2. Are the outbreaks of *Pelagia noctiluca* (Forsskål, 1775) more frequent in the Mediterranean basin?

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Introduction

In pelagic ecosystems, medusae are considered key predators, affecting zooplankton abundance and fish recruitment by preying on their larvae or competing for food (Purcell, 1997, 2003; Lynam *et al*., 2005). Thus, these gelatinous carnivores may be considered top predators as well as fish competitors (Purcell and Arai, 2001; Purcell, 2003). Several studies have demonstrated a significant increase in jellyfish abundance in different areas of the northern hemisphere, probably related to climate change and foodweb modifications (Brodeur *et al*., 1999; Mills, 2001; Lynam *et al*., 2004). *Pelagia noctiluca* is a holoplanktonic and oceanic, non-selective, top predator that exercises top–down control in marine foodwebs and whose importance in the Mediterranean Sea became evident in the early 1980s during the so-called "*Pelagia* years" (CIESM, 2001).

Pelagic ecosystems in the Mediterranean Sea, and specifically in the western basin, are extremely sensitive to the influence of North Atlantic climate (Molinero *et al*., 2005a). In this region, northern hemisphere climate patterns related to the North Atlantic drive the interannual variability of sea surface temperature (SST) and shape the prevailing northern hemisphere winter conditions.

To date, most relevant climate-related changes in marine ecosystems have been identified at high latitudes and in productive temperate seas, where the underlying mechanisms linking climate and oceanographic patterns have been recognized (Hare and Mantua, 2000; Beaugrand *et al*., 2002; Edwards *et al*., 2002). In northern European marine ecosystems, changes appear to be related to significant modifications in the North Atlantic ocean–atmosphere circulation, and were noticed particularly in the mid-1980s (Alheit *et al*., 2005). As the North Atlantic climate strongly affects atmospheric conditions in the western Mediterranean, similar forcing is expected to act on its hydrological structure and marine foodweb. Accordingly, coupling between the North Atlantic climate and the marine ecosystem of the Mediterranean is possible by using appropriate chronological records and statistical techniques (Molinero, 2008). In fact, downscaling methods of climate–ocean interactions have revealed close relationships between some copepods and jellyfish species in the western Mediterranean and climate variability in the North Atlantic (Molinero *et al*., 2005a, 2005b).

In this paper, we present an overview of the recent outbreaks of *P. noctiluca* in the Mediterranean basin, with the aim of assessing the potential link between climate oscillations and long-term changes in the abundance of *P. noctiluca*.

Material and methods

Information was taken from long-term records of *P. noctiluca* in four selected regions of the Mediterranean Sea (Figure 2.1):

1) The Balearic Sea, located in the western Mediterranean (WM), is characterized by a thermohaline circulation that is governed by meridional

exchanges between the relatively saline, cold, and nutrient-rich waters of the northern basin and the less saline, warmer, and more oligotrophic waters of the Algerian basin. This region is of interest because interannual changes in hydrographic patterns are indicative of basin-scale dynamics of the water masses.

2) The Gulf of Tunis is located in the southwestern Mediterranean. The region is under the influence of Modified Atlantic Waters (MAWs). Interannual variations in hydrographic features in the Gulf of Tunis may therefore be related to changes in the variability of the Algerian Current.

3) The Adriatic Sea is linked to the eastern Mediterranean by the Otranto Strait and is shallow in its northern part, with an average depth of 35 m. It is strongly influenced by the northern Italian rivers, particularly the Po River. The southern Adriatic is considerably deeper, with an average depth of 900 m. In the Adriatic, there are two different water mass formations:

   3.1) Northern Adriatic Dense Water, occurring in the northern half of the basin and formed during winter in the Gulf of Trieste;

   3.2) Adriatic Bottom Water (ABW), formed by mixing between the Ionian surface waters and the relatively warmer and more saline Modified Levantine Intermediate Water (MLIW) entering the southern Adriatic.

4) The Aegean Sea is a distinct subsystem of the eastern Mediterranean, with a very complex morphology characterized by an alternation of shallow and deep basins and a large number of islands, gulfs, and bays. The general circulation within the Aegean Sea is cyclonic; the highly saline (>38.8 psu) and very oligotrophic water of Levantine origin, dominant in the southern Aegean, travels northwards along the west coast of Turkey (Theocharis *et al.*, 1999). A surface layer of brackish (~30 psu) water is formed in the northeastern Aegean by the inflow of modified Black Sea Water through the Dardanelles Strait.

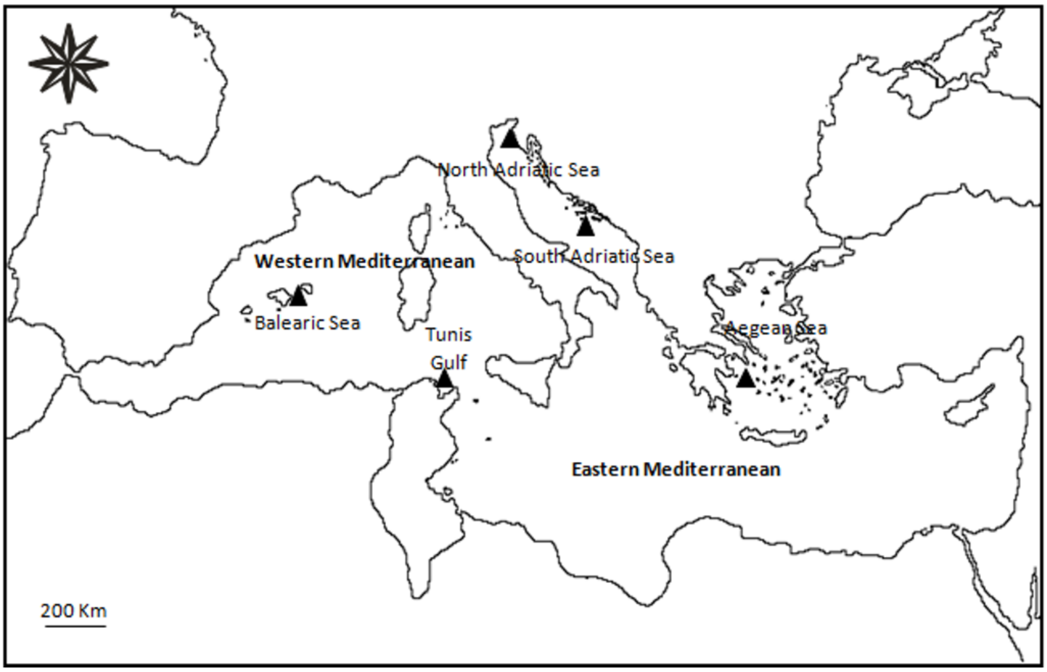

Figure 2.1. Map of the eastern and western Mediterranean basins showing the stations where *Pelagia noctiluca* was monitored and collected.

Biological data and sampling strategy

Pelagia noctiluca outbreaks were recorded semi-quantitatively in the Balearic Sea (1994–2008), the Adriatic Sea (1978–2006), and the Aegean Sea (1983–2008). The frequency of the observations varied between seasonal and monthly. In coastal waters of the Gulf of Tunis, quantitative records of *P. noctiluca* were collected between 1993 and 2008 by vertical tows (20 m to the surface) using a WP-2 net (200 µm mesh) and a handnet (estimated filtered volume 1000–5000 m^3 in surface and subsurface). The sampling frequency was monthly to weekly during *P. noctiluca* outbreaks.

Data analysis

The abundance of *P. noctiluca* was estimated semi-quantitatively. The species was classed as absent, rare (1–10 individuals 1000 m^{-3}), abundant (10–100 individuals 1000 m^{-3}), or very abundant (>100 individuals 1000 m^{-3}).

Various climatic and hydrological indices were used to test a possible relationship between *P. noctiluca* outbreaks and hydroclimatic variability:

i) the North Atlantic Oscillation (NAO), which drives climate variability over the North Atlantic, North Sea, Europe (Beaugrand *et al.*, 2002; Lynam *et al.*, 2004), and western Mediterranean Sea, affecting marine ecosystems;

ii) the northern hemisphere temperature (NHT), a proxy of temperature anomalies in the northern hemisphere;

iii) SST in the Mediterranean Sea;

iv) the regional atmospheric index (RAI), calculated by means of principal component analysis on a climatological matrix comprising 500 hPa geopotential height, precipitation, sea level pressure, and SST (a detailed description of the methods is given in Molinero *et al.*, 2005a);

v) at a local scale, climatological variables, i.e. atmospheric average annual temperature (AAT), calculated from the monthly average air temperature at Tunis–Carthage meteorological station; annual temperature deviation (ATD), which represents the annual difference between minimum winter temperature and maximum summer temperature; and total annual precipitation (TAP).

Results and discussion

The model developed by Goy *et al.* (1989) suggested a 2- to 3-year cycle for the western Mediterranean, characterized by *Pelagia* outbreaks and followed by a period of very low abundance of the species. A period of 11–12 years has also been observed between two sets of *Pelagia* years when analysing qualitative data collected over two centuries in the northwestern Mediterranean.

The analysis of semi-quantitative records of *P. noctiluca* indicates a different seasonal cycle in the five areas (Figure 2.2). According to the decadal model of Goy *et al.* (1989), the peaks of *P. noctiluca* observed in the Balearic Sea and the Gulf of Tunis in 1993–1995 and 2004–2006 may be considered normal or predictable outbreak events. However, the outbreaks observed in these two regions in 1998 and 1999 did not match the expected periodicity. In addition, a further anomalous change was the increasing occurrence and persistence of *Pelagia* outbreaks from 1998 in both ecosystems.

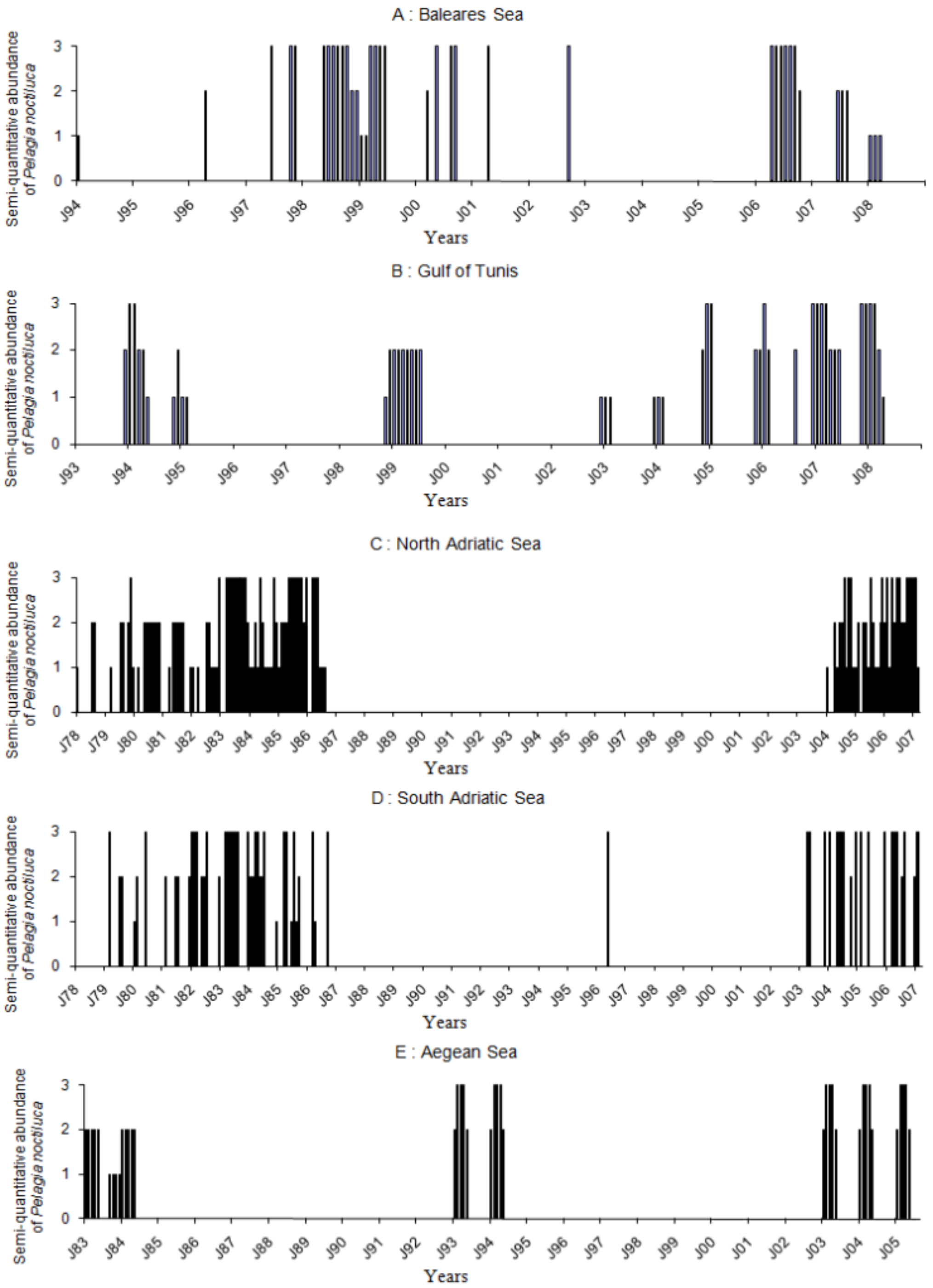

Figure 2.2. Abundance of *Pelagia noctiluca* in different ecosystems in the Mediterranean basin: A = Balearic Sea; B = Gulf of Tunis; C = north Adriatic Sea; D = south Adriatic Sea; E = Aegean Sea. Estimates are semi-quantitative: 1 = rare (1–10 individuals 1000 m^{-3}); 2 = abundant (10–100 individuals 1000 m^{-3}); 3 = very abundant (>100 individuals 1000 m^{-3}).

In the Adriatic Sea, *Pelagia* years seem to follow a different variability, with a 20-year cycle and with outbreaks persisting during the 8–10 years when hydrological and trophic conditions are favourable. In the Aegean Sea, we observed decadal outbreaks over 2–3 years, in agreement with the model of Goy *et al*. (1989).

To assess possible relationships between regional modifications in the abundance and timing of *P. noctiluca* and interannual changes in large-scale and/or local hydro-climatic processes, we performed a principal components analysis on hydroclimatic variables and quantitative abundance of *P. noctiluca* recorded in the Gulf of Tunis from 1999 to 2007 (Figure 2.3).

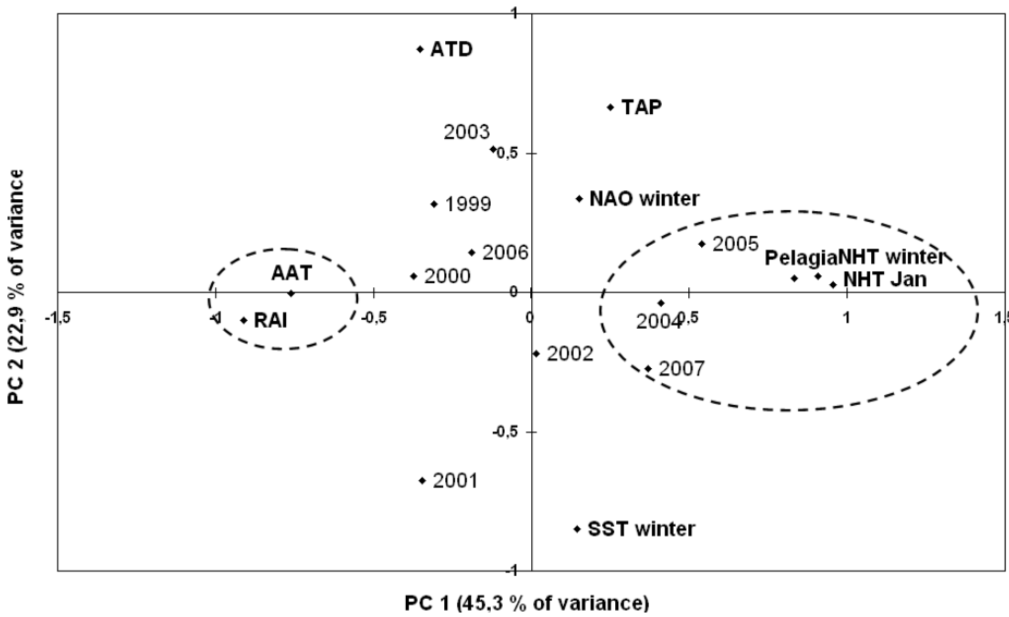

Figure 2.3. Principal Component Analysis between hydroclimatic variables and abundance of *Pelagia noctiluca* in the Gulf of Tunis for the period 1999–2007. AAT = average annual temperature; ATD = annual temperature deviation; NAO winter = North Atlantic Oscillation index from December to March; NHT winter = northern hemisphere temperature index from December to March; NHT Jan = NHT January; Pelagia = *Pelagia* average abundance; RAI = regional atmospheric index for north Tunisia; SST winter = sea surface temperature in winter; TAP = total annual precipitation.

In Figure 2.3, the results (PC1, 45.3% of total variance) indicate that, during 2004, 2005, and 2007, *P. noctiluca* abundance was associated with variations of the NHT index from December to March (NHT winter) and with the NHT index in January (NHT January), and negatively associated with the RAI and the atmospheric AAT. In contrast, the NAO index seems not to be related to the *P. noctiluca* abundance. In the southwestern Mediterranean (Gulf of Tunis), the positive anomalies of the NHT winter index are associated with negative phases of RAI and a decrease in atmospheric AAT. These climatic conditions correspond to mild winters, which seem to favour *P. noctiluca* reproduction and probably determine optimal conditions for the success of *P. noctiluca* outbreaks and their maintenance for several months and even years.

Pelagia noctiluca can be considered an indicator of climate variability in the Mediterranean. The recent climatic and hydrological conditions of the Mediterranean seem to promote higher frequency of *P. noctiluca* peaks.

The preliminary results of this work raise new questions.

1) Why have *P. noctiluca* outbreaks in the western Mediterranean not followed the periodicity described by Goy *et al.* (1989) after 1998? Is this attributable to global warming, which affects hydrological and trophic winter conditions in the western Mediterranean, thus creating a new environmental niche more favourable for *P. noctiluca* reproduction and development success?

2) What alterations are likely to occur in the structure of the western Mediterranean pelagic foodweb because of the persistent presence of *P. noctiluca*?

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