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RESEARCH PAPER

First record of the freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 in Greece suggests distinct European invasion events

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Abstract This contribution presents the first record of the freshwater jellyfish *Craspedacusta sowerbii* Lankester, 1880 in Greece. The species was found in a water transfer canal adjacent to Lake Marathon, 45 km northeast of Athens; this is the southernmost record of this invasive alien medusa in the Balkan Peninsula and Europe. A review of recently published records shows that this species has expanded its range in Europe and the Mediterranean countries. Genetic analysis of the Greek specimen suggests that the phylogeny of *C. sowerbii* needs further evaluation since we are probably dealing with a distinct species within the genus *Craspedacusta*, and that the Greek population represents a distinct invasion event from that previously recorded in central Europe. However, due to a lack of molecular information on the native and invasive ranges, further phylogenetic studies are necessary to clarify this issue.

Keywords Medusa · Invasive · Alien species · DNA · Phylogeny

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Introduction

Craspedacusta sowerbii Lankester, 1880 is a small freshwater cnidarian (less than 25 mm in diameter) with a wide ecological niche, which has enabled it to colonize virtually all types of freshwater ecosystems (Boothroyd et al. 2002; Moreno-Leon and Ortega-Rubio 2009; Galarce et al. 2013). Even though deliberate introductions of this species have not been reported, this species has successfully colonized all of the continents apart from Antarctica (Dumont 1994; Jankowski 2001), and is thus considered one of the most widespread freshwater invaders.

Although initially alleged to have originated from South America, *C. sowerbii* is native to the Yangtze valley in China (Kramp 1961). It was first recorded and described from the "Victoria regia" (*Victoria amazonica*) tank at the Royal Botanic Society's gardens in Regent's Park, London, United Kingdom (Lankester 1880). The most plausible vector of introduction was water lily plants from Brazil (Payne 1924). The earliest reports of the occurrence of *C. sowerbii* in Europe and United States of America observed this species in artificial impoundments or botanical ponds (Bushnell and Porter 1967). In recent times, this medusa has been widely reported in artificial water bodies and, sporadically, in a variety of natural freshwater bodies such as pool habitats of streams and rivers, ponds, lakes, and reservoirs (Duggan and Eastwood 2012). Due to its high morphological plasticity, the taxonomy of the *Craspedacusta* genus has been contentious, with several conflicting species and variations being described from China and Japan (Dumont 1994; Kubota and Tanase 2006). Recently, with the aid of molecular tools, Fritz et al. (2009) revealed the existence of at least three very divergent lineages of *C. sowerbii*: the "kiatingi," the "sowerbii," and the "sinensis." In that work, all of the sequences from the specimens found in Germany and Austria belonged to the "kiatingi" lineage, indicating that the Kiating region of China is the most plausible origin of the jellyfish found in Central Europe. The predominant presence of this species in artificial water bodies suggests that it has been released due to the transportation of aquatic plants (Bushnell and Porter 1967).

This species exhibits a preference for mesotrophic to eutrophic lentic freshwater ecosystems (Jankowski et al. 2008; Moreno-Leon and Ortega-Rubio 2009; Gomes-Pereira and Dionísio 2013) and relatively warm waters (Lewis et al. 2012). It feeds on zooplankton and often develops blooms, especially during warmer periods of the year (Stefani et al. 2010). Despite the existence of many studies on the biology and distribution of this freshwater jellyfish, its impact on inland freshwater ecosystems has been inadequately studied and remains unclear (Stefani et al. 2010; Oscoz et al. 2010). Usually, *C. sowerbii* is discovered by chance or when looking for some other organisms of interest. Thus, the time of introduction, the establishment, and the main dispersal pathways of this species in new regions often remain unknown. In this contribution, *C. sowerbii* is reported for the first time in Greece, making this the southernmost record of the species in the Balkan Peninsula. *Craspedacusta sowerbii* was found in an artificial slow-flowing canal adjacent to the supplementary drinking-water reservoir of Lake Marathon. Physicochemical characteristics of this habitat are also given.

Materials and methods

Examined material

Two medusa individuals of *C. sowerbii* were collected manually from the water column of a concrete water transportation canal (3 m in width and 2 m in depth) adjacent to the Lake Marathon reservoir by the authors on 30 September 2014 (Figs. 1, 2). Both specimens were fixed in pure ethanol (100 %), and one was deposited in the

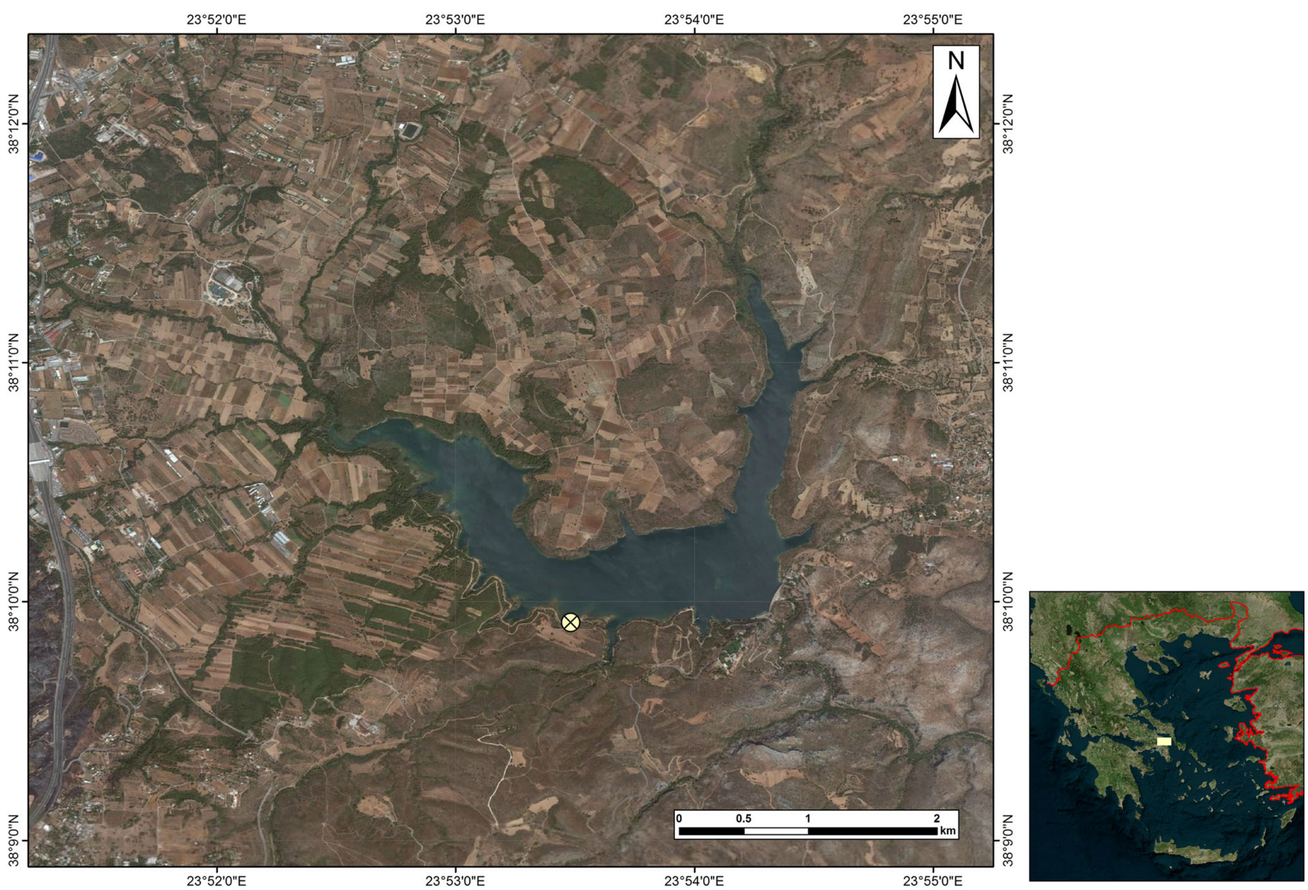

Fig. 1 Lake Marathon and the exact location where *Craspedacusta sowerbii* was found

Fig. 2 Mature male *Craspedacusta sowerbii* medusa approximately 15 mm in diameter from Lake Marathon with a range of tentacle sizes and four large gonads in the center

collection of the Interdisciplinary Centre of Marine and Environmental Research, University of Porto (Portugal) while the other was deposited in the Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research (Greece). Physicochemical parameters of the canal were measured with a GPS Aquameter from Aquaread Ltd.

Study area

Lake Marathon is a drinking-water supply reservoir that was formed after the construction of Marathon Dam at the confluence of the Charadros and Varnavas streams. In order to replenish this supplementary drinking water reservoir, water is transferred to the lake by canals from two major artificial lakes (Mornos and Evinos) and the natural lake. Lake Marathon is located 45 km NE of Athens, Attica Prefecture, at 225 m a.s.l. (38°09′N and 23°53′E). Its catchment area is 118 km^2, with an average runoff of 14,400,000 m^3 $year^{-1}$ and an average rainfall of 580 mm $year^{-1}$. Its surface area is 2.45 km^2, its maximum water depth is about 54 m, and its maximum capacity is 41,000,000 m^3 (EYDAP 2015). Since the dam was completed in 1929, its aquatic and shoreline vegetation has increased in richness. Riparian and marshland zones include *Phragmites australis* (Cav.) Trin. ex Steud. and *Vitex agnus-castus* L., which are fringed by rich terrestrial maquis and forest dominated by *Pinus halepensis* Miller. The lake's aquatic vertebrate community is also rich, and includes several fishes (in the genera *Scardinius*, *Rutilus*, *Luciobarbus*, and *Pelasgus*) and a rich variety of water birds (Hellenic Centre for Marine Research, unpublished observations). As it is a drinking-water storage facility, Lake Marathon is protected, anthropogenic pressures are limited, and human access is prohibited.

Genetics analysis

Due to the taxonomic uncertainty over the genus *Craspedacusta*, the identity of one of the specimens was tested by genetic analysis. To achieve this, the whole genomic DNA was extracted from a small tissue sample (2 mm^3) using the Jetquick tissue DNA Spin Kit (Genomed) according to the manufacturer's protocol. A fragment of approximately 700 bp of the mtDNA *cox1* gene (CO1) was amplified by polymerase chain reaction (PCR) using universal primer modified versions, i.e., dgLCO1490 and dgHCO2198 (Meyer et al. 2005). The PCR conditions (25-μL reactions) were as follows: each reaction contained 2.5 μL Invitrogen PCR buffer, 0.5 μL of each primer at 10 mM, 1.5 μL 50 mM $MgCl_2$, 0.5 μL 10 mM dNTP, 0.1 μL Invitrogen Taq DNA polymerase, and approximately 100 ng per μL DNA template. The cycle parameters were: initial denaturation at 94 °C for 3 min, denaturation at 94 °C (30 s), annealing at 50 °C (45 s), and extension at 72 °C (45 s), repeated for 38 cycles, before a final extension at 72 °C for 5 min. Amplified DNA templates were purified and sequenced (forward and reverse) by the commercial company Macrogen Europe, using the same primers. Chromatograms were checked by eye using ChromasPro 1.7.6 (http://technelysium.com.au). The obtained sequences were aligned with all the *Craspedacusta* spp. CO1 sequences available on GenBank (Table 1) using ClustalW on Bioedit v.7.2.5. (Hall 1999) and adjusted manually, resulting in a final alignment of 574 bp. Four additional Limnomedusae sequences were also included in the alignment as outgroups (Table 1). The newly obtained sequence was submitted to GenBank (Table 1).

In order to confirm the species identification and to estimate evolutionary relationships, the final alignment was then analyzed using the neighbor-joining (NJ) and Bayesian inference (BI) methods. The NJ analysis was performed on MEGA 6.06 (Tamura et al. 2013) with a random sequence addition (ten replicate heuristic searches), with the support for nodes estimated using the bootstrap technique with 1000 replicates. The best-fit model of nucleotide substitution evolution based on the corrected Akaike's information criterion was estimated using JModelTest 2.1.4 (Darriba et al. 2012). The BI analysis was achieved on MrBayes version 3.2.3 (Ronquist et al. 2012) under the model GTR+I. Analyses started with program-generated trees, with four incrementally default-heated Markov chains; two independent runs 1×10^6 generations long were sampled at intervals of 100 generations, producing a total of 10,000 trees. Burn-in was determined upon the convergence of log-likelihood and parameter estimation

Table 1 List of *Craspedacusta sowerbii* CO1 sequences that were analyzed and their GenBank accession numbers

Locality of specimen	GenBank accession number	Study
Marathon, Greece	KP231217	This study
Sichuan province, China	KF510026	Cai et al.[a]
Hubei province, China	NC_018537	Zou et al. (2012)
Hessen, Germany	FJ423613	Fritz et al. (2009)
Baden-Wuerttemberg, Germany	FJ423614	Fritz et al. (2009)
Baden-Wuerttemberg, Germany	FJ423615	Fritz et al. (2009)
Saxony Anhalt, Germany	FJ423616	Fritz et al. (2009)
Northrhine-Westphalia, Germany	FJ423617	Fritz et al. (2009)
Saxony-Anhalt, Germany	FJ423618	Fritz et al. (2009)
Baden-Wuerttemberg, Germany	FJ423619	Fritz et al. (2009)
Rheinland-Pfalz, Germany	FJ423620	Fritz et al. (2009)

[a] Unpublished

values using Tracer 1.6 (Rambaut et al. 2014). Estimates of sequence divergence (uncorrected *p*-distances) were assessed using MEGA 6.06 (Tamura et al. 2013).

Results and discussion

The collected jellyfish (Fig. 2) presented an umbrella/bell diameter of 15 mm and its gonads were well defined. The gonads, which were located on the radial canals, appeared to be well developed and elongated at their distal ends, thus indicating a mature male specimen. The physicochemical characteristics of the canal adjacent to Lake Marathon during the sighting of the medusae are presented in Table 2. The population of *C. sowerbii* medusae was scattered sporadically and the density seemed to be low. At a distance of 20 m along the canal, only 8 individuals were visually recorded. No individuals were spotted within the reservoir, even though it was inspected at several locations. As medusa can be found as deep as 3 m below the water's surface (Beckett and Turanchik 1980), individuals may have been present in the reservoir.

Table 2 Values of physical and chemical parameters measured in the irrigation ditch adjacent to Lake Marathon on the date of collection (30 September 2014)

Parameter	Value
Temperature (°C)	15.6
Pressure (mbar)	999
pH	7.91
Redox potential (mV)	20.4
Dissolved oxygen (mg L^{-1})	7.87
Electric conductivity (μS cm^{-1} @ 20 °C)	245
Total dissolved solids (mg L^{-1})	159
Salinity (ng L^{-1})	0.09

The aligned CO1 sequences had a total length of 574 bp, with 207 polymorphic and 176 parsimony-informative sites. No indels and no unexpected stop codons were observed after translating all sequences to amino acids. The tree topologies resulting from the single tree recovered using the NJ and BI approaches were congruent, and results of both analyses are shown in Fig. 3. Two major mtDNA clades were retrieved with strong support: the first included the new Greek specimen sequence plus the one from Hubei province, China; the second included all the sequences from the German specimens and also the one from Sichuan province, China (Fig. 3). This pattern suggests that the phylogeny of *Craspedacusta sowerbii* needs further evaluation, since both clades display 15 % divergence (uncorrected *p*-distance), indicating that we are probably dealing with distinct species within the genus *Craspedacusta*. Unfortunately, the CO1 sequences available in GenBank come from only two countries in Europe: Germany and now Greece. Our results show that, as the newly sequenced Greek individual does not cluster together with the German ones, there would appear to have been at least two invasion events in Europe, one in which the species invaded Germany and another in which it recently invaded Greece, which most likely also correspond to two distinct *Craspedacusta* spp. Further studies concerning the phylogeny of this species in the native and invaded ranges should be performed in order to clarify this issue.

In most cases of biological invasion it is very difficult to trace the vectors and pathways of introduction and the subsequent dispersion (Simberloff et al. 2013). For this particular species, dispersal may include the transfer of the cnidarians in aquaria and commercial plant nursery grounds that host water plants (Gasith et al. 2011). Dumont (1994) proposed that aerial dispersal by birds of the cnidarian's drought-resistant resting stages may lead to movement among wetlands. The Marathon area has several

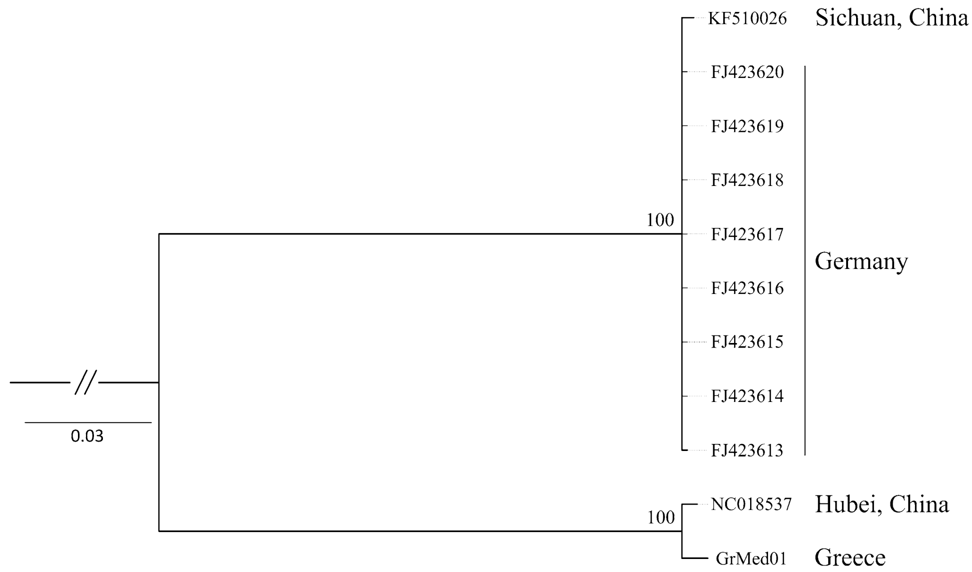

Fig. 3 Phylogenetic tree obtained by Bayesian inference and neighbor-joining analyses using mtDNA fragments (CO1). KP231217 pertains to the Lake Marathon sample. Support values are given as Bayesian posterior probabilities above nodes and as bootstrap support values below nodes. Available sequences downloaded from GenBank and the new sequence codes refer to Table 1

plant nursery gardens and hosts a large number of migratory water birds.

As with most hydrozoans, the life cycle of *C. sowerbii* includes both benthic polyp and free-swimming medusa stages (Lewis et al. 2012). Its successful worldwide distribution is usually attributed to several traits, such as its capacity for vegetative reproduction, its prolonged survival in new habitats with limited or no sexual reproduction (Payne 1924; Reisinger 1957), and its ability to develop a durable chitin-covered resting body phase under unfavorable conditions (Bouillon and Boero 2000), thus enhancing its survival and capacity to disperse to different freshwater habitats.

In Europe, the first records of *C. sowerbii* can be traced back to the end of the nineteenth century (from the UK, France, and Germany), whereas there has been more recent documentation of this species from many localities in Italy, Spain, Sweden, and Portugal (Ferreira 1985). In the Balkan Peninsula, the species was first recorded in 1958 from several localities in Serbia (Jakovčev-Todorović et al. 2010) and Montenegro (Milovanović and Živković 1965), while it was recorded in Croatia and Bulgaria in 1992 and 1994, respectively (Jaslovska and Stloukal 2004). The species has recently been documented in Albania (Dhora 2011) and near the Mediterranean coast of Turkey (Aysel et al. 2011) as well. This is the first record of the freshwater jellyfish *C. sowerbii* in Greece, and we speculate that it could be more common and widespread than is apparent from this incidental observation. Greece's freshwaters, even many protected lakes and sensitive reservoirs, are poorly monitored for alien species (Zenetos et al. 2009), so populations of this alien may have been overlooked until now.

In temperate regions, medusae of *C. sowerbii* have mostly been recorded during the summer period (Dumont 1994); these observations are often related to rising water temperatures and increased nutrient input (Gasith et al. 2011). Most records of polyps report observations made during the summer, thus indicating increased growth and reproduction during warm periods (De Vries 1992; Pérez-Bote et al. 2006). Although the literature mentions the species in several types of artificial water bodies such as quarry ponds, gravel pits, reservoirs, aquaria, and even wastewater treatment facilities, records of the species within concrete-based flowing canals are limited or infrequently reported (Gasith et al. 2011). However, many reports from several regions document its occurrence in artificial freshwater habitats, especially reservoirs, such as in the Iberian Peninsula (Pérez-Bote et al. 2006; Gomes-Pereira and Dionísio, 2013) and in Serbia (Jakovčev-Todorović et al. 2010). In Monte da Rocha Dam in southern Portugal, the species probably arrived via the Sado River that enters the dam (Gomes-Pereira and Dionísio 2013). Similarly, in Lake Marathon, the species may have entered from the Charadros stream or Varnavas stream, from canal inputs from the natural Lake Yliki, or from the artificial lakes Mornos and Evinos which feed Lake Marathon. This means that all of the freshwater bodies connected to the lake must be inspected for the possible occurrence of *C. sowerbii*.

Several studies have attempted to investigate the potential effects of *C. sowerbii* on freshwater ecosystems; however, their effects on local communities remain inadequately studied (Stefani et al. 2010; Oscoz et al. 2010; Gasith et al. 2011). Several studies have reported that the diet of *C. sowerbii* includes a variety of cladocerans, copepods, and rotifers (Dodson and Cooper 1983; Boothroyd et al. 2002; Moreno-Leon and Ortega-Rubio 2009). When abundant, the medusae can affect the population dynamics of zooplankton and significantly decrease their abundance (Jaslovska and Stloukal 2004). Dumont (1994) speculated that *C. sowerbii* medusae consume fish eggs and larvae, although—perhaps due to its small size—it is generally not considered an important predator of fish eggs or larvae. In contrast, polyps are able to consume hatched young fry, algae, nematodes, oligochaetes, crustaceans, water mites, insects, and arachnids (Bushnell and Porter 1967). Although the medusa may reduce zooplankton stocks, this reduction is not large enough to affect fish populations (Dodson and Cooper 1983). Overall, it appears that impacts on zooplankton are density dependent and can be more profound during warm temperatures when medusa populations increase. There is no information on the extent of limnological disturbance caused by *C. sowerbii* to a drinking water reservoir or its adjacent waters.

Conclusions

This is the first record of the freshwater jellyfish *C. sowerbii* in Greece. We speculate that this species may be more widespread in Greece than is apparent from this incidental observation because artificial reservoirs and wetlands are rarely surveyed for alien organisms in Greece. Additionally, genetic analysis showed that the phylogeny of *C. sowerbii* needs further evaluation, since we are probably dealing with different species within the genus *Craspedacusta* and the Greek population represents a distinct invasion event from that previously recorded in central Europe. Further molecular analysis of specimens from both its native and invaded regions is needed to understand the dynamics of the invasion of this genus around the world.

Alien species are important influences on ecosystem structure and functioning, and it is known that *C. sowerbii* can affect zooplankton communities. Therefore, surveys addressing the population dynamics of this species should be performed that target both the medusa and the polyp forms in the Greek freshwater ecosystem in which the species occurs. Finally, since the species appears to be restricted to a small area and still has a low abundance, this specific phase of population development is the most appropriate period to implement efficacious measures to eradicate or at least control further dispersion and reduce the impacts of this unintentional introduction.

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