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RESEARCH PAPER

Different lineages of freshwater jellyfishes (Cnidaria, Olindiidae, *Craspedacusta*) invading Europe: another piece of the puzzle from Sicily, Italy

Enrico Schifani[1] · **Arturo Viviano**[2] · **Roberto Viviano**[2] · **Luigi Naselli-Flores**[3] · **Federico Marrone**[1]

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Abstract

Correctly identifying and mapping the distribution patterns of passively dispersing freshwater organisms is an important task to understand the mechanisms through which these organisms move across the world and to counteract the introduction of invasive alien species in a timely way; moreover, in the light of the growing evidence of the pervasiveness of cryptic species and cryptic biological invasions among all animal groups, the use of molecular identification tools is strongly advisable. In this context, we present the first record of the freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 in the Mediterranean island of Sicily, Italy. This invasive species, native to China, was found during a routine survey campaign aimed at assessing the freshwater species richness in the Sicilian region. Individuals were collected in November 2017 and identified to species level through the sequencing of fragments of both mitochondrial and nuclear genes, and their comparison to the sequences available on public databases. The analysis of molecular data proved that the Sicilian population belongs to *C. sowerbii* s.s., i.e. one of the two major *Craspedacusta* lineages which have been discovered to have invaded Europe and which were until recently erroneously jointly reported under the binomen *Craspedacusta sowerbii*. In order to get a clearer picture of the history and patterns of freshwater jellyfish invasion worldwide, the need for molecular identification of all the non-native *Craspedacusta* populations currently reported as *C. sowerbii*, and the opportunity of monitoring human-impacted ecosystems is stressed.

Keywords *Craspedacusta sowerbii* (=*sowerbyi*) · Biological invasions · Invasive species · Cryptic invasions

Introduction

Several freshwater organisms produce resting stages which give them the potential to passively disperse across the "dry ocean" surrounding continental water bodies (Incagnone et al. 2015). Human activities have interfered in several ways with the natural dispersal and colonization patterns by altering the ecological state of inland water bodies, by enhancing global changes and by acting as dispersal vectors for several native and non-native species (Lockwood et al. 2005; Marrone and Naselli-Flores 2015). Biological invasions, i.e. the human-mediated successful establishment of species outside their native distribution ranges, are one of the most serious threats to the conservation of world biological diversity, and are known to be particularly harmful in inland waters (e.g. Gallardo et al. 2016; Chandra and Gerhardt 2008). Moreover, biological invasions in inland waters have been often overlooked due to the misidentification of cryptic alien taxa as native, sometimes even endemic, species (e.g. Marrone

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✉ Luigi Naselli-Flores
luigi.naselli@unipa.it

[1] Department of Biological, Chemical and Pharmaceutical Sciences and Technologies (STEBICEF), Section of Zoology, University of Palermo, Via Archirafi 18, 90123 Palermo, Italy

[2] Via Michele Cipolla 106, 90123 Palermo, Italy

[3] Department of Biological, Chemical and Pharmaceutical Sciences and Technologies (STEBICEF), Section of Botany and Plant Ecology, University of Palermo, Via Archirafi 28, 90123 Palermo, Italy

et al. 2011; Saito et al. 2018; Morais and Reichard 2018). This stresses the need for the implementation of molecular identification tools when dealing with biological invasions (Blanchet 2012), especially for those taxa whose taxonomy is more unstable and/or morphology is poorly informative.

The olindiid freshwater jellyfishes of the genus *Craspedacusta* Lankester, 1880, native to eastern Asia (Kramp 1950), are worldwide human-spread species that have been reported to occur in all continents except Antarctica, usually under the binomen *Craspedacusta sowerbii* Lankester, 1880 (Dumont 1994; Jankowski et al. 2008). The morphology-based traditional taxonomy of the group has been largely disputed (Bouillon and Boero 2000; Jankowski 2001; He 2003) and no sound consensus has been reached to date. However, recent molecular studies (Fritz et al. 2009; Zhang et al. 2009) agree in proposing the existence of at least three different lineages of species rank within the genus, i.e. *Craspedacusta sowerbii*, *C. kiatingi* Gaw & Kung, 1939, and *C. sinensis* Gaw & Kung, 1939, plus another taxon of uncertain rank (“*C. ziguensis”* He & Xu, 1985).

Currently, *Craspedacusta sowerbii* is considered to be one of the most widespread freshwater invaders (Duggan and Eastwood 2012; Karaouzas et al. 2015) although molecular identification of most of the invasive populations is currently lacking and their actual identity should be checked. Fritz et al. (2009), for instance, proved that all the freshwater jellyfish populations they investigated from Germany and Austria do actually belong to the “kiatingi cluster” of the genus *Craspedacusta* (i.e. to *Craspedacusta kiatingi*), not to *C. sowerbii* s.s. Therefore, despite different *Craspedacusta* taxa invading water bodies throughout the world, the plurality of these biological invasions has been, to date, overlooked due to taxonomically inadequate data, and this pattern represents a clear example of the widespread phenomenon of cryptic invasions in inland waters.

Craspedacusta jellyfishes have complex life histories. The medusa stage is the only one easily visible as free swimming in all kinds of freshwater environments (Jankowski et al. 2008). Conversely, polyps are benthic, a few millimetres long, and much less visible unless actively sought. The polyp-stage can encyst (podocysts) and produce drought-resistant resting spherical frustules, which again develop into polyps when environmental conditions improve (Dumont 1994). These diapausing stages thus facilitate human-mediated dispersal with fish stocking, relocation of aquatic plants and invertebrates, or passive dispersal through waterfowl, mammals and other animals (Incagnone et al. 2015; Failla Siquier et al. 2017). While the polyp form dominates its life history, the three other stages (medusa, frustule, resting body) occur in response to specific environmental conditions (Acker and Muscat 1976). The polyp stage can live for years until suitable environmental conditions make it develop to medusa (Kato and Hirabayashi 1991). Such conditions, not well understood yet, were suggested to be associated with changes in water temperatures, water level and food abundance (Acker and Muscat 1976; DeVries 1992; Minchin et al. 2016).

As occurrence records are mostly due to random observations of medusae (which can form blooms) and polyps are usually overlooked, and due to their great habitat plasticity (DeVries 1992), *Craspedacusta* jellyfishes are expected to be much more widely distributed than currently known (Duggan and Eastwood 2012). In summary, the factors related to their dispersal capacity are (1) the ability to produce a durable, chitin-covered resting body (Kato and Hirabayashi 1991; Bouillon and Boero 2000); (2) their several strategies of vegetative reproduction (Reisinger 1957) and (3) long-term survival without sexual reproduction (Petrusek et al. 2005; Fritz et al. 2007).

Medusae blooms can have significant effects on zooplankton abundance and composition, thus affecting food webs (Spadinger and Maier 1999; Jankowski and Ratte 2000; Boothroyd et al. 2002; Jankowski et al. 2005; Smith and Alexander 2008). Apart from direct predation, this is also due to unselective killing which affects non-prey organisms alike (Smith and Alexander 2008). Moreover, native freshwater predators may have limited impact on the medusae (DeVries 1992). Conversely, very little information is available about the ecological impacts of polyps (DeVries 1992).

Although the genus *Craspedacusta* is widely reported throughout the West-Palaearctic region, the only molecular data available to date refer to Central Europe, where only *C. kiatingi* proved to be present (Fritz et al. 2009), and Greece, where a different lineage of uncertain identity was reported based on sequences of the mitochondrial DNA cytochrome c oxidase subunit I (mtDNA COI) (Karaouzas et al. 2015). In this paper, we investigated a recently found *Craspedacusta* population from the Mediterranean island of Sicily (southern Italy) with the aim of checking which species is actually present in the Mediterranean area, and to contribute to the understanding of the history and patterns of freshwater jellyfish invasion in the Western Palaearctic area.

Materials and methods

In the context of an extensive sampling campaign aimed at investigating the biological diversity of Sicilian inland waters, samples were collected on the 8th and 14th of November 2017 in a concrete reservoir located inside the campus of the University of Palermo, Sicily, Italy (WGS84 geographical coordinates: 38°06′25.2″N, 13°21′03.1″E).

The sampled water body stores about 450 m^3 of water (size: 13.20 × 15.50 m, h 2.20 m) and is used to irrigate the experimental fields of the Department of Agricultural, Food and Forest Sciences (University of Palermo). The reservoir is subjected to considerable water level fluctuations and it was observed to be almost dry on several occasions (L. Naselli-Flores, pers. obs.); its re-filling occurs by pumping municipality waters with average physical and chemical characteristics as reported in the Electronic Supplementary materials, Table S1. Water temperature was measured in situ with a Hanna HI9835 probe.

The presence of aquatic vertebrates was registered based on direct observations. Qualitative invertebrate samples were collected by means of three different nets: a 125-µm-mesh conical net was used in the open waters, a 1-mm hand net was specifically used for the visual collection of the jellyfish, and a further 200-µm hand net was used for sampling invertebrates along the walls of the reservoir. Collected samples were fixed in situ in 90% ethanol and sorted in the laboratory under a stereomicroscope. Crustacean samples were identified according to Alonso (1996), Dussart (1969), and Meisch (2000). A *Craspedacusta* voucher specimen was deposited in the collection of the Zoology Section, Natural History Museum, University of Florence (Italy) (MZUF), Cnidaria collection number MZUF 1501.

Phytoplankton for qualitative analysis were collected using a 20-µm conical net. Species were identified in living samples immediately after collection, according to the most updated taxonomic literature, using a Zeiss Axiovert microscope.

DNA was extracted from one of the collected jellyfish specimens on 8th November, 2017. Prior to DNA extraction, the specimen was soaked in double-distilled water for 1 h; DNA was then extracted from the whole specimen using the Ron's Tissue Mini Kit (BIORON) following the manufacturer's protocol. Fragments of the mtDNA cytochrome oxidase subunit I (COI) and of the nuDNA internal described spacers (ITS) were amplified following the protocols described in Karaouzas et al. (2015) and Fritz et al. (2009), respectively. PCR products were purified using the Exo-SAP-IT kit (Affymetrix USB) and sequenced with an ABI 3130xL (Applied Biosystems) sequencer. MEGA7 (Kumar et al. 2016) was used to translate the COI sequence to amino acids in order to check for the possible presence of frameshifts or stop codons, which would indicate the presence of sequencing errors or pseudogenes. The novel *Craspedacusta* sequences were deposited in GenBank (accession numbers: MH230079 & MH500048); moreover, all the available *Craspedacusta* COI and ITS sequences were downloaded from GenBank to be included in the analyses (see accession numbers in Figs. 2, 3). A single sequence of *Cubaia aphrodite* Mayer, 1894 (Hydrozoa, Olindiidae) was included in the mtDNA analyses to be used as an outgroup, whereas the ITS tree was rooted on *Craspedacusta sinensis*, i.e. the adelphotaxon of the clade including *C. sowerbii* s.s. and *C. kiatingi* (Zhang et al. 2009).

Novel and GenBank sequences were aligned in ClustalX (Thompson et al. 1997) and used in the phylogenetic analysis. Bayesian inference (BI) of phylogeny and maximum likelihood (ML) analyses were performed as implemented by MrBayes 3.2 (Ronquist et al. 2012) and PhyMl v.3 (Guindon and Gascuel 2003) for both datasets. The best evolutionary model for each dataset was chosen using the software MrModeltest 2.2 (Nylander 2004) on the basis of Bayesian information criterion (BIC) resulting in a general time reversible model with gamma distributed rate variation among sites (GTR + G; nst = 6) for the COI dataset, and in a Kimura 2-parameter with gamma distributed rate variation among sites (K2P + G; nst = 2) for the ITS dataset. Node supports were evaluated by their posterior probabilities in the BI and by 1000 bootstrap replicates in the ML analyses. The BI analyses were performed with two independent runs of 1,000,000 generations and four Markov chains using default heating values. Trees and parameter values were sampled every 100 generations resulting in 10,000 saved trees per analysis. An initial fraction of 2000 trees (20%) was conservatively discarded as burn-in. For all analyses and both datasets, standard deviation of split frequencies reached values lower than 0.018288, and values of the potential scale reduction factor (PSRF) comprised between 0.999 and 1.002 for all the partitions with frequency ≥ 0.10 in at least one run, indicating the convergence of the runs.

Results

Samplings and species identification

Water temperature on the two sampling dates was 16.1 °C and 15.9 °C, respectively. In accordance with Stefani et al. (2010) and Caputo et al. (2018), jellyfish abundance appeared higher in the shaded parts of the reservoir, and *Craspedacusta* individuals were present at a density lower than 1 specimen m^{-2}. Overall, ten *Craspedacusta* specimens in the medusa stage, all bearing well-developed gonads, were collected on the two sampling dates. The collected specimens had a diameter ranging between 1.5 and 2.0 cm (Fig. 1).

Co-occurring fauna and microalgae are reported in Table 1. The samples collected by scratching the walls of the reservoir did not reveal the presence of the polyp stage, which probably are more concentrated on the bottom of the reservoir, as a result of the water-level fluctuations to which this irrigation water body is subjected.

Molecular analyses

Upon aligning our *Craspedacusta* sequences and those downloaded from GenBank, and having trimmed the tails of the

Fig. 1 *Craspedacusta sowerbii* specimen from Palermo, Italy Photo by Enrico Schifani

sequences which were not present in all the individuals, we obtained a 337-bp-long fragment for the COI dataset, and a 607-bp-long fragment for the ITS dataset.

The relative shortness of the analysed COI fragment is due to the only partial overlap of the Chilean *Craspedacusta* COI fragments available on GenBank with the other available COI sequences, so that excluding the Chilean sequences from the analyses would have led to an aligned COI fragment of 574 bp. BI and ML exploratory analyses were thus also carried out based on the longer mtDNA dataset which did not include the *Craspedacusta* sequences from Chile; the clustering of the *Craspedacusta* sequences obtained proved to be consistent with the one based on the shorter mtDNA dataset presented in Fig. 2 (see Electronic Supplementary Material available online, Fig. S1).

The BI and ML analyses of COI and ITS datasets presented consistent topologies at their major nodes (Figs. 2, 3). The tree based on the COI dataset showed the affinity of the studied Sicilian sample with those from Chile, Marathon (Greece) and Hubei (China), plus a further sequence of unclear origin (GenBank A.N.: LN901194); moreover, in addition to the two divergent *Craspedacusta* COI lineages already described by Karaouzas et al. (2015), a third lineage, currently including a single sequence (GenBank A.N.: MG000493), was observed. The ITS dataset grouped the studied Sicilian *Craspedacusta* sample with Chinese samples belonging to the *Craspedacusta sowerbii* s.s. clade described by Zhang et al. (2009) and Fritz et al. (2009) (Fig. 3).

Table 1 Taxa co-occurring with *Craspedacusta sowerbii* at the study site on November 2017 (see text)

- Chordata
  - Reptilia
    - *Trachemys scripta* (Thunberg in Schoepff, 1792)*
  - Pisces
    - *Gambusia holbrooki* Girard, 1859*
    - *Carassius auratus* Linnaeus, 1758*
- Arthropoda
  - Ostracoda
    - *Cypridopsis vidua* (O.F. Müller, 1776)
  - Copepoda
    - *Acanthocyclops trajani* Mirabdullayev and Defaye, 2004*
    - *Macrocyclops albidus* (Jurine, 1820)
  - Branchiopoda
    - *Bosmina longirostris* (O. F. Müller, 1776)
    - *Coronatella rectangula* (Sars, 1861)
  - Insecta
    - Diptera *unident.*
    - Ephemeroptera *unident.*
- Mollusca
  - Gastropoda
    - *Physella acuta* (Draparnaud, 1805)*
- Phytoplanktic algae
  - Bacillariophyceae
    - *Ulnaria acus* (Kützing) Aboal
    - *Nitzschia acicularis* (Kützing) W.Smith
  - Chlorophyceae
    - *Gonium pectorale* O.F.Müller
    - *Coelastrum astroideum* De Notaris
    - *Monactinus simplex* (Meyen) Corda
    - *Pediastrum duplex* Meyen
    - *Tetradesmus lagerheimii* M.J.Wynne & Guiry
    - *Desmodesmus* sp.
    - *Golenkinia radiata* Chodat
    - *Monoraphidium* spp.
    - *Ankistrodesmus arcuatus* Korshikov
  - Zygnematophyceae
    - *Staurastrum pingue* var. *planctonicum* (Teiling) Coesel & Meersters
    - *Mougeotia* sp.
  - Euglenophyceae
    - *Trachelomonas* sp.
  - Chrysophyceae
    - *Dinobryon* sp.

*Non-native taxon

Discussion

Identification of European *Craspedacusta* populations

To date, few molecular data are available for *Craspedacusta* populations from both its native distribution ranges and invaded regions. Moreover, for some populations, only ITS sequences or COI sequences are available, thus preventing an exhaustive total evidence analysis of the molecular diversity patterns of the genus, and on the taxonomical identity of some populations. The branching pattern of the phylogenetic tree based on ITS sequences is in good accordance with those published by Fritz et al. (2009) and Zhang

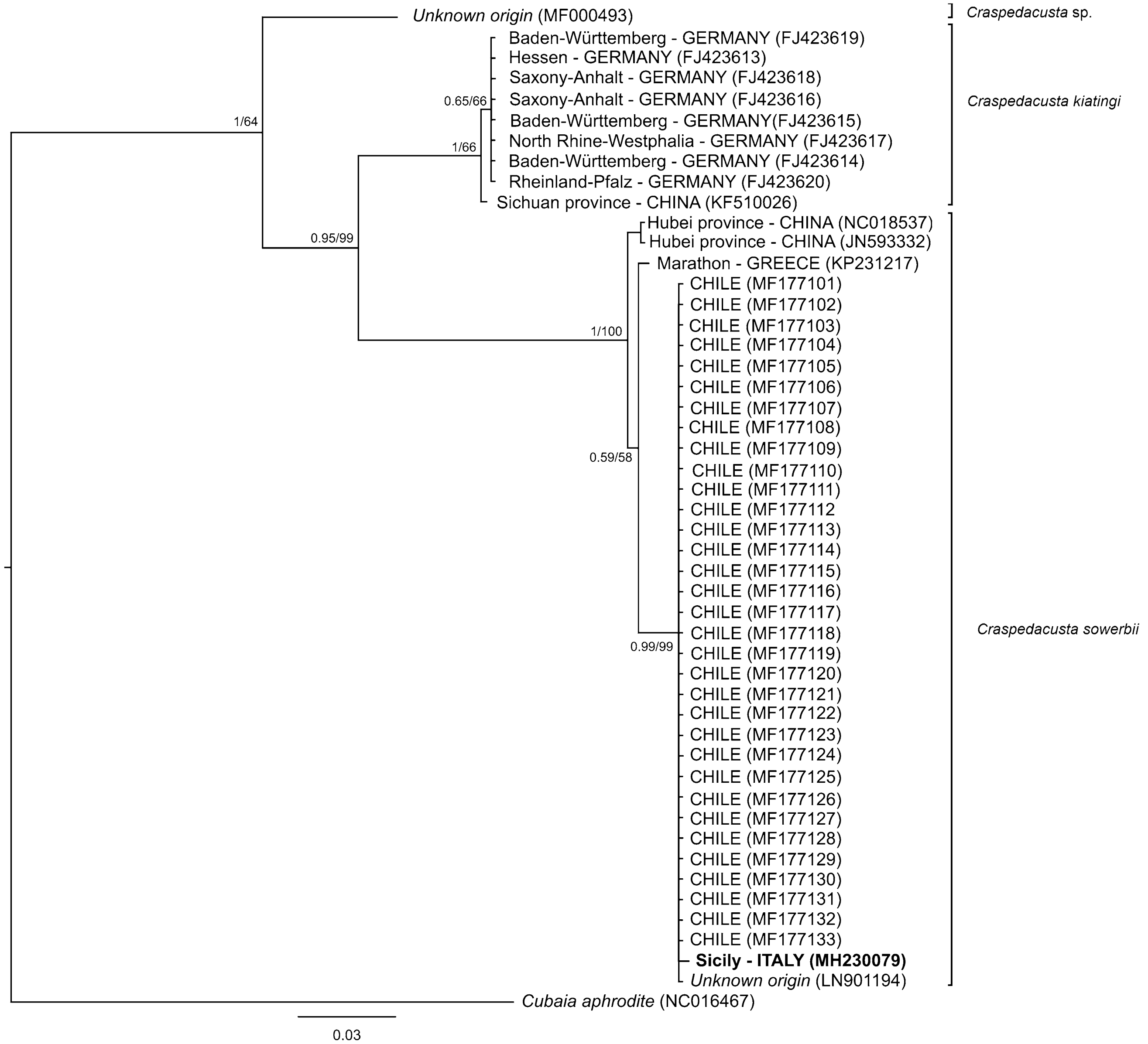

Fig. 2 Bayesian consensus phylogram based on a 337-bp-long fragment of the mitochondrial gene encoding for the cytochrome oxidase subunit I (mtDNA COI). Node support is reported as nodal posterior probabilities/ML bootstrap. Accession numbers of both novel and GenBank sequences are shown in *parentheses*. Original Sicilian sequence is reported in *bold*

et al. (2009), and distinctly separates the Central European *Craspedacusta* populations, belonging to *C. kiatingi*, from the Sicilian one, belonging to the *C. sowerbii* s.s. clade. Unfortunately, no ITS sequences are available for the Chilean and Greek *Craspedacusta* populations. However, the phylogenetic tree based on COI sequences shows the existence of three clades: a first clade including a single sequence of unknown origin, a second clade, which can be ascribed to *C. kiatingi*, including German and Chinese sequences from Sichuan Province, and a third clade including Sicilian, Chilean, Greek and Chinese sequences from Hubei Province. The presence in this clade of the Sicilian sequence, belonging to an individual identified as *C. sowerbii* s.s. based on its ITS sequence, allows the Chilean populations and the Greek population from Marathon to be ascribed as *C. sowerbii* s.s.

Therefore, it can be assumed that European water bodies have been invaded at least twice by two different *Craspedacusta* species of Asian origin: *C. kiatingi*, which invaded Central European countries, and *C. sowerbii*, which invaded Sicily and Greece in Europe, and Chile, in South America. To date, the occurrence of two distinct *Craspedacusta* biological invasions in Europe was largely overlooked since different invasive species had been lumped under the binomen

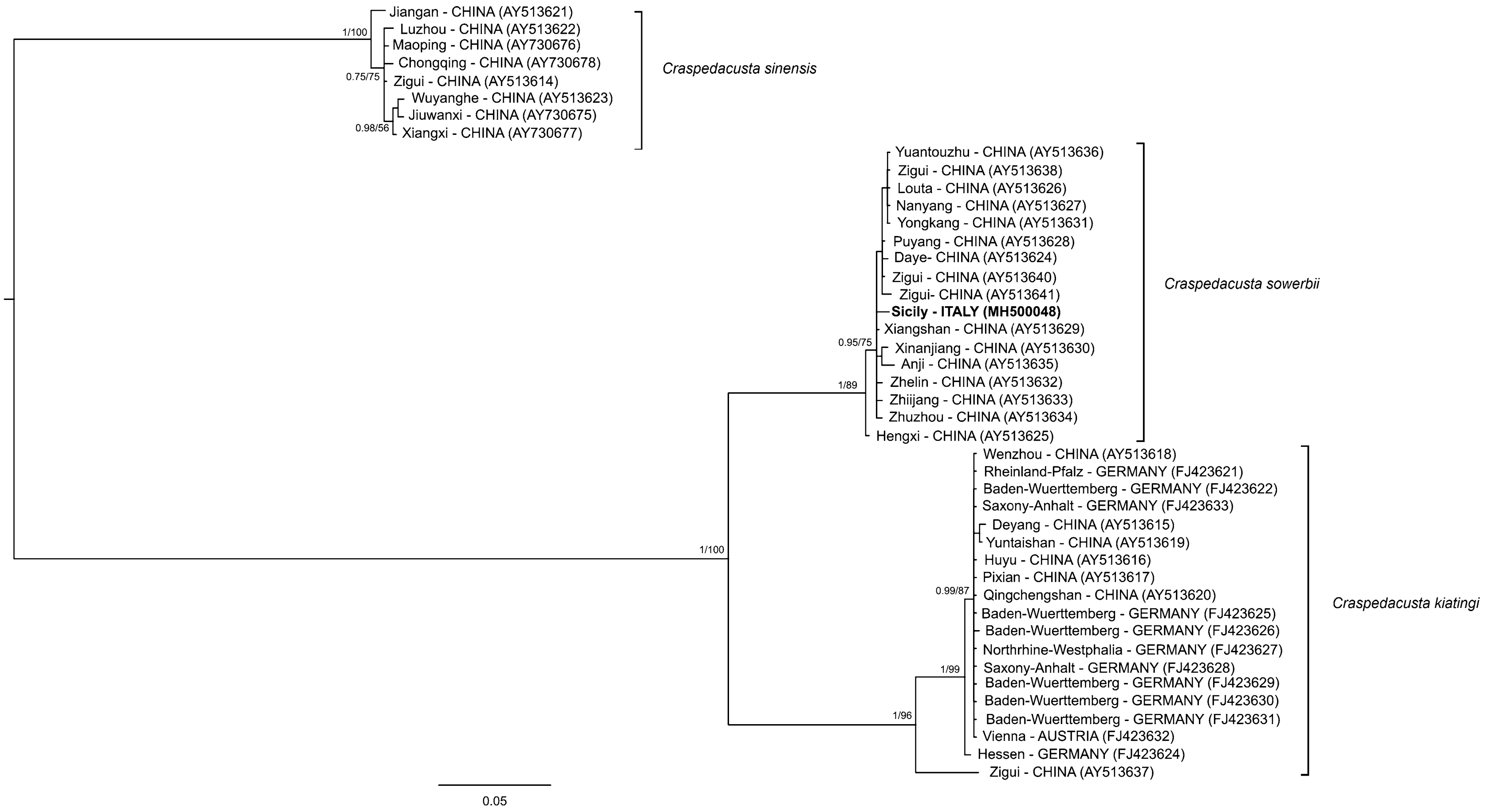

Fig. 3 Bayesian consensus phylogram based on a 607-bp-long fragment of the nuclear internal described spacers (nuDNA ITS). Node support is reported as nodal posterior probabilities/ML bootstrap. Accession numbers of both novel and GenBank sequences are shown in *parentheses*. Original Sicilian sequence is reported in *bold*

C. sowerbii, and the actual identity of the *Craspedacusta* populations for which no molecular data are available is still to be verified. Further efforts aimed at reviewing and defining the identity and distribution of these species and other *Craspedacusta* lineages throughout their distribution ranges will allow a better understanding of the history and vectors of the biological invasion of freshwater jellyfish around the globe.

Ecological remarks

Stefanelli (1948) reported for the first time the presence of *Craspedacusta sowerbii* in Italy, based on polyps and medusae which "appeared" in an aquarium hosting individuals of the Asian dwarf gourami *Trichogaster lalius* (F. Hamilton, 1822) fed with zooplankton collected in ponds in the vicinity of Rome. Indeed, aquaria often represent the location of first observation for this species, suggesting that escape or release from aquaria is likely a frequent human-mediated facilitation to its dispersal (Gasith et al. 2011). Since its first Italian record, freshwater jellyfishes have been sporadically recorded in several water bodies in central and northern Italy (see e.g. Ramazzotti 1962; Cotta Ramusino 1972; Stefani et al. 2010; Ciutti et al. 2017, and references therein). In particular, the species bloomed in several small lakes in the Italian Alps, where it has been repeatedly observed since the 1990s (Morpurgo and Alber 2015), during the summer of 2015, a record year in all the surface temperature analyses (RealClimate 2018), and in Ireland, the first observations of *C. sowerbii* coincided with unusually high water temperatures (Minchin et al. 2016). However, the Sicilian finding occurred in autumn, and the recorded water temperature values in the studied sites were well below 19 °C, which is considered the lower limit of temperature for optimal growth (Acker and Muscat 1976). Accordingly, this was probably the final phase of the medusa stage: their density value (around 1 individual m^{-2}) was lower than those reported in the literature (e.g. Pérez-Bote et al. 2006), and could not be considered a jellyfish bloom.

The population discovered in Sicily belongs to the same cluster as that found in Marathon (Greece), a town located at the same latitude as Palermo, and in Mediterranean and Valdivian Chilean ecoregions; all these areas are characterized by similar Mediterranean climatic features (Karaouzas et al. 2015; Fuentes et al. 2018). Moreover, it was found in Hubei Province, located in Central China, which is characterized by a subtropical monsoon climate, with seasonal temperature excursions similar to those recorded in the Mediterranean area (Zou et al. 2012). It is possible that *Craspedacusta* species have different invasive potential under different climatic scenarios, and that *C. kiatingi* is more adapted to continental or temperate climates, while *C. sowerbii* finds its optimum in warmer climates, but this hypothesis should be tested based on a much wider sampling of the *Craspedacusta* populations occurring worldwide.

At a local scale, given the great ability of *C. sowerbii* to quickly spread among geographic areas, as well as its ability to remain mostly undetected due to the overlooking of the polyp form, its presence in Sicily could be wider than currently known and is likely to increase even outside urban contexts. In the studied Sicilian reservoir, the observed phytoplankton species structure was typical of those commonly found in meso-eutrophic ponds, although with a relatively low number of species, and the jellyfish coexisted with several non-native vertebrate [*Trachemys scripta* (Thunberg in Schoepff, 1792), *Gambusia holbrooki* Girard 1859, and *Carassius auratus* Linnaeus, 1758] and invertebrate [*Acanthocyclops trajani* Mirabdullayev and Defaye, 2004, *Physella acuta* (Draparnaud, 1805)] species (Marrone and Naselli-Flores 2015), along with a few euryecious crustacean autochthonous taxa already known from Sicily (Marrone et al. 2005; Pieri et al. 2006), making up quite a simplified community.

To date, insufficient data exist to predict the consequences of the presence of *C. sowerbii* on the invaded ecosystems. However, it is worth noting that in this artificial and highly disturbed ecosystem, characterized by a relatively species poor community, several allochthonous species coexisted. This highlights the importance of human-made and/or human-impacted inland water ecosystems as invasion bridgeheads for several exotic species (e.g. Alfonso et al. 2010). The continuous disturbance to which these ecosystems are subjected does not allow the establishment of a "mature" community and removes the role of those priority effects which may constitute a barrier against new colonizers. It is therefore particularly important to establish more accurate surveys of these "banal" environments in order to create an early detection observatory for exotic and invasive species.

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Compliance with ethical standards

Ethical standards The authors declare that this study complies with the current Italian laws.

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