Jellyfish Cassiopea andromeda

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Cassiopea andromeda entered the Mediterranean from the Red Sea through the Suez Canal and colonized several areas of the basin. This species is an epibenthic scyphozoan with a maximum umbrella diameter of about 30 cm commonly found in tropical and subtropical shallow coastal ecosystems such as mangroves, estuaries, and sandy mudflats. This species has a metagenetic cycle with the following phases: planula, benthic polyp, ephyra, and adult medusa. The symbiotic relationship with dinoflagellates allows the jellyfish species to feed via direct predation and through photosynthesis by the zooxanthellae (mixotrophy).

Keywords: non-indigenous species ; upside-down jellyfish ; Megabenthos Underwater Video ; species distribution ; stable isotopes ; mixotrophic behavior

1. Introduction

The presence of non-indigenous species (NIS), also called alien species, is considered an important cause of biodiversity loss and changes in an ecosystem [1]. In the Mediterranean Sea, NIS can also be introduced via maritime traffic, by means of ballast waters and hull fouling. The diffusion of NIS has also been correlated with climate changes, which allows tropical and subtropical species to expand their distribution to other habitats [2][3][4]. For these reasons, harbors are hotspots for the introduction of NIS, and, usually, the host populations need to be studied to fill the knowledge gap in their pathways of invasion and in their impacts on the surrounding ecosystems. In 2014, the Lessepsian upside-down jellyfish *Cassiopea andromeda* (Forsskål, 1775) (Cnidaria, Rhizostomeae) invaded a touristic harbour of Palermo (Sicily, Italy) named Cala. Over the years, its abundance within Cala has increased [5].

C. andromeda (**Figure 1**) entered the Mediterranean from the Red Sea through the Suez Canal [5][6] and colonized several areas of the basin. This species is an epibenthic scyphozoan with a maximum umbrella diameter of about 30 cm commonly found in tropical and subtropical shallow coastal ecosystems such as mangroves, estuaries, and sandy mudflats. This species has a metagenetic cycle with the following phases: planula, benthic polyp, ephyra, and adult medusa [7].

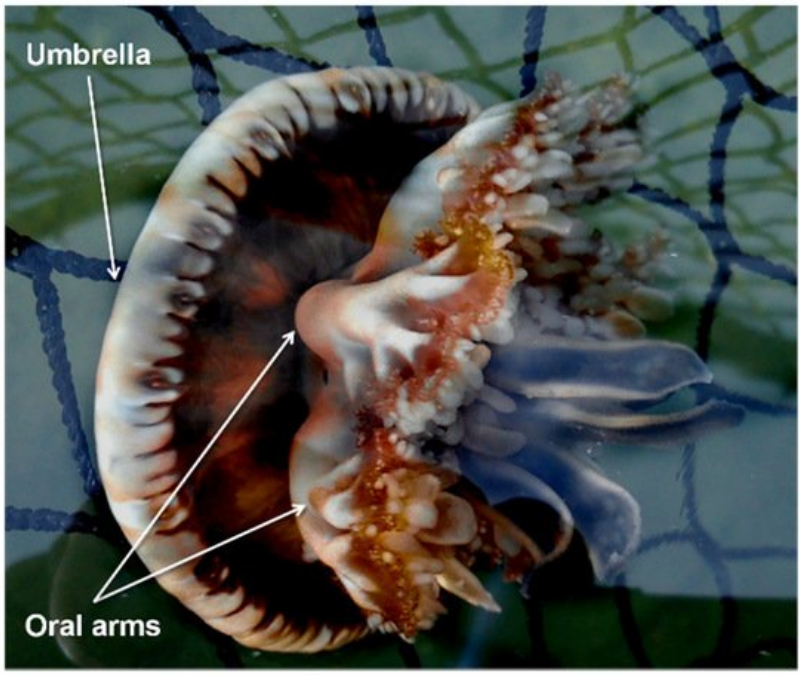

Figure 1. *Cassiopea andromeda* (Forsskål, 1775).

Contrary to jellyfish with pelagic behaviors, these benthic jellyfish prefer habitats with less water movements [8][9][10]. They often lay down on their umbrella, exposing their oral arms to the sun. Similar to other Rhizostomeae jellyfish, they frequently exhibit a symbiotic relationship with dinoflagellates, such as *Symbiodinium* spp., which are present in the tentacular tissue on their oral arms [11]. This relationship allows the jellyfish species to feed via direct predation and through photosynthesis by the zooxanthellae [12][13]; this mixed feeding of the jellyfish is called mixotrophy (concurrent autotrophy and heterotrophy).

In this symbiotic interaction, the carbon needed for the basal metabolism of the host is provided by the photosynthetic process [14][15][16][17], whereas nitrogen is taken up from the environment through the digestive processes [12][13]. However, this amount of nutrient intake is not fixed but rather depends on the species and the environments in which they grow (see, e.g., [16][17][18][19][20]). As with other symbiotic cnidarians, *Cassiopea* jellyfish may acquire dissolved nutrients from the surrounding environment to meet the energetic needs of their photosynthetic partners [21], while zooxanthellae may provide much of the carbon requirements to the host, which are critical to the metamorphosis of ephyrae and to the survival of the jellyfish [8]. Stable carbon and nitrogen isotopes might be valuable indicators of the relative importance between the autotrophy and heterotrophy pathways [22][23][24]. Subsequent studies have found that several factors such as inorganic nitrogen uptake [25], terrestrial nitrogen loads [26], eutrophication [26][27][28][29], zooxanthellae population dynamics [30], light [31], and bleaching [32] may affect the nitrogen isotopic ($\delta^{15}N$) signature of mixotrophic coral organisms with zooxanthellae symbionts.

Some authors have demonstrated the success of a mutualistic interaction with *C. andromeda* under stressful environmental conditions in shallow waters, i.e., high temperatures, high levels of irradiation, eutrophic conditions, and changes in salinity [33]. These life history traits also permitted this species to become an invader in the Mediterranean Sea, where, being one of the earliest Lessepsian migrants, *C. andromeda* has spread, reaching the western Mar Menor in Spain, being randomly spotted in the Levant Sea, Aegean Sea, and Strait of Sicily [6][34][35][36]. Mediterranean *C. andromeda* populations form short-term outbreaks up to 20 individuals m^{-2} in semi-enclosed human-impacted coastal systems with eutrophic waters and low hydrodynamics [5]. Stoner et al. [8] observed that *Cassiopea* spp. populations were significantly denser, and that individuals from these populations were larger in areas with high human population densities (a proxy of nutrient enrichment) with respect to more natural sites. Equally, The et al. [37] reported high densities of *Cassiopea* jellyfish within shrimp farms where environmental conditions were stable and the concentrations of nutrients and organic matter were high.

2. Distribution of *Cassiopea andromeda*

Studying NIS in harbor environments is not always easy due to the presence of obstacles (e.g., floating docks, anchored or moving nautical vehicles, and ropes) which hinder the use of standard visual methods and tools. A Megabenthos Underwater Video (MUV) device specially designed and built to overcome these sampling difficulties [38] allowed recording several *C. andromeda* specimens of different sizes in the different sub-areas of Cala. Their abundance and density varied across the four sampling dates. The large number of individuals of small sizes observed in February 2018 compared with that during previous months, when the intermediate size was the most abundant, suggests a previous reproductive event and indicates that the population of jellyfish in this study area is quite established.

The lowest values of abundance and density were recorded in April 2018, when the medusa stage population was clearly in decline. Since then, the medusa stage disappeared for two years and was subsequently spotted in October 2020 and in November 2021 (unpublished data from the authors' on-site visual inspections), when a few small and medium-sized specimens were observed. The period of apparent absence of the species in this harbour of Palermo could correspond to the polyp phase, which is not macroscopically visible. After a long period of two years, the transition from the polyp to medusa (strobilation) phases could have been triggered by exogenous factors (according to [11]), which led to the reappearance of a visible population.

The presence of *C. andromeda* down to 7.5 m depths may be due to the jellyfish's photosynthetic symbionts needing light, and its presence in the internal and intermediate zones of Cala could be due to the more eutrophic conditions [8]. Moreover, the dense packing of the smallest individuals in the internal zone could depend on the hypothetical presence of a close polyp population due to the lower hydrodynamics and the presence of many artificial substrates in this area of the harbour. Equally, the lack of *C. andromeda* observed at deeper and external sites (i.e., at the Cala mouth) may also be due to the greater amount of water movement typically caused by the continuous passage of boats.

From the results of the GIS-based statistical analyses, the jellyfish aggregation seen during June and November in different sub-areas and with different orientations suggests that the *C. andromeda* population is established in various

zones of Cala. This is probably due to the environmental variability of the harbour, which is severely influenced by various factors (e.g., terrigenous and anthropogenic inputs) heterogeneously distributed over time and space, as well as by the variation in some environmental parameters (e.g., water turbidity due to vessel movements and external inputs).

The ranges of the environmental parameters measured in the study area (temperature, salinity, and transparency) were consistent with the conditions necessary to maintain a *Cassiopean* population [37] and did not influence the distribution of specimens, which clustered around both low and high parameter values. In fact, *Cassiopea* spp. tolerate a wide range of temperatures (up to about 29 °C), salinities (up to 36), and levels of light exposure (from 200 to 500 µmol photons m^{-1} s^{-1}) [10][39]. The cluster behavior is possibly generated by other factors, such as a greater concentration of nutrients or organic matter in these areas, which would attract jellyfish to specific areas, as hypothesized by [37].

3. Trophic Behavior of *Cassiopea andromeda*

In the literature, the use of $\delta^{15}N$ from aquatic autotrophic organisms and consumers to trace anthropogenic sources of N has often been reported [40][41][42][43][44]. The generally most useful observation is that, in nutrient-rich environments, the $\delta^{15}N$ of algae can track the $\delta^{15}N$ from nitrate. The transformation of inorganic nitrogen compounds into an organic form during biosynthesis by living autotrophic organisms influences the reduction of oxidized forms of N to NH_4^+ and, then, its assimilation into organic matter. This process generally prefers the incorporation of an isotope with a lower mass. Some authors [45][46] measured a large range of N fractionations (−30 to 0‰) for nitrate and ammonium assimilation by algae and bacteria. The atmospheric N_2 bacterial fixation by the enzyme nitrogenase is reflected in organic material having $\delta^{15}N$ values slightly less than 0 ‰ and lower than the environmental values for organic materials produced by other mechanisms [47]. For this reason, low $\delta^{15}N$ values in organic matter are generally thought to indicate N_2 fixation. Assimilation produces isotope fractionation by favoring the incorporation of lighter isotopes. Several authors measured a wide range of N fractionations (−30 to 0‰) in field studies [45][46] and in laboratory experiments for nitrate and ammonium assimilation by algae [48][49][50]. For ammonium assimilation, the authors of [47] reported a range of fractionation from −4 to −27‰, depending on whether the algae cells were nitrogen limited, enzyme limited, or diffusion limited.

The *Cassiopea andromeda* trophic position and energy assimilation strategy may vary according to the availability of food sources, allowing the species to subsist in water masses ranging from eutrophic to oligotrophic conditions [51][52][53].

In the study area, the lower values of $\delta^{15}N$ for *C. andromeda*, indicating a depletion of ^{15}N compared with ^{14}N, were unexpected, but they could be the result of the availability of nitrogen sources rich in ^{14}N, such as those from untreated urban waste [54]. These lower values could be more affected by the characteristic of the two sampling sites of Cala (Calamida and Canottieri), which are confined and feature low hydrodynamics. The stable isotope values in *C. andromeda* were consistently lower than those in the other community components, suggesting the production of organic components based on the metabolism of associated symbionts.

Septic tank effluent contains predominantly organic and inorganic carbon, organic nitrogen, and ammonium. The septic sludge $\delta^{15}N$ reported by [54] had low values (–2.1 ‰), whereas the corresponding particulate and dissolved fractions generally had different nitrogen and carbon ratios as a result of fractionation in the anaerobic or aerobic processes. Nevertheless, an influence of atmospheric precipitation was not excluded given that the $\delta^{15}N$ of nitrate reported for a wet deposition showed values ranging from −11‰ to +3.5‰, with a mean value of −3.1‰ [55][56][57].

For both sampling sites, the lower $\delta^{15}N$ values observed for the oral arms of jellyfish suggest a lower trophic level with respect to the umbrella, highlighting the higher concentration of autotrophic symbionts in these tissues [11][58]. Indeed, the pattern suggested is that the zooxanthellae, which colonize the oral arms of *C. andromeda*, uptake the dissolved inorganic nitrogen with a low $\delta^{15}N$ value from the environment [52][53][59], while the umbrella uses a mix of the uptake of nitrogen with higher $\delta^{15}N$ values, due to fractionation along the food web through predation [24][51][60], and degradation of the colonizers.

Less negative $\delta^{13}C$ values (typically from −10 ‰ to −14 ‰) than those of particulate organic matter and plankton (ca. −20 ‰ [51]) are typical for the uptakes of dissolved inorganic carbon by zooxanthellae [20][22][61][62]. The $\delta^{13}C$ values obtained for the umbrella in this entry were higher than those obtained for the oral arms, in particular at the Calamida site, suggesting less translocation of the metabolites derived from symbionts and greater dependence on the heterotrophic metabolism of the jellyfish [52][53].

During synthesis, the isotopic signature evidenced that the metabolites derived from inorganic nutrient uptake and predation are then exchanged and recycled between the zooxanthellae and the host (e.g., [63]). The photosynthesis that occurs in the oral arms could involve processes depleting the nutrient pools derived from untreated discharge civil effluents and mixed with the discharge of wet depositions.

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