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Population dynamics and predatory impact of the alien jellyfish *Aurelia solida* (Cnidaria, Scyphozoa) in the Bizerte Lagoon (southwestern Mediterranean Sea)

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Abstract

Understanding the life cycle strategies and predatory impact of alien jellyfish species is critical to mitigate the impact that these organisms may have on local populations, biodiversity, and ultimately on the functioning of food webs. In the Mediterranean Sea, little is known about the dynamics of alien jellyfish, despite this biodiversity hotspot being one of the most threatened areas by increasing numbers of alien jellyfish. Here, we investigated the population dynamics and predatory impact of a non-indigenous scyphomedusa, *Aurelia solida* Browne 1905, in the Bizerte Lagoon, Tunisia. The study was based on bimonthly surveys performed over two consecutive years, from November 2012 to August 2014. Field observations showed that the planktonic phase of *A. solida* occurs from winter to early summer. Prey composition was investigated by means of gut content and field zooplankton analyses. Calanoid copepods, mollusc larvae, and larvaceans represented the main food items of *A. solida*. To determine the jellyfish feeding rate and their predatory impact on zooplankton populations, the digestion time for zooplankton prey was assessed at three different temperatures: 13, 18, and 23°C in laboratory conditions, corresponding to the average range of temperatures encountered by *A. solida* in the Bizerte Lagoon. We found that *A. solida* consumed 0.5–22.5% and 0.02–37.3% of the daily zooplankton standing stock in 2013 and 2014, respectively. These results indicate a non-negligible but restricted seasonal grazing impact on some mesozooplankton groups, explained by the relatively short lifespan of the medusa stage (5–6 months).

Keywords: Scyphomedusae; abundance; predation; mesozooplankton; SW Mediterranean.

Introduction

Jellyfish blooms are conspicuous and natural events in marine ecosystems. The intensity and recurrence of jellyfish blooms in the last decades have been on the rise (Purcell *et al*., 2007; Molinero *et al*., 2008), at least at the scale of Large Marine Ecosystems, particularly in coastal waters and semi-enclosed basins (Brotz & Pauly, 2012; Brotz *et al*., 2012). Indeed, in some areas, jellyfish have not shown any increase or have even declined (Brotz, 2011). There is, however, consensus on the influence of habitat modifications, and their synergies with warming and fishing, on jellyfish increases through the promotion of a larger space for settlement of the polyps in coastal waters (Duarte *et al*., 2013). The consequences of jellyfish blooms, especially scyphozoan blooms, may have wide implications, with substantial impacts on the structure and dynamics of marine ecosystems, as well as different economic sectors of human activities, such as fisheries, tourist activities, and power plant industries (review in Purcell *et al*., 2007).

Aurelia spp. jellyfish represent, so far, the most investigated scyphozoan taxon. The genus is widely distributed between 70°N and 40°S (Lucas, 2001), with many species subject of intense monitoring due to their high blooming potential, particularly in coastal waters (Olsen *et al*., 1994; Toyokawa *et al*., 2000; Mutlu, 2001). *Aurelia* spp. blooms may have dramatic predatory impacts on invertebrate zooplankton and fish larvae (Möller, 1984; Ishii & Tanaka, 2001), eventually leading to local disruption of the traditional phytoplankton-copepod-fish pathway (Boero, 2013).

The population dynamics of some *Aurelia* spp. show a great variability among life history traits (reviewed in Lucas, 2001). Originally considered as represented by few species with wide geographical distributions, the *Aurelia* clade is a morphologically cryptic species complex that is now known to include at least 16 valid molecular spe-

cies (Dawson & Jacobs, 2001; Dawson & Martin, 2001; Schroth *et al*., 2002; Gómez Daglio & Dawson, 2017). The wide ecological and phenotypic plasticity of *Aurelia* spp. appears to be a genetic adaptation of different sibling species to local conditions, rather than physiological acclimation processes of a few cosmopolitan species to a variety of different habitats (e.g. Berstad *et al.*, 1995).

The first report of *Aurelia* medusae, originally thought to be *Aurelia aurita*, in the Bizerte Lagoon dates back to May 1994 (Chakroun & Alouin-Bejaouin, 1995). Molecular analyses based on mitochondrial (COI) and nuclear (28 S) sequences have shown that the species is *Aurelia solida* Browne 1905, a native from the Red Sea (Scorrano *et al*. 2017). The pattern and history of the arrival of *A. solida* in the Bizerte Lagoon remains unclear so far. The harbour of Bizerte was established in the 20th century and currently sustains the transit of thousands of commercial vessels every year, which suggests a possible introduction via ballast waters (Schroth *et al*., 2002).

Research on gelatinous plankton along the southwestern Mediterranean coasts has generally been limited to reports on seasonal and annual distributions of medusae (Daly-Yahia *et al*., 2003; Touzri *et al*., 2010, 2012), while little is known on their population dynamics and trophic ecology. In clear contrast, this question has been widely addressed in the northern Mediterranean Sea, showing a substantial predatory role of particular species, such as *Pelagia noctiluca* and *Velella velella*, in structuring plankton communities (Sabatés *et al*., 2010; Purcell *et al*., 2015; Tilves *et al*., 2016; Milisenda *et al*., 2018), while the trophic ecology of *Aurelia* species has been overlooked. In recent years, several *Aurelia* spp. blooms were reported across the Mediterranean Sea in the MED-JELLYRISK framework, an international coordinated effort launched to mitigate ecological and societal impacts of jellyfish blooms (http://www.jellyrisk.com). In this work, we used a combined approach based on field surveys and laboratory experimental settings, as well as statistical modelling, to investigate the population dynamics of *A. solida*, and to quantify the top-down effect of this non-indigenous jellyfish on the native mesozooplankton of the Bizerte lagoon.

Material and Methods

Field sampling

Field work was carried out in the Bizerte Lagoon located in the north of Tunisia (southwestern Mediterranean Sea). The lagoon covers an area of 128 km^2 and has an average depth of 7 m (maximum 12 m), connected to the Mediterranean Sea *via* a 7 km-long artificial channel (Bizerte channel) opened in the early 20th century. This semi-enclosed coastal ecosystem is subject to various anthropogenic pressures such as domestic sewage input, industrial activities (oil refineries, ceramic industry, metallurgy activities), fishing, and intensive shellfish farming (mussels, oysters, and clams) (Khessiba *et al*., 2001). The sampling was carried out at a single station (coordinates: 37.20617°N; 9.85888°E) (Fig. 1).

A total of 33 sampling campaigns took place from November 2012 to August 2014 on a bi-weekly to monthly basis depending on weather conditions. Sea subsurface (-0.5 m) temperature (SST) and salinity were recorded using a WTW multi-parameter probe (Cond model 3110/SET).

Mesozooplankton was collected during daytime hours (≈ 08:00–09:00) by vertical towing using a WP2 net (0.56 m mouth diameter, 200 µm mesh size, 8 m depth). All samples were preserved in buffered 4% formaldehyde-seawater solution (formalin). Mesozooplankton counting and identification to major taxonomic groups, and to Order for copepods, were performed on a sub-sample under a Leica MZ125 stereomicroscope.

As medusae were in low abundance and highly dispersed, their abundances were assessed using a protocol developed by Verity *et al*. (2011) that consisted of visual counting from a boat running at a constant slow speed (1 kt) for a fixed distance (4.54 km). Over the transect, all medusae lying within 1 m either side of the boat bow were counted. For the sake of simplicity, we considered that the observed medusae lie generally in the upper 1 m depth. Thus, the volume surveyed was estimated as: 4,540 m long survey transect × 2 m wide swath × 1 m depth = 9,080 m^3. Sampling was conducted on calm days to maximise visibility. Considering the shallow depth of the Bizerte Lagoon (average depth 7 m), as well as the homogeneity of abiotic (temperature, salinity, nitrites, nitrates, phosphates, silicate, DOC, and Chl-*a*) and planktonic (bacteria, picophytoplankton, microphytoplankton, and microzooplankton) parameters throughout the water

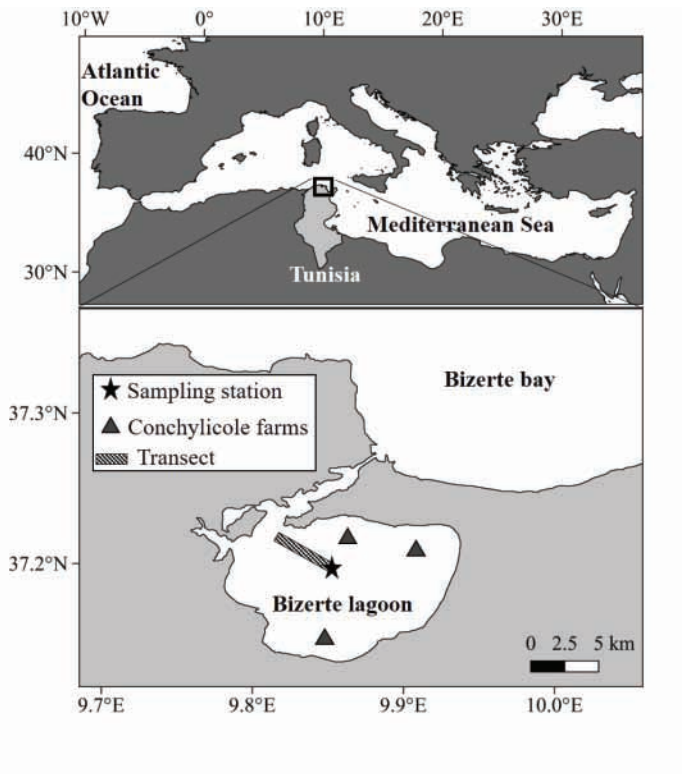

Fig. 1: Map of the Mediterranean Sea showing with locations of the sampling station and the transect in the Bizerte Lagoon between November 2012 and August 2014.

column (Sakka Hlaili *et al*., 2008), a similar pattern was considered for medusae distribution. In each sampling date, the bell diameter of medusae (n ≥ 30 individuals) was measured within two hours following collection.

Aurelia solida *predation impact*

Since no light/dark difference in feeding rate was found for *A. aurita* (Bailey & Batty, 1983), and the homogeneity of the shallow water column (Sakka Hlaili *et al*., 2008) suggested the absence of vertical migration for *A. solida*, we considered that diet, feeding rate, and predation impact were homogeneous over 24 h.

Since March 2013, 5–20 *A. solida* were sampled in the first 1 m depth layer with a hand net and immediately preserved individually in 4% formalin for gut content analysis. In the laboratory, the formalin solution was filtered to collect any possible egested material, and the jellyfish was dissected to examine canals, stomach, and gastric pouches for prey organisms, which were identified to major taxonomic groups, and to Order for copepods. The relative importance of *A. solida* prey was expressed as the percentage of each prey taxon relative to all prey items in the gut contents, the percentage of numerical abundance of prey items in the gut contents (*N*; %), the index of frequency of occurrence in the gut (FO; %) and the index of relative importance (IRI; %) (Laroche, 1982).

Pearre's selectivity index (*C*) (Pearre, 1982) was applied to estimate prey taxon selectivity of *A. solida*. *C* ranges between -1 and +1 and depicts the magnitude of negative and positive selection of prey. This method is based on the Chi-square (X^2) analysis, comprising 2 × 2 configured comparisons between the average abundance of each taxon in the medusa gut contents and the corresponding abundance in the ambient environment (Pearre, 1982). The selectivity *C* is given by the equation:

$$C = \pm \left[\frac{\left(\left| a_d b_e - b_a a_e \right| - \frac{n}{2} \right)^2}{abde} \right]^{\left(\frac{1}{2}\right)}$$

where *a* is the number of individuals in a particular species and *b* is the number of individuals of all other taxa in the diet (subscript *d*) and in the environment (subscript *e*), respectively; $a = a_d + a_e$; $b = b_d + b_e$; $c = a_e + b_e$; and $d = a_d + b_d$; and $n = a + b + c + d$. This was repeated for each taxon of interest. A Chi-square test was applied to test the significance of the values.

Jellyfish digestion time for zooplankton was determined at three temperatures (13, 18, and 23°C) using the protocol established by Purcell (2003). To avoid a thermal shock caused by a difference between *in situ* water and incubation temperature, the experiments were conducted when the *in situ* water temperature was close to one of the three experimental temperatures. The experiments were conducted during March and May (2014) when the SST values were close to the experimental temperatures (Δ = 0.8 ± 0.1 °C). Sixty medusa individuals were collected by hand net from the Bizerte Lagoon and maintained in an 80 L tank with fresh zooplankton collected with a WP2 net from the lagoon to assure continuous feeding until return to the laboratory (30 min after sampling). Five medusae were preserved immediately (t_0). In the laboratory, after 1 h of acclimation, the medusae were transferred from the 80 L tank to 11 20 L tanks (i.e. five medusae per tank) filled with 20 µm-filtered seawater maintained at a constant temperature (average salinity = 37 ± 0.5). Five medusae were preserved at 30 min or 1 h intervals for up to 8 h for gut content analyses. Digestion time was determined by solving (prey = 0) the linear regressions evaluating the relation between the time and the number of available prey in the gut contents (Purcell, 2003). Medusa bell diameter was measured to the nearest 1.0 mm.

Individual rates of feeding on mesozooplankton were expressed as the number of prey items consumed per medusa per day: $F = C_m / D \times 24h$ where *F* is the number of prey items consumed per medusa per day, C_m is the number of prey items in medusa gut, and *D* is the digestion time (h). Digestion time was estimated by the previous experiment, and SSTs recorded in the sampling campaigns were used as a reference to choose the right digestion time estimated from the three experimental temperatures. Since bivalve larvae survive their transit through the jellyfish gut and are egested alive, only 1% of the bivalve larvae found in the gut content were used to estimate the feeding rate in order to avoid an overestimation (Purcell *et al*., 1991).

Predation impact was expressed as the percentage of prey standing stock consumed per day: $P = F \times M / C \times 100$ where *P* is the percentage of prey standing stock consumed per day, *F* is the feeding rate, *M* is the abundance of medusae per cubic metre, and *C* is the abundance of prey per cubic metre.

SEM modelling

Structural equation modelling (SEM) (Alsterberg *et al*., 2013) was used to depict interactions between the environmental variability and plankton, and to quantify the top-down effect exerted by *A. solida* on mesozooplankton abundance. The strength and sign of links and the quantification of the overall model were determined by simple and partial multivariate regression and Monte Carlo permutation tests (1,000 replicates), while Chi-square values were used to assess robustness and fit of the overall path model (Grace *et al*., 2010). The standardised path coefficients (i.e. partial regression coefficients) indicated the strength of the relationship between causal and response variables. Significance levels for individual paths between variables were set at α = 0.05. SEM was run in AMOS (version 21).

Results

During the survey period, the SST showed a marked seasonal pattern ranging from 11–28.4°C (Fig. 2A). The

lowest values were shown in February (11°C in 2013; 12.4°C in 2014), followed by a gradual increase as the seasons progressed, reaching 28.4°C in July 2013. The sea surface salinity (SSS) decreased during the late winter–spring period, reaching 34.2 in May 2013 and 33.6 in March 2014, then increased to 38.3 in October 2013.

The mesozooplankton density in the Bizerte Lagoon varied markedly from 425 ind m^{-3} in December 2012 to 11,071 ind m^{-3} in September 2013 (Fig. 2B). Mesozooplankton density showed two distinct peaks in July (10,759 ind m^{-3}) and September (11,071 ind m^{-3}) 2013. The density decreased dramatically during the winter of 2013, then remained relatively constant during the spring. Chlorophyll concentration averaged 1.6 ± 2.3 mg m^{-3}, with values ranging between 0.02–12.3 mg m^{-3}.

Regarding the composition of mesozooplankton (Fig. 2C), copepods were dominant during almost the entire period, with a relative abundance ranging between 50–96.7% of the mesozooplankton community, except in May and October 2013 when cladocerans dominated (relative abundance of 64 and 47%, respectively). Calanoid copepods were the dominant order among copepods (50–100%), followed by mollusc larvae (1.3–28.6%), and larvaceans (up to 22.3%), with a dominance of mollusc larvae during the first half of the study period (November 2012–September 2013).

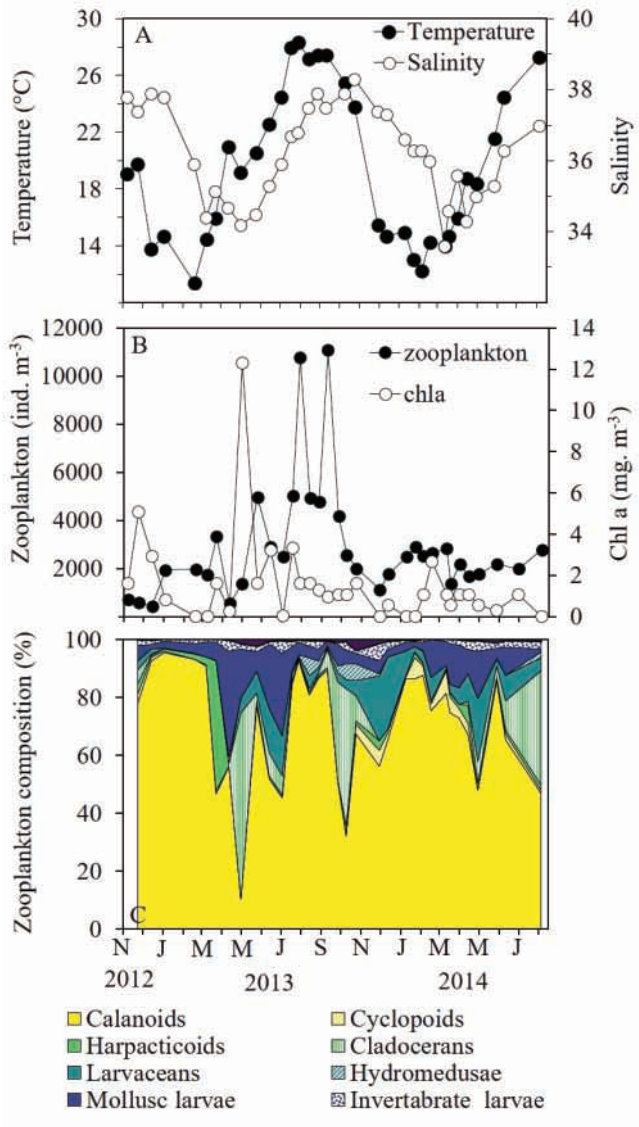

Fig. 2: Seasonal variation of (A) abiotic factors (temperature and salinity), (B) zooplankton abundance and chlorophyll biomass, and (C) zooplankton composition in Bizerte Lagoon between November 2012 and August 2014.

Aurelia solida *dynamics*

A. solida were present in the water column from winter until early summer (Fig. 3A). The net hauls showed that *A. solida* ephyrae occurred from December to January, whereas medusae were observed 1–2 months after the start of ephyra strobilation (February 2013 and January 2014). Maximum abundances of ephyrae were found in December (1.2 ind m^{-3} in 2012; 3.9 ind m^{-3} in 2013). All individuals sampled in February 2013 (6.5 ind m^{-3}) and January 2014 (0.07 ind m^{-3}) were juveniles, while the maximum abundance of adults was observed in March 2013 and April 2014 (2 ind m^{-3} and 1.8 ind m^{-3}, respectively). No significant difference (*t*-test; p = 0.39) in population abundance was observed between 2013 and 2014 (1.2 ± 2 ind m^{-3} in 2013; 0.6 ± 1.3 ind m^{-3} in 2014). The occurrence period of *A. solida* seemed to be related to the SST. Ephyrae only appeared after the SST fell below 15°C (13.8°C in December 2012; 14.7°C in December 2013), whereas the last observation for adults (in both

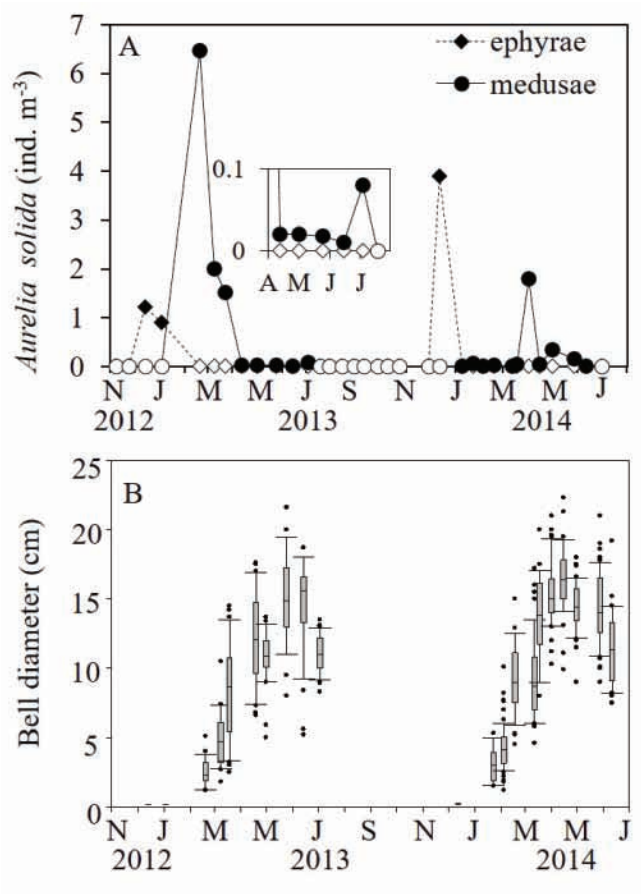

Fig. 3: Seasonal variation of *Aurelia solida* (A) abundance and (B) bell diameter in Bizerte lagoon between November 2012 and August 2014; white spots: 0 ind.m^{-3}.

Bizerte Lagoon and Channel, *pers. obs.*) coincided with 24.5°C SST (early July 2013 and mid-June 2014). While ephyra abundance was higher during the second year (3.9 ind m^{-3}), abundance of the adult stage was not significantly different between the two years (*U*-test, $p = 0.5$; 2013 = 0.5 ± 0.9 ind.m^{-3}; 2014 = 0.3 ± 0.9 ind.m^{-3})

A. solida mean ($\bar{x}$ ± SD) bell diameter increased gradually to reach a maximum of 14.6 ± 3.3 cm ($n = 35$) in June 2013 and 16.4 ± 2.4 cm ($n = 36$) in mid-April 2014. The largest sampled medusae reached 23.4 (April 2013) and 22.3 cm (April 2014) (Fig. 3B). Bell diameter shrinkages were observed since June 2013 and April 2014, occurring one to two months after the first appearance of brooding females (April 2013–March 2014). The first occurred in May 2013, while the two others occurred gradually since June 2013 and April 2014 after the spawning event. Overall, no significant difference in bell diameter was observed between the two years (*t*-test, $p = 0.89$).

Diet and predation impact

A total of 126 medusae were examined for gut content analysis. The numbers of captured prey items averaged 114.9 ± 92.9 medusa^{-1}. A total of 14,472 prey items were identified and grouped in 16 food types (Table 1; Fig. 4), mainly mesozooplankton (14 types). Copepod nauplii and tintinnids were the only identified microzooplankton. Overall, the most abundant prey items were gastropod larvae (N: 33.7%; IRI: 40.4%), calanoid copepods (N: 29.4%; IRI: 36%), bivalve larvae (N: 12.4%; IRI: 11%), tintinnids (N: 10.1%; IRI: 4.1%), larvaceans (N: 5.5%; IRI: 4.2%), and copepod nauplii (N: 3.4%; IRI: 2%). The comparison between the diet in 2013 and 2014 showed

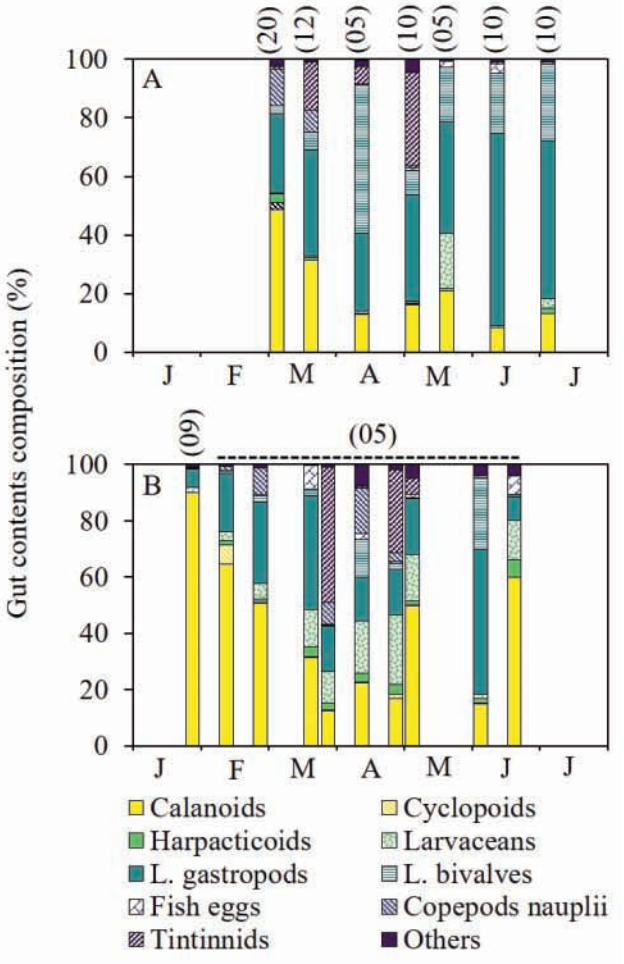

Fig. 4: Variation of the diet composition of *Aurelia solida* in Bizerte Lagoon in (A) 2013 and (B) 2014; (*n*) number of analyzed specimens.

Table 1. Diet composition of *Aurelia solida* in Bizerte Lagoon in 2013 and 2014 (2013: N = 71; 2014: N = 54; Total: N = 125).

Items		%N			%FO			%IRI		
		2013	2014	All	2013	2014	All	2013	2014	All
Mesozooplankton (200-2000 µm)	Cladocerans	0.6	0.3	0.5	19.7	13.0	16.8	0.1	0.1	0.1
	Chaetognates	0	< 0.1	< 0.1	0	1.9	0.8	0	< 0.1	< 0.1
	Calanoid copepods	21.1	40.8	29.4	100	100	100	24.8	50.7	36.0
	Cyclopoid copepods	0.4	1.3	0.8	9.4	37.5	25.9	< 0.1	0.6	0.2
	Harpacticoid copepods	1.0	1.9	1.4	43.8	66.7	56.8	0.5	1.5	1.0
	Larvaceans	2.2	10.2	5.5	40.8	90.7	62.4	1.0	11.5	4.2
	L. gastropod	42.1	22.3	33.7	98.6	90.7	97.6	48.8	25.1	40.4
	L. bivalve	17.9	4.9	12.4	84.5	55.6	72.0	17.8	3.4	11.0
	L. crustacean	0.8	1.1	0.9	42.3	42.6	42.4	0.4	0.6	0.5
	L. cirrhiped	0.2	0.6	0.4	15.5	22.2	18.4	< 0.1	0.2	0.1
	Fish Eggs	0.9	1.3	1.1	36.6	35.2	36.0	0.4	0.6	0.5
	Fish larvae	0.0	0.1	0.1	< 0.1	7.4	3.2	0	< 0.1	< 0.1
	Ostracods	0.1	0.3	0.2	9.9	16.7	12.8	< 0.1	0.1	< 0.1
	Hydromedusae	0.1	0.1	0.1	4.2	1.9	3.2	< 0.1	< 0.1	< 0.1
Microzooplankton (20-200 µm)	Copepods nauplii	3.1	3.9	3.4	47.9	46.3	47.2	1.7	2.2	2.0
	Tintinnids	9.5	11.0	10.1	38.0	25.9	32.8	4.3	3.5	4.1

differences among the prey dominance. While gastropod larvae dominated the prey (N: 42.1%; IRI: 48.8%) in 2013, they only represented 22.3% (IRI: 25.1%) in 2014, supplanted by calanoid copepods (N: 40.8 %; IRI: 50.7%). Larvaceans were twice as abundant in 2014 (N: 10.2%; IRI: 11.5%) as in 2013 (N: 21.1%; IRI: 1%). Fish eggs were less abundant (N: 1.1%; IRI: 0.5%), but occasionally reached 8.4% of the gut contents (March 2014). Prey number and diversity in stomachs of *A. solida* were significantly correlated (N = 126; $p < 0.001$) to the medusa size (Fig. 5). Linear regressions showed that bell diameter explained the greatest amount of variation in prey diversity, indicating a larger diversity in the diet composition of larger medusae. The juvenile (bell diameter 1–4 cm) preyed on two to four types of prey, mainly copepods (73–90%) while adult medusae contained up to 11 different prey items. Overall, no significant correlation was found between the proportions of most of the prey items in the gut contents and their proportion in the environment ($p > 0.5$). Copepods were ingested at low rates relative to the proportion available *in situ*. Conversely, cladocerans, fish eggs, and microzooplankton (tintinnids and copepod nauplii) were largely eaten when their abundance was highest in the environment.

Among the 14 mesozooplankton prey items ingested by *A. solida*, only eight presented a significant selectivity ($p < 0.5$) (Fig. 6). Among the copepods, only cyclopoid copepods did not present significant selectivity index values. While calanoid copepods dominated the gut contents, they were negatively selected (C = –0.05 to –0.4), as well as the cladocerans (C = –0.32). Other crustaceans, represented by harpacticoid copepods (C = 0.14 to 0.48) and crustacean larvae (C = 0.07), were occasionally positively selected. Larvaceans and mollusc larvae were constantly selected, with significance values (C) ranging from 0.06–0.27 and 0.1–0.46, respectively. Fish eggs were barely selected (C = 0.07 to 0.26).

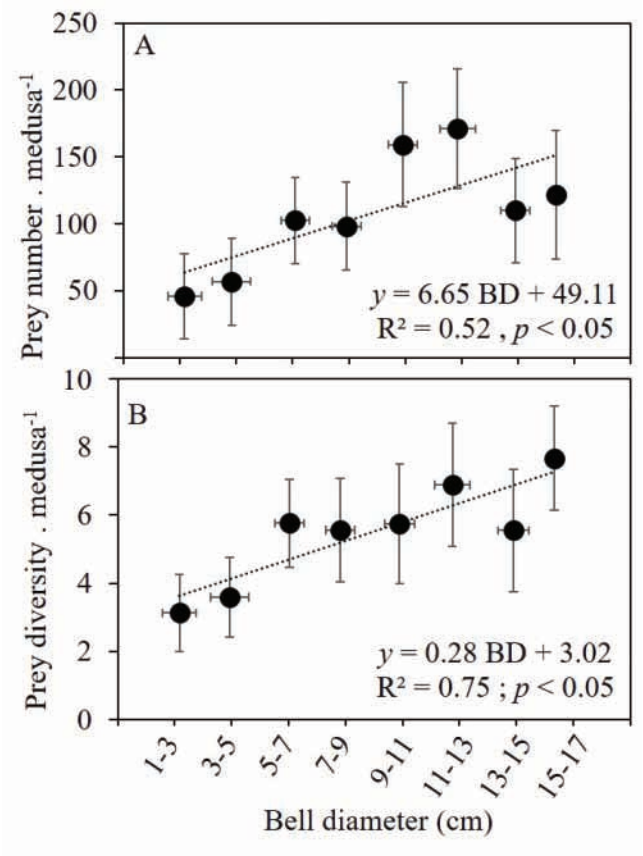

Fig. 5: Relation between *Aurelia solida* bell diameter (cm) and (A) the prey in the gut contents and (B) the prey diversity.

A. solida digestion time decreased with an increase in temperature. The linear regressions evaluating the relation between the time and the number of available prey in the gut contents at each of the three temperatures (13, 18, and 23°C) are summarised in Table 2. Solving the equations for 0 prey (regardless of zooplankton taxon) yielded 6.2, 3.8, and 2.4 h at 13, 18, and 23°C, respectively. Copepods, gastropod larvae, and fish eggs were the most frequent and abundant prey items, enabling determination of their specific digestion times. The regression analyses indicated that no copepods remained in the gut after 6.9, 3.8, and 2.4 h at 13, 18, and 23°C, respectively. Gastropod larvae digestion decreased from 4.5 to 2.4 h between 13 and 23°C. Fish eggs disappeared faster and were digested after 4.7 and 1 h at 13 and 23°C, respectively. At the three temperatures (13, 18, and 23°C), we did not observe any larvaceans after the first 30 min.

Feeding rates were estimated using different digestion rates taking into account the SST at each sampling event. The daily feeding rate for mesozooplankton (regardless of the group) varied markedly from 168 ± 39 (n = 20) up to 2682 ± 277 (n = 5) prey items consumed medusa^{-1} day^{-1} (Fig. 7A). No significant difference was observed (t-test; $p = 0.12$) between feeding rates in 2013 (1078.2 ± 683.8, n = 7) and 2014 (582.4 ± 382.6, n = 10). Feeding rates were positively correlated with bell diameter (r^2 = 0.33; $p < 0.001$) and temperature (r^2 = 0.33; $p < 0.05$). Individual ingestion rates of gastropod larvae ranged between 32 ± 14 (n = 8) and 898 ± 191 (n = 10) gastropod larvae day^{-1}, with the highest values in 2013 following the background composition of the diet (Fig. 7B). The highest feeding rate of copepods and fish eggs reached 531 ± 58 (n = 5) and 106 ± 8 (n = 10) ind day^{-1}.

The predation impact of *A. solida* on the daily mesozooplankton stock varied markedly from 0.4–23.7% in 2013 and from 0.02–39.2% in 2014 (Fig. 7C). The high

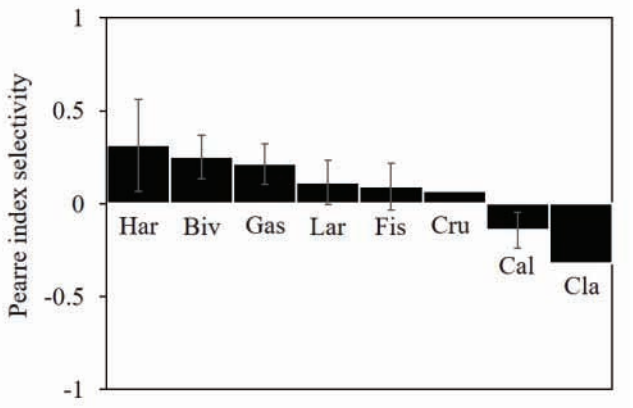

Fig. 6: Prey selectivity of *Aurelia solida* in Bizerte Lagoon during the present study; Har = Harpacticoids; Biv = bivalve larvae; Gas = gastropods larvae; Lar = larvaceans; Fis = Fish larvae; Cru = crustacean larvae; Cal = Calanoids; Cla = Cladocerans.

Table 2. Digestion time of *Aurelia solida* at 13, 18 and 23 °C.

A. solida bell diameter ± SD (cm)	T (°C)	Prey	DT (h)	Linear regression	R^2
9.8 ± 1.9	13				
		Mixed zooplankton	6.2	y = 35.05 - 5.6x	0.6
		Copepods	6.9	y = 16.23 - 2.35x	0.7
		Gastropods larvae	4.5	y = 12.77 - 2.85x	0.5
		Fish eggs	4.7	y = 4.93 - 1.03x	0.6
10 ± 1.7	18				
		Mixed zooplankton	3.8	y = 90.23 - 23.78x	0.5
		Copepods	3.8	y = 49.15 - 12.98x	0.5
		Gastropods larvae	3.8	y = 24.7 - 12.6x	0.6
		Fish eggs	2.7	y = 6.6 - 2.4x	0.8
10.6 ± 1.0	23				
		Mixed zooplankton	2.4	y = 105.53 - 44.23x	0.6
		Copepods	2.4	y = 60.55 - 25.58x	0.6
		Gastropods larvae	2.4	y = 30.05 - 12.33x	0.7
		Fish eggs	1	y = 2.08 - 4x	0.9

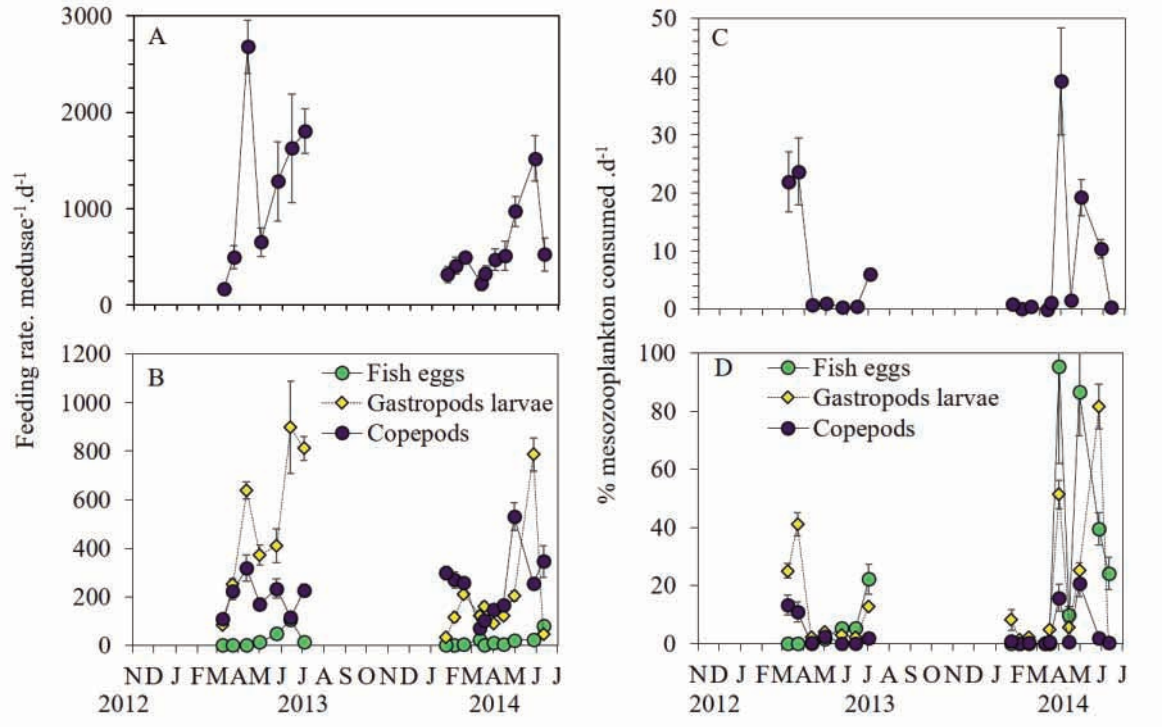

Fig. 7: Seasonal variation of *Aurelia solida* (A-B) feeding rate (prey consumed medusae^{-1}) and (C-D) predation impact (% prey standing stock consumed day^{-1}) in Bizerte Lagoon in 2013-2014.

values recorded (22–23.7% in March 2013; 39.2% in April; 10.4–19.2 % in May 2014) corresponded to relatively high abundances of adult jellyfish. Overall, no significant difference (*t*-test; $p = 0.34$) was observed for the impact of *A. solida* predation on the mesozooplankton between the two years. Although gastropod larvae were the most ingested prey, the predation impact was limited, barely exceeding 25% (Fig. 7D), a finding that was similar for copepods (0.1–20% of the daily stock). The non-motile prey, fish eggs, were the main ingested item, accounting for up 95% of the daily stock.

Structural Equation Modelling

Results of the SEM model showed direct and indirect relationships among biotic and abiotic factors in the plankton food web. Temperature emerged as the leading environmental factor over the period investigated, as shown by the positive and significant values of path coefficients: 0.22, 0.58, and 0.48 with chlorophyll, mesozooplankton, and *A. solida*, respectively. In contrast, salinity did not show an overall significant effect on plankton compartments. SEM results showed a close negative influence of *A. solida* on mesozooplankton (path coeffi-

cient -0.67), which, together with temperature, drove a large part of mesozooplankton variability (74% of total variability) (Fig. 8).

Discussion

Several *Aurelia* spp. populations have been recorded across the Mediterranean Sea, from the northern coasts of the Alboran Sea to the Marmara Sea. However, much of our current knowledge on life histories and population dynamics comes from studies on the northern Mediterranean coasts, while investigations are particularly scarce in the southern countries (Papathanassiou *et al*., 1987; Bonnet *et al*., 2012; Kogovšek *et al*., 2012; Malej *et al*., 2012; Marques *et al*., 2015).

Seasonal population dynamics

The planktonic life stages of *A. solida* (ephyrae, juveniles, and adults) in the Bizerte lagoon occur from winter (ephyrae) to summer months, with a unique generation by year and a lifespan of seven to eight months. Com-

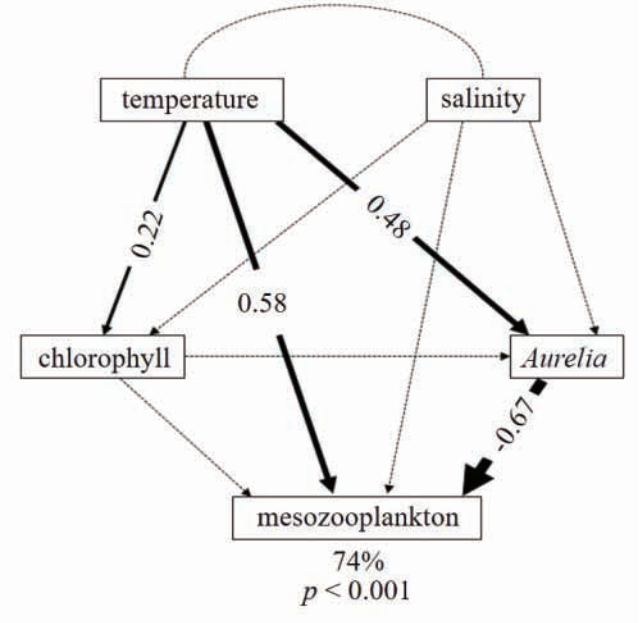

Fig. 8: Path diagram of the interaction between the abiotic (temperature, salinity) and biotic parameter (chlorophyll biomass, mesozooplankton and *Aurelia solida*) in Bizerte lagoon in 2013 and 2014.

Table 3. Literature review of *Aurelia* spp. occurrence period and maximum abundance. Reference: (1) Olsen *et al.*, 1994; (2) Lucas, 2001; (3) Lucas & Williams, 1994; (4) Lucas, 1996; (5) Möller, 1980; (6) Gröndahl, 1988; (7) Lo & Chen, 2008; (8) Toyokawa *et al.*, 2000; (9) Aoki *et al.*, 2012; (10) Marques *et al.*, 2015; (11) Kogovšek *et al*., 201; (12) Malej *et al*., 2012; (13) This study.

Area	Location	Species	Months		Max. abundance (ind. m^{-3})		T (°C)	Reference
			Ephyrae	Medusae	Ephyrae	Medusae		
Northestern Atlantic	Kertinge Nor & Kerteminde Fjord, Denmark	*A. aurita*	February - March	April - September	304 ± 129	248 ± 292	na (min) – 22 (max)	1, 2
	Southampto Water, UK	*A. aurita*	January / February - March	April - June	8.71	2.8	10 – 16	3
	Horsea Lake, UK	*A. aurita*	December - June	March - January	-	24.9	5.5 – 23	4
	Kiel Bigt, Germany	*A. aurita*	November - August	April - November	0.07	0.12	na	5
	Gullmarfjord, Sweden	*A. aurita*	October - March	March - September	-	-	-1.4 – 16	6
North-western Pacific	Tapong Bay, Taiwan	*A. aurita*	September - February	January - December	328	14.5	17 – 30	7
	Tokyo Bay, Japan	*Aurelia* sp.1	October - May	January - December	2.4	1.6	12 – 25	8
	Mikawa Bay, Japan	*Aurelia* sp.1	-	March - Augudt	-	0.91	8.3 – 26.5	9
Mediterranean Sea	Thau Lagoon, France	*Aurelia* sp.	November - May	March - June	14.7	3.3	13 – 20	10
	Berre Lagoon, France	*Aurelia* sp.	November - April	January - May	0.43	0.18	7 – 17	
	Bages-Sigean Lagoon, France	*Aurelia* sp.	-	May - June	-	0.18	14 – 28	
	Mljet Lake, Adriatic	*Aurelia* sp.5	May - January	January - December	-	-	11 – 28	11
	Northern Adriatic	*Aurelia solida*	November - February	February - June	-	-	15 – 24	12
	Bizerte Lagoon, Tunisia	*Aurelia solida*	December - January	January/Fabruary - June/July	3.9	6.5	14 – 24.5	13

parable life cycle tuning, with strobilation after seasonal low temperatures in winter or early spring months, is exhibited by different *Aurelia* spp. in Northern European and Japanese seas. There is, however, a certain degree of variability in life history traits (e.g. abundance, growth, medusa longevity) driven by specific environmental features (Lucas & Williams, 1994; Olsen *et al*., 1994; Riisgård *et al*., 1995; Lucas, 1996; Toyokawa *et al*., 2000; Miyake *et al*., 2002), and likely also by the ecological variability among the different cryptic species (Table 3).

During the two years of surveying, *A. solida* strobilation started in December. Overall, animal metamorphosis and life stage transitions are driven by epigenetic influences (Heyland & Moroz, 2006; Fuchs *et al*., 2014; Fellous *et al*., 2015): especially for the polyp-to-jellyfish transition, chemico-physical and biological factors such as temperature, photoperiod, salinity, and food regime are known to play key roles (Purcell *et al*., 2012; Holst, 2012; Hubot *et al*., 2017), with temperature leading the activation of strobilation processes in Scyphozoa (Purcell, 2005, 2007). In particular, for several *Aurelia* spp., a critical low water temperature seems to regulate strobilation and pre-strobilation phases. For instance, *Aurelia* spp. polyps from the northern Mediterranean Sea strobilate at 13–14°C but not at 21°C (Purcell *et al*., 2012), while in the northern Adriatic Sea, *A. solida* strobilation occurs at cold water temperatures (from 15 to 8°C, from November to February, respectively) (Malej *et al*., 2012). In the Bizerte Lagoon, *A. solida* ephyrae are produced when water temperature drops below 15°C; a lower temperature than that reported for *A. solida* polyp strobilation in the Red Sea (19°C) (Schroth *et al*., 2002), which can be attributed to divergent selection and adaptation to the habitat.

The *Aurelia* spp. life span extends from several months to over a year (Lucas & Williams, 1994), disappearing from the water column after sexual reproduction and/or sudden changes in environmental parameters. *A. solida* adult medusae thrive and reproduce in the Bizerte Lagoon from spring until early summer and disappear when water temperature rises to 25°C or above. In the northern Adriatic, the reported observations highlight a similar seasonal pattern, with occurrence of *A. solida* medusa from February to June (Malej *et al*., 2012). This suggests that, in the Mediterranean Sea, the species do not occur in waters above 25°C, tuning the timing of developmental events (e.g. strobilation, reproduction, spawning) and life history traits to the environmental conditions. In contrast, *Aurelia* medusae collected in the Suez Canal are known to occur at temperatures far exceeding 25°C (El-Serehy and Al-Rasheid 2011, described as *A. aurita*).

The abundance of *A. solida* planktonic stages in the Bizerte Lagoon displayed a marked variability particularly in the ephyra stage. The relatively lower ephyra abundance in December 2012 to January 2013 (1.2 and 0.9 ind m^{-3}, respectively), compared to December 2013 (3.9 ind m^{-3}), might be related to difference in food supply during the polyp stage. In fact, low zooplankton density (644 ± 63 ind m^{-3}) was recorded in summer and autumn 2012 (Gueroun *et al*., 2014), while much higher prey density was available to *A. solida* polyps for the same period during the second year (i.e. summer and autumn 2013). Although *Aurelia* spp. polyps strobilate at low food concentration, the number of produced ephyrae per polyp, as well as the number of strobilation cycles per polyp, increased with food (Wang *et al*., 2015a, b). Ephyrae abundance was three times higher in 2013 than in 2012, but adult abundance did not exhibit significant variation between the two years.

Adult medusa abundance relies not only on ephyra production, but also on recruitment success (Hernroth & Gröndahl, 1985; Lucas *et al*., 2012). Apparently, the success of ephyra-to-medusa recruitment in the Bizerte lagoon was lower in 2013 than in 2012. Available information suggests that both adult jellyfish or ephyra mortality can be induced by several mechanisms, including a long starvation period (Fu *et al*., 2014), predation, metabolic intolerance to variation of environmental factors (e.g. temperature, salinity), or parasitism (Pitt et al. 2014). In the Bizerte lagoon, mortality of *A. solida* ephyrae remains unexplained. However, mortality might not be assigned to changes of environmental factors, since temperature (13–14.7°C) and salinity (36.3–37.7) were comparable in both years, and nearly constant during ephyra occurrence.

Aurelia solida *predation*

A. solida in the present study, similar to *A. aurita* s.l. populations worldwide, showed prey heterogeneity, mostly reflecting opportunistic predation on available food within each ecosystem (Matsakis & Conover, 1991; Olsen *et al*., 1994; Ishii & Tanaka, 2001; Barz & Hirche, 2005). Jellyfish are opportunistic tactile predators whose prey selection depends on various predator and prey characteristics (reviewed in Purcell, 1991). With the exception of two samples, significant positive selection was found for mollusc larvae in the analysed gut contents. This positive selectivity may have been slightly overestimated due to the large mesh size (200 µm) of the plankton net used during the present study. However, mollusc larvae are easier prey to catch than active mesozooplankton taxa such as copepods and larvaceans. Although mollusc larvae are the dominant prey, the predatory impact of *Aurelia* spp. may be limited by bivalve recruitment, since they are not digested and survive the passage through the jellyfish gastric cavity (Purcell *et al*., 1991). A significant positive prey selectivity exhibited by *A. solida* for larvaceans in the present study diverges from results obtained by Purcell and Sturdevant (2001). In contrast to copepods, larvaceans do not actively swim, but are very sensitive to vibrations. At the slightest touch of their gelatinous casing or 'house', larvaceans react with a burst of swimming (Bone & Mackie, 1975). This behaviour should allow them to escape predation by *Aurelia* medusae. However, in the natural environment, responses of zooplankton to their predators can be reduced due to shear flow (Singarajah, 1975). Larvacean size might also explain their selection by *A. solida* as the contact probability with a predator is positively correlated to prey size (Madin, 1988). The four species constituting larvacean

Table 4. Literature review of digestion time estimated from the stomach contents of *Aurelia* spp. Reference: (1) Heeger & Möller, 1987; (2) Matsakis & Conover, 1991; (3) Sullivan *et al.*,1994; (4) Båmstedt & Martinussen, 2000; (5) Martinussen & Båmstedt, 2001; (6) Ishii & Tanaka, 2001; (7) Dawson & Martin, 2001; (8) Purcell, 2003; (9) This study; ND = no data.

Species	Bell diameter (±SD) (cm)	Prey	Temperature (°C)	Digestion time (h)	Source
A. aurita	0.6 - 2.5	Herring larvae	10-12	5	Möller (1980b)
A. aurita	1.8-2.4	Herring larvae	22	3.8	Heeger and Möller (1987)
A. aurita	ND	Copepods , Fish eggs, *Rathkea octopunctata*	4	3.85	Matsakis and Conover (1991)
A. aurita	ND	Copepods	7.5	3.5 ± 1.2	Sullivan et al. (1994)
		Fish larvae	7.5	2.3 ± 0.1	
A. aurita	3.6 (± 0.7)	Copepods (*Calanus finmarchicu*)	10	1.3	Båmstedt and Martinussen (2000)
A. aurita	1.2 (± 2.2) - 1.5 (± 0.2)	Small copepods (*Temora longicornis*)	5-20	5.1 ± 1.3 (5°C), 3.1 ± 0.7 (20°C)	Martinussen and Båmstedt (2001)
		Big copepods (*Calanus finmarchicus*)	5-20	23.1 ± 2.7 (5°C), 4.6 ± 1.1 (20°C)	
A. aurita	17.9 - 20.7	Mixed zooplankton	22	0.95	Ishii and Tanaka (2001)
A. aurita	4-8	copepods,	30	0.71	Dawson and Martin (2001)
		Bivalves veligers	30	2.3	
A. labiata	11 (± 3)	Copepods - Cladocerans	14	3	Purcell (2003)
		Larvaceans	14	1.5	
A. solida	10 (± 2.5)	Mixed zooplankton	13 ; 18 ; 23	6.2 (13°C) ; 3.8 (18°C) ; 2.4 (23 °C)	This study
		Copepods		6.9 (13°C) ; 3.8 (18°C) ; 2.4 (23 °C)	
		Larveceans		< 0.5	
		Fish eggs		4.7 (13°C) ; 3.8 (18°C) ; 1 (23 °C)	
		Gastropod larvae		4.5 (13°C) ; 2.7 (18°C) ; 2.4 (23 °C)	

populations in the Bizerte Lagoon, namely *Oikopleura longicauda*, *Oikopleura fusiformis*, *Oikopleura dioica*, and *Fritillaria pellucida* (Touzri *et al*., 2012) can reach up to 3 mm in length (Brunetti *et al*., 1990; Scheinberg *et al*., 2005). While the copepods were the second main prey, they were always negatively selected by *A. solida.* Copepods are known to be active swimmers with a complex and variable behaviour to escape from predators, such as escaping at submaximum velocity or jumping away from predators (Suchman, 2000). Their escape behaviour, associated with their ability to detect the water movement created by jellyfish bell contraction, may explain why less than 1% of encountered copepods are ingested by these short-tentacled medusae (Suchman, 2000).

A. solida diet varied qualitatively and quantitatively depending on the medusa size. Diet of small medusae (bell diameter < 5 cm) showed low prey diversity (1–5 different prey types), mainly copepods, compared to large medusae. Similar observations have been made in other areas (Graham & Kroutil, 2001; Barz & Hirche, 2005). The composition of zooplankton in the field did not show a temporal variation during the studied period, indicating that dietary changes are linked to jellyfish predatory and clearance ability. Clearance rate rising with medusa bell diameter (Möller, 1980; Olsen, 1995), probability to encounter less abundant prey, and therefore increasing diet diversity, is much higher in larger medusa than in smaller ones.

The digestion time of jellyfish varies according to temperature and prey availability; high temperature reduces digestion time (Martinussen & Båmstedt, 2001; Purcell, 2009), whereas it increases with both prey size and number (Martinussen & Båmstedt, 1995; Båmstedt & Martinussen, 2000). In our study, only the influence of temperature was investigated. The observed digestion

times were quite low compared to previous studies (Table 4). These differences may be due to the different prey availability (type, size, and abundance) and experimental conditions, as well as the different physiological responses of various *Aurelia* species. It is tempting to suggest that digestion time variability in *Aurelia* spp. might be interpreted as species-specific ecological adaptations to different environments.

Although there was a great variability in predation impact estimations, *A. solida* exerted a non-negligible pressure on the mesozooplankton daily standing stock that can reach up to 39.2%, mainly when the jellyfish abundances were high. The sporadic high predation on copepods (21%) and fish eggs (95%) can directly impact their recruitment in case of matching with reproduction and/or spawning events. In case of fish recruitment, the pressure can be amplified indirectly through competition with zooplanktivorous fish (Purcell, 2003; Lynam *et al*., 2005). Compared with other jellyfish populations, *A. solida* predation impact in the Bizerte Lagoon was considerably lower than the *A. aurita* s.l. pressure reported in Tokyo Bay (5–162%) (Kinoshita *et al*., 2006), and Kertinge Nor cove (Denmark) (351% of the daily rotifer biomass) (Olsen, 1995), and was greater than in Chesapeake Bay (0.3 ± 0.3% and 6.9 ± 3.9% of copepod and larvacean daily standing stocks, respectively) (Purcell, 2003).

While predation impact estimates jellyfish pressure during its occurrence, SEM, taking into account the whole period (with and without jellyfish), highlighted mesozooplankton control by *A. solida* through a prominent top-down control.

Nonetheless, *A. solida* pressure appears non-negligible; its low abundance and limited occurrence (6–7 months) probably restricted its predatory impact, avoiding a higher depletion on the mesozooplankton community, and might characterise its persistence in the lagoon (Boudouresque, 1999) and enable the establishment of a resident population. However, *A. solida* is not the only jellyfish recorded in the Bizerte Lagoon. Since 2012, two other non-indigenous species, *Phyllorhiza punctata* (Gueroun *et al*., 2014) and *Rhopilema nomadica* (Balistreri *et al*., 2017) occur during the summer–autumn period, causing increasing pressure on the zooplankton community, with wide implications for the pelagic food web dynamics in the Bizerte Lagoon.

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