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Nanoplastic uptake temporarily affects the pulsing behavior in ephyrae of the moon jellyfish *Aurelia* sp

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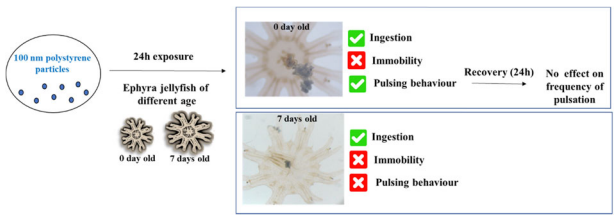
Abstract

The aim of this study is to investigate for the first time the uptake and ecotoxicological effects of nanoplastics (NPs) in a marine cnidarian. Ephyrae of the moon jellyfish *Aurelia* sp. of different ages (0 and 7 days old) were exposed to *negatively charged* polystyrene NPs for 24 h; then, the uptake was assessed through traditional and novel techniques, namely microscopy and three-dimensional (3D) holotomography. Immobility and behavioral responses (frequency of pulsations) of ephyrae were also investigated to clarify if NP toxicity differed along the first life stages. NP uptake was observed in ephyrae thanks to the 3D technique. Such internalization did not affect survival, but it temporarily impaired the pulsation mode only in 0 day old ephyrae. This may be ascribed to the negative charged NPs, contributing to jellyfish behavioral alteration. These findings promote 3D holotomography as a suitable tool to detect NPs in marine organisms. Moreover, this study recommends the use of cnidarians of different ages to better assess NP ecotoxicological effects in these organisms, key components of the marine food web.

Graphical Abstract



Keywords Behavior · Bioassay · Ecotoxicology · Immobility · Nanoplastics · Toxicity

Introduction

Plastics have revolutionized our daily lives so much that our age has been defined as the "Plastic Age" (Thompson et al. 2009). Global plastic production has increased exponentially

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in the last decades (UNEP 2021), reaching 367 million tons globally in 2020 (Plastics Europe 2021). Due to their resistance and hydrophobicity, plastics are easily dispersed from terrestrial to aquatic ecosystems (Wang et al. 2021). Once in the aquatic environment, plastics undergo degradation, breaking down into smaller particles at micro and nanoscales, also known as microplastics (materials between 0,1 µm and 5 mm) and nanoplastics (NPs, between 1 and 100 nm; Lambert and Wagner 2016). Due to their wide distribution and size, microplastics and NPs can be ingested by marine biota and transferred along the trophic chain, representing a serious problem (Nelms et al. 2018; Botterell et al. 2019; Markic et al. 2019; Barria et al. 2020; Natarajan et al. 2022). Moreover, these particles may induce toxicity due to the additives that are incorporated during their manufacture, and to other chemicals able to concentrate during their time in marine environments (Rios et al. 2007; Oehlmann et al. 2009; Heskett et al. 2012). Once ingested, toxins can be leached from the particles and enter tissues, resulting in endocrine disruption or cellular toxicity (Galloway 2015; Rochman 2015; Rummel et al. 2019). Recently, microplastics have been reported in gelatinous zooplankton (Lengar et al. 2021), *such as cnidarians* (Sucharitakul et al. 2020**;** Rapp et al. 2021**;** Eom et al. 2022), where they temporarily affected jellyfish survival and behavior (Costa et al. 2020a) Sucharitakul et al. 2020; Lengar et al. 2021; Rapp et al. 2021; Eom et al. 2022). Jellyfish exert an important ecological role in the ecosystem (Boero et al. 2008; Brodeur et al. 2016), being key components of the marine food web (Purcell et al. 2007). They are regulators of marine biogeochemical fluxes (Faimali et al. 2017; Baez et al. 2022) and sensitive to a wide class of contaminants, including plastics (Faimali et al. 2014, Costa et al. 2015, 2020a; Gambardella et al. 2015). Thus, they can ingest microplastics in a direct or indirect way through trophic transfer from contaminated prey (Costa et al. 2020b).

Thanks to their ability to ingest microplastics and considering that jellyfish and plastic distribution is influenced by currents and winds (Macali et al. 2018), jellyfish have been proposed as innovative bioindicators for plastic pollution in pelagic waters and in monitoring surveys (Macali and Bergami 2020), but not in in discharged treated wastewater (Sucharitakul et al. 2021). Although microplastic ingestion and ecotoxicological effects in marine jellyfish have recently been documented (Costa et al. 2020a), research on NPs in jellyfish and in other cnidarians is still sparse.

The properties of NPs differ from microplastics (Gigault et al. 2021). NPs can have emerging properties (i.e., increasing hydrophobic interactions that lead to protein conformational changes; Auclair et al. 2017) at the nanoscale. Due to their small size and high surface area to volume ratio, NPs can permeate biological membranes (Lambert and Wagner 2016), resulting in a toxicity increase relative to micro sized particles and their bulk counterparts (Andrady 2017; Triebskorn et al. 2019). The high NP surface area to mass ratio may also retain more toxic chemicals than micro or bulk material, increasing overall hazard (Koelman et al. 2015). Moreover, the counterbalance of several parameters (presence of salts, natural organic matter and colloids) of seawater may modify NP properties and behavior (Corsi et al. 2014; Bergami et al. 2016; Corsi et al. 2020, 2021; González-Fernández et al. 2021) and therefore, NP toxicity. Considering the growing concern around unexplored NP toxicity in the marine environment and jellyfish's ecological role in the marine food web, the potential uptake and ecotoxicological effects of NPs in the ephyrae of the moon jellyfish *Aurelia* sp. were investigated. In this study polystyrene nanoparticles were used, this polymer is one of the most abundant worldwide, representing about 10% of total plastic production (Verschoor et al. 2017). Recently, polystyrene NPs have been detected in the freshwater cnidarian *Hydra attenuata*, where they caused morphological changes and sub-lethal effects (Gagnè et al. 2019; Auclair and Gaugnè 2020; Auclair et al. 2020). In the present study NP uptake was assessed in marine jellyfish ephyrae by means of an epi-fluorescent and novel technique, namely three-dimensional (3D) holotomographic microscopy (Costa et al 2020a). Immobility and behavior, i.e., frequency of pulsations (Fp), were investigated as ecotoxicological endpoints in jellyfish ephyrae of two different ages—0 day old and 7 days old—in order to understand if the sensitivity to NPs differs along the first developmental stage of the life cycle.

Materials and methods

Polystyrene nanoparticles

Visible blue-dyed and fluorescent polystyrene NPs (nominal diameter: 100 nm) were purchased (cat. nr. 1100B, 2002; Phosphorex) and supplied as a 10 g/L in deionized water. Visible blue-dyed and fluorescently labeled (345 nm excitation/435 nm emission) NPs were used for jellyfish toxicity bioassays and uptake respectively. Fluorescently labeled NPs were supplied in deionized water containing a small amount of surfactant and 2 mM of sodium azide as an antimicrobial agent; NPs had no funcionalization. Nanoplastics were sonicated for 1 min and suspended in 0.22 µm filtered natural seawater (FSW) up to 100 mg/L suspension. The latter was used to bring NPs to 0.1, 1 and 10 mg/L. Since no environmentally relevant or high concentrations are available for NPs (Koelmans et al. 2015), we selected those reported for microplastics (Gambardella et al. 2017, 2018).

After NP suspension preparation, toxicity tests were immediately performed.

Aurelia sp. ephyrae recruitment

Colonies of *Aurelia* sp. polyps were provided by Acquario di Genova, Costa Edutainment S.p.A., and transported to CNR-IAS. They were placed in a thermostatic room (20 °C) in 1.5 L tanks, filled with FSW, gently aerated and fed daily with nauplii of *Artemia salina* (about 40 nauplii/mL); sea water was changed every two days. Strobilation was induced by thermic shock and food starvation: polyps were moved to 1.5 L tanks at 10 °C and were not fed; seawater was not changed for one month. After strobilation,120 ephyrae (0 day old) were collected and transferred by using a pipette into a beaker to evaluate NP ingestion and toxicity. Another 120 ephyrae were isolated from polyp culture and kept at 20 °C in a 2 L glass beaker with central aeration for a week in order to allow free movement of the organisms (Widmer 2008). During this period, ephyrae were fed every day with *Artemia sp*. nauplii and water was changed twice a week according to Olesen et al. (1996). Ephyrae were kept unfed 24 h prior to the experiments according to methods detailed in Shafer et al. (2021).

NP ingestion

Visible blue-particles and fluorescent blue polystyrene particles were used to detect NPs in the jellyfish ephyrae. Ephyrae collected after strobilation (0 day old) and those that were maintained in FSW for 1 week were individually placed into a multiwell plate with 2 mL of NP suspensions (0-0.1-1-10 mg/L) for 24 h. Three replicates were prepared for each dilution; each replicate contained 8 ephyrae individually placed in each well according to Faimali et al. (2014). Plates were kept in a thermostatic room (20 °C) in dark conditions for 24 h (35 ± 2‰ salinity; 8.0 pH). After this time exposure, the ephyrae were washed 3 times with new FSW to remove potential NPs bound to the exterior of the body (Nasser and Lynch 2015). They were anesthetized with menthol crystals fixed in 4% paraformaldehyde solution in FSW, and mounted in glycerol-PBS (1:1) for the observation under the microscope (Olympus) and three-dimensional (3D) holotomographic microscope (Tomocube Inc. model HT-2), according to Costa et al. (2020a). This technology can acquire a fluorescence signal and a three-dimensional map of the sample refractive index at the same time. The resulting 3D holotomography map shows the different structures (characterized by different refractive index ranges) stained with different colors, together with the fluorescence signal associated to the NPs.

Toxicity test

Visible blue particles were used to perform toxicity tests in jellyfish ephyrae. The same dilutions described for NP uptake were used and prepared according to the previous section. 0 and 7 days old ephyrae were individually placed into a multiwell plate containing 2 mL of NPs dilutions (at 0, 0.1, 1, 10 mg/l) for 24 h, as reported in the previous paragraph. For each dilution, three replicates (each one consisting of 8 ephyrae) were prepared. After 24 h, acute and behavioral endpoints were investigated. The Immobility percentage (% I) - meaning ephyra capability to perform any movement - was considered the acute endpoint; this percentage was calculated for each dilution and compared to controls. The percentage of the Alteration of the frequency of pulsations (% AFp) was considered the behavioral endpoint, meaning the pulsation number made by each ephyra in one minute. This percentage was calculated recording the Fp made by each ephyra in 1 minute, according to literature (Faimali et al. 2014, Costa et al. 2015, 2020a, 2020b). For each dilution and controls, the average Fp was calculated; then, the AFp percentage was calculated for each treatment and for each replicate against controls according to the formula: %AFp = [(Fp treated - Fp control)/ Fp control]/ 100. For toxicity tests, three independent experiments were repeated and carried out in three replicates. Both endpoints were assessed by using an automatic recording system coupled with a specifically designed video graphics analyzer, called the Swimming Behavioral Recorder (SBR, Faimali et al. 2014). This system is based on a video camera coupled with image analysis software (BIOMONITOR, developed by On Air srl, Genova, Italy) designed to track and analyze linear swimming behavior of aquatic invertebrates. The ephyrae were dark-adapted for 2 min (time fixed by preliminary tests to reach steady frequency of pulsations), before video-recording, according to Faimali et al. (2006).

Recovery test

After recording immobility and Fp for each treatment of NP tested, jellyfish exposed to visible blue NPs were washed three times with fresh FSW to remove NPs attached to the gelatinous body. Then, ephyrae were placed in new multiwell plates filled with clean FSW under the same experimental conditions following the toxicity tests. After 24 h, the pulsations made by each ephyra from the recovery of both treatments (ephyrae previously exposed to NPs and then in clean seawater) and the control, were measured by SBR system, according to Costa et al. (2020a).

Statistical analysis

The median Effective Concentration (EC50: NP concentration resulting in 50% Immobility or Alteration of Frequency pulsation) in the exposed ephyrae and related 95% Confidence Limits (CL) were calculated after 24 h of

exposure, by using Trimmed Spearman–Karber (TSK) analysis (Finney 1978). Significant differences between controls and NP-exposed jellyfish of the same ephyra age were identified using one-way analysis of variance (ANOVA) followed by the Tukey test. When data failed to meet normality assumption, non-parametric Kruskal Wallis test and Mann Whitney tests were used. For the recovery test, the analysis was performed comparing the Fp between ephyrae collected immediately after the toxicity test to 10 mg/L NPs and ephyrae placed in clean FSW. Data were considered significantly different when $p < 0.05$. For data analysis, SPSS statistical software (Statistical Package for the Social Sciences, Version 20) was used.

Results

Uptake

The presence of NPs in 0 and 7 days old ephyrae after exposure to environmental and high concentrations is reported in Figs. 1 and 2, respectively.

A small percentage of ephyrae at both ages ingested NPs at 0.1 mg/L (<10%, Table 1); such NPs were mainly localized in the gastric filaments of 0 day old ephyrae and in the manubrium of 7 days old ephyrae, bearing the mouth at its tip (Fig. 1). About 30% of ephyrae at both ages showed blue stained NPs at 1 mg/L exposure (Fig. 2B, E; Table 1), while all ephyrae ingested NPs at the highest tested treatment (10 mg/L; Fig. 2C, F; Table 1). NPs formed agglomerates in all treatments within 24 h (i.e., Fig. 2C).

The internalization of polystyrene NPs into the jellyfish body was assessed using holotomography. Fluorescent blue NPs were localized in the ephyrae jellyfish body after exposure to all treatments (Fig. 3).

The 3D representation acquired with the holotomogram allowed us to locate polystyrene NPs (refractive index: 1.58) inside the ephyra jellyfish body, in proximity of the cnidocytes containing the nematocysts (Suppl. Data).

Suppl. Data. Uptake of blue fluorescent (refractive index 1.58) NPs in *Aurelia* sp. ephyrae jellyfish, acquired with the 3D holotomographic microscope. NPs are localized inside the gelatinous body (yellow regions indicate the body; 1.355–1.378 refractive index range), among the nematocysts (purple regions; 1.398–1.412 refractive index range).

Toxicity

Polystyrene NPs did not affect immobility of 0 day old or 7 days old *Aurelia* sp. ephyrae (Fig. 4). Less than 10% immobility was found at any treatments, thus no significant difference between NP-treated ephyrae and controls was observed ($p > 0.05$) and it was not possible to calculate an EC50 (>10 mg/L).

However, NPs impaired jellyfish behavior after 24 h exposure in a dose-dependent way (Fig. 5).

An alteration of the frequency of pulsations was found in jellyfish of both ages; specifically, 2–57% and 9–24% effect were observed in 0 and 7 days old ephyrae, respectively. Despite it, a toxic effect was only observed in 0 day old ephyrae (EC50: 7.20 mg/L, confidence limits: 4.82–10 mg/L). After 24 h recovery in clean FSW, ephyrae of both ages previously exposed to 10 mg/L NP concentrations showed a pulsation frequency comparable to controls, since the observed effect ranged from 10 to 14% (Fig. 6).

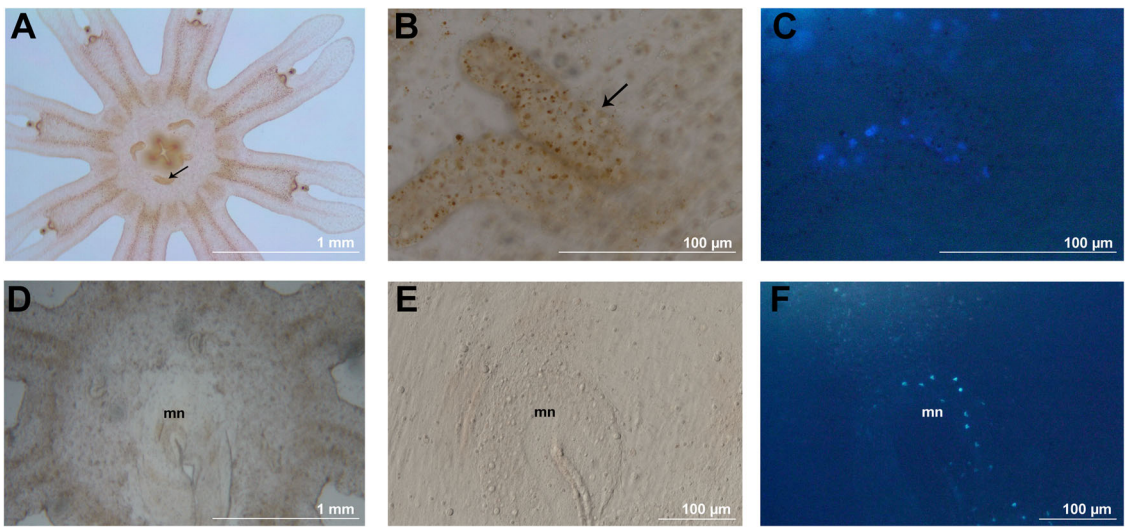

Fig. 1 Zero day old(**A**–**C**) and 7 days old (**D**–**F**) ephyrae of *Aurelia* sp. exposed to 0 and 0.1 mg/L of polystyrene nanoparticles (NPs) for 24 h. **A**, **D**: control (0 mg/L). **A**, **B**, **D**, **E**: bright field. **C**, **F**: fluorescence images using DAPI. Arrows indicate ephyrae gastric filaments. mn: manubrium. **A**, **D**: Bars equal 1 mm. **B**, **C**, **E**, **F**: Bars equal 100 µm

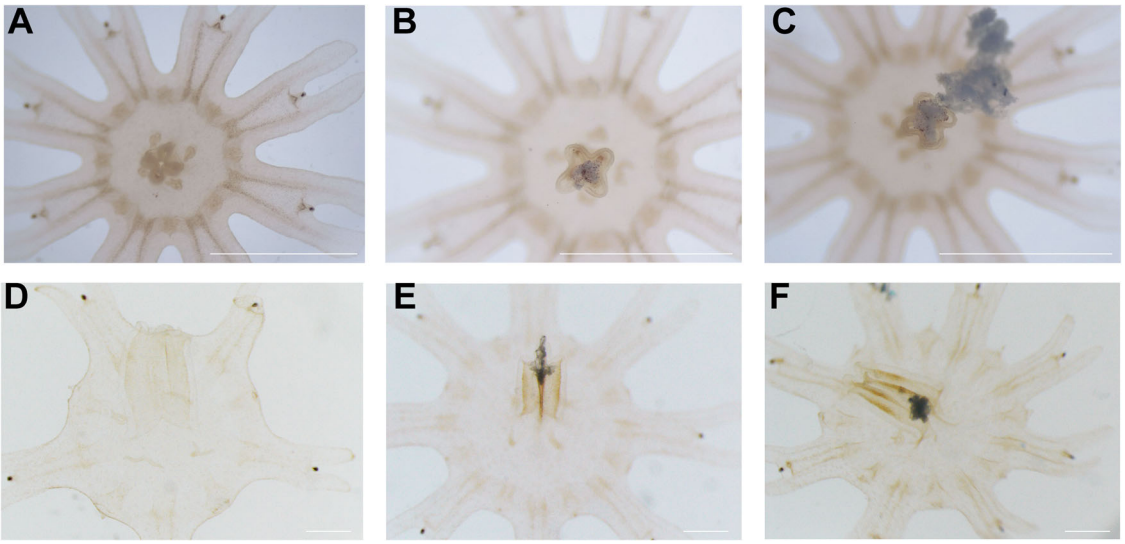

Fig. 2 Zero day old (**A**–**C**) and 7 days old (**D**–**F**) ephyrae of *Aurelia* sp. exposed to 0, 1 and 10 mg/L polystyrene nanoparticles (NPs) for 24 h. A, **D** control (0 mg/L); **B**, **E**: 1 mg/L of NPs; **C**, **F**: 10 mg/L of NPs. Ephyrae ingested NPs from 1 mg/L (**B**, **E**) up to 10 mg/L (**C**, **F**). Bars equal 1 mm

Table 1 Percentage of ephyrae containing blue stained NPs (% ± standard error)

NP concentrations	0 day old	7 days old
0.1 mg/L	8.9 ± 1.8%	9.5 ± 1.7%
1 mg/L	28.5 ± 1.6%	31.2 ± 2.0%
10 mg/L	99.7 ± 0.5%	99.4 ± 1.1%

Discussion

In this study NP uptake and ecotoxicological effects in a marine jellyfish are reported. *Aurelia* sp. is a pelagic jellyfish, known to incorporate microplastics at ephyra and medusa stages (Costa et al. 2020a, 2020b; Sucharitakul et al. 2020), but to date no evidence of NP ingestion in any marine cnidarians is available. NPs are difficult to detect due to their low mass and small size (Nguyen et al. 2019); in this study NP uptake was observed in 0 day old and 7 days old jellyfish ephyrae by using conventional and novel microscopy techniques.

The uptake was first detected by using traditional microscopy, since NPs form aggregates in seawater, resulting in easy identification, as reported in previous studies where the same polystyrene NPs were observed in marine crustaceans and rotifers (Gambardella et al. 2017, 2018). Specifically, NPs aggregated up to reach an average size of 2471 nm, 1640 nm and 4156 nm after 24 h in seawater at 0,1, 1 and 10 mg/L concentrations, respectively (Gambardella et al. 2018).

Polystyrene NPs were localized in the mouth of jellyfish ephyrae, but conventional light microscopy constraints did not allow confirmation of NP internalization in jellyfish tissues. Recently the use of different techniques has been applied to detect and verify NP ingestion in biota (Nguyen et al. 2019), including innovative interferometric techniques such as the tomographic microscopy (Mariano et al. 2021), that successfully verified microplastic ingestion in jellyfish (Costa et al. 2020a). In this study, NP internalization was demonstrated in the gelatinous body of jellyfish ephyrae by using the holotomographic approach. The latter can provide a 3D refractive index distribution of the sample based on a 2D projection series, revealing the intra-cellular structure (Kus 2022). NPs were previously observed in mammalian cells by using this technique (Roshanzadeh et al. 2021); however, to our knowledge no applications on NPs in marine biota has been reported to date. In this study, we suggest the holotomographic approach as a promising novel tool to detect NPs in marine organisms.

By measuring fluorescence changes using a molecular rotor probe, polystyrene NP has been recently detected in freshwater cnidarians (i.e., *Hydra*; Gagnè et al. 2019; Auclair et al. 2020). Here, we report that marine jellyfish were capable of internalizing and retaining polystyrene NPs within their body for 24 h Costa et al. 2020a, 2020b. Although ephyrae of both 0 day and 7 days internalized NPs, the pulsing behavior was only affected in the younger ephyrae. These findings may be related to the rhopalia development, complex sensory organs associated with the pulse mode and swimming (Schwab 1977).

Studies report that a distinct rhopalium is not developed until 72 h after strobilation induction in jellyfish; thus rhopalia growth and differentiation take place after 3 days and specifically in 3 day old ephyrae up to 5 day old ephyrae (Spangenberg 1991). The rhopalial nervous system differentiates first, the gravity sensing organ, followed by the

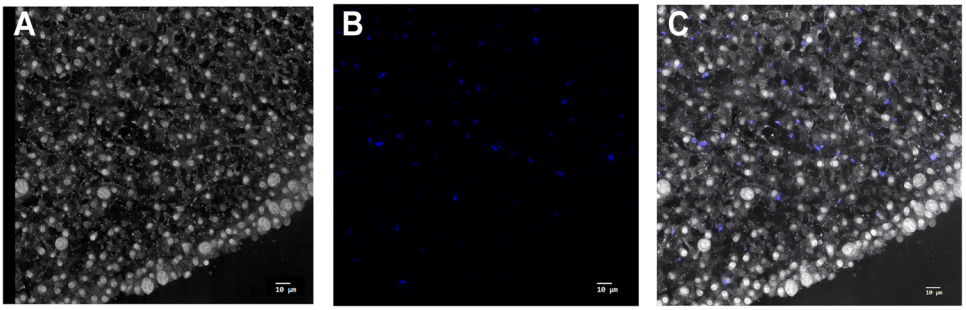

Fig. 3 Internalization of NPs in 0 day old jellyfish ephyrae. Images are acquired with holotomogram. NPs (blue color representing the fluorescence channel visible) are localized inside the gelatinous body. **C** shows a stitched image of the tomogram (**A**) and fluorescent (**B**) images. Bars equal 10 µm

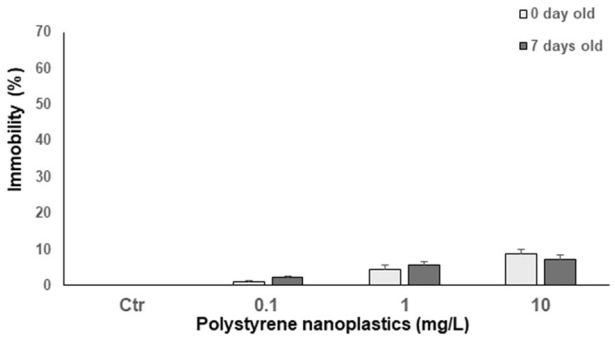

Fig. 4 Immobility percentage of *Aurelia* sp. ephyrae of 0 day old and 7 days old after 24 h exposure at increasing NP treatments ($M \pm SE$, $n = 3$). Ctr control

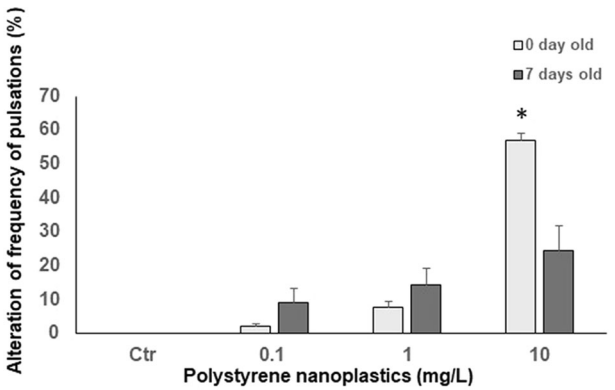

Fig. 5 Alteration of the frequency of pulsations of *Aurelia* sp. ephyrae of 0 day old and 7 days old after 24 h exposure at increasing NP treatments ($M \pm SE$, $n = 3$). Asterisk indicated a significant difference between controls and 10 mg/L NP treated ephyrae of 0 day old age ($^*p < 0.05$). Ctr control

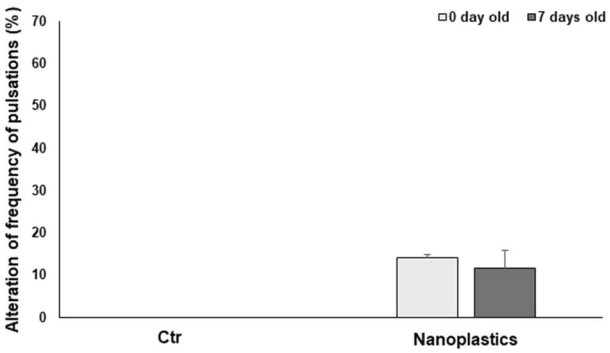

Fig. 6 Alteration of the Frequency of pulsations of *Aurelia* sp. ephyrae of 0 day old and 7 days old- previously exposed to 10 mg/L of NPs- after 24 h recovery in clean filtered seawater (FSW) ($M \pm SE$, $n = 3$). Ctr control

"marginal center" that controls swimming activity, and lastly the presumptive photoreceptors, namely the ocelli (Spangenberg et al. 1996). Moreover, after 72 h the formation of new rhopalial cell types develop, including the mechanoreceptor cells (Spangenberg 1991), with a key role in prey capture and defense (Galliot et al. 2009). The youngest ephyrae used in this study were 0 day, lacking developed mechanoreceptors and a distinct rhopalium organization. This may explain the difference in pulsing behavior at 0 day ephyra age if compared to 1 week old ephyrae. Our findings on the relation between ephyra age and the rhopalial development are also supported by the expression of Atohl genes, which control photo- and mechanoreceptor development in Bilateria (Jarman and Groves 2013). Such genes have been found in the rhopalia of the cnidarian jellyfish (i.e., *Podocoryne carnea* and *Aurelia aurita*), where they seem to be specifically expressed in a high level at the first ephyrae stages (Seipel et al. 2004; Brekhman et al. 2015), although they are also expressed at the adult stage when the rhopalium nervous system is not completed yet. Since a different pulsing behavior was found in 0 and 7 day old ephyrae exposed to NPs and considering that Atohl genes are highly expressed at ephyra stage, further research on Atohl gene expression in jellyfish of different ages will clarify if such genes may be considered an important stage-specific transcription factor in driving behavioral changes.

The neuro-sensory system of cnidarians is strongly connected with pacemaker activity, such as modes or swimming contractions (Nakanishi et al. 2009). It consists of rhopalia, the motor nerve net (MNN) and the diffuse nerve net (DNN; Nakanishi et al. 2010). MNN is formed by large cells in the oral epithelium, that innervate swimming

muscle fibers (Anderson and Schwab 1981). The rhopalium forms regular electrical impulses through the MNN to elicit jellyfish pulsations (Horridge 1956). All non-rhopalial sensory cells and their neuronal processes are present in the DNN. The latter can be found outside of the rhopalium, being distributed in *Aurelia sp*.ectoderm. Its function is to act as a sensory nerve net to elicit feeding: moreover, it can also be used as an escape response behavior upon sensory stimuli (Horridge 1956). After strobilation, DNN early differentiation begins in newborn ephyrae, then the development of the MNN and the pacemaker activity of the rhopalium take place (Nakanishi et al. 2009). Hence, 0 day old ephyrae do not have a fully differentiated DNN and MNN and overall sensory cells. The detection of mechanical disturbances (due to nanoparticles and microplastics) in seawater may generate sensory responses, modulating behavior, as reported in the larval swimming speed of crustaceans and in 0 day old ephyrae pulse frequency (Gambardella et al. 2015; Costa et al. 2020a, b). Likewise, the NP presence and NP aggregation may affect the frequency of pulsations, since undifferentiated sensory cells unable to perceive mechano-sensory stimuli, may not modulate and control pulse frequency. This may explain the significant increase in the pulsation mode in 0 day old ephyrae rather than in older ephyrae.

Internalization of NPs may alter energy metabolism, inducing changes in behavior (Li et al.2014; Mattson et al. 2015). Thus, the ingestion of polystyrene NPs in fish larvae disrupt glucose metabolism and cortisol, leading to changes in locomotive activity (Brun et al. 2019). Although in this study we did not investigate energy metabolism, we found changes in behavior due to NP exposure. Since this exposure induced a toxic effect in terms of EC50, further investigations on metabolic responses in jellyfish ephyrae may be addressed to better clarify the mechanisms that may cause behavior impairment.

Significant changes in frequency of pulsations were found in 0 day old ephyrae, although they were temporary, as demonstrated by the recovery test. Similar results were obtained by exposing ephyrae of the same age of those used in this study to microplastics (Costa et al. 2020a). When jellyfish were placed in clean sea water, no mechanical stress occurred, likely due to the absence of NPs and their agglomerates. The interaction between NPs and jellyfish may have exerted pressure on undifferentiated sensory cells of the young ephyrae, and as a consequence it may have altered the electrical impulses. Although the pulsation frequency resumed the same level seen in not exposed ephyrae, damages at lower organization levels (i.e., molecular, cellular) cannot be excluded, since NPs were ingested and internalized in jellyfish ephyrae gelatinous body. Recent findings suggest that intra-cellular uptake of nano-sized polystyrene particles could increase hydrophobic interactions leading to protein conformational changes in fish (Auclair et al. 2017), also due to NP surface charge. The latter is a key parameter of NP behavior and toxicity (Corsi et al. 2020); polystyrene NPs used in the present study showed a negative surface charge and a high hydrodynamic size (Gambardella et al. 2017), typical of all plain polystyrene NPs with no functionalization (Corsi et al. 2020). Negatively charged polystyrene NPs could induced lysosomal perturbations, oxidative stress, DNA damage, detoxification dysfunction or triggering the innate immune response in marine invertebrates (i.e., bivalves, echinoderms; (Cole et al. 2020; Gonçalves et al. 2022). Thus, NP negative charge and the high hydrodynamic size resulting in NP aggregation overtime may contribute to temporarily affect jellyfish behavior, rather than positive charged NPs, although further studies are needed to confirm this hypothesis.

Exposing the freshwater cnidarian *H. attenuata* to polystyrene NPs, Auclair et al. (2020) found that NPs are responsible for decreasing biomass, inducing lipid peroxidation, increasing polar lipid levels and forming lipid-like liquid crystals at the intracellular level; however, after a 24 h depuration period in clean water, such biomarker levels returned to control values. Accordingly, the behavioral results reported in this study after the recovery test were comparable to those obtained in unexposed jellyfish. Nevertheless, it will be worth investigating biomarker levels in ephyrae of different ages exposed to NPs and after a recovery period in clean seawater to correlate behavioral and enzymatic responses.

Jellyfish are formed of water, glycoproteins, and lipids (Hubot et al. 2022). The latter characterize jellyfish mucus, that contributes to jellyfish chemical defenses, besides toxins and antimicrobial compounds (Ovchinnikova et al. 2006). Since jellyfish mucus is able to sequester polystyrene microplastics and the presence of polystyrene NPs is responsible for temporary changes in lipid contents in cnidarians (Lengar et al. 2021), the investigation of biomarkers specific for lipids, coupled with the analysis of behavioral endpoints, should be further addressed in jellyfish in order to clarify the potential toxicity derived from polystyrene NPs after acute exposure.

These findings provide new evidence on NP uptake in marine jellyfish ephyrae and the adverse consequences on behavioral dysregulation, that may be due to NP behavior in seawater. Further investigations at cellular and molecular levels are required to better understand possible consequences of NPs into jellyfish fitness and therefore in the marine ecosystem.

Author contributions EC, CG, and FG conceived of the presented idea. CG and MDG performed the microscopical observations; EC, VP, and RM carried out the ecotoxicological experiments on jellyfish

thanks to the support of SL. FS acquired the images and the video with the holotomographic microscopy. EC and CG wrote the manuscript with the support of all co-authors. MF and FG supervised the project. All authors discussed the results and commented on the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

Consent to participate Informed consent was obtained from all individual participants included in the study.

Consent to publish All authors confirm that the work has not been published elsewhere, completely, in part, or any other form, and that the manuscript has not been submitted to another journal.

Ethical approval Materials used in this study were invertebrate larvae, and this study does not involve human participants or vertebrates.

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