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Molecular approach indicates consumption of jellyfish by commercially important fish species in a coastal Mediterranean lagoon

Marques Raquel [2, *], Darnaude Audrey M. [2], Crochemore Sandrine [1], Bouvier Corinne [2], Bonnet Delphine [1]

[1] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Montpellier, France
[2] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Montpellier, France

* Corresponding author : Raquel Marques, email address : raquel.fonseca-da-silva-marques@etu.umontpellier.fr

Abstract :

Until recently, jellyfish have been ignored as an important source of food, due to their low nutritional value. Here, quantitative PCR was used to detect and quantify the DNA of the jellyfish *Aurelia coerulea* in the gut contents of commercially important fish species from the Thau Lagoon. Individuals from five fish species were collected during two different periods: the bloom period, when the pelagic stages of *A. coerulea* are abundant, and the post-bloom period, when only the benthic stage – polyps – is present in the lagoon. The DNA of A. coerulea was detected in the guts of 41.9% of the fish analysed, belonging to four different species. The eel Anguilla anguilla and the seabream Sparus aurata were important jellyfish consumers during the bloom and post-bloom periods, respectively. These results provide new insights on the potential control of jellyfish populations and on jellyfish importance as a food source for exploited fishes.

Highlights

► DNA of the jellyfish *Aurelia coerulea* was detected by qPCR in the guts of four commercially important fish species. ► All the individuals of European eel analysed had jellyfish DNA in their guts. ► Gilthead Sea bream likely indirectly consumed jellyfish polyps, by preying on their settling substrates (bivalves). ► Jellyfish might be a non-negligible important food source for commercially exploited fish species.

Keywords : Predation, *Aurelia coerulea*, Eel, Seabream, Polyps, Medusae, Quantitative PCR, Gut content, Thau lagoon

1. Introduction

Gelatinous organisms (scyphozoan, ctenophores, siphonophores, salps, pyrosomes and appendicularians, hereafter called jellyfish) are ubiquitous components of marine food webs and their noticeable outbreaks have been promoting recent research on their ecology. However, these studies have long focused on the drivers of jellyfish blooms (*e.g.* Purcell 2012) while little is known still on the causes of jellyfish mortality (Purcell and Arai 2001), although this information is fundamental though to understand their population dynamics.

So far, jellyfish were consistently considered as "dead ends" in marine food webs, due to their high water content and low nutritional value (e.g. 2.3-3.6 KJ.g.dry mass^{-1} for *A. aurita vs.* 15.6 – 27.9 for various fishes, Doyle et al. 2007). They were largely believed to be ignored by most predators, with the exception of a few specialists, feeding exclusively on gelatinous organisms, such as the ocean sunfish (*Mola mola*), the butterfish (*Peprilus triacanthus*) and the leatherback turtle (*Dermochelys coriacea*) (Mianzan et al. 1996; Purcell and Arai 2001; Arai 2005). Recent research though, has led to a shift in this paradigm (Hays et al. 2018).

Historically, diet assessments were performed by gut content analysis, which may provide biased information regarding jellyfish consumption as it gives excessive importance to hard prey that are more resistant to digestion (Hyslop 1980). Gelatinous organisms are digested rapidly and often destroyed or shrunk by preservative methods (Arai 2005). Although gut contents still provide new evidences of the importance of jellyfish as prey (Díaz Briz et al. 2018), contemporary studies have been using new techniques to identify jellyfish predators, such as stable isotope analysis, animal-borne cameras, remotely operated vehicles and molecular analysis (Hays et al. 2018). Due to these modern techniques, the list of jellyfish predators has been growing and now includes commercially important fishes such as herring (*Clupea harengus*), whiting (*Merlangius merlangus*), bluefin tuna (*Thunnus thynnus*) and swordfish (*Xiphias gladius*) (Cardona et al. 2012; Lamb et al. 2017). Jellyfish were also shown to be of high importance in the diet of the larvae of a critically endangered fish, the European eel, *Anguilla anguilla* (Ayala et al. 2018) and to be ingested even by herbivorous fishes (Bos et al. 2016). Likewise, cephalopods, anemones, crabs, echinoderms and several species of birds have been reported to feed on jellyfish (Ates 2017; Hoving and Haddock 2017; McInnes et al. 2017; Phillips et al. 2017; Thiebot et al. 2017). Jellyfish consumption apparently even occurs in deep benthic habitats of the Norwegian fjords, where mass falls of jellyfish carcasses can provide food for several scavengers, including the commercially exploited lobster *Nephrops norvegicus* (Sweetman et al. 2014; Dunlop et al. 2017).

The life cycle of many blooming jellyfish species (i.e. scyphozoans) is complex, though, comprising two pelagic stages (the young immature ephyrae and the sexually mature medusae) and an asexual reproductive benthic stage (the scyphistomae, hereafter called polyps). The magnitude of most jellyfish blooms is therefore dependent on the density of polyps and ephyrae survival. Therefore, the mortality during these two early life stages may have a major effect on

jellyfish population dynamics (Lucas et al. 2012; Fu et al. 2014). Insights on the predation on polyps and ephyrae and its potential impact on jellyfish outbreaks are still limited though (*e.g.* Ishii et al. 2004; Takao et al. 2014). In a recent laboratory experiment (Marques et al. 2016), the jellyfish *Aurelia coerulea* was found to be a potentially non-negligible source of food for an opportunistic fish, the gilthead seabream *Sparus aurata*. This fish was able to feed on all life stages of this jellyfish (including polyps) with potentially high ingestion rates. However, the predation of jellyfish by this fish has never been shown in the field, so far.

Jellyfish from the *Aurelia* Genus, are among the most common scyphozoans that form blooms (Dawson and Martin 2001; Mills 2001). They are widely distributed in coastal areas and semi-enclosed seas (Mills 2001). The Thau lagoon (NW Mediterranean, south coast of France) presents the rare particularity to harbour a completely resident population of *A. coerulea*, seemingly isolated from the Mediterranean Sea (Bonnet et al. 2012; Marques et al. 2015a). In this lagoon, *A. coerulea* ephyrae first appear in the early winter (in November - December) and grow during winter to give rise, at the beginning of spring (in March –April), to the adult medusae that form the annual bloom (Marques et al. 2015b). The medusae remain in the water column until the late spring (June), but disappear from the system afterwards. Polyps of *A. coerulea*, on the contrary, are found all year round in the lagoon (Marques et al. 2019), mainly settled on biofouling organisms, such as oysters and mussels (Marques et al. 2015a). Therefore, the Thau lagoon offers an ideal framework to investigate whether marine predators benefit from the jellyfish annual blooms and identify which life stages of *A. coerulea* are consumed in the field. This is imperative to address the role of predation in controlling jellyfish population dynamics and the potential importance of jellyfish as food for exploited fish species.

To this end, commercial fish species were sampled at different periods of the year and molecular analyses of their gut content were used to study their consumption of *A. coerulea*, during and after its local pelagic bloom.

2. Material and Methods

2.1. Sampling and samples preparation

Fishing is the oldest economic activity in the Thau lagoon, which is mainly performed by small enterprises (50 to 65 fishing boats operating in the lagoon), who target different species of fish using different fishing gears (CÉPRALMAR 2006). Different fish species were collected in the Thau lagoon by a professional fisherman. Fishes were collected during the annual bloom of *A. coerulea* (hereafter called bloom period, between April and June; Bonnet et al. 2012; Marques et al. 2015b) in 2012, 2013 and 2018, and during a period (from September to November) in 2018, when the pelagic stages of *A. coerulea* are not present in the lagoon (hereafter called post-bloom period, Bonnet et al. 2012; Marques et al. 2015b). During the bloom period, fishes were collected by trammel nets, with an active fishing effort of maximum 3h. During the post-bloom period, the

traditional ‘capéchade’, which is the most used fishing technique in Thau (Crespi 2002), was used to collect fish for this study. The ‘capéchade’ is a fishing trap gear, placed at the same location for several days. Fishes are collected when the sun rises, after 24h of fishing effort. The number of species and individuals collected were therefore dependent on their occurrence in the nets. Immediately after collection, the fish were placed in separate plastic bags by the fisherman in order to avoid possible loss (or mixing) gut contents during sampling. Bags were then filled with absolute ethanol and stored in individual containers. Once in the laboratory, the fish were weighted (Total weight in g), dissected and their entire gut contents were removed and preserved at -30°C until DNA extraction. For positive DNA templates, samples of both the pelagic (medusae) and benthic (polyps) stages of *A. coerula* were collected in the lagoon. Medusae were collected by a hand net and immediately preserved in absolute ethanol. Polyps attached to mussel shells were collected by SCUBA divers and transported in sea water to the laboratory. The samples were examined under a dissecting microscope (Olympus SZ40; Olympus KL 1500 LCD) and individual polyps were collected using needles. Fifty polyps were pooled per sample, frozen in liquid nitrogen and maintained at -30ºC until DNA extraction.

2.2. DNA extraction

After thawing, the fish gut contents were mechanically ground in a mixer mill (MM400, Retsch). Three subsamples of 25 mg were collected from each gut content (when possible) and DNA was extracted using DNeasy blood and tissue kit (QIAGEN) (Stopar et al. 2010). The extraction was performed according to the instructions of the manufacturer, with an extra lysis step, performed overnight at 56ºC. The same protocol was used for *A. coerulea* medusae samples, which were previously washed with pure molecular MilliQ water for ethanol removal. This protocol was, however, inefficient for the extraction of the polyp’s DNA, and therefore, their DNA was extracted by nucleic acid purification automated Maxwell ® instrument (Promega) and 16 LEV Blood DNA kit (Promega), with a modification of the lysis procedure, which was performed overnight at 56ºC, using 30 µl of Proteinase K (Promega). In all cases, the extracted DNA was quantified in Nanodrop (NanoDrop One, Thermo Scientific).

2.3. Detection of A. coerulea DNA

Detection and quantification of *A. coerulea* DNA in the fish gut contents was performed by quantitative PCR (qPCR). This technique has been employed to detect and quantify the DNA of a specific prey in gut contents and faecal pellets, when traditional visual methods fails to do so (Matejusová et al. 2008; Nejstgaard et al. 2008; Töbe et al. 2010). This sensitive approach allows the detection and quantification of very small amounts of DNA so even highly digested jellyfish can still be detected. All amplifications reactions were analysed using a Roche LightCycler 480 Real-Time thermocycler (qPHD-Montpellier GenomiX platform, Montpellier University,

France). The total qPCR reaction volume was 1.5 µl and consisted of 0.5 µl DNA and 1 µl LightCycler 480 SYBR Green I Master mix (Roche) with 0.6 µM PCR primer (Eurofins Genomics). A 245 base pair gene fragment (partial sequences of mt-16S rDNA) was amplified by the species-specific (*A. coerulea*) primers AS3-F (5'- ATTGGTGACTGGAATGAATG - 3') and AS3-R (5'- TATGACAGCCCTTAGAGTTC - 3') designed by Wang et al. (2013). The best suited primer concentration (0.4, 0.6 or 0.8 µM) was determined in preliminary tests on three samples of *A. coerulea* polyps and medusae. A Labcyte Acoustic Automated Liquid Handling Platform (ECHO) was used for pipetting each component of the reaction mixture into a 384-well plate (Roche). The qPCR program consisted in an enzyme activation step at 95ºC for 2 min, followed by 45 cycles of denaturation at 95ºC for 10 s, hybridization at 60ºC for 10s and elongation at 72ºC for 10 s. A final melting temperature curve (Tm) of the amplicon was performed (95ºC for 5 s and 65ºC for 1 min), in order to ensure the specificity of the primers. The same amplification conditions and reaction concentrations were used in all assays performed in this study.

The efficiency and specificity of target gene detection by the primer was tested on a 2-fold dilution series of *A. coerulea* medusae and polyps positive templates. Triplicate reactions were performed at each dilution in order to generate the standard curves for each template. An ANCOVA analysis was performed, in order to assess if the efficiency (*i.e.* the slopes) of the two standard curves were significantly different. Absolute quantification of *A. coerulea* DNA in the fish gut contents was estimated using the regression equation of the standard curve obtained for the polyps positive template. The observed Cp values of each dilution of the positive template were plotted against its known DNA concentration to obtain the regression equation. The Cp value is defined as the cycle when the sample fluorescence exceeds the threshold above the background fluorescence. The Cp value is therefore related with the amount of DNA present in the sample (Dorak 2006).

The quantification of DNA in fish gut contents was only performed in the samples showing Cp values below 31, which was found to be the Cp correspondent to the minimum quantifiable concentration (1.37 x 10-4 ng μL^{-1}). Samples with the same Tm values as the positive templates (Tm peak at 81.5) and Cp values between 31 and 32.62 (maximum Cp observed for the positive templates) were considered as positive detection but non-quantifiable. Samples showing Cp values above 32.62 were considered as negative detection. For each gut content sample, a minimum of 9 replicates (3 experimental replicates, *i.e.* for DNA extraction, of the same gut content and 3 technical replicates for each experimental replicate), were performed, except for some samples with very low material, from which only one experimental replicate was collected. Only gut contents samples that showed positive detection in at least two technical replicates were considered to contain *A. coerulea* DNA.

The specificity of the primers and the detection of *A. coerulea* DNA was further confirmed by sequencing the positive templates and the qPCR product of 16 samples with positive amplifications. For that, 10 µL of molecular MilliQ water was added to the qPCR products. The DNA was purified using a commercial kit (QIAquick PCR Purification kit, QIAGEN), following the manufacturer protocol. The purified DNA was amplified by traditional PCR using PCR kit illustra puretaq ready to go (GE Healthcare), with 5 µL of purified DNA sample, 0.6 µM of each forward and reverse primers (primer pair AS3) and 27.5µl of molecular MilliQ water. The thermal profile for the PCR reaction was composed by 3 min at 95°C, 35 cycles of 1 min at 95°C, 1 min at 60°C and 90 s at 72°C, followed by 1min at 72°C (Stopar et al. 2010; Ramšak et al. 2012). The products of PCR reactions were analysed through electrophoresis (Mupid-One; Advance) at 100V for 30min in 0.5 X TAE buffer (Euromedex). An aliquot of 3 µL of samples were load on Agarose gel 1.5%, using loading buffer (AppliChem, Panreac) and 1Kb DNA ladder (Euromedex). Gels were stained with GelRed ® Nucleic Acid Gel Stain (Biotium), visualized and photographed on UV table using Molecular Imager Gel Doc ™ XR System (Bio-Rad) for quality control of DNA amplification. Sequencing was performed at the genotyping and sequencing facilities in Montpellier University. The purification of PCR products was performed by magnetic beads, using the CleanPCR kit (GCBiotech), performed by an automated liquid handler (Biomek 4000, Beckman Coulter). Sequencing was then performed with 55-60 ng of DNA using the BigDye Terminator Cycle sequencing v3.1 kit (Life Technologies), with the following PCR program: 3 min at 96ºC, 25 cycles of 10 sec at 96ºC, 5 sec at 50ºC and 4min at 60ºC. The products of the sequencing reaction were purified using magnetic beads, following the same protocol as previously described. The purified products were then analysed on an ABI 3500 xL capillary sequencer (Applied Biosystems, Darmstadt, Germany). A BLAST analysis of the resulting sequences against the GenBank nucleotide database was performed.

3. Results

3.1. Standard curve and DNA quantification

Both positive templates (polyps and medusae) were identified as *A. coerulea*, after the BLAST analysis. The standard curves of the qPCR assay (Fig. 1), determined with polyps and medusae positive templates, showed high assay efficiencies (86.64 and 93.80 %, respectively) and high correlation coefficient, R^2 (both 99%). The slope of both positive templates did not differ significantly (ANCOVA; $F = 0.03$, $P = 0.85$). However, the initial template concentration of polyps was higher (55.79 ng μL^{-1}) than that of medusae (11.89 ng μL^{-1}) and therefore, more dilution steps showed Cp values below 31. In consequence, the standard curve of polyps comprises more dilution steps and wider range of quantifiable template concentration, increasing the accuracy of the regression fit. For this reason, its correspondent equation ($y = -3.69\ x + 16.74$) was selected to estimate the concentration of *A. coerulea* DNA in the fish gut content.

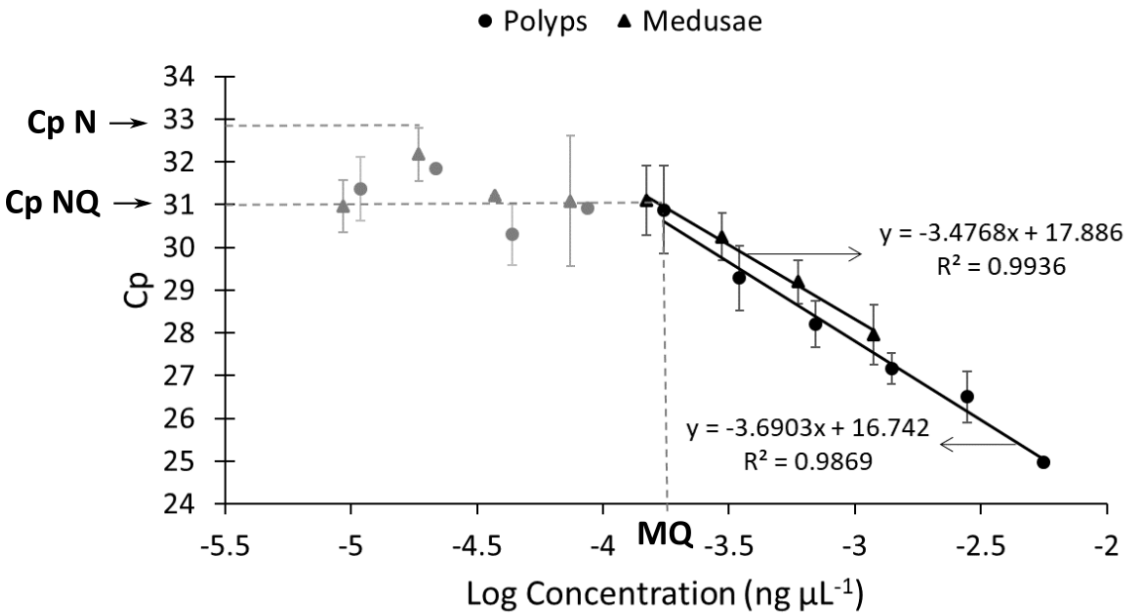

Fig. 1: Standard curves determined from 2-fold dilutions of polyps (circles) and medusae (triangles) positive templates. The dilutions included in the standard curve of each template are represented in black, while the dilutions excluded from the standard curve are in grey. In each case, the standard curve equation is shown, but only that of the polyp's template was used to estimate DNA concentration in fish gut contents (efficiency of 86.63%). The minimum quantifiable concentration (MQ = 1.37 x 10^{-4} ng μL^{-1}) corresponded to a Cp of 31 (*i.e.* the threshold for quantification; Cp NQ). Samples with Cp values between 31 (Cp NQ) and 32.62 (*i.e.* the threshold for detectability; Cp N) were considered positive but Non-quantifiable. Samples with Cp values above Cp N were considered negative (see methods section for further information). Error bars are standard deviations.

Although the more diluted samples of the positive template for *A. coerulea* polyps and medusae were positive (*i.e.* with proper melting curves), they showed low Cp values, indicating that their DNA concentrations were too low to be accurately quantified. Therefore, those dilutions were excluded from the standard curve. Among the three technical replicates analysed for each dilution sample, six false negatives (*i.e.* deviated Tm peak values) were observed. Although non-quantifiable, *A. coerulea* DNA was still detected at a maximum Cp of 32.62, which was therefore considered as the threshold of detectability.

The BLAST analysis revealed that all sequenced qPCR products of gut contents samples matched the previously designated *Aurelia* sp.1 (> 96.7% similarity), recently accepted as *A. coerulea* (Scorrano et al. 2016).

3.2. Fish ingestion of A. coerulea

During the period of *A. coerulea* bloom (from April to June) 50 fish individuals were provided by the fisherman. They belonged to five different species: the European eel (*Anguilla*

anguilla, Linnaeus, 1758), the sand smelt (*Atherina boyeri*, Risso, 1810), the golden mullet (*Liza aurata*, Risso, 1810), the salema (*Sarpa salpa*, Linnaeus, 1758) and the gilthead sea bream (*Sparus aurata*, Linnaeus, 1758) (Table 1). During the post-bloom period, when only polyps are present in the lagoon (September to November), only 12 individuals could be collected for this work. They belonged to three different species: the golden mullet (*L. aurata*), the salema (*S. salpa*) and the gilthead sea bream (*S. aurata*).

Table 1: Numbers of fish gut contents analysed (N) and of fish guts with positive detection of *A. coerulea* DNA (N Positives). In each case, the species, the range of weight and length of the sampled fish are indicated with the sampling period, from April to June (bloom) and from July to November (Post-bloom).

Period	Common name	Fish Species	Weight (g)	Length (mm)	N	N Positives (%)
Bloom	European eel	*Anguilla anguilla*	4.8 [a]	150 [b]	10	10 (100 %)
Bloom	Sand smelt	*Atherina boyeri*	0.41 - 8.1 [c]	40 - 99 [c]	5	0 (0 %)
Bloom	Golden mullet	*Liza aurata*	251.2 - 900	306.0 - 488.4 [a]	12	4 (33.3 %)
Bloom	Salema	*Sarpa salpa*	260.6 - 650	263.7 - 360.2 [a]	11	1 (9.1 %)
Bloom	Gilthead sea bream	*Sparus aurata*	133.6 - 300	95.5 - 126.7 [a]	12	4 (33.3 %)
Post-bloom	Golden mullet	*Liza aurata*	219 - 660.7	291.0 - 436.1 [a]	3	1 (33.3 %)
Post-bloom	Salema	*Sarpa salpa*	219.5 - 324.1	248.7 - 284.1 [a]	2	1 (50 %)
Post-bloom	Gilthead sea bream	*Sparus aurata*	159.9 - 234.6	101.7 - 116.3 [a]	7	5 (71.4 %)

[a] Calculated from length-weight relationships (Melià et al. 2006; Crec'hriou et al. 2012)
[b] Data not collected during the study, an approximate length of the individuals is provided.
[c] Data not collected during the study, but data from individuals collected in the Thau lagoon during the same period of the year is provided.

In total, DNA from *A. coerulea* was detected in the gut content of 26 fish (41.9 % of the 62 individuals analysed), among which 73% had been collected during the bloom period and 27% during the post-bloom period (Table 1). With the exception of the sand smelt, all species were shown to have consumed *A. coerulea*, irrespective of the period of sampling. During the bloom period, medusae DNA was detected in the gut contents of all the eels collected (10 individuals). One third of the golden mullets and gilthead sea breams analysed were also shown to have consumed *A. coerulea*, while positive detection was only observed in one individual of salema (9.1%). During the post-bloom period, *A. coerulea* was detected in only one golden mullet, one salema, and in 5 (71.4 %) gilthead sea bream.

The concentration of DNA in the fish gut contents was higher during the bloom than in the post-bloom period (Fig. 2). At this time of the year 63.2 % of the jellyfish consumers had a sufficient amount of DNA to be quantified (*i.e.* > 1.37×10^{-4} ng μL^{-1}). The maximum concentration (11.1×10^{-4} ng μL^{-1}) was detected in a golden mullet, but four other fish (two eels and two gilthead sea breams) showed DNA concentrations above 4×10^{-4} ng μL^{-1} in their gut contents. During the post-bloom period, the concentration of DNA in the guts was very low and, in most cases, non-quantifiable (Fig. 2).

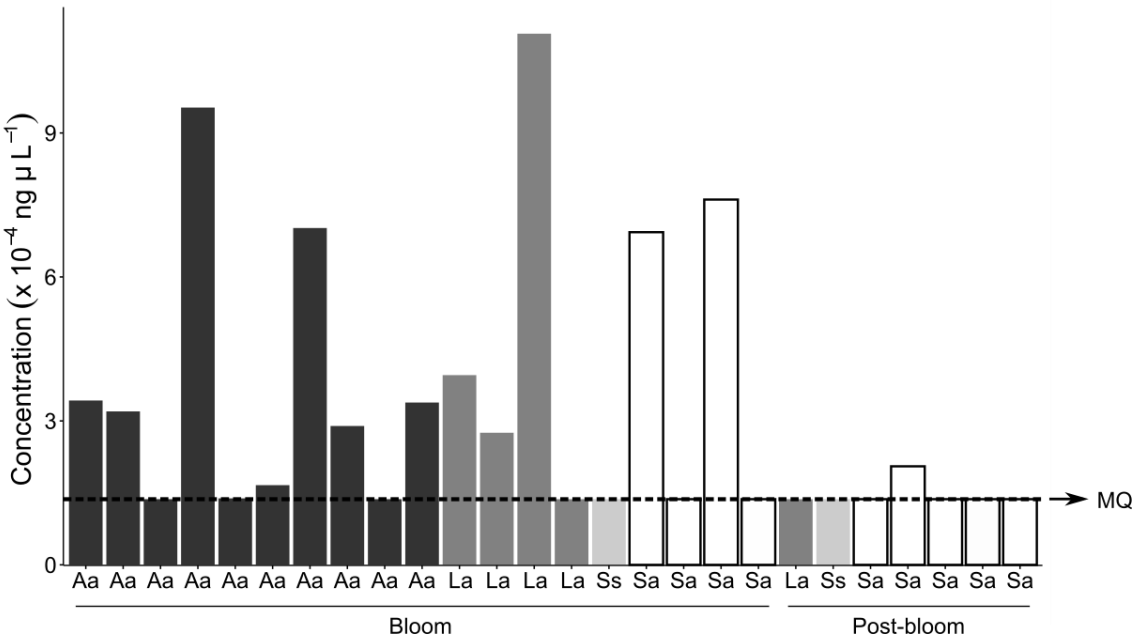

Fig. 2: Estimated concentration of *A. coerulea* DNA in the gut contents of the fish with positive detection: (Aa) European eel (*Anguilla anguilla*), (La) Golden mullet (*Liza aurata*), (Ss) Salema (*Sarpa salpa*), (Sa) Gilthead sea bream (*Sparus aurata*). The horizontal dashed line (MQ) indicate the minimum quantifiable DNA concentration (1.37 x 10^{-4} ng µL^{-1}, *i.e.* Cp = 31; see methods section for further information), below which the detection was positive but non-quantifiable.

4. Discussion

The present work brings new insights on the prey-predator relationships between fish and jellyfish in the Thau lagoon. Indeed, four of the five fish species analysed in this study were found to feed on *A. coerulea*. For some species, all the individuals tested had *A. coerulea* DNA in their gut, suggesting that this jellyfish might be a non-negligible source of food for commercial fish in the Thau lagoon.

The concentration of the target DNA in the gut contents was frequently low, with many individuals showing non-quantifiable DNA concentrations. This is not very surprising because jellyfish are rapidly digested in fish guts, compared to other prey (*e.g.* > 93% of the jellyfish biomass can be digested within 1h in controlled laboratory studies, Arai et al. 2003). In particular, due to the fishing method used, most of the fish captured during the post-bloom period, probably had largely digested their prey during their prolonged captivity in the net. Therefore, we consider our results to be conservative and likely to underestimate *A. coerulea* consumption by commercial fish in the Thau lagoon. However, since only few individuals of each species were analysed, especially during the post-bloom period, additional studies are needed to confirm the actual importance of *A. coerulea* as a source of food for fishes in the Thau lagoon.

300 During *A. coerulea* bloom periods, the only fish species which did not seem to consume
301 jellyfish was the sand smelt. The diet of this species is opportunistic but mainly based on pelagic
302 organisms such as zooplankton, phytoplankton, arachnids, insects and fish larvae (Vizzini and
303 Mazzola 2005, Dias et al 2014, Yagci et al 2018). However, due to the small size of the specimens
304 examined (< 7cm), they might have avoid jellyfish blooms, since they may become prey for large
305 jellyfish medusae.
306 In contrast, the European eel was shown to be a potential important consumer of jellyfish
307 in the Thau lagoon. All the individuals tested showed positive detection of *A. coerulea* in their
308 gut contents, with relatively high DNA concentrations. The consumption of gelatinous organisms
309 by eels was also previously reported for their larvae (leptocephali) in the Sargasso Sea (Riemann
310 et al. 2010; Ayala et al. 2018). Although there is a progressive ontogenic change in the diet of the
311 eels (Costa et al. 1992; Proman and Reynolds 2000), it is not surprising that they retain the ability
312 to feed on gelatinous organisms. After their migration from their spawning areas in Sargasso Sea
313 (Ginneken and Maes 2005), European eels reach the Mediterranean lagoons as glass eels, with an
314 average length of ca. 60–65 mm (Melià et al. 2006). At this stage, eels are considered to be non-
315 feeding, starting to feed only when reaching the elver eel stage (Tesch et al. 2003). The individuals
316 collected in this study were all at the elver stage (*i.e.* pigmented with a length of ca. 150 mm).
317 The diet at this stage is mostly based on small sized prey like amphipods, isopods, mysids and
318 insects (Costa et al. 1992; Proman and Reynolds 2000) but it depends highly on prey availability
319 (Costa et al. 1992; Bouchereau et al. 2006). Therefore, it is likely that the high abundances of
320 jellyfish during the bloom might result in their ingestion by this opportunistic species.
321 The rate of standard metabolism of an European eel at 25ºC (*in situ* temperature in June
322 2013 was 20 ± 0.7 ºC) is 83.3 J g^{-1} day^{-1} (Owen et al. 1998). Assuming a similar energy
323 requirement for the individuals collected in Thau, an eel with 4.72 g (estimated for a 15 cm eel,
324 from length-mass relationships; Carss et al. 1999), would require 0.4 KJ d^{-1} of energy. One gram
325 (wet weight) of *Aurelia* sp. provides 0.1 KJ of energy (Arai 1997 in Doyle et al. 2007, after wet
326 weight estimation according to Lucas 1994). Therefore, one eel would require 3.8 g of medusae
327 wet weight per day to meet its energy requirements. The eels analysed in this study were collected
328 in June 2013, when the abundance of medusae was at its highest (75.5 ind 100 m^{-3}; Marques et
329 al. 2015b). Because medusae are big in this time of the year (16.4 ± 2.8 cm; Marques et al. 2015b,
330 which corresponds to 195.1 g of wet weight, estimated after Hirst and Lucas 1998, at the same
331 salinity conditions), it is possible that the eels had bitten their umbrellas, taking advantage of the
332 soft consistency of jellyfish body. Indeed, many jellyfish predators do not ingest the whole
333 medusae, but instead, they bite the umbrella margins and/or select particular parts of the medusae
334 with higher nutritional values, such as gonadal tissue (Milisenda et al. 2014; Marques et al. 2016;
335 Dunlop et al. 2017; Hoving and Haddock 2017). Therefore, in theory, one medusae could provide
336 enough energy to sustain the standard metabolism of one eel for 51 days. Even though a large

amount of jellyfish consumption is needed to meet such energy requirements (*i.e.* 80.5 % of the eel weight per day), the rapid digestion and gut clearance rates (Arai et al. 2003) allow the fish to increase its ingestion rates. Similar results were also reported for the leptocephali stage of the European eel (Ayala et al. 2018) and for other commercially important organisms (*e.g*. fish top predators, eel larvae, lobsters, deep water octopus), which, during blooms, jellyfish are able to meet and maybe overcome the entire energy requirements of these predators (Cardona et al. 2012; Dunlop et al. 2017; Hoving and Haddock 2017). Here we confirm the potential important role of jellyfish as food for young stages of the European eel. These results are of great importance since the European eel is listed as a critically endangered species by IUCN (Freyhof and Kottelat 2010) and information regarding its diet is still limited.

The consumption of *A. coerulea* during its bloom period was also recorded for the gilthead sea bream and the golden mullet, both species showing, in some cases, high *A. coerulea* DNA concentration in their gut contents. This result is not surprising for sea bream as this species has been shown to prey on all life stages of *A. coerulea* in laboratory experiments, with high ingestion rates of polyps and small medusae (Marques et al. 2016). The sea breams with the highest concentrations of the target DNA in their guts were collected in April 2013, when medusae bell diameter is < 3 cm (Marques et al. 2015b). In the laboratory, small medusae (1 cm bell diameter) were preferred by this fish, but larger ones (up to 8 cm bell diameter) were also preyed upon, by taking several bites on the edge of their umbrella (Marques et al. 2016). Therefore, our results provide evidence of a possible active predation of sea bream individuals on pelagic jellyfish in the field. Jellyfish, though, were not selected in the laboratory when prey with higher nutritional value were equally available (Marques et al. 2016). In the field, gilthead seabreams prey mainly on polychaetes, small fishes, crustaceans, gastropods and bivalves but adapt their diet to local prey availability (Pita et al. 2002; Escalas et al. 2015). Therefore, we suspect that the high abundance and accessibility of *A. coerulea* medusae during the bloom periods, benefit this opportunistic predator by providing a suitable source of food when its preferred prey are less accessible (Marques et al. 2016; Díaz Briz et al. 2018).

More surprisingly, one third of the golden mullet specimens analysed had the target DNA in their gut contents. Mullets are detritivores, eating a mixture of sand, detritus, microphytobenthos, macroalgae, zooplankton and benthic macrofauna (Laffaille et al. 2002; Almeida 2003). To our knowledge, the consumption of jellyfish by this species has never been described so far. It is possible that *A. coerulea* was consumed unintentionally, since dead medusae are occasionally found decomposing on soft bottoms (Marques, personal observation) and the resulting organic matter may be incorporated in the surface sediment layer. One individual of this species, though, showed high concentration of the target DNA in its gut content (the maximum concentration recorded in this study). Although, the active predation of jellyfish by the golden mullet cannot be excluded, this particular individual was collected during the peak of *A. coerulea*

abundance (in May 2018), when high biomass of jellyfish was also caught in the fishing nets (J. Fabrice, personal communication). Therefore, the high concentration of *A. coerulea* DNA in its gut contents might have been the consequence of its unintentional ingestion of medusae in the fishing net during sampling.

The ingestion of *A. coerulea* by salema might also be unintentional. Indeed, this species has been described so far as a true herbivore, with a diet largely based on seagrass leaves (Havelange et al. 1997). Because decaying medusae are also occasionally observed entangled among the seagrass leaves in the Thau lagoon (R. Marques, personal observation), they might have been ingested together with the target seagrass leaves. However, recent observations have shown that even herbivorous fish may actively prey on jellyfish (Bos et al. 2016), which cannot be excluded here. Still, additional individuals of this species should be analysed to test this hypothesis.

The consumption of *A. coerulea* was also observed when its pelagic stages were absent, which suggests that polyps might also be ingested by commercial fish species in Thau. The most important consumer of polyps in our study was the gilthead seabream (71.4% of the individuals showed positive detection of *A. coerulea* DNA in their gut contents). In previous laboratory experiments (Marques et al. 2016), the sea bream was shown to consume polyps, likely in an indirect way. In this recent study, it was suggested that the actual target of the fish during the predation experiments, could have been the settling substrate of polyps (*i.e*. living mussels), rather on the polyps themselves. In Thau, most of the polyps of *A. coerulea* are found fixed on oysters or mussel shells (Marques et al. 2015a). Because bivalves are highly important in the diet of adult sea bream (Pita et al. 2002; Tancioni et al. 2003; Russo et al. 2007) and very abundant in Thau lagoon, we hypothesize that the consumption of *A. coerulea* polyps in the field results from an indirect ingestion, when fishes are preying on their settling substrates. In addition, pieces of mussel shells were recurrently observed in the sea bream gut contents. These findings highlight the likely underestimated impact of sea bream predation on the regulation of the benthic population of *A. coerulea* in the lagoon, potentially contributing to the reduction of medusae abundances and to the magnitude of jellyfish blooms in this lagoon.

A. coerulea polyps consumption was also detected for both the salema and the golden mullet. This is surprising, since polyps generally settle on the underside surface of hard substrates and have never been found on soft sediments or fixed to seagrass leaves (Marques et al. 2015a). Even though unintentional consumption can not be excluded, very few individuals of these two species were analysed in this study. Therefore, the importance of the consumption of *A. coerulea* polyps by their individuals in the lagoon still needs further investigation.

5. Conclusion

Our results demonstrate that the jellyfish *A. coerulea* is ingested by several commercially important fishes in Thau lagoon during its bloom period, when the abundance and biomass of its pelagic stages are high, but also in post-bloom periods, when only *A. coerulea* polyps are present in this semi-enclosed ecosystem. This provides evidence that the vulnerability of jellyfish to fish predation has been underestimated in the lagoon but also, potentially, elsewhere. Indeed, predation pressure by a large number of fish species with broad diets is more ecologically important than that by a few specialized ones (Purcell and Arai 2001; Arai 2005). Here we highlight potential ecological implications for both fish and jellyfish ecology. On the one hand, direct predation on jellyfish pelagic stages or indirect predation on polyps might contribute to control jellyfish blooms, through top-down regulation. In this sense, the overexploitation of fish stocks might contribute to the increase of jellyfish outbreaks, by releasing the predation pressure over jellyfish populations (Roux et al. 2013). On the other hand, the availability and accessibility of jellyfish during their blooms provide an alternative food source for fish populations, that might actively consume jellyfish when their primary prey are less available (Diaz Briz et al. 2018; Mianzan et al 2001).

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7. Declaration of interest: none

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