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Research Article

Short-range diversity and invasion dynamics of the freshwater jellyfish *Craspedacusta sowerbii* in Lake Kinneret, Israel, and its watershed: field sampling combined with hydrodynamical simulations

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Abstract

The hydrozoan *Craspedacusta sowerbii*, native to the Yangtze River system in China, has become an invasive species in freshwater ecosystems worldwide. Multiple genetic lineages have been introduced globally, yet the species' taxonomic identity has not been comprehensively resolved. The species life cycle alternates between a benthic polyp stage and a pelagic medusa stage, the latter being the primary focus of most distributional studies. In Israel, the species was previously reported from the Lake Kinneret watershed, though recent records are lacking. Here, we surveyed streams and ponds in the Golan Heights for both medusae and polyps and conducted genetic analyses on collected specimens. Three distinct cytochrome c oxidase subunit I (COI) haplotypes were identified, corresponding to those previously described from European and Asian populations. Most sites exhibited homogeneous COI haplotype composition, apart from a single site where different COI haplotypes co-occurred. This pattern suggests restricted short-distance dispersal and exchange, consistent with multiple independent colonization events. While our survey did not confirm the presence of *C. sowerbii* in its pelagic stage, the detection of polyps in multiple inflowing streams suggests that colonization of Lake Kinneret itself is likely in the future. To facilitate a proper monitoring program, we simulated the movement and distribution of possible medusae aggregations, originating from the inflowing Jordan River as well as from all surrounding shorelines of the lake. We first conducted 3D hydrodynamic simulations of the lake, incorporating the transport of medusae released from the main inflowing streams. The simulations suggest specific positions for coastal 'hotspots' of medusae distributions appearing yearly or seasonally. Furthermore, the simulations indicate seasonal variations in the penetration potential of medusae into the lake. In winter, they would penetrate deeper and away from the coasts, whereas in summer they are likely to remain concentrated near the lake surface and close to the coasts.

Key words: Cnidaria, COI, hydrodynamical simulations, invasion genetics, Lagrangian particle tracking

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Introduction

The expansion of invasive cnidarians is a global phenomenon, largely facilitated by international shipping, aquaculture, and climate change (González-Duarte et al. 2016; Marchessaux et al. 2021). In freshwater ecosystems, the diversity of cnidarians possessing a pelagic life stage (=medusa or jellyfish) is very low compared to marine environments, and invasive taxa are rare (Dumont 1994; Bouillon and Boero 2000b; Jankowski 2001; Jankowski et al. 2008; Lüskow et al. 2024). A notable exception is the globally widespread *Craspedacusta sowerbii*, a freshwater hydrozoan native to the Yangtze River (China) (Kramp 1950), which represents an ecologically novel trophic guild in invaded systems (Gießler et al. 2023). Since its first description (Lankester 1880) it has spread to all continents except Antarctica (Dumont 1994).

Invasion success of *C. sowerbii* is attributed to a complex life cycle, comprising a benthic polyp stage capable of asexual budding and dispersal via frustules, and a medusa stage that reproduces sexually (Dejdar 1934; Reisinger 1957). Polyps can also form resting stages, known as podocysts, under adverse conditions (Acker and Muscat 1976). Medusa production is temperature-dependent, with blooms typically occurring in summer and early fall (McClary 1959; Jakovčev-Todorović et al. 2010; Marchessaux and Bejean 2020). These blooms are conspicuous and well documented, while polyps, only 1–2 mm in size, are cryptic and poorly studied (Duggan and Eastwood 2012).

Medusae can induce trophic cascades through heavy predation on zooplankton, potentially altering food web dynamics (Boothroyd et al. 2002; Jankowski 2004; Jankowski et al. 2005; Smith and Alexander 2008; Schachtl et al. 2026). Stable isotope studies demonstrate niche overlap between medusae and planktivorous fishes, indicating possible competition (Gießler et al. 2023). The ecological role of polyps, however, remains less understood.

Most medusae populations worldwide are unisexual, and there is still limited evidence for regular sexual reproduction of *C. sowerbii* in non-native regions (Acker and Muscat 1976; Boothroyd et al. 2002; Lundberg et al. 2005; Fritz et al. 2007). Genetic analyses have revealed three major mitochondrial lineages of *C. sowerbii* based on medusae data (Fritz et al. 2009; Schifani et al. 2019; Morpurgo et al. 2020, 2024; Lüskow et al. 2025). Little data on genetic diversity in benthic polyp populations is available (but see dissertations of Schachtl 2019; Klotz 2022 and Wang 2022) due to the permanent sedentary lifestyle and inconspicuous appearance of the polyp stage. For sampling the polyp stage, collection of substrate and subsequent careful examination under the microscope is more reliable than established stream sampling techniques (Duggan and Eastwood 2012; Moore et al. 2025).

Reports of *C. sowerbii* from the Middle East are increasing, with records from Turkey, Iran, Iraq, and Syria (Balık et al. 2001; Saadalla 2006; Bekleyen et al. 2011; Bagheri et al. 2017; Dhahir and Ali 2017; Kutlu 2020; Ozbek and Sömek 2020; Mamish and Zeini 2022; Seçer et al. 2025). In Israel, the species was first detected in an aquarium of the Hebrew University of Jerusalem (Rahat 1961; Rahat and Campbell 1974). The first observation of the species (medusa stage) in the natural habitat was made from 2003 onwards in small ponds along the Zavitan and Meshushim streams in the Golan Heights, which are connected to Lake Kinneret.

In one of these ponds (Iris Pond) medusae were repeatedly reported over multiple years (Gasith et al. 2011; Gophen and Shealtiel 2012). These previous medusae records within the watershed suggest that the species is already established in the region. As lotic systems can facilitate the spread of invasive species (Leuven et al. 2009), a colonization of Lake Kinneret via inflowing streams appears likely in the future. Given Lake Kinneret's ecological and economic importance as the region's largest freshwater reservoir (Berman 1998; Zohary et al. 2014), monitoring the introduction of *C. sowerbii* is important.

To improve future detection of *C. sowerbii* in the Lake Kinneret and monitoring efficiency, we simulated a potential colonization of the lake by predicting possible medusae aggregations. These simulations represent two scenarios: (a) an early stage of colonization, in which the lake is colonized from established populations in the Golan Heights; and (b) a later stage, following successful colonization, in which medusae swarms originate from all surrounding shorelines of the lake.

Predicting distribution of medusae, as pelagic stages with limited active movement, requires a detailed understanding of the three-dimensional circulation patterns and thermal structure of the lake. To address this, we employed a high-resolution three-dimensional hydrodynamic model (the Massachusetts Institute of Technology General Circulation Model, MITgcm; Marshall et al. 1997a, 1997b), which has been successfully applied to lakes and other enclosed basins (e.g., Bennington et al. 2012; Dorostkar et al. 2017; Amitai et al. 2024). The model is coupled with a Lagrangian particle-tracking framework, a widely used approach for investigating the transport and dispersion of materials and organisms in aquatic systems (Carlson et al. 2017; Cimatoribus et al. 2019; Shi et al. 2026). In the context of enclosed freshwater environments, for example, Cimatoribus et al. (2019) applied a three-dimensional Lagrangian model in Lake Geneva to study how inflowing river water disperses, demonstrating that wind-driven gyres and water column stratification strongly regulate the spatial and temporal patterns of particle transport. Similarly, our modeling framework resolves currents and predicts the seasonal stratification, allowing us to identify the changing depth of the thermocline. By simulating the trajectories of medusae as passive particles within this specific layer, we can examine how they are advected from riverine inflows and littoral zones under varying seasonal conditions.

The objectives of this study are therefore: (i) to assess the presence of *C. sowerbii* within the Lake Kinneret watershed at any life stage, (ii) in the absence of medusae, to examine genetic diversity patterns of local polyp populations, thereby providing insights into the invasion pathways and (iii) as the colonization of the lake is likely, to identify potential coastal locations that may act as accumulation hotspots of the medusae for future monitoring.

Material and methods

Study area

Lake Kinneret is a warm, monomictic, meso-eutrophic subtropical lake with a surface area of 168 km^2, a volume of 4.3×10^9 m^3, and a watershed of 2,730 km^2. Its main inflow is the Jordan River, which flows from north to south into the lake (Ostrovsky et al. 2012; Berman et al. 2014). The region has a Mediterranean climate, characterized

by hot, dry summers and cool, wet winters. The lake is strongly stratified in summer and well mixed in winter with surface water temperatures ranging from ~15 °C in winter to ~30 °C in summer (Hambright et al. 1994; Amitai et al. 2025).

Particulate phosphorus concentrations range from ~1 μM in the epilimnion during spring blooms to ~3 μM in the hypolimnion in early winter. Ammonium peaks at ~110 μM in the hypolimnion in early winter and declines sharply during spring blooms, while epilimnetic concentrations remain below 20 μM. Summer pH values are high (~9.0) in surface waters and below 8 in the hypolimnion. Nitrate accumulates over winter and peaks in May (~30 μM in the hypolimnion and ~20 μM in the epilimnion), while nitrite reaches ~3 μM in winter in both layers (Berman et al. 2014).

The Golan Heights form a volcanic plateau northeast of Lake Kinneret, composed mainly of basalt and paleosols (Inbar 2024). Annual rainfall ranges from ~1,200 mm in the north to ~500 mm in the south. Streams originating in the Golan Heights cut deep ravines toward the lake, with major inflows including the Meshushim, Zavitan, Yehudiya, Daliyot, and Samach streams (Rimmer and Givati 2014). Sampling sites in the Meshushim and Zavitan lie within the Yehudiya Nature Reserve, where upper catchments are dominated by oak woodland and shrub steppe, primarily Tabor oak (*Quercus ithaburensis*) (Danin 1988; Yona et al. 2020). As typical Mediterranean streams, during late summer low-flow periods, the streams typically contract into a series of weakly connected or isolated natural pools, resulting in reduced longitudinal connectivity and increased habitat fragmentation (Gasith and Resh 1999; Bonada and Resh 2013). This general pattern is characteristic of the perennial yet highly seasonal streams of the Golan Heights, where discharge declines markedly during summer, enhancing the relative importance of deep pool habitats as refugia (e.g. Meshushim Pond, reaching maximum depth of 7 m, and Iris Pond with a maximum depth of 3 m), while supporting diverse invertebrate communities, mainly cladocerans, copepods, and chironomid larvae (Gasith et al. 2012; Gophen and Shealtiel 2014).

Field Sampling

Sampling was conducted in September 2023, focusing on the eastern inflows of Lake Kinneret (originating in the Golan Heights) and the lake itself. Altogether seven sampling locations were selected based on the last reported occurrence of *C. sowerbii* medusae at Iris Pond (Gasith et al. 2011; Gophen and Shealtiel 2012), including streams and ponds in the Zavitan and Meshushim (downstream of Iris Pond), a section of the Jordan River, and two sites on the Lake Kinneret shore near the Lake Kinneret Limnological Laboratory and Magdala. Additionally, to see if the colonization is only limited to the Meshushim and Zavitan, two sites in the separated Daliyot stream, not connected to the Zavitan/Meshushim, were surveyed (for details see Suppl. material 1: table S1).

Medusae were surveyed by intensive snorkeling transects in stream rock pools. Potential polyp occurrences were assessed by collecting substrate samples, which mostly consisted of small rocks (less than 10 cm) found nearshore. Samples were examined microscopically using a stereomicroscope at 400× magnification. Both single polyps and polyp colonies (multi-polyp units formed by asexual reproduction) were fixed in 95% ethanol for subsequent genetic analysis.

DNA extraction, amplification, and sequencing

DNA was extracted from individual polyps or colonies using the DNeasy Blood and Tissue Kit (Qiagen, Hilden Germany), and a segment of the cytochrome c oxidase subunit I (COI) gene was amplified. In the initial polymerase chain reaction (PCR), an established primer set was used (Primer set 1: CF7 5'-TCGCTGAGTATTTTCAACAAATC-3'; CR7 5'-GATTATCATGGTAGCAGACGTG-3') (Schachtl 2019) to amplify an 879 bp fragment. Since not all polyps could be successfully amplified with primer set 1, a second set of primers, amplifying a 100 bp fragment located within the CF7–CR7 region, was designed using GENEIOUS v2025.1.1 (Primer set 2: 453F 5'-GCCATCTTTAGCCTTCATGCG-3'; 578R_b 5'-ATGACCATGGATCGCGTTCC-3').

PCR reactions were prepared in a total volume of 25 µL containing 1 U DNA polymerase (Bioline, MangoTaq), 0.1 mM dNTPs, 4.5 mM $MgCl_2$, 5 µL reaction buffer, 0.2 µM of each primer, 7 µl of template DNA and DNA-free water. The cycling protocol consisted of an initial denaturation at 94 °C for 5 min, followed by 30 cycles of denaturation at 94 °C for 50 s, annealing at 58 °C (primer set 1) or 55 °C (primer set 2) for 50 s, and extension at 72 °C for 60 s. A final extension step was performed at 72 °C for 5 min. PCR products were visualized on 1% agarose gels, purified using the Monarch PCR DNA Cleanup Kit (New England Biolabs, USA), and sequenced using the Sanger method at the Sequencing Centre of the Ludwig-Maximilians-University in Munich (LMU).

Amplified fragments were sequenced bidirectionally using the same primer pairs as in the PCR. Consensus sequences were generated in BioEdit v.7.2.5 (Hall 1999) and aligned using ClustalW. Obtained sequences were assigned to reference haplotypes which were defined from the most common mitochondrial DNA (mtDNA) haplotypes (COI and 16S) identified in a large European *Craspedacusta sowerbii* dataset compiled in previous studies (Schachtl 2019; Klotz 2022; Wang 2022). These haplotypes fall into two major clades of *C. sowerbii*, each comprising two well-supported subclusters. The complete COI sequences of the four reference haplotypes are available in GenBank: Type 1.1 (MZ508273), Type 1.2 (MZ508274), Type 2.1 (MZ508275), and Type 2.2 (MZ508276). New sequences were classified using either the long fragment (primer set 1; dataset 1) or the short fragment (primer set 2; dataset 2; see Suppl. material 1: figs S1, S2). Local COI haplotype frequencies were mapped in QGIS v.3.40.1 using modified hydrological data from de Jager and Vogt (2003) and topographic data from Ryan et al. (2009).

For comparative analyses, selected COI sequences of *C. sowerbii* from GenBank (accessed October 2025), representing known clades, were included in dataset 1 together with the four reference COI haplotypes. Sequences from Chile (MN601813–MN601814; MF177101–MF177133; Fuentes et al. 2019; Caputo et al. 2021) and one sequence from India (MG924343) were excluded to maximize alignment length. The final alignment of the long fragment comprised 39 *C. sowerbii* sequences (for details see Suppl. material 1: table S2). The same sequence of *Limnocnida tanganjicae* Günther, 1893 as in Schachtl (2019) served as the outgroup. Assignment to reference COI haplotypes was performed by phylogenetic inference in MEGA v.11.0.13 (Tamura et al. 2021). The best-fitting substitution model was selected using the Bayesian Information Criterion (BIC) under complete deletion. A maximum likelihood tree was reconstructed under the K2+I

model with 1,000 bootstrap replicates. Identical sequences were collapsed in the tree visualization. Six COI sequences from distinct sampling sites in the Golan Heights were deposited in GenBank (PX499474–PX499479; 674–840 bp).

Hydrodynamical model

For simulating the three-dimensional velocity fields in Lake Kinneret, we used the Massachusetts Institute of Technology General Circulation Model (MITgcm; Marshall et al. 1997a, 1997b). The model was configured in its hydrostatic, free-surface, partial-cell mode with a horizontal resolution of 400 × 400 m and 47 vertical layers of different thickness ranging from 0.25 m near the surface to 1 m at 43 m depth. The integration time step was 300 s. Sub-grid scale processes were parameterized using the Smagorinsky horizontal diffusivity (Smagorinsky 1993) and Turbulent Kinetic Energy (TKE) vertical mixing (Gaspar et al. 1990) schemes. The Jordan River, providing approximately 70% of total inflow (Gal et al. 2003), served as the only open boundary and accounts for the Zavitan and Meshushim streams as well.

Hourly air temperature, humidity, precipitation, and wind fields were obtained from the COSMO model covering the entirety of Israel in a resolution of 2.5 km (Khain et al. 2021). Observed shortwave and longwave radiation were used directly from the Kinneret Limnological Institute Meteorological Station located in Ginosar (35.5243°N, 32.8475°E). All atmospheric variables were interpolated and adjusted to the hydrodynamic grid to provide consistent external forcing.

Lagrangian particle toolbox

In this study, a Lagrangian transport analysis was performed using the Particle Tracking and Analysis Toolbox (PaTATO) for MATLAB (Fredj et al. 2016). We embedded PaTATO within the MITgcm runs to compute Lagrangian trajectories representing medusae with relatively low motility. The inflow entering Lake Kinneret was set in the simulations to arrive from the Jordan River area, including the Zavitan and Meshushim streams. The particles were tracked for 72 hours under hourly varying flow fields, for representative days in January and June. In a separate simulation, we generated monthly mean maps of all particles settling positions after three days of tracking. For these analyses, we simulated a particle release every six hours along the entire littoral zone of Lake Kinneret to simulate continuous inflow from all potential sources from the lake watershed.

Results

Presence and COI haplotype diversity of *Craspedacusta sowerbii*

Individuals of *Craspedacusta sowerbii* were found only in the polyp stage; no medusae were detected at any location. Polyps were detected at four of the seven sampled locations: Meshushim (two sites: pond and stream), Zavitan (three sites: two ponds, stream), Iris Pond (one site) and Daliyot (one of two stream sites). No polyps were detected in Lake Kinneret, the Jordan River or the Daliyot Pond (Fig. 1A). Of these, a total of 66 polyps were successfully sequenced in the Zavitan (pooled stream and ponds; n = 28), the Meshushim (pooled stream and pond; n = 22), the Iris Pond (n = 15), and the Daliyot Stream (n = 1) (Fig. 1A).

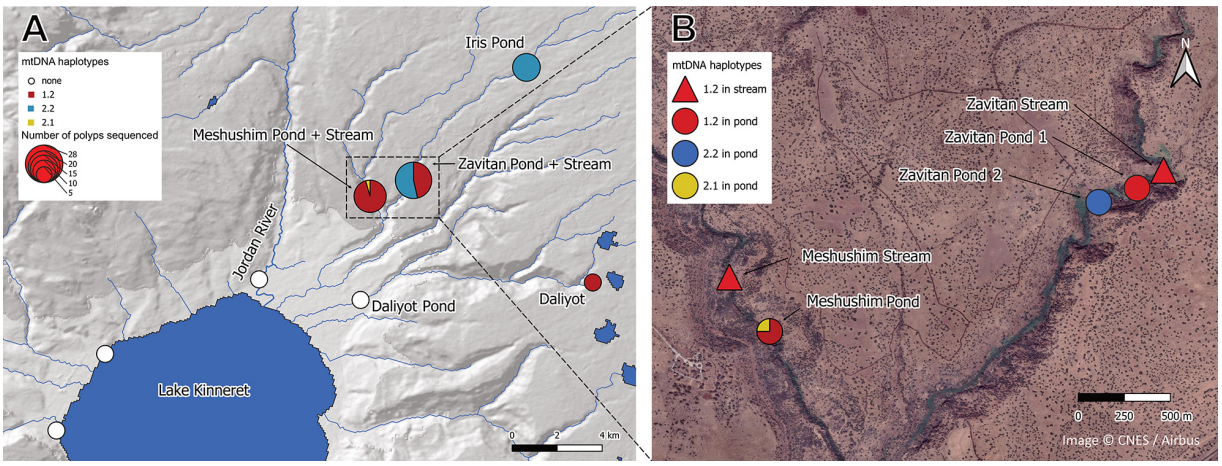

Figure 1. A. Map of the study area showing seven sampling locations in the Golan Heights and Lake Kinneret from west to east: two sites along the Lake Kinneret shoreline, the Jordan River, Daliyot Pond, Meshushim, Zavitan, Iris Pond and the Daliyot Stream. Sites where *C. sowerbii* polyps were detected are indicated with the color corresponding to their COI haplotype and the size to their abundance; sites with no detections are shown as small white circles; **B.** Fine-scale distribution of *C. sowerbii* and relative abundance of COI haplotypes near the Meshushim–Zavitan confluence. Each symbol represents a sampling site where polyps were detected, with the color corresponding to the COI haplotype and the shape corresponding to the type of waterbody. Sites fixed for a single COI haplotype are shown with a solid color; two COI haplotypes (1.2 and 2.1) were detected in the Meshushim Pond (n = 4).

Amplification with primer set 1 yielded 47 sequences (659 bp after complete deletion, dataset 1), containing 104 polymorphic sites (103 parsimony-informative), and resolving three distinct COI haplotypes. Primer set 2 produced 19 shorter sequences (100 bp, dataset 2), with 12 polymorphic parsimony-informative sites and two COI haplotypes. All sequenced polyp specimens from Israel showed identical COI haplotypes to those reported elsewhere and fall into the two well-known major clades represented by: Types 1.2 (n = 35), 2.2 (n = 30), and 2.1 (n = 1) (Fig. 2; for specific sequence identity see Suppl. material 1: figs S1, S2).

COI haplotype distribution across the watershed was heterogeneous (Fig. 1B). The Iris Pond contained only COI haplotype 2.2, the Zavitan sites contained COI haplotypes 1.2 and 2.2, and the single Daliyot Stream specimen belonged to COI haplotype 1.2. Two COI haplotypes (1.2 and 2.1) at the same sampling site were observed in the Meshushim Pond despite low sample size (n = 4). At the other studied localities, only one COI haplotype per site was detected: for example, all specimens from Zavitan Pond 1 were 1.2 (n = 12), whereas all specimens from Zavitan Pond 2 (approx. 280 m downstream) were 2.2 (n = 15).

Hydrodynamic simulations

Results from the Lagrangian analyses of representative days in January and June 2023 are presented in Fig. 3. Here, 72-hour trajectories of 32 particles, entering the lake from the Jordan River (the Kinneret main inflow) were obtained from the particle tracking and analysis toolbox (PaTATO), and calculated using 3D velocity fields. The trajectories within the lake differed markedly, depending on the prevailing velocity fields, the degree of thermal stratification at the time of their arrival, and the Jordan River water temperature. In January, when the water column is unstratified and stream discharge can be relatively high (30–120 $m^3 s^{-1}$), particles may either penetrate deeper layers (if the Jordan water temperature is lower than that of the lake water) or be transported far from the river inlet along the surface (if

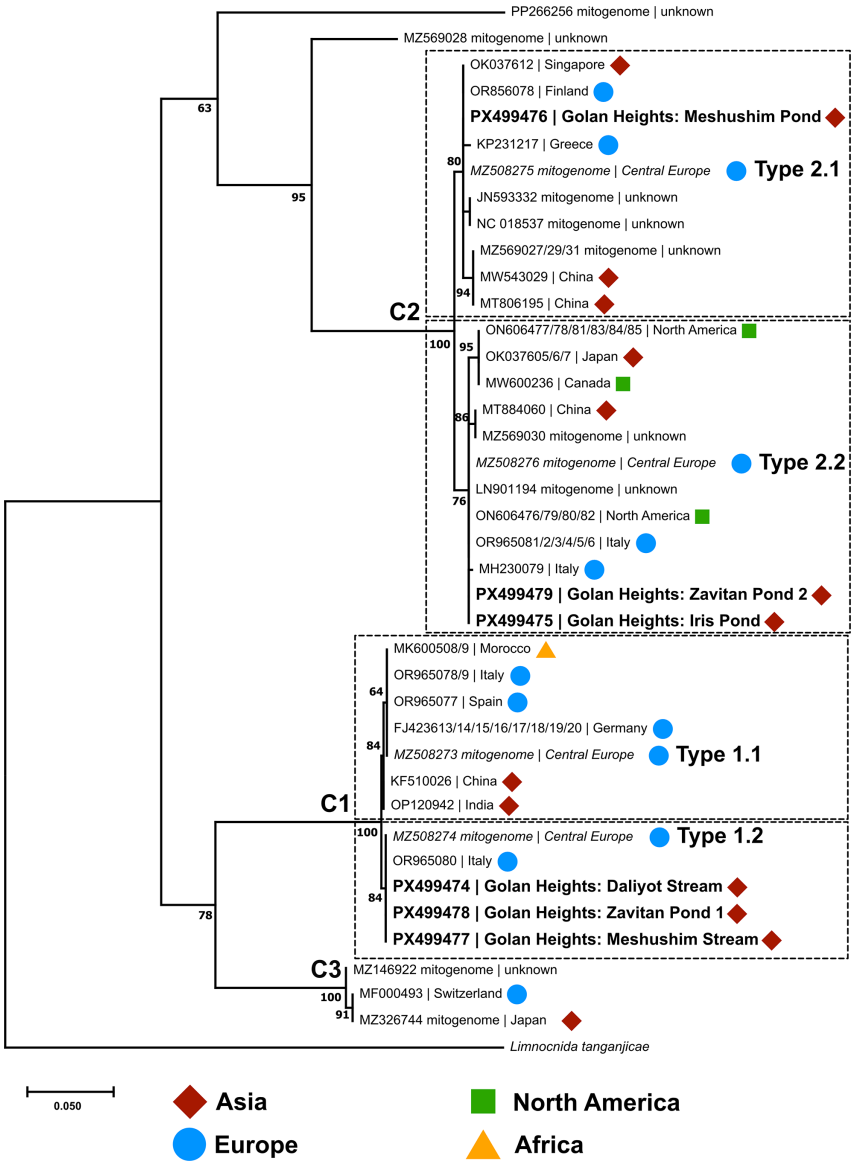

Figure 2. Maximum likelihood tree reconstructed from 39 COI sequences from *C. sowerbii* (originating from this study and GenBank), with *Limnocnida tanganjicae* as the outgroup. Bootstrap support values (1000 replicates) are shown at nodes. Sequences from the Golan Heights (PX499474–PX499479) cluster within clades C1 (COI haplotype 1.2) and C2 (COI haplotypes 2.1 and 2.2).

the river water is in thermal equilibrium with the lake). In contrast, in June, stream discharges are weak, and the lake is strongly stratified. Consequently, particles remain confined along the northern coast of the lake, at the upper ~10 m (Fig. 3).

In a different set of numerical experiments, we examined the potential distribution of medusae when released from the overall littoral areas of Lake Kinneret. The normalized particle densities of all final trajectory positions released from the littoral areas, are shown in Fig. 4 for the months June, July, October and November (for all months see Suppl. material 1: fig. S3). Particles were tracked for three days, with releases of every six hours to ensure statistical significance. The resulting monthly accumulation maps revealed a permanent 'hotspot' along the western coast near Tiberias, and a seasonal 'hotspot' in the northern part of the lake near Capernaum during July and October–December. An additional, somewhat weaker, seasonal accumulation zone was observed along the southern edge of the lake during the winter months (November–February).

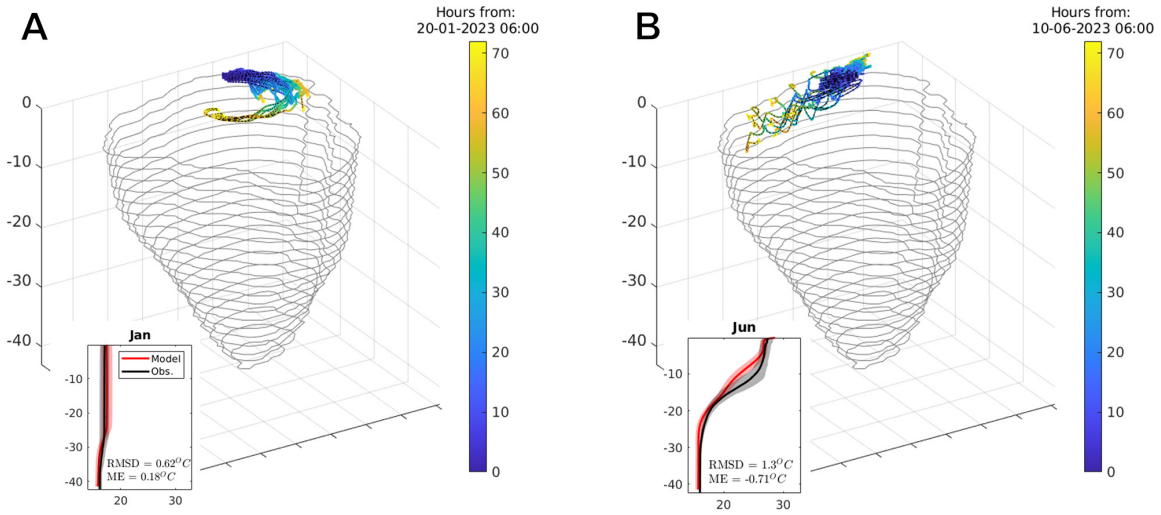

Figure 3. Representative 72-hour trajectories of 32 particles obtained from the particle tracking and analysis toolbox (PaTATO), calculated using 3D velocity fields for a day in January (**A**) and June (**B**). The particles are entering Lake Kinneret from the Jordan River inflow. The inset panels compare simulated and observed lake temperature profiles for the corresponding months.

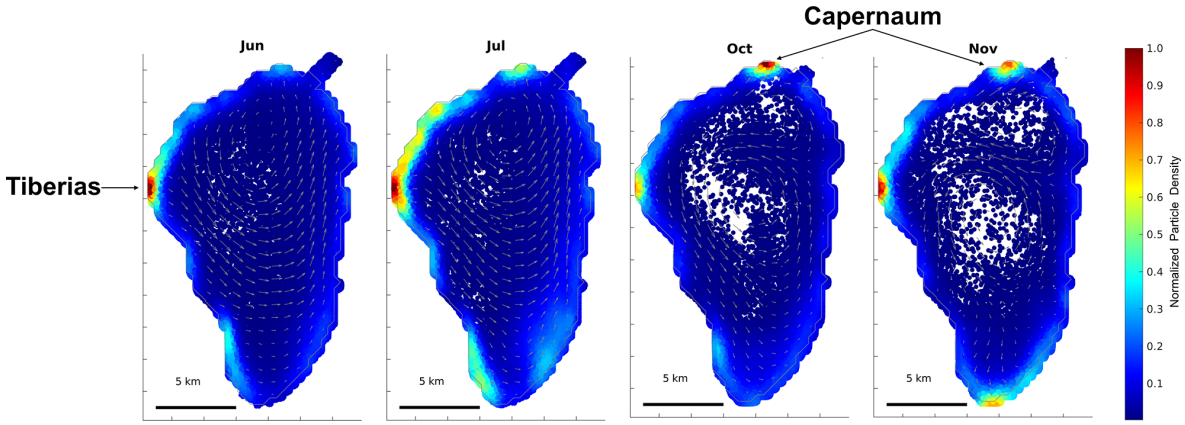

Figure 4. Normalized densities over the months June, July, October and November of the final positions of particles released from the littoral areas of Lake Kinneret. Particles were tracked for three days, with releases every six hours. Arrows indicate the lake monthly mean surface circulation. Areas where no accumulation of medusae was modeled are shown in white.

Discussion

This study represents the first detection of the polyp stage of *C. sowerbii* in Israel, following the earlier observation of medusae by Gasith et al. (2011) and Gophen and Shealtiel (2012). Our findings indicate that the species has a wider distribution in the Lake Kinneret watershed than previously assumed, particularly when polyps are considered. Importantly, several populations appear to have established independently, as evidenced by the presence of multiple COI haplotypes at various sites. While *C. sowerbii* in its pelagic medusa stage has not yet been observed in Lake Kinneret, 3D hydrodynamic simulations indicated specific coastal areas with potentially high medusae accumulation, which could serve as focal sites for future monitoring field campaigns. These simulated coastal hotspots could facilitate sexual reproduction if male and female medusae co-occur due to potential high medusae densities. The simulations also indicated a seasonal pattern in the penetration potential of medusae from the Kinneret watershed's rivers into the lake. Based on the model results, during winter, medusae are expected to migrate to greater

depths and toward the central region of the lake, resulting in increased dispersion throughout the water column. In contrast, during summer, the model suggests that they tend to remain concentrated near the surface and along the coastal margins.

Global distribution of *Craspedacusta sowerbii*

The polyp specimens found in the Kinneret watershed belonged to two known major mtDNA-clades of *C. sowerbii* (Fritz et al. 2009; Schifani et al. 2019; Morpurgo et al. 2020, 2024; Lüskow et al. 2025) based on COI sequence similarities. One major clade (named C2 here, representing Types 2.1 and 2.2) is more heterogeneous and has a cosmopolitan distribution, with numerous records from Europe, Asia, and both North and South America (Fritz et al. 2009; Fuentes et al. 2019; Schifani et al. 2019; Caputo et al. 2021; Morpurgo et al. 2024). Based on medusa data, individuals from these two sequence groups are commonly assigned to "*C. sowerbii*" (Fritz et al. 2009; Fuentes et al. 2019; Oualid et al. 2019; Schifani et al. 2019; Lüskow et al. 2021). Polyps belonging to Types 2.1 and 2.2 were also found among the Israeli samples. Another major clade (named C1 here, representing Types 1.1 and 1.2) was most often detected in the Mediterranean region and Central Europe with rare reports from Africa and Asia (cf. Fig. 2). COI haplotypes of clade C1 have not been detected in the Americas (Fuentes et al. 2019; Caputo et al. 2021; Lüskow et al. 2021, 2023). Interestingly, the present study provides the first record of Type 1.2 specimens outside Europe. In contrast, specimens of Type 1.1, which are the most abundant among medusae records from Europe (formally assigned to "*C. kiatingi*" in Fritz et al. 2009), have not been detected among polyp samples from Israel. As most global records are based on medusae observations without genetic data, the true haplotype diversity and distribution is probably underestimated (Oualid et al. 2019; Lüskow et al. 2024).

Evidence for multiple introductions

Despite the limited geographic scope of our survey, we identified three distinct COI haplotypes (1.2, 2.1, and 2.2). In Israel, COI haplotype distributions showed little overlap between nearby sites, as most sites were dominated by a single COI haplotype. This is consistent with separate location-specific founder events and limited short-distance dispersal, rather than expansion from a single introduction. Thus, the genetic pattern in Israeli polyp populations points to multiple introduction events that have not yet homogenized through dispersal. Comparable patterns have been found in Central Europe, with some localities showing higher within-site COI haplotype diversity (Schachtl 2019; Wang 2022; Morpurgo et al. 2024). Repeated introductions are known to counteract population-wide founder effects and increase genetic diversity (Kolbe et al. 2004; Roman 2006; Lavergne and Molofsky 2007; Ghabooli et al. 2013; Putelli et al. 2025) and have been reported for other invasive cnidarians, including the brackish-water hydrozoan *Cordylophora* (Folino-Rorem et al. 2008).

Connections to European populations

The COI haplotypes identified in Israel were identical to those previously described from Europe, suggesting that the populations in the watershed of Lake Kinneret may represent secondary introductions rather than direct transfers from the native range in China. Multiple dispersal vectors have been hypothesized in the literature but have

not been comprehensively validated. Natural short-distance dispersal via hydrochory is possible but likely limited, as indicated by the strong local founder effects within streams. Human-mediated vectors such as recreation, fisheries, or aquaculture are likely to facilitate long-distance dispersal (Dumont 1994; Lewis et al. 2012). The Zavitan and Meshushim, situated in the Yehudiya Forest Nature Reserve, may serve as corridors for spreading between otherwise isolated habitats. Zoochory by migratory birds could also play a role, as Israel lies along the main flyway between Europe and Africa, and the nearby Hula Valley serves as a major stopover site (Alon et al. 2004). Podocysts, which can function as dispersal propagules, may be transported externally or internally by waterfowl (Figuerola and Green 2002; Green 2016). Although their desiccation tolerance remains debated (Reisinger 1957; Bouillon and Boero 2000a; Bouillon and Boero 2000b; Winata et al. 2024), survival after prolonged periods of desiccation during attachment to human or animal vectors would allow a successful establishment in distant locations. Further investigation of their survival ability and tolerance to various environmental conditions could shed more light on this mode of dispersal. To clarify connectivity and gene flow between different *C. sowerbii* populations, future studies should apply higher-resolution markers (e.g. microsatellites), as COI alone provides limited resolution (Calderon et al. 2006; Muñoz et al. 2013).

Importance of polyp-based surveys

Our results highlight the necessity of including polyp sampling in distributional surveys. Because medusae were absent during our sampling period, the species would have gone undetected if only pelagic surveys had been conducted. Previous studies have similarly shown that polyp-based surveys reveal broader distributions than medusae records alone (Duggan and Eastwood 2012; Morpurgo et al. 2024; Moore et al. 2025; supported by data in the dissertations of Schachtl 2019; Klotz 2022; Wang 2022). In streams, polyps may establish cryptic colonies that act as reservoirs for subsequent lake colonization. Environmental DNA approaches could also greatly improve detection in such habitats (Blackman et al. 2022; Jeunen et al. 2022; Fueyo et al. 2024; Moore et al. 2025).

Implications for Lake Kinneret

Although we did not detect *C. sowerbii* in Lake Kinneret itself, its occurrence in inflowing streams suggests that colonization of the lake remains possible and likely, particularly given the species' proven capacity for long-distance dispersal. Abiotic and biotic conditions may currently limit establishment: Lake Kinneret exhibits higher salinity (Lake Kinneret: 190–350 ppm Cl^-; streams: 15–40 ppm Cl^-), elevated nitrate levels, and possibly intense benthic grazing pressure compared to upstream habitats (Rimmer and Gal 2003; Rimmer and Nishri 2014; Sukenik et al. 2014; Gophen 2023). However, experimental data on the effects of these stressors on polyp survival are lacking.

If established in Lake Kinneret, *C. sowerbii* could impose additional stress on this lake ecosystem already under pressure from climate change, water-level fluctuations, and other invasive species (Zohary and Ostrovsky 2011; Ostrovsky et al. 2012; Heller et al. 2014; Sternberg et al. 2015; Gophen 2024; Zohary and Gasith 2025). The medusa stage, in particular, may compete with planktivorous fishes for zooplankton prey (Gießler et al. 2023), exacerbating existing competition between native and introduced fish species (Spataru and Gophen 1985; Goren and Galil 2005).

Considering Lake Kinneret's ecological and economic importance, intensified monitoring, especially at stream inflows and the Jordan River delta, combined with experimental studies on tolerance to local abiotic stressors, is strongly recommended. This, combined with predicting invasion dynamics by simulating the spread of medusae aggregations, is crucial for future monitoring.

Relevance of simulating medusae aggregations during the mixing period in winter

Concerning the simulations in Lake Kinneret in the winter months, we assume delayed blooms and prolonged survival of *C. sowerbii* medusae. Medusa budding is typically reported at temperatures above 20 °C (e.g. Folino-Rorem et al. 2015; Marchessaux et al. 2022; Winata et al. 2024), although our own observations indicate that budding can even occur at lower temperatures. In temperate regions, blooms of *C. sowerbii* medusae usually only occur in the warm summer months when the water temperatures are high (McClary 1959; Jakovčev-Todorović al. 2010; Marchessaux and Bejean 2020). Yet, at similar latitudes as the Golan Heights (Nevada USA, Japan, Morrocco, Croatia), medusae have been found in December and January (Deacon and Haskell 1967; Lewis et al. 2012; Oualid et al. 2019; Violić et al. 2022). Moreover, medusae can persist at temperatures well below 20 °C (Dodds and Hall 1984; Karaouzas et al. 2015; Marrosu et al. 2023), and climate suitability indices suggest that subtropical systems may support their year-round occurrence (Marchessaux et al. 2022). Climate change is expected to shift both the timing and geographic range of medusae blooms (Marchessaux et al. 2021, 2022). In Lake Kinneret, recent warming has extended stratification periods and maintained temperatures above 20 °C into late December (Amitai et al. 2025), increasing the likelihood of winter persistence. Water temperatures in nearby stream areas, where polyps have been found in close proximity to the lake, are similar to those in Lake Kinneret, potentially enabling continued budding. As stream discharge into the lake is higher during the winter months, two contrasting effects may be observed. During increased production of medusae during summer and fall, a weak connectivity between ponds due to low precipitation could impede effective transport of medusae into the lake. Only during the winter months, the hydrological regime in the Golan Heights streams may permit the propagation of medusae. It is essential to consider hydrological parameters in conjunction with biological factors in order to effectively predict invasion pathways. Modeling of medusae distributions during the mixing period is important to understand medusae swarm behavior in temperate regions as well, when medusae blooms persist until fall (DeVries 1992; Shifani et al. 2019; Morpurgo et al. 2024; Lüskow and Pakhomov 2024). Therefore, including simulations of medusa aggregations during the winter period is important for understanding and predicting future swarm dynamics under changing environmental conditions.

Limitation of the Lagrangian particle toolbox and the need for an active matter model for *C. sowerbii* medusae

In Figs 3, 4, we presented results of passive tracer dynamics, as the differences between the simulations with the active tracer transport mode of Particle Tracking and Analysis Toolbox (PaTATO) were relatively small. This may be

understood when considering the fluid eddy diffusivity, used by the Massachusetts Institute of Technology General Circulation Model (MITgcm). Eddy diffusivity describes how passive tracers are mixed and carried by the flow. Its value is about 10^{-2} m^2/s. In comparison, the extra mixing caused by active tracer dynamics is usually two orders of magnitude smaller. The passive tracer dynamics provides general description on the spreading of medusae distribution transported downstream by the watershed rivers inside the lake. However, by this we tacitly assumed low motility of the medusae. This should be refined in follow-up analyses, as *C. sowerbii* in their pelagic stage are relatively good swimmers (Peterson et al. 2022; Winata et al. 2024), especially with a strong ability for vertical self-propulsion (hence, might be able to move vertically even in stably stratified waters). To be able to simulate a more complete dynamics and in particular the generation and maintenance of small scale blooms or aggregations (Condon et al. 2013), one needs to develop a detailed active matter agent-based model for *C. sowerbii* medusae, embedded in the lake hydrodynamic simulations, similar to the one developed by Gengel et al. (2023, 2024) for marine medusae. This formidable task, however, is outside the scope of the current research. Likewise, modeling the spread of other life stages of *C. sowerbii* is an endeavor for future research, but could prove as well to be valuable in the light of other aquatic invaders with similar larval stages.

Conclusion

This study provides the first documentation of the polyp stage of *Craspedacusta sowerbii* in Israel in the field and reveals that the species is more widespread in the Lake Kinneret watershed than previously recognized. Genetic analyses identified three distinct COI haplotypes, indicating multiple independent introductions rather than expansion from a single founder population. The restricted overlap among sites suggests limited short-distance dispersal, similar to populations in Central Europe. Although the species has not yet been confirmed in Lake Kinneret, its presence in inflowing streams underscores the risk of eventual establishment and its consequences. Experimental studies on the environmental tolerance of not only the medusae and polyps but also the podocysts are important to further understand the distribution pattern and introduction pathways. Therefore, continued monitoring is essential to evaluate invasion dynamics and potential impacts on this ecologically and economically critical lake.

Toward this goal, hydrodynamic simulations identified specific coastal locations (Tiberias and Capernaum) with potentially high medusae concentrations along the Kinneret shore, providing guidance for more focused follow-up field campaigns. Early detection and a better understanding of the invasion dynamics are critical for assessing potential impacts on fisheries and ecosystem functioning.

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Supplementary material 1

Methodology, phylogenetic, localities

Authors: Stefan Dehos, Sabine Gießler, Herwig Stibor

Data type: docx

Explanation note: PCR Amplification and sequencing protocol, phylogenies and table of localities.

Link: https://doi.org/10.3897/neobiota.107.179109.suppl1

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

Regarding the use of AI in the preparation of this manuscript, the authors declare the following:
DeepL was used for linguistic improvement only.

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Author contributions

Conceptualization: HS, ZK, EH. Data curation: NS, SG, YA, SD. Formal analysis: YA, SD, NS. Funding acquisition: EH, HS. Investigation: YA, SD, ZK. Methodology: YA, SG, SD. Project administration: HS, EH. Resources: EH, HS, ZK. Software: SD, YA, NS. Supervision: EH, HS. Visualization: YA, SD, NS. Writing – original draft: YA, SD. Writing – review and editing: HS, ZK, EH, SG.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.