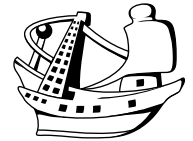


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Seasonal changes in the population dynamics of *Aurelia aurita* in Thau lagoon

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Abstract: Seasonal dynamics of the scyphomedusae, *Aurelia aurita*, was investigated twice a month from January 2010 to June 2011 and related to environmental conditions in Thau lagoon, southwestern Mediterranean Sea. Strobilation, indicated by the presence of 1 mm ephyrae, occurred from November to the middle of April. Maximum abundances up to 330 ind.100 m⁻³ were reached in May 2011, few weeks after the last ephyrae release. The population declines afterwards steadily until disappearing from the water column. Concurrent with increased water temperature and mesozooplankton predation during May, growth rates increased from 0.04 mm.day⁻¹ to a peak of 4.5 mm.day⁻¹, with a maximum bell diameter of 11.3 cm reached on the 7th May. During the study period, there was no advection of *A. aurita* between Thau lagoon and the coastal waters.

Résumé : *Etude des changements saisonniers de la dynamique de population d'Aurelia aurita dans la lagune de Thau.* La dynamique de population de la scyphoméduse *Aurelia aurita* a été étudiée en relation avec des variables environnementales via des prélèvements bimensuels de janvier 2010 à juin 2011 dans la lagune de Thau, en Méditerranée Orientale. La strobilation, indiquée par la présence d'éphyrules de taille d'environ 1mm, se déroule de Novembre à la mi-avril. Les abondances maximales de 330 ind.100 m⁻³, sont observées en mai 2011, quelques semaines après les dernières émissions d'éphyrules. Les effectifs diminuent ensuite très rapidement jusqu'en juin où *A. aurita* disparaît de la colonne d'eau. Les faibles taux de croissance de 0,04 mm.j⁻¹ observés de janvier à avril augmentent jusqu'à 4,5 mm.j⁻¹ lorsque la température augmente et qu'une forte pression de prédation est exercée sur le zooplancton en Mai. Un diamètre d'ombrelle maximum de 11,3 cm est observé le 7 mai. Il n'y a pas eu d'advection d'*A. aurita* entre les eaux de la lagunes de Thau et la zone côtière pendant la période de l'étude.

Keywords: *Aurelia aurita* • Lagoon • Mediterranean Sea

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Introduction

The scyphomedusa *Aurelia aurita* (Linnaeus, 1758) is widespread in coastal waters around the world and it is probably the most studied jellyfish (Lucas, 2001; Lo & Chen, 2008). Although a number of studies on the life cycle of *A. aurita* have been conducted, the multi-site comparisons of the seasonal patterns of *A. aurita* remain scarce (i.e. Miyake et al., 1997), particularly in the Mediterranean Sea where only one publication refers to the population dynamics of this species (Chakroun & Aloui-Bejaouin, 1995).

Lagoons are semi enclosed ecosystems that offer an ideal place to study the life histories of benthic-planktonic populations such as *A. aurita*, since both benthic and pelagic phases coexist. Furthermore, mass reproduction of *A. aurita* occurs in inshore waters that warm up much earlier than offshore waters (Vinogradov et al., 1992). Thau lagoon is the widest lagoon of the Languedoc Roussillon area with 7500 ha. It is a shallow environment with a main depth of 8 m. In Thau, oyster and mussel productions are of high importance as they represent 10% of the French national production. The wood structures supporting bivalve productions are probably very suitable substrata for the reproductive sessile stage of *A. aurita* (Uye et al., 2003; Uye & Ueta, 2004). Our objectives were (1) to provide the first description of *Aurelia aurita* pelagic life cycle in the Western Mediterranean Sea, (2) to compare its population dynamics with other lagoons worldwide and (3) finally to determine the temperature and salinity roles in *Aurelia aurita* life cycle.

Material and Methods

Plankton samples are collected twice a month at 4 monitoring sampling stations from January 2010 to June 2011. Three of these stations are located inside the lagoon: in a harbour (43°19'082N-3°33'532E, 3 m depth), between oyster production tables (43°24'644N-3°36'016E, 4.5 m depth) and nearby a disused shipyard (43°25'329N-3°40'862E, 4.5 m depth). A coastal station (43°21'925N-3°41'453E, 23 m depth) was also monitored in waters surrounding the lagoon to assess possible links between changes in *A. aurita* abundance and inflow/outflow water masses exchanges. Gelatinous plankton was collected by horizontal tows near surface with a Hansen net (700 µm mesh aperture). A large plexiglass collector was used to keep the organisms in good shape. Samples were then preserved in 4% buffered formaldehyde. We considered *A. aurita* ephyrae i.e. < 10 mm, while immature organisms were determined from the absence of developed gonads. Bell diameter, sex and the presence of planula larvae were

determined. As bell size measurements were done on preserved individuals, size was corrected for formalin shrinkage according to Möller (1980). Temperature and salinity were recorded in sub-surface (< 0.5 m) simultaneously during sampling with a probe (EC 300 VWR international/ WTW model 350i).

To detect associations between the abundance of *Aurelia* life stages and environmental variables (i.e. temperature, salinity) we used a cumulative frequency method and a Monte Carlo randomization, as in Perry & Smith (1994) and Paramo et al. (2003). First, the relative cumulative frequency distribution (CFD) was calculated for temperature and salinity. Afterwards, we weighted the CFDs for each environmental variable by multiplying the curve by the abundance of *Aurelia* life stages, as in Paramo et al. (2003). The absolute difference between the two CFD curves, unweighted and weighted, shows whether the life stages were associated with a certain environmental window or whether they were randomly distributed. In the latter case two curves will accrue similarly and will not be significantly different. However, when life stages were associated with a particular thermal or salinity window, the slope of the weighted CFD was steeper than that of the unweighted environmental variable.

The test of significance of the difference between the curves was performed by a Monte Carlo test (1000 randomizations) under the hypothesis of a random distribution.

Results and Discussion

Seasonal occurrence

Ephyrae production occurs mainly from November until April (Fig. 1A). Similar patterns have been observed in temperate ecosystems of the Northern hemisphere where ephyrae production usually occurs in winter through spring, although in some fjords, autumn and spring productions have been also observed (Lucas & Williams, 1994). Maximum abundances of ephyrae were observed in April 2010 and February 2011 (50 and 200 ind.100 m⁻³ respectively), whereas the maximum abundances of adults were found in June 2010 and May 2011 (100 and 330 ind.100 m⁻³, respectively). Similar values have been observed in the Bay of Tokyo (153 ind.100m⁻³) (Lucas, 2001). Immature organisms are observed in March-April, and sexual adults from April to June (Fig. 1B). Abundance decreased drastically from April to June allowing the population decline, both ephyrae and adults. This sharp decrease in abundance, likely due to natural mortality, is well known and has been repeatedly observed, for example in mid-summer, June-July, in the Black Sea (Vinogradov &

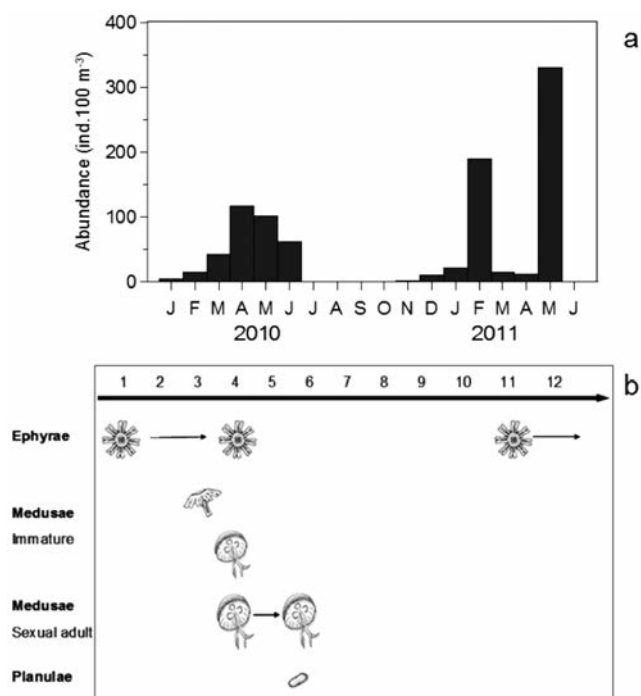


Figure 1. *Aurelia aurita*. **A.** Abundance (ind.100 m⁻³) in Thau lagoon. **B.** Pelagic life cycle.

Figure 1. *Aurelia aurita*. **A.** Abondance (ind.100m⁻³) dans la lagune de Thau. **B.** Partie pélagique du cycle de vie d'*Aurelia aurita*.

Shushkina, 1992; Mutlu, 2001) soon after the gametes release from the mature adults. From the two-year survey in Thau lagoon, it appeared that only one generation per year occurs, while in the Black Sea for example, one or two generations (winter and spring) might occur (Shushkina & Musayeva, 1983; Mutlu, 2001). Our observations suggest a *A. aurita* life span of 7-8 months in Thau lagoon, which is concurrent with former results in other European ecosystems (Lucas & Williams, 1994) while Miyake et al. (1997) suggest that its life span in some bays of Japan could reach up to two years.

The spatial survey here used suggests that *A. aurita* originated from the lagoon as it was not found in the coastal station. As shown elsewhere, the semi-enclosed system of the lagoon might provide refuge, food and substratum to polyp colonies. Indeed, Tokyokawa et al. (2011) indicated that in semi enclosed ecosystems, such as harbours protected by breakwaters, if ephyrae were encountered then it could be concluded that the polyp colonies could be found nearby.

Breeding and growth

A. aurita presented a slow growth rate from January to mid-April around 0.04 mm.d⁻¹. Then during the next 2-3 weeks, the growth rate suddenly increased of 100 times up to

4.5mm.d⁻¹ leading to sexual adults with an average size of 8.42 cm and a maximum observed size of 11.33 cm. Similar size ranges have been observed in Tomales Bay, USA (Miyake et al., 1997). While growth rates in the range of 3.4 cm.week⁻¹ and 4 cm.week⁻¹ were observed respectively by Möller (1980) in Kiel Bight and Lucas & Williams (1994) off Southampton, larger *A. aurita* are usually found in coastal waters (references in Lucas & William, 1994; Miyake et al., 1997).

The period of intense growth coincides with a sharp increase in temperature (from 11 to 20°C in April) and an intense predation on the mesozooplankton stock (decrease in abundance of ~ 81%). It is not clear however, why medusae in Thau lagoon do not attain the sizes found in other areas where organisms can reach > 20 cm. A possible, non-exclusive explanation is a food limitation constrain as a result of either their own predatory impact, or through competition for food resources with bivalves which are very abundant in the lagoon.

Between May and June 2010, the bell size decreased from 19% at the rate of 1.4 mm.d⁻¹, and the population started disappearing from the water column. While the reasons for this decrease in bell size are still discussed (food limitation, decrease in the metabolic activity), the size reduction is in the range of those usually observed, between 10 and 20% (Möller, 1980; Lucas & Williams, 1994). The sex ratio was well balanced with 49% of males and 51% of females. Light microscopic examination of the organisms showed that up to 1528 eggs were carried in the brood sacs of a single individual.

Temperature and salinity

The time of occurrence of *A. aurelia* in the pelagic plankton is highly variable among localities because of environmental differences (reviewed by Miyake et al., 1997). In Thau, maximum abundances of *A. aurita* ephyrae occurred at 16°C, although they could be observed within a large temperature window, between 5 and 26°C (Fig. 2B). The presence of ephyrae was continuous from November to April, and afterwards disappeared from the water column as temperature increased over 16°C. Lo & Chen (2008) have recorded an inverse correlation between *A. aurelia* ephyrae abundance and temperature in Tapong Bay. They indicated that ephyrae were almost absent during the warm and wet season (May-October). In Thau, the mature adults were preferentially encountered around 19°C (Fig. 2A). When temperature increased above this optimum, there was a total disappearance of the adults from the water column. However, the review in Lo & Chen (2008) indicated that *A. aurita* medusae were repeatedly encountered at temperature > 20°C.

Salinity optima are similar for both *A. aurita* ephyrae and adults (34.8 and 35.3 respectively, Fig. 2C & D).

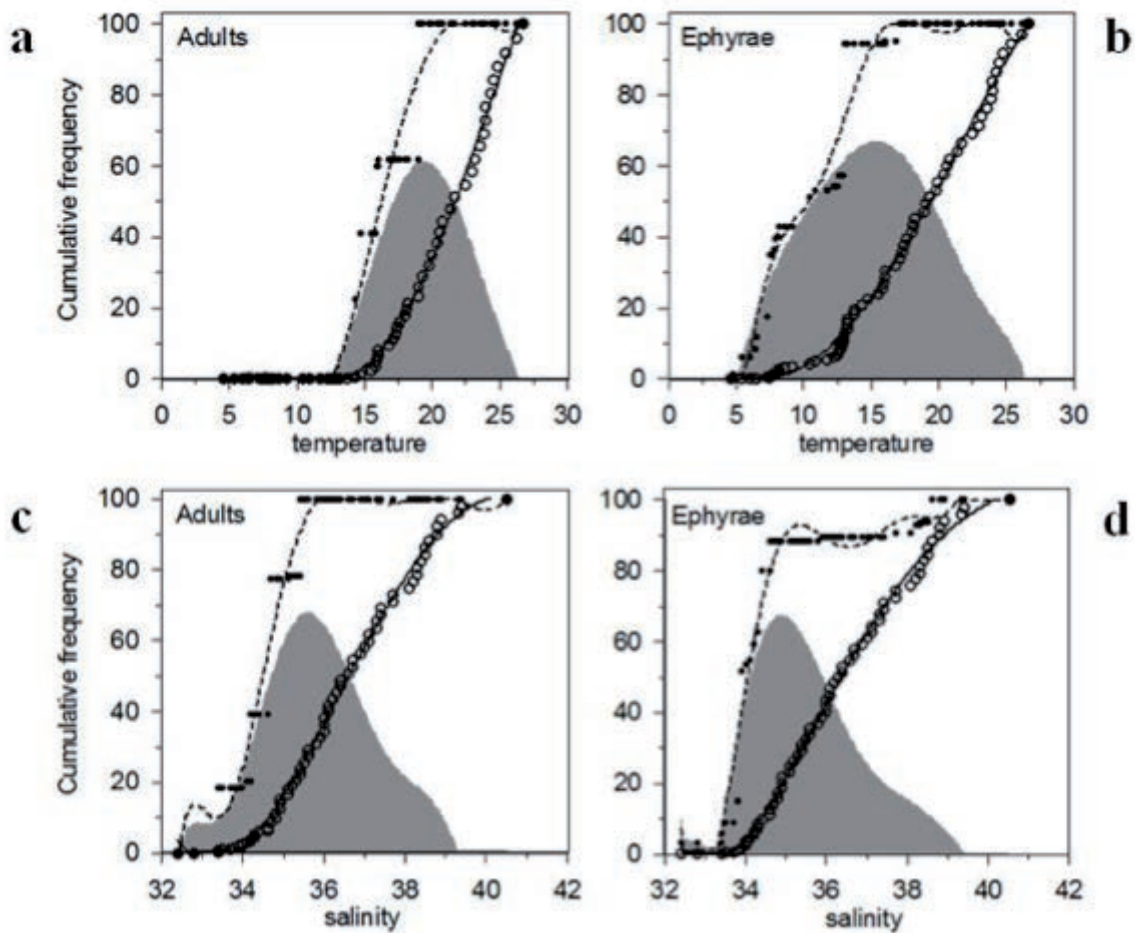


Figure 2. *Aurelia aurita*. Cumulative frequency distribution (CFD) of the habitat variables. **A & B.** Temperature. **C & D.** Salinity. unweighted CFD: thick line, weighted CFD: dotted line, absolute difference between unweighted and weighted: filled areas.

Figure 2. *Aurelia aurita*. Distribution des fréquences cumulées (CFD) des variables définissant l'habitat. **A & B.** Température. **C & D.** Salinité. Les CFD non pondérés sont représentés par une ligne épaisse, les CFD pondérés par une ligne pointillée, les aires grises représentent la différence absolue entre les CFD non pondérés et pondérés.

Supporting Lo & Chen's results (2008), no significant correlation between salinity and *A. aurelia* abundance (ephyra or adult) was found. This is probably due to extreme inflow events which can affect abruptly the salinity. Indeed, intense precipitations often occur in fall. Salinity conditions strongly vary as the freshwater inflows into the lagoon vanish in summer which leads to an increase of salinity up to 39.3. The contrasting hydrological seasons characterized by strong temperature and salinity changes are hypothesized as a further reason why *A. aurelia* disappears from the water column in Thau lagoon from July to November.

Figure 3 synthesises the occurrence of *A. aurelia* in 3 Western Mediterranean lagoons. The medusae occur roughly at the same salinity in Bizerte and in Thau (32.5 to 38 and 33 to 39.3, respectively), however, they are present

at temperatures (between 12.5 and 27.5°C) higher than in Thau (between 7 and 24°C). In Berre, with contrasting environmental conditions in comparison with the two first lagoons, i.e. brackish waters, *A. aurelia* is encountered between 16.5 and 26.5. In addition, the thermal niche overlaps with those of Bizerte and Thau with a range of 4 to 27°C.

These results highlight the plasticity of the species to live and reproduce in contrasted environments. They further support former observations showing that *A. aurelia* might inhabit a broad window of environmental conditions ranging from salinity from 10 to 32 and temperature from -2 up to 30°C (Miyake et al., 1997). The variability in the environmental ranges *A. aurelia* inhabits in the western Mediterranean raise several questions to thoroughly assess its life history, in particular the plasticity of the species to

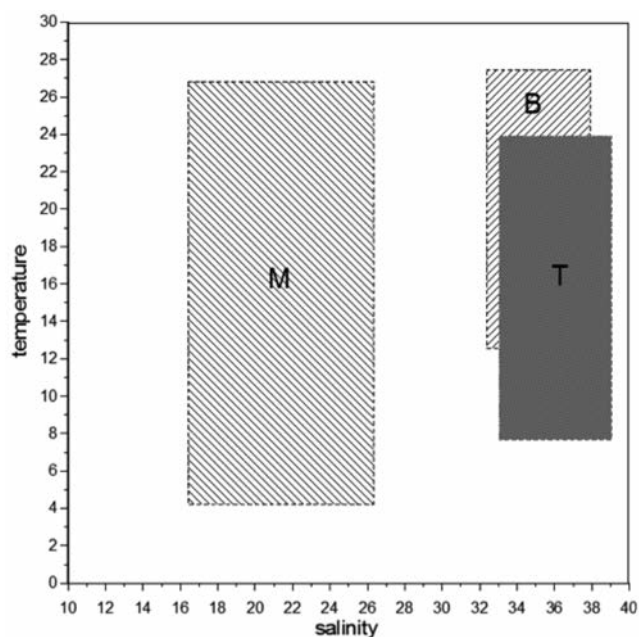


Figure 3. *Aurelia aurita*. Temperature and salinity windows of occurrence in 3 Mediterranean lagoons: Berre (M), Bizerte (B) and Thau (T).

Figure 3. *Aurelia aurita*. Fenêtres de distribution en fonction de la température et de la salinité dans 3 lagunes Méditerranéennes : Berre (M), Bizerte (B) et Thau (T).

evolve in changing environments and whether cryptic species exist in the Mediterranean lagoons. This first study could be used as baseline for further investigations on the *A. aurita* dynamics in the Mediterranean Sea with some molecular biology approaches urgently needed.

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