughout this period, plankton was sampled at weekly intervals from a depth of 80 m (Point B: 43˚41′N; 7˚19′E) in the Ligurian Sea (north-west Mediterranean). Details of sampling locality are given in Molinero *et al.* (2005). Sampling was performed by means of vertical hauls of a zooplankton net (Juday-Bogorov, 330 µm mesh size) from bottom to surface. The gelatinous carnivores analyzed were the holoplanktonic hydromedusae *Liriope tetraphylla*, *Solmundella bitentaculata*, and *Rhopalonema velatum* and the siphonophores *Abylopsis tetragona* and *Chelophyes appendiculata*. All these species are common inhabitants of the Western Mediterranean basin. The mesh size of the net prevented assessments of individuals smaller than 330 µm, but the total number of samples collected was considerable (1405 samples), and consistency of sampling and quantification protocols produced a biological data set that we believe to be comparable through time.

Data analysis. Time series were log-transformed and analysed in standardized and non-dimensional form (*i.e.* zero mean and unit variation). Statistical analysis was performed using Matlab Software.

The inter-annual variability of seasonal SST gradient between winter (JFM) and summer (JAS) was calculated and used as a proxy of environmental variability. Long term records of SST identify alterations in pelagic ecosystems, particularly with changes in phytoplankton community structure (Richardson & Schoeman, 2004). We further calculate the thermal stratification of the water column as the average temperature difference m^{-1} of the 0–75 m depth layer.

The cumulative sum of the standardized time series (*z*-scores) was used to assess periods of similar variability. The method consists of plotting the cumulative sum of *z*-scores. Each data point, y_t, corresponding to time t (t from 1 to n) was added to the preceding data point. A constant deviation from the mean of the time series shows a constant slope on the chart, and interpretation is based on the slope of the line. Persistent changes from the mean of the time series cause a persistent change of the slope. The cumulative sum allows detecting in a simple way the timing of changes and homogeneous periods in a time series.

The effect size of temperature treatment on the gelatinous carnivore population was investigated for 1967-1993 and for each temperature regime identified. Pearson product moment correlations, as well as the probability density distribution of correlation coefficients after bootstrap resampling were computed. The analysis involved a random pairwise sampling with replacement where each time series was resampled 5,000 times. The number of elements in each bootstrap sample equals the number of elements in the original data set. The probability density distribution of the corresponding correlation coefficients was computed using nonparametric Kernel smoothing.

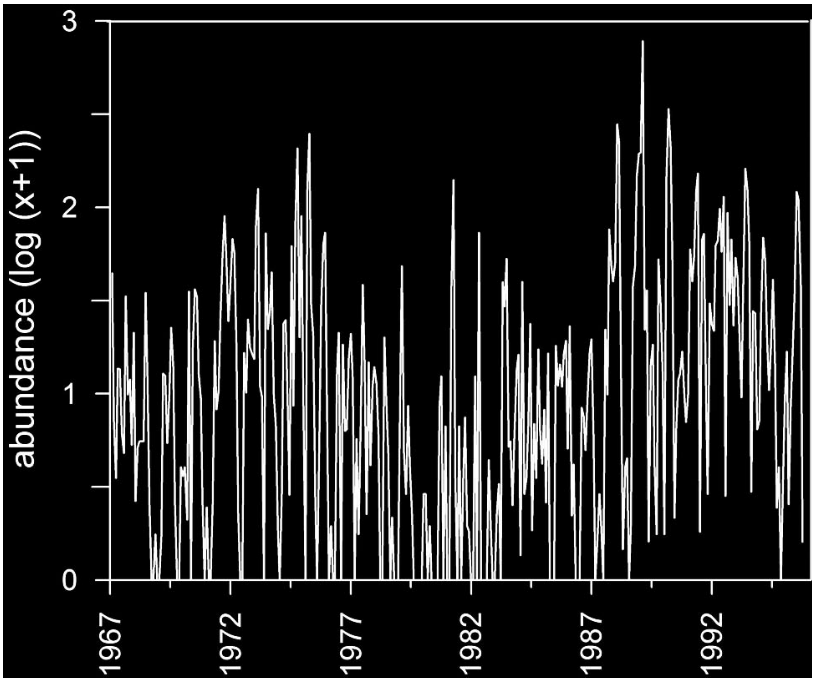

Fig. 1: Long-term variability of the abundance of holoplanktonic gelatinous carnivore species. Abundances are expressed as log_{10} (x+1).
Sl. 1: Dolgoročna variabilnost številčnosti holoplanktonskih želatinoznih mesojedih vrst. Številčnost je izražena kot log_{10} (x+1).

The dynamics of gelatinous carnivore outbreaks was assessed by means of peak-to-peak plots (Rinaldi *et al.*, 2001). The method consists in extracting from the time series, *y*, significant peaks (*i.e.* outbreaks), say y_i (i = 0, 1, 2, ...,n), and plot them one against the previous one, thus obtaining a set of points (y_i, y_{i+1}). The points in the peak-to-peak plot (PPP) lie on a closed regular curve (the slice of a torus) when the dynamics of the phenomenon is quasiperiodic and lie roughly on a curve when the attractor is a low-dimensional strange attractor.

RESULTS AND DISCUSSION

The inter-annual variability of the gelatinous carnivore community displays a high intermittency and two dome-shaped periods, before and after the early 1980s (Fig. 1). High abundances (peaks) indicating outbreaks were recorded throughout the investigated years. However, before the early 1980s, a higher number of events with low or null abundances were observed, whereas after the early 1980s permanently high values characterized the gelatinous carnivore abundance, and the number of events with low or null abundances was significantly reduced.

The inter-annual variability of the temperature difference between winter (JFM) and summer (JAS) in the northern Mediterranean over the second half of the twentieth century is shown in figure 2a. Values are expressed as standard deviations from the long term mean of the time series. The variability of the signal reveals two major regimes of temperature that were characterized by lower values than the long-term mean, from 1950 to the late 1970s, and higher ones after the early 1980s. A remarkably similar pattern is observed in the water column stratification during the years 1967–1993 (Fig. 2b), which also show generally low values before the early 1980s and higher values afterwards. The link between large- and local-scale temperature variability was statistically significant, as shown by the Pearson's correlation coefficient and the effective probability after correction for temporal autocorrelation (r = 0.66; p <0.05). The cumulative sum of z-scores depicted the main temperatures regimes that characterized the pelagic environment for gelatinous carnivores. Such regimes were used afterwards as treatment effect.

The relationship between variations in the population size of gelatinous carnivores and temperature is shown in figure 3a. Considering the whole period, the Pearson's correlation coefficient and the effective probability after correction for temporal autocorrelation were $r = 0.50$ and $p < 0.05$, respectively, although the probability density estimation of correlation coefficients obtained after bootstrap resampling (5000 times) revealed a high variability in the link (mean = 0.42; std = 0.30). However, analysis of the relationship during the regime of low temperatures does not provide statistical support

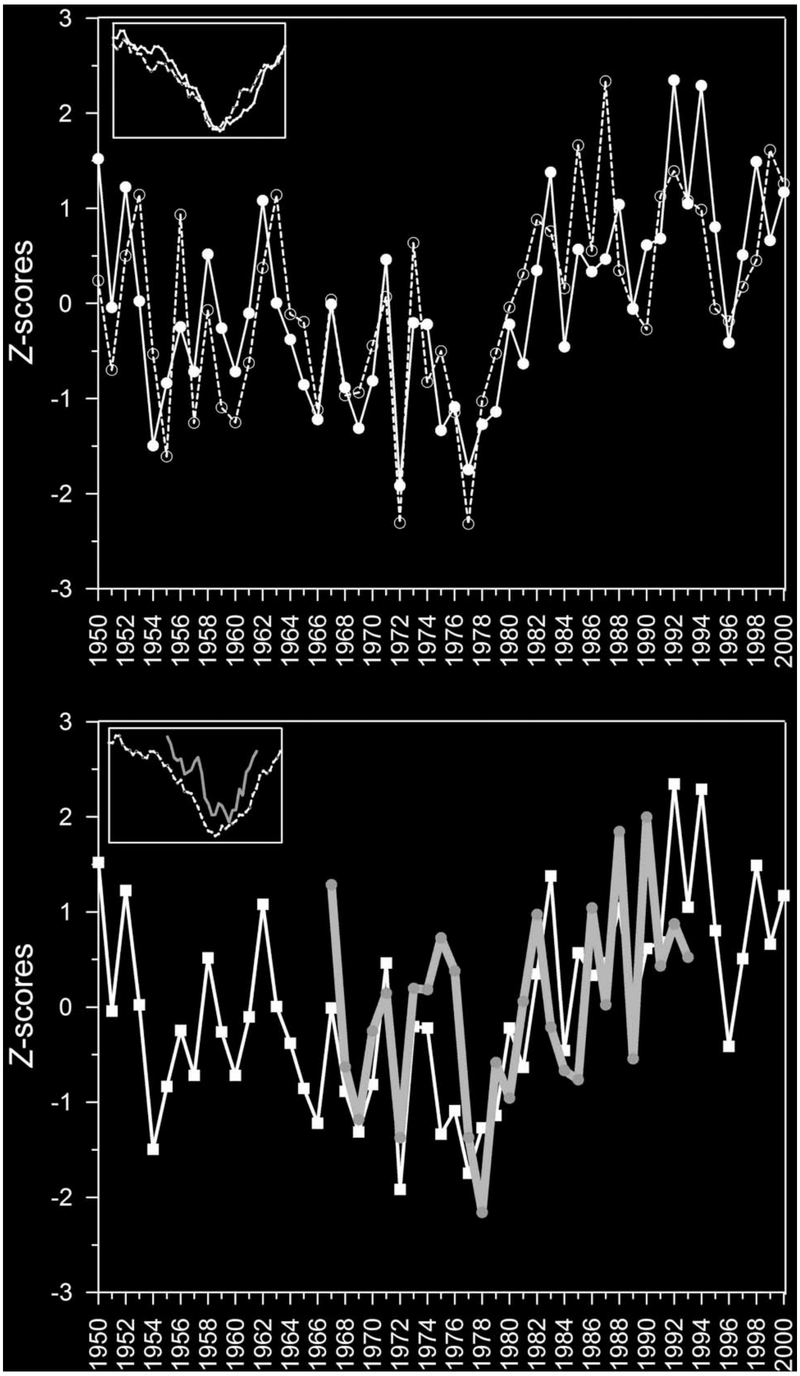

Fig. 2: (a) Inter-annual variability of the seasonal sea surface temperature (SST) gradient between winter (JFM) and summer (JAS). The time series was obtained from mean (dotted line) and maximum (continuous line) seasonal values. (b) Time series of SST gradient (mean values) and thermal stratification of the water column (0–75 m; grey line). The cumulative z-scores diagram of the time series (inset) illustrates the inflexion point that separates the two temperature regimes in the northern Mediterranean.

Sl. 2: (a) Medletna variabilnost gradienta sezonske površinske temperature morja (SST) med zimo (JFM) in poletjem (JAS). Časovni razpored je bil narejen na podlagi srednjih (črtkana črta) in najvišjih (polna črta) sezonskih vrednosti. (b) Časovni razpored SST gradienta (srednja vrednost) in termalne stratifikacije vodnega stolpa (0–75 m; siva črta). Kumulativni diagram časovnega razporeda (vloženi graf) prikazuje prevoj, ki ločuje dva temperaturna režima v severnem Sredozemlju.

Tab. 1: Relative abundance of gelatinous carnivore species in the thermal regimes investigated. The structure led by the species contribution to the total abundance is similar in the two periods, with* L. tetraphylla *and* R. velatum *as the dominant species in the two periods.
Tab. 1: Relativna številčnost želatinoznih mesojedih vrst v obravnavanih temperaturnih režimih. Struktura s prispevkom vrste k polni številčnosti je podobna v obeh obdobjih, z vrstama* L. tetraphylla *in* R. velatum *kot dominantnima vrstama v obeh obdobjih.

	Period 1 (1967–1980)	Period 2 (1981–1993)
Rhopalonema velatum	23.83	18.73
Liriope tetraphylla	61.19	57.12
Solmundella bitentaculata	3.81	9.55
Chelophyes appendiculata	6.77	11.39
Abylopsis tetragona	4.40	3.21

that variations in population size of gelatinous carnivores are related to temperature, as illustrated by the probability density estimation of correlations coefficients (Fig. 3a; mean = 0.26; std = 0.46). In contrast, during the high temperature regime the link was significantly enhanced and the population size changes were closely coupled to temperature variations (Fig 3a; mean = 0.57; std = 0.30). These results suggest that the relationship of gelatinous carnivores with temperature evolves according to the strength of climate signal. It is worth noting that the structure led by the species contribution to the total abundance is similar in the two periods, with *L. tetraphylla* and *R. velatum* as the dominant species in the two periods (Tab. 1).

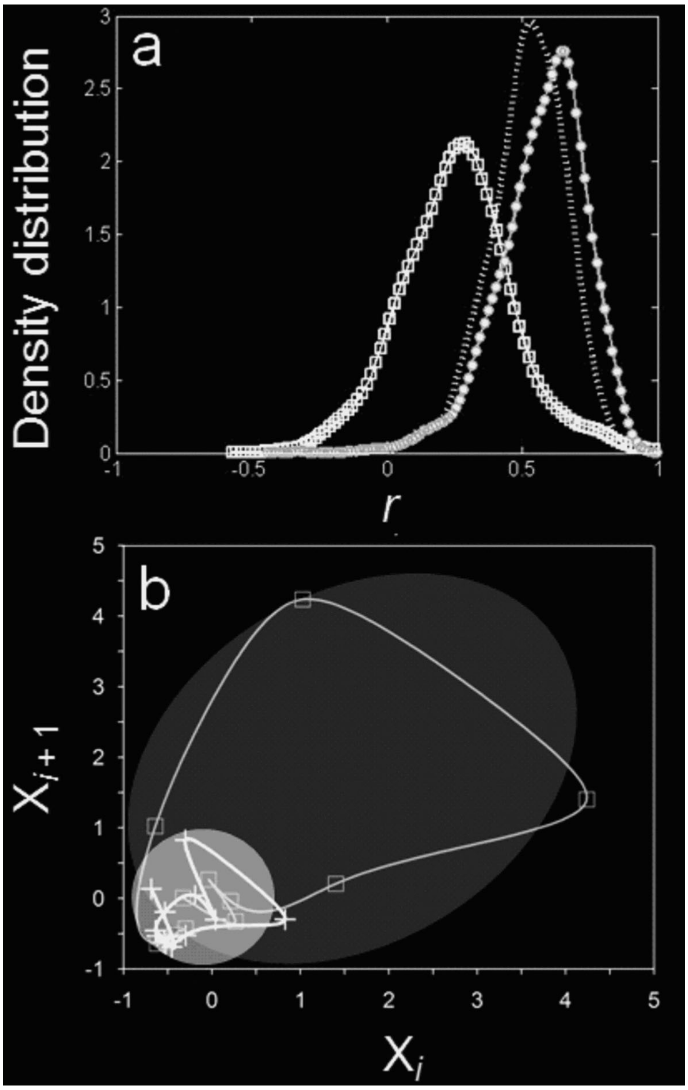

Fig. 3: (a) Probability density estimation of the correlation coefficients between temperature and the population size of gelatinous carnivores. The density distribution was obtained by bootstrap resampling (5,000 times) in the whole study period (dotted line) and in the two temperature regimes corresponding to the years 1967–1980 (low temperature: open symbols); and 1981–1993 (high temperature: filled symbols). (b) Long term dynamics of gelatinous carnivores outbreaks illustrated by the peak-to-peak plot, X_i, X_i+1, where X_i denotes a significant peak of abundance (e.g. outbreak) at time t and X_i+1 the next significant peak at time t+1. The dark circle illustrates the outbreak dynamics under the low temperature regime, whereas the ellipsoid points out the new outbreak dynamics under the high temperature regime.
Sl. 3: (a) Ocena gostote verjetnosti korelacijskega koeficienta med temperaturo in velikostjo populacije želatinoznih mesojedov. Podatki za distribucijo gostote so bili pridobljeni z bootstrap vzorčenjem z vračanjem (5000-krat) tekom celotne raziskave (črtkana črta) in v dveh temperaturnih režimih v letih 1967–1980 (nizka temperatura: kvadrati); in 1981–1993 (visoka temperature: polni krogci). (b) Dolgoročna dinamika masovnega pojavljanja želatinoznih mesojedov, prikazana z grafom vrhov X_i, X_i+1, kjer X_i označuje izrazit vrh številčnosti (npr. izbruh masovnega pojavljanja) ob času t in X_i+1 naslednji izrazit vrh ob času t+1. Temnejši krog prikazuje dinamiko masovnega pojavljanja v nizkem temperaturnem režimu, medtem ko elipsa prikaže novo dinamiko masovnega pojavljanja v visokem temperaturnem režimu.

Although no significant changes were observed in the contribution of species to the total abundance of gelatinous carnivore population, the peak-to-peak plot unveils contrasting dynamics depending on the temperature regime (Fig. 3b). The low temperature regime showed boom cycles that were roughly described by a circle of low diameter. Conversely, the long exposure to high temperature and to the concomitant associated water column changes (*i.e.* high stratification) allowed the significant change in boom cycles. Cycles were roughly described by an ellipsoid which dimensions were 5-fold higher than the cycles noticed during the low temperature regime.

Beside the direct effect that temperature changes may have on the population dynamics of gelatinous carnivores, the observed changes are likely related to concomitant effects of climate forcing on the pelagic environment of the western Mediterranean (Menard *et al.*, 1994). For instance, Gomez & Gorsky (2005) identified modifications in the western Mediterranean related to high temperatures and high atmospheric pressure that affected changes at the bottom of the food web *(i.e.* a flagellate dominance on the microplankton community). The high temperature regime was related to persistently high values of the North Atlantic Oscillation (NAO), particularly to the longest and higher positive phase over the twentieth century. The generally warm and stable water column associated with high temperatures after the 1980s has provided suitable environmental conditions for the development of gelatinous carnivore outbreaks (Molinero *et al.,* 2008), and substantially altered their outbreak dynamics. This is in accordance with previous investigations in the same area that found a positive relationship between the survival of gelatinous carnivore larvae and stratified water (Goy *et al.*, 1989; Buecher, 1999). These results suggest that the northern Mediterranean pelagic populations are potentially vulnerable to climate change and long term variations of gelatinous carnivore populations are indicative of ecosystem-state modifications.

In the global change context, climate projections suggest a dominance of the positive phases of the NAO (IPCC, 2007). This means that generally high atmospheric pressure, high temperatures and low wind stress are expected to dominate atmospheric conditions in the northern Mediterranean, which in turn point towards enhancement of water column stratification. As shown by our analysis, these conditions seem to alter the dynamics of gelatinous carnivore outbreaks, which may jeopardize the pelagic diversity and ecosystem function and resilience.

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PODNEBJE IN SREDOZEMSKE MEDUZE: OCENA VPLIVA TEMPERATURNIH REŽIMOV NA DINAMIKO MASOVNEGA POJAVLJANJA MEDUZ

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POVZETEK

Izvedena je bila analiza 27-letnega časovnega razporeda pojavljanja želatinoznega mesojedega zooplanktona, z namenom ocene učinka različnih temperaturnih režimov na številčnost. Razmerje med temperaturo in velikostjo populacije želatinoznih mesojedov je diskontinuirano, za nizke temperaturne režime pa ni ugotovljena statistična povezava. Je pa dinamiko masovnega pojavljanja populacije spremenilo podaljšano izpostavljanje visokim temperaturam. Še posebej visoke temperature in močna stratifikacija vodnega stolpa so izrazito povezane z razvojem masovnih populacij želatinoznih mesojedov. Ti rezultati kažejo na velik pomen želatinoznega mesojedega zooplanktona kot ekološkega indikatorja ekosistemskih sprememb v Sredozemskem morju.

Ključne besede: klimatske spremembe, Sredozemsko morje, temperaturni režim, želatinozni mesojedi zooplankton, masovno pojavljanje

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