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# The quagga mussel (*Dreissena bugensis*) south of the Alps: an ongoing biological invasion in Lake Garda

**Francesca Ciutti · Luca Bonacina · Andrea Chemello · Adriano Boscaini · Fabio Buzzi · Silvia Costaraoss · Giorgio Franzini · Laura Fravezzi · Federica Giacomazzi · Giovanna Pellegrini · Sabrina Pozzi · Chiara Zampieri · Chiara Agostinelli · Eugenia Bettoni · Ketty Caraffini · Elisa Carena · Riccardo Formenti · Romana Fumagalli · Paola Montanari · Francesco Nastasi · Nico Salmaso · Cristina Cappelletti**

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**Abstract** Over the past century, Lake Garda has been increasingly affected by the introduction of several non-indigenous species. In early 2022, the identification of *Dreissena bugensis* (quagga mussel) marked the first record of a naturalized population in lakes south of the Alps. To investigate the colonization patterns of this invader and its potential interaction with the established invader *D. polymorpha* (zebra mussel), a comprehensive field survey was conducted in 2022 across twelve stations, encompassing littoral, sublittoral, and profundal zones, during both spring and autumn. By spring 2022, quagga mussels had colonized the littoral and sublittoral zones of nearly all stations, with higher density in the northern part of the lake and a growth rate dependent on depth. Between spring and autumn, their population continued to grow, surpassing zebra mussels at all stations and expanding into the profundal zone as well. Analysis of population structure and veliger monitoring suggest that quagga mussels likely arrived in the lake in 2019. The evidence of *D. bugensis* already being firmly established in Lake Garda, as well as in nearby Lake Ledro, highlights the need for biosecurity protocols to prevent further invasions and the spread of established invaders to other Italian lakes.

**Keywords** Invasive alien species · Freshwater bivalves · *Dreissena polymorpha* · *Dreissena bugensis* · Deep southern subalpine lakes

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F. Ciutti (✉) · A. Chemello · C. Cappelletti
Technology Transfer Center, Fondazione Edmund Mach,
Via E. Mach 1, 38098 San Michele All'Adige, TN, Italy
e-mail: francesca.ciutti@fmach.it

L. Bonacina · A. Boscaini · N. Salmaso
Research and Innovation Centre, Fondazione Edmund
Mach, Via E. Mach 1, 38098 San Michele All'Adige, TN,
Italy

F. Buzzi · C. Agostinelli · E. Carena · R. Formenti ·
R. Fumagalli · F. Nastasi
ARPA Lombardia, Via 1° Maggio 21/B,
23848 Oggiono (Lecco), Italy

S. Costaraoss · L. Fravezzi · G. Pellegrini · S. Pozzi
APPA Trento, Via Lidorno 1, 38123 Trento, Italy

G. Franzini · F. Giacomazzi · C. Zampieri
ARPA Veneto (ARPAV), Dipartimento Qualità
Dell'Ambiente, Sede Di Verona, Via A. Dominutti 8,
37135 Verona, Italy

E. Bettoni · K. Caraffini · P. Montanari
ARPA Lombardia, Via Antonio Cantore 20,
25128 Brescia, Italy

N. Salmaso
NBFC (National Biodiversity Future Center), Piazza
Marina 61, 90133 Palermo, Italy

## Introduction

There is a broad consensus that invasive alien species (IAS) are among the main drivers of biodiversity change and alterations in ecosystem services, together with other factors such as habitat alterations, climate change, overexploitation of species and pollution (World Resources Institute 2005). Biotic exchange plays a pivotal role in aquatic ecosystems, especially lakes, due to intentional (e.g., fish stocking) and unintentional (e.g., ballast water) introduction of organisms (Sala et al. 2000; Beeton 2002). Moreover, on a global scale, the number of non-indigenous species (NIS) continues to rise globally, with the rate of first records for most taxa increasing over time, particularly in recent years (Seebens et al. 2017).

Among the most well-known freshwater invasive species are zebra mussels, *Dreissena polymorpha* (Pallas, 1771), and quagga mussels, *Dreissena bugensis* (Andrusov, 1897), both recognized for their significant ecological and economic impacts (Beekey et al. 2004; Karatayev et al. 2007, 2015; Bossenbroek et al. 2009). Their success as invaders is attributed to their functional traits and ecosystem engineering abilities, as they attach to substrates and form reef-like structures that alter benthic habitats, leading to environmental changes and compromising water quality (Karatayev et al. 2002; Vanderploeg et al. 2002; Gutiérrez et al. 2003; Zhu et al. 2006; Sousa et al. 2009; Emery-Butcher et al. 2020; Karatayev and Burlakova 2025). While zebra and quagga mussels share similar life cycles, they differ in certain ecological traits, leading to significant differences in their spread and competition patterns (Ram et al. 2012). Both species have a free-swimming planktonic veliger stage and an attached adult stage, but zebra mussels spawn in water temperatures ranging from 12 to 15 °C, with peak spawning in cold spring and early summer in warm polymictic waters (Bacchetta et al. 2010). In contrast, quagga mussels can spawn at lower temperatures and under varying food availability, with veligers observed year-round rather than only in summer (Ram et al. 2012; Karatayev et al. 2022). Additionally, quagga mussels often invade waterbodies already colonized by zebra mussels (Burlakova et al. 2014), with their dynamics primarily influenced by biological traits (e.g., fecundity) and environmental conditions (such as substrate, water conditions, and depth preferences) that are not yet fully understood (Ram et al. 2012; Karatayev and Burlakova 2025). In deep lakes, quagga mussels tend to surpass zebra mussels in terms of impact, especially in deeper areas where they achieve higher densities (Zhulidov et al. 2010; Karatayev et al. 2011b). Zebra mussels prefer hard substrates and areas with wave action, colonizing rocks, shells, silty sand, and aquatic vegetation, whereas quagga mussels can additionally colonize silty sediments in the profundal zones of deep lakes. However, both species exhibit highly patchy distributions in littoral zones (Karatayev et al. 2015).

Native to the Ponto-Caspian basin and the southern Dnieper River drainage, both zebra and quagga mussels spread across Europe and North America. Zebra mussels, originally confined to the river basins of Russia, Bulgaria, Hungary, and surrounding regions, began to spread rapidly in the nineteenth century (Aldridge et al. 2004). By the 1870s, zebra mussels invaded most European countries, with their spread accelerating due to shipping activities. By the 1980s, zebra mussels reached North America, rapidly spreading across the Great Lakes and beyond (Karatayev et al. 2011a; Benson 2014). In contrast, quagga mussels started expanding in the 1940s from Ukraine (Bij de Vaate et al. 2013) and later spread to the Volga River in 1997 and to other downstream watersheds by 2000 (Orlova 2013) with significant differences in colonization patterns across river basins (Zhulidov et al. 2010). In Western Europe, quagga mussels followed two main invasion pathways: one through the southern corridor (Danube River, Main-Danube Canal, and Main and Rhine rivers), and another from North America via trans-Atlantic shipping (Bij De Vaate 2010; Bij De Vaate and Beisel 2011; Marescaux et al. 2016). Through the Rhine River, *D. bugensis* reached the Netherlands in 2006 (Molloy et al. 2007; Matthews et al. 2014), Germany in 2007 (Van Der Velde 2007), Belgium between 2009 and 2010 (Marescaux et al. 2012) and France in 2011 (Bij De Vaate and Beisel 2011; Trunfio et al. 2023). In the last decades, it has also been observed Baltic Sea in 2014 (Wozniczka et al. 2016, Wawrzyniak-Wydrowska et al. 2019), in the UK (Aldridge et al. 2004; Ainscough et al. 2021) and Ireland (Baars et al. 2022). The first evidence of quagga mussels in the Alpine region came from Swiss waterways, where eDNA samples collected from the Rhine River in Basel suggested their presence as early as 2014, although no adults were observed at that time

(De Ventura et al. 2017). In the following years, adult quagga mussels were found in Swiss and French lakes, including Lake Geneva (2015), Lake Constance (2016), Lake Neuchâtel (2017), Lake Hongrin (2019), Lake Bourget (2019) (Kurmayer et al. 2021), Lake Biel (2019), Lake Murten (2021) (Haltiner et al. 2022) and Lake Serre-Ponçon (2023) (Combrisson 2023). Furthermore, the presence of quagga mussels south of the Alps was hypothesized through genetic surveys in lakes Lugano and Maggiore in 2020, suggesting an early arrival of the species, although no specimens were observed at that time (Capelli et al. 2023).

Until 2017, investigations carried out in Lake Garda demonstrated the presence of at least 45 non-indigenous species (NIS) (Ciutti et al. 2011; Ciutti and Cappelletti 2017; Lopez-Soriano et al. 2018), an estimate that was considered certain to increase. Lake Garda was the first Italian waterbody where zebra mussels were observed in 1970 (Giusti and Oppi 1972), while in the nearby Lake Ledro, located just 6 km from Lake Garda and connected by a hydroelectric power plant, the species was recorded as early as 1973 (Bianchi et al. 1974).

More recently, in early 2022, quagga mussels were observed for the first time in Lake Garda, with their identification confirmed through both morphological and genetic analyses (Salmaso et al. 2022). However, no attempts were made to evaluate the spatial colonization pattern. Following this first observation, a field survey of both zebra and quagga mussels was conducted in order to: a) characterize the colonization dynamics of quagga mussel and its timeline introduction; b) assess its early impact on the established zebra mussel; c) compare the population structures of both species, d) monitor the growth of the quagga mussel population over time, and e) estimate the timeline of quagga mussel introduction.

## Methods

### Study area and survey plan

The field investigation was conducted in Lake Garda, a deep, oligomictic, subalpine lake with a surface area of 368 $km^2$, a volume of $49 \times 10^9$ $m^3$, a maximum depth of 350 m, and an altitude of 65 m a.s.l. The lake is part of the Italian Long Term Ecological Research network (IL-TER IT08-005-A) (Salmaso et al. 2021). Lake Garda consists of two basins: the north basin, characterized by steep shores and depths ranging from 300 to 350 m, and the south basin, with gentler shores and a maximum depth of approximately 80 m. The lake is oligo-mesotrophic (Salmaso et al. 2018) and, according to the Water Framework Directive, its ecological status is “good” in both the sub-basins. Lake Garda is connected to Lake Ledro, a relatively small lake, with a “moderate” ecological status. Covering an area of 2.17 $km^2$ and having a volume of $75.8 \times 10^6$ $m^3$, Lake Ledro reaches a maximum depth of 48 m. Situated at an altitude of 652 m above sea level, it is connected to Lake Garda via a pumping pipe used for hydroelectric energy production.

Twelve stations along the entire perimeter of Lake Garda were sampled across a depth gradient in spring and autumn 2022 by operators of the Environmental Protection Agencies of the Provinces of Trento (TN), Verona (VR) and Brescia (BS) (Fig. 1). Additional investigations were carried out in spring 2023 to evaluate the potential expansion of quagga mussels in Lake Ledro.

### Dreissenids samplings and quantification

Zebra and quagga mussels were sampled following European and Italian protocols for benthic macroinvertebrates to assess the ecological status according to the Water Framework Directive WFD 2000/60/CE (European Parliament 2000; Parlamento italiano 2006; Governo italiano 2010; Boggero et al. 2014). At each one of the twelve stations (fixed geographic locations within the lake reported in Fig. 1), three distinct depth zones were identified (littoral, sublittoral, and profundal), and within each zone, three replicate samples of 0.0225 $m^2$ were collected using a Petit-Ponar grab. This sampling was conducted in both spring and autumn 2022, yielding a total of 216 samples (12 stations $\times$ 3 zones $\times$ 3 replicates $\times$ 2 seasons; Table 1). The littoral zone exhibited marked habitat variability, influenced by the presence or absence of vegetation and substrate type (sand, pebbles, or coarse organic debris). In contrast, the sublittoral zone had more homogeneous, silty, and sandy sediment with lower vegetative coverage, while the profundal zone was characterized by organic-rich silt, low temperature, and limited photosynthetically active radiation. The same stations had been sampled in 2017 following the

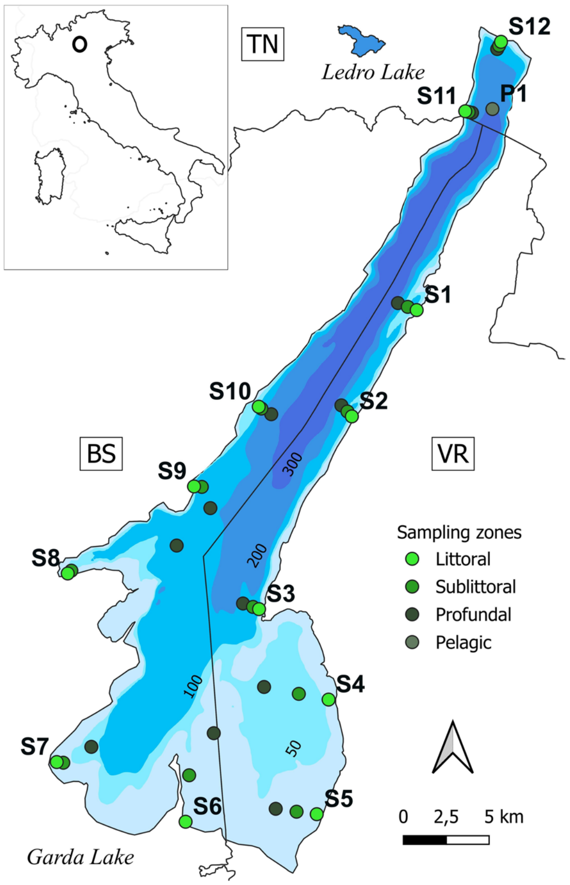


**Fig. 1** Study area and sampling zones

same procedure; therefore, those data were included in the analysis to obtain a more complete overview of the persistence of the invasive mussels over the last years. In the laboratory, mussels were sorted, counted and taxonomically identified and a stereomicroscope was used for specimens with a total length of less than 2 mm. Shell length of zebra (n = 1939) and quagga (n = 6275) mussel specimens were measured from spring samples collected at sites S1, S2, S3, S4, S5, S11, and S12 to analyze population structure, and from autumn samples at site S2 to investigate quagga growth.

An early method for detecting dreissenids involves monitoring veligers in the water column. This study incorporates observations of dreissenid veligers found in zooplankton samples collected from depths of 0–20 m between 2013 and 2024. The presence of these veligers is useful for estimating the arrival timeline of *Dreissena bugensis*, as quagga mussel veligers have been observed throughout the year, not just during the summer months.

## Data analysis

To characterize the colonization patterns of quagga mussel throughout the lake and assess its impact on the established invader zebra mussel, the densities of both species and their relative abundances were calculated for each sample. To visualize the spatial and temporal variations across zones and along a latitudinal gradient (from north to south), boxplots of mussel densities were presented for each station in both spring and autumn.

**Table 1** Monitoring stations and their corresponding sampling depth in the littoral, sublittoral and profundal zones of Lake Garda

| Monitoring station | Municipality (province) | Sampling depth (m) in the different zones: | | |
|---|---|---|---|---|
| | | Littoral | Sublittoral | Profundal |
| S1 | Malcesine (VR) | 10 | 25–30 | 96–105 |
| S2 | Brenzone sul Garda (VR) | 16 | 30 | 94 |
| S3 | Torri del Benaco (VR) | 8 | 30 | 100–115 |
| S4 | Bardolino (VR) | 4–6 | 48 | 78 |
| S5 | Lazise (VR) | 7 | 32 | 60 |
| S6 | Sirmione (BS) | 5 | 19–20 | 60–62 |
| S7 | Padenghe (BS) | 10 | 28–29 | 93–96 |
| S8 | Salò (BS) | 22 | 35–38 | 177–180 |
| S9 | Toscolano Maderno (BS) | 15–16 | 23–34 | 177–179 |
| S10 | Gargnano (BS) | 15 | 36–40 | 230 |
| S11 | Riva del Garda (TN) | 11–18 | 26–29 | 109–113 |
| S12 | Riva del Garda (TN) | 11–12 | 29–30 | 117–122 |

The influence of the sub-basins (north vs. south), zones and their interaction on mussel density across different periods (spring and autumn of 2017 and 2022) was assessed using a generalized linear mixed model (GLMM) with a negative binomial distribution (nbinom2) to account for overdispersion in the abundance data (Zuur et al. 2009). Sub-basins and zones were treated as fixed effects, while stations were included as a random effect (GLMM.NB: Density ~ Basin * Zone + (1|Station)). Replicates were not included, as they did not improve model performance.

Additionally, to describe the expansion of quagga mussel over time and evaluate the competition with the zebra mussel population, pie charts showing the relative abundances of both species across zones of each station were compared between seasons.

To analyze the population structure of both species across zones, size frequency distributions were plotted using specimens collected from stations S11, S12, S1, S3, S4, S5, with the shell length of each specimen measured to the nearest 0.1 mm and grouped into 1 mm step classes. Moreover, to investigate the growth of quagga mussels over the summer and the potential influence of depth, the size-frequency distribution of quagga mussels collected at S2 was compared between spring and autumn across zones. Bar plots were used to represent the population structures of both species and to highlight temporal (seasonal) and spatial (zonal) variations. The mean length of each cohort was calculated using the modal progression analysis of the Bhattacharya (1967) method, implemented in FISAT II software (Version 1.1.2, FAO-ICLARM Fish Assessment Tools; (Gayanilo et al. 2005).

The timeline of quagga mussel arrival was estimated based on the cohort's mean length and by analyzing the presence of veligers in the water samples collected from the pelagic zone P1 across the different months of the period 2013–2024.

Where not explicitly stated, all the statistical analyses were performed using R software (version 4.5.1).

## Results

### Distribution, density and relative abundance of Dreissenids

Dreissenid sampling provided a total of 8214 adult specimens, identified as two species: 6275 quagga mussels and 1939 zebra mussels. In 2017, zebra mussels were the only dreissenid species present across all stations except S10, colonizing both littoral and sublittoral zones up to a maximum depth of 48 m at station S4 (Bardolino). Their mean density ranged from 1628 ± 3175 ind/m$^2$ in spring to 1567 ± 2376 ind/m$^2$ in autumn, with the highest density observed at station S11 (Riva del Garda) in both spring (10,311 ± 4905 ind/m$^2$) and autumn (6755 ± 823 ind/m$^2$) (Fig. 2 and Table S1). No zebra mussels were recorded in the profundal zones at any of the stations in 2017. In 2022, zebra mussels were found in the littoral or sublittoral zones of all stations except S4, with generally lower abundances compared to 2017, and were completely absent from the profundal zones. Their mean density in spring was 1487 ± 2255 ind/m$^2$ decreasing to 493 ± 710 ind/m$^2$ in autumn. Conversely, quagga mussels, absent in 2017, were found at all stations in spring 2022, except in the littoral zone of S6, limited to the littoral and sublittoral zones. Their density increased from spring to autumn, rising from 4188 ± 6888 to 7846 ± 15,361 ind/m$^2$, with maximum densities found in the littoral zone at S2 in spring (2745 ± 2908 ind/m$^2$), and at S11 in autumn (64,429 ± 17,308 ind/m$^2$) (Fig. 2). In autumn 2022, quagga mussels were also observed in the profundal zones of S3 and S7, at depths of 115 and 93 m, respectively, with very few specimens (mean densities of 44 and 89 ind/m$^2$, respectively) (Fig. 2 and Table S1).

According to the GLMM.NB results, in 2022 densities of both species were significantly higher ($p < 0.05$) in the north sub-basin. No significant effect of sub-basin was observed in 2017, when only zebra mussels were present. Additionally, no significant differences were detected between littoral and sublittoral zones within the same sub-basin across any period or species, and no significant interaction between sub-basin and zone was observed (Table 2).

The rapid expansion of quagga mussels during the summer of 2022 partially replaced the established invader zebra mussels whose relative

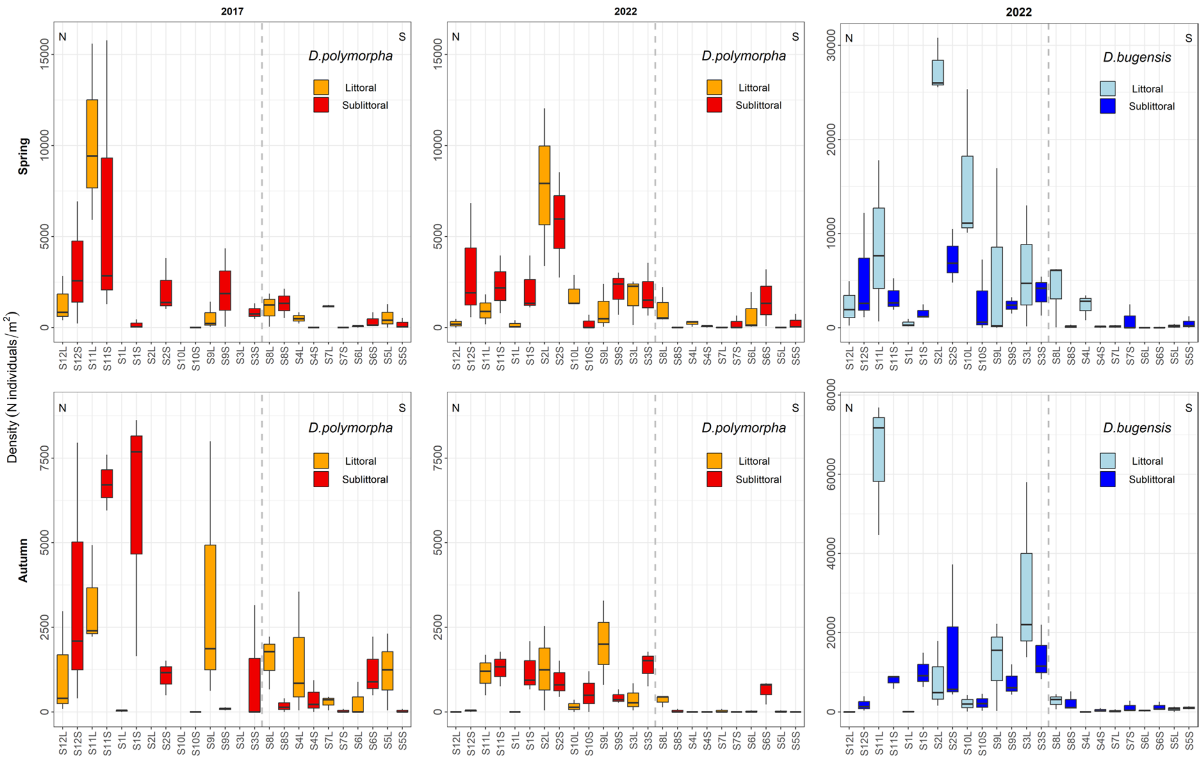


**Fig. 2** Densities of *D. polymorpha* and *D. bugensis* mussels at the monitoring stations in the littoral and sublittoral zones of the north (N) and south (S) sub-basins. (Boxplots represent median, interquartile range and whiskers). Note the different scales on the y-axes. The profundal zone is not included because specimens were found only in S3 and S7 in autumn 2022

**Table 2** Influence of sub-basin (north vs. south), zone (littoral vs. sublittoral), and their interaction on mussel density across different periods (spring and autumn of 2017 and 2022)

| Species | Year | Season | Intercept<br>Slope ± se | | South basin<br>Slope ± se | Sublittoral zone<br>Slope ± se | South basin: sublittoral zone<br>Slope ± se |
|---|---|---|---|---|---|---|---|
| *D.bugensis* | 2022 | spring | 9.1531 ± 0.4154 | *** | − 1.9422 ± 0.6435 ** | − 0.9286 ± 0.5874 | − 0.5517 ± 0.9102 |
| *D.bugensis* | 2022 | autumn | 9.1913 ± 0.5296 | *** | − 2.9729 ± 0.7574 *** | − 0.1534 ± 0.5722 | 1.0834 ± 0.7899 |
| *D.polymorpha* | 2017 | spring | 8.1354 ± 0.8644 | *** | − 1.6099 ± 1.0499 | − 0.5135 ± 0.8714 | − 0.1623 ± 1.2651 |
| *D.polymorpha* | 2017 | autumn | 7.5841 ± 0.5862 | *** | − 0.7141 ± 0.7865 | 0.291 ± 0.7348 | − 1.2626 ± 1.044 |
| *D.polymorpha* | 2022 | spring | 7.4495 ± 0.4588 | *** | − 1.4516 ± 0.7116 * | 0.369 ± 0.5968 | − 0.461 ± 0.9465 |
| *D.polymorpha* | 2022 | autumn | 6.0666 ± 0.9752 | *** | − 2.1938 ± 1.4951 | 0.7662 ± 0.8336 | − 2.6884 ± 1.6869 |

Values correspond to regression coefficient (slope) ± standard error (se). Significance levels are indicated as follows: *: $0.01 \leq p < 0.05$; **: $0.001 \leq p < 0.01$; ***: $p < 0.001$

abundance decreased in almost all stations, particularly at S6 (–95% in the littoral zone and –65% in the sublittoral zone) (Fig. 3).

In 2023 adult specimens of quagga mussel were observed in Lake Ledro, attached to a buoy and its

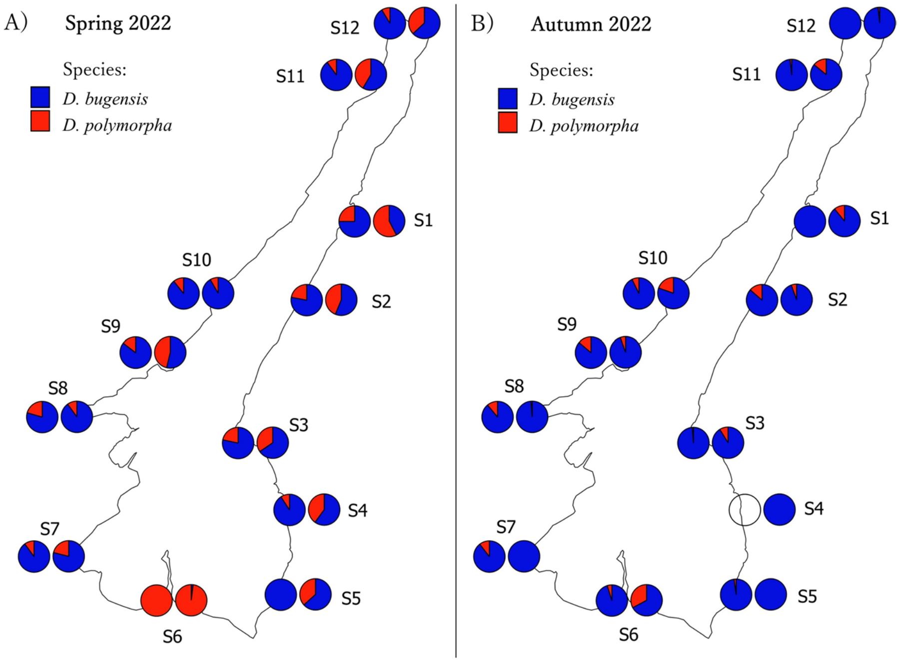


**Fig. 3** Relative abundance of *D. bugensis* and *D. polymorpha* in spring (panel A) and autumn 2022 (panel B). At each station shown in each panel, two pie charts are displayed side-by-side: the pie chart on the left corresponds to the littoral zone, and the pie chart on the right corresponds to the sublittoral zone

anchoring rope, with a maximum shell length of 15.2 mm.

## Population structure and growth

In spring 2022, the shell length of both quagga and zebra mussels ranged from 1 to 24 mm, with most specimens measuring between 4 and 12 mm.

Generally, quagga mussels exhibited well-structured populations, particularly in stations with high abundance (S11, S12, S1 sublittoral, S3, and S4 littoral), with two clearly distinguishable groups at some of these stations, especially in the littoral zone (S11, S12, S1, and S3) (Fig. 4). In contrast, zebra mussels displayed poorly structured populations, particularly in stations with low abundance (S12 littoral, S1 littoral, S4, and S5) (Fig. 4). In stations with higher abundance (S11, S12 sublittoral, S1 sublittoral), no distinct groups were detectable. However, these data were not easily interpretable and were used primarily for descriptive purposes.

Comparisons of length-frequency distributions between spring and autumn in station S2 revealed well-structured populations of quagga mussels in both the littoral and sublittoral zones, with clearly distinguishable length classes, corresponding to two cohorts plus an additional cohort represented by 2 specimens with shells longer than 25 mm belonging to a possible third cohort (Fig. 5).

According to the modal progression analysis, in the littoral zone, the first and second spring cohorts measured 5.5 ± 1.9 mm and 16.1 ± 2.4 mm long, respectively, while in the sublittoral zone, they measured 4.4 ± 2.0 mm and 13.0 ± 2.3 mm, respectively. On the other hand, the autumn cohort reached 15.7 ± 1.9 mm in the littoral zone and 13.7 ± 2.4 mm in the sublittoral zone. Both populations were characterized by a peak in juvenile shells measuring 2 mm, which accounted for approximately 40% of the total abundance. In autumn, the 0 + cohort grew to 15.7 mm in the littoral and 13.7 mm in the sublittoral (Fig. 5).

## Veligers

Analysis of the veliger distributions collected at station P1 from 2013 to 2024 shows that, until 2020, veligers were observed between June and December. However, from 2021 onwards, they first appeared in March, and from 2022 to 2024, they were observed as early February, with occasional appearances in April and May (Fig. 6).

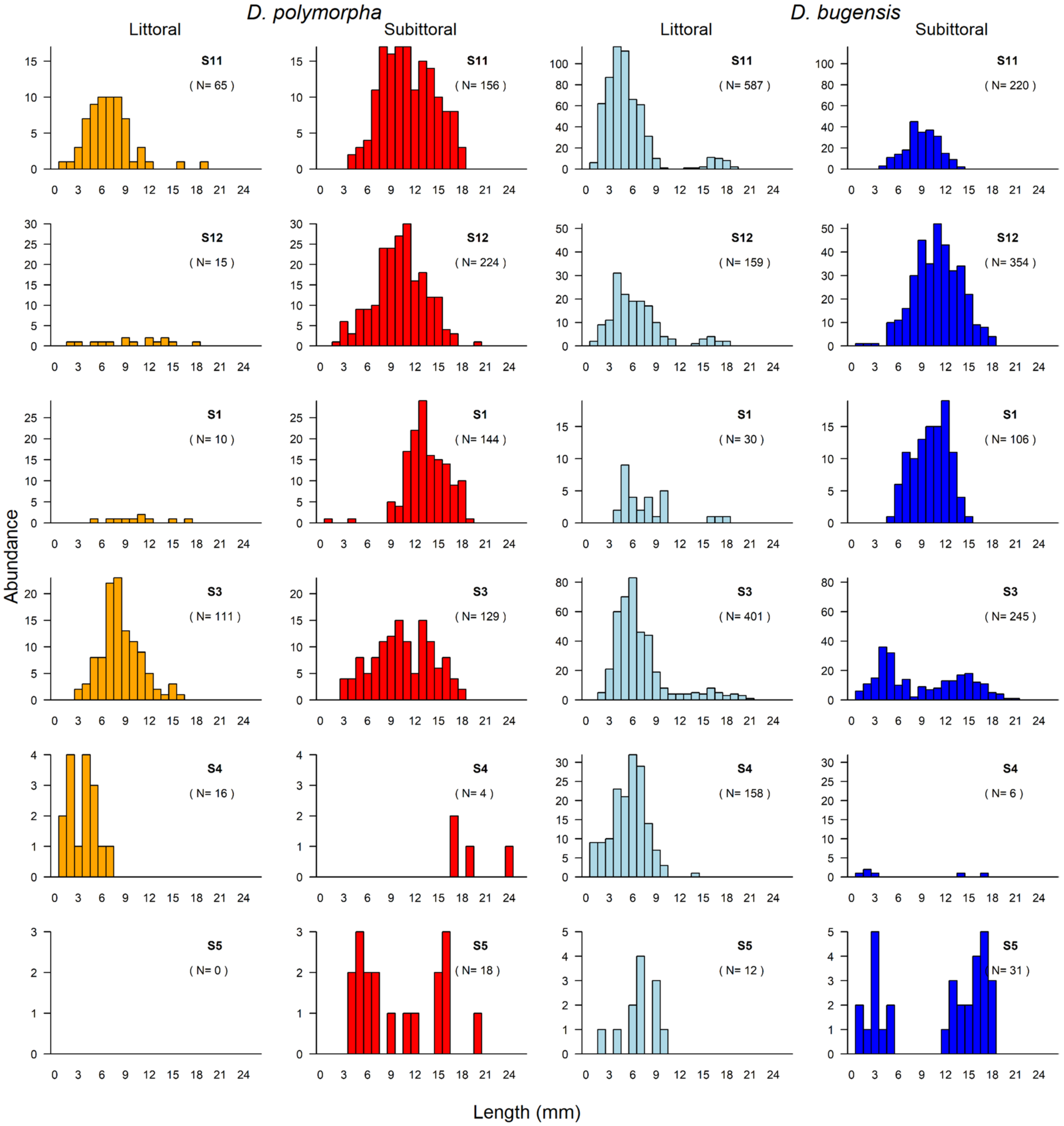


**Fig. 4** Shell length-frequency distribution of *D. polymorpha* and *D. bugensis* shells collected in the littoral and sublittoral zones of stations S11, S12, S1, S3, S4, and S5 during spring 2022. In the stations with low abundance (N < 50) length-frequency distributions should be interpreted with caution. Note the different scales on the y-axis

## Discussion

The results of this study highlight the expansion of *D. bugensis* in Lake Garda, showing notable interactions with the established species, *D. polymorpha*. The following discussion examines the implications of these findings concerning colonization patterns, population structure, ecological impacts and the potential of Lake Garda in the spread of invasive species.

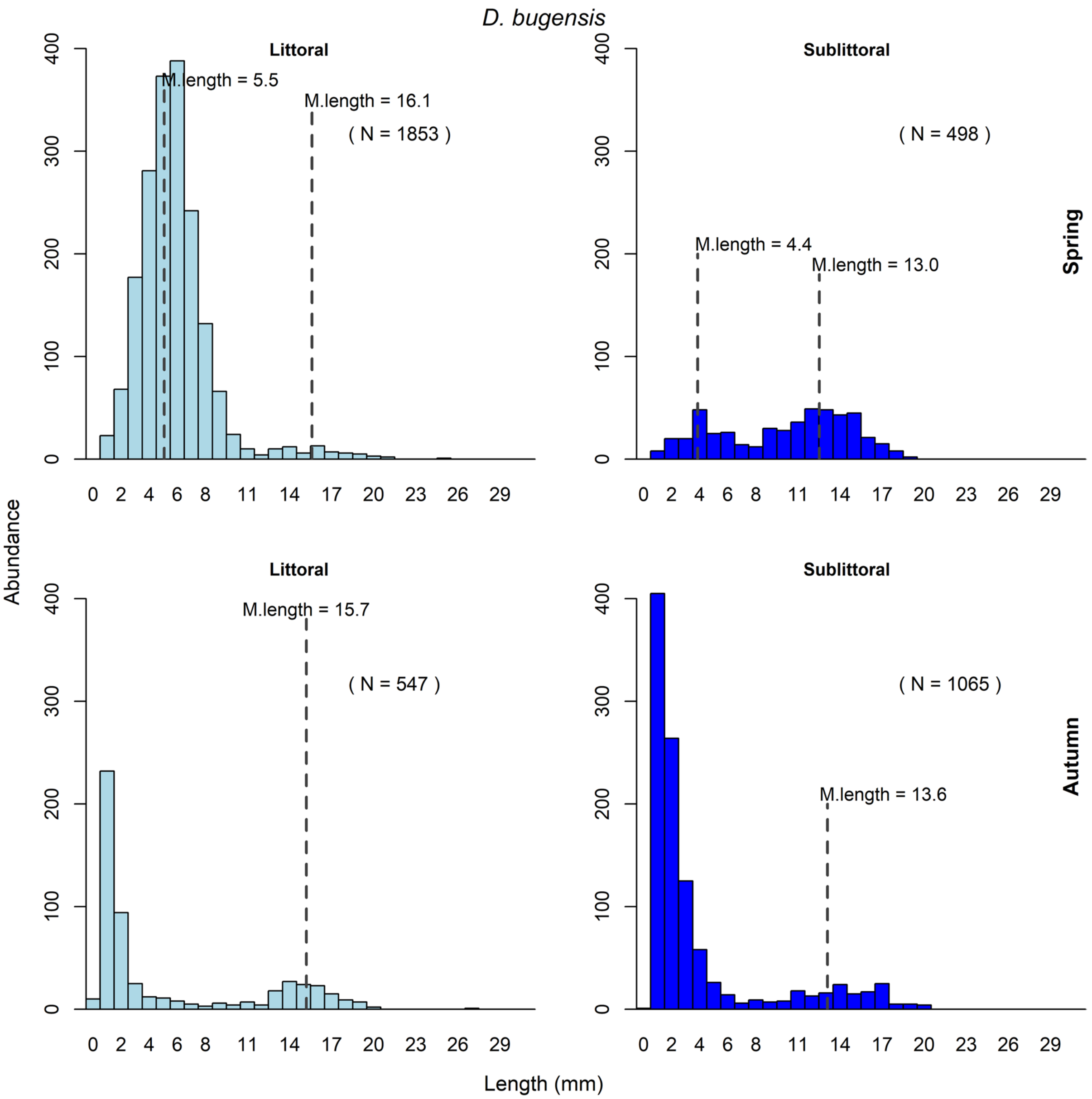
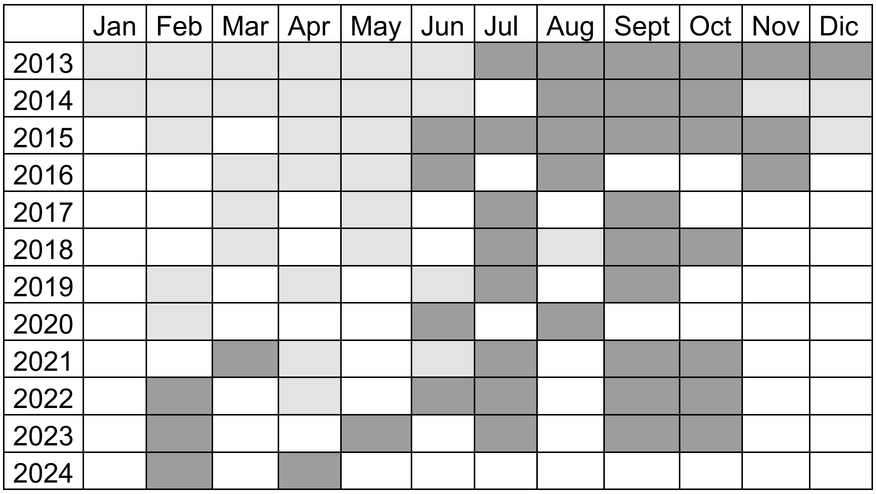


**Fig. 5** Comparison of the shell length-frequency distributions of *D. bugensis* shells collected in the littoral and sublittoral zones of station S2 during spring and autumn 2022

### Morphology, colonization and population structure

In 2022, the first year of observation, quagga mussels had already spread throughout Lake Garda, occupying both the littoral and sublittoral zones of nearly all stations. From spring to autumn, their density exceeded that of zebra mussels in most areas, replacing the established invader in the littoral zones of stations S1 and S12, as well as in the sublittoral zones of S4, S5, and S7. This pattern mirrors observations in Lake Constance, where quagga mussels rapidly replaced zebra mussels (Haltiner et al. 2022). By spring 2022, quagga mussels reached a maximum depth of 48 m at station S4, although by autumn, they were found also in the profundal zones (115 m in S3 and 93 m in S7). This suggests that while their



| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dic |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2013 | ░ | ░ | ░ | ░ | ░ | ░ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| 2014 | ░ | ░ | ░ | ░ | ░ | ░ | | ▨ | ▨ | ▨ | ░ | ░ |
| 2015 | | ░ | | ░ | ░ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ░ |
| 2016 | | | ░ | ░ | ░ | ▨ | | ▨ | | | ▨ | |
| 2017 | | | ░ | | ░ | | ▨ | | ▨ | | | |
| 2018 | | | ░ | | ░ | | ▨ | ░ | ▨ | ▨ | | |
| 2019 | | ░ | | ░ | | ░ | ▨ | | ▨ | | | |
| 2020 | | ░ | | | | ▨ | | ▨ | | | | |
| 2021 | | | ▨ | ░ | | ░ | ▨ | | ▨ | ▨ | | |
| 2022 | | ▨ | | ░ | | ▨ | ▨ | | ▨ | ▨ | | |
| 2023 | | ▨ | | | ▨ | | ▨ | | ▨ | ▨ | | |
| 2024 | | ▨ | | ▨ | | | | | | | | |

**Fig. 6** Dreissenid veligers collected at station P1 from 2013 to 2024. White indicates months when water samples were not collected, light grey indicates months when water samples were collected but no veligers were found, and dark grey indicates months when water samples were collected, and veligers were observed

expansion is ongoing, quagga mussels may continue to colonize greater depths in the future.

Profundal waters, which are cold, food-poor, and oxygen-limited, are unsuitable for zebra mussels (Karatayev and Burlakova 2025), which typically occupy the littoral and sublittoral zones, as observed both in this study and in previous surveys (Franchini 1978). Conversely, quagga mussels, which can successfully settle on soft substrates, have a broader ecological niche and can extend into deeper and colder environments, as has been documented in other water bodies, including Lake Constance (Haltiner et al. 2022) and the Great Lakes (Karatayev et al. 2022), where quagga mussels colonized lakebeds at depths exceeding 200 m.

The rapid expansion of quagga mussels in Lake Garda resulted in a decline of zebra mussels, like patterns observed in other lakes where the two species compete (Karatayev et al. 2015; Rudstam and Gandino 2020). However, in deep lakes, quagga mussels often surpassed zebra mussels after nine or more years of coexistence (Karatayev et al. 2015); therefore, it is likely that both species will persist in Lake Garda for several years. According to typical colonization patterns (Matthews et al. 2014; Karatayev et al. 2015) quagga mussel densities are likely to decrease in the littoral and sublittoral zones after reaching their peak, while expanding into deeper areas. Analysis of abundance data revealed significant differences between the two sub-basins of Lake Garda. Higher densities of both species were found in the northern part of the lake, likely due to more favorable environmental conditions such as lower turbidity, colder and more oxygenated waters (Huang et al. 2016). Additionally, the steep northern shores, which are less exposed to the continuous lapping of waves than the shallow southern shores traversed by boats and ferries (Ghirardi et al. 2022), experienced reduced wave action, which enhances substrate settlement and favors bivalve populations (Lorenz and Pusch 2013). The colonization success of *D. bugensis* is reflected in the observed population structure, with distinct age-class distributions across zones.

Shell length-frequency distribution analysis of mussels revealed well-structured populations of *D. bugensis* in stations with a consistent number of specimens while zebra mussels were generally poorly structured, likely due to the impact of the new invader. Quagga mussels showed distinct cohorts in most sampling stations during spring 2022, with differences between the littoral and sublittoral populations, while *D. polymorpha* didn't display clear cohorts. Results also indicated a recent juvenile settlement of *D. bugensis*, similar to patterns observed in Lake Mead (Gerstenberger et al. 2011; Wong et al. 2012). A comparison of the length-frequency distributions of quagga mussels between spring and autumn revealed depth-dependent growth, with the littoral population growing faster than the sublittoral one (10.18 mm vs. 9.24 mm). This difference is likely influenced by water temperature, which ranged from 9.2 to 19.6 °C at 16 m depth and from 9.2 to 12.8 °C at 30 m depth between February and October. The estimated growth rates for Lake Garda were

0.042 mm/day for the littoral zone and 0.038 mm/day for the sublittoral zone of S2. These rates are higher than those observed in Lake Ontario, where growth rates in caged mussels were 0.031 mm/day and 0.018 mm/day at depths of 15 m and 45 m, respectively (Elgin et al. 2022) but consistent with the 0.041 mm/day rate reported for the littoral zones of Lake Oneida (USA) by (Karatayev et al. 2015) and Lake Geneva by (Zhang et al. 2023).

Veligers were historically observed from June to December, during periods when zebra mussels were the sole dreissenid species present in the lake, consistent with findings reported in previous studies (Rolla et al. 2020; Haltiner et al. 2022). Since 2021, however, veligers have been detected between February and May, suggesting the presence of *D. bugensis*, which is known to spawn year-round (Gerstenberger et al. 2011; Haltiner et al. 2022) (Fig. 6). This earlier detection of veligers, particularly in spring, serves as an early warning signal for *D. bugensis* invasion, as similar observations have been made in other lakes colonized by zebra mussels (Whitehead et al., 2024). The observation of spring veligers in March 2021 suggests that quagga mussels reached detectable density that year; however, the occurrence of three size-age cohorts in 2022 indicates that introduction likely occurred before 2020, meaning the quagga mussel population had likely already been introduced in the lake by 2019.

### Ecological effects of bivalve invasion

The high filtration rates of invasive mussels can impact water quality by reducing phytoplankton primary production and sequestering nutrients (Burlakova et al. 2023). However, the potential effects of the new invader *D. bugensis*, together with established species as *Corbicula* spp. clams and *D. polymorpha*, on biological communities and water quality have yet to be investigated in Lake Garda as done by Binelli et al. (1997) on Lake Como. Both zebra and quagga mussels, as ecosystem engineers, can alter lakebed features by creating a three-dimensional structure, which increases substrate diversity and provides refuges for benthic invertebrates, leading to increased density in some species (Ricciardi 2003; Karatayev et al. 2022; Zhang et al. 2022). For example, Kobak et al. (2013) observed that detritivores and herbivorous species, such as gammarids and snails, benefit from the nutrient release in mussel pseudofaeces. Conversely, the rapid settlement of mussels and their high filtration rates can negatively affect the benthic community by reducing total richness and density of some taxa (McNickle et al. 2006). This study, although focused on the colonization of *D. bugensis* in Lake Garda and its interaction with *D. polymorpha*, did not examine the broader ecological impacts of the species on the aquatic biota and ecosystem functioning. Further research is needed to assess the interactions between quagga mussels and the benthic community, as well as their effects on native (Unionidae, Pisidiidae) and non-native (*Corbicula* spp. clams and *Sinanodonta woodiana*) bivalves, other macroinvertebrates, and macrophytes inhabiting both hard and soft substrates in various lake zones.

### Xenodiversity of Lake Garda and human activities

The introduction of the Ponto-Caspian *D. polymorpha* in 1970 (Giusti and Oppi 1972) marked the beginning of bivalve invasions in Lake Garda, followed by the arrival of *Corbicula fluminea* (Müller, 1774) in 2000 (Nardi and Braccia 2004; Ciutti et al. 2007), *Corbicula fluminalis* (Müller, 1774) in 2008 (Cappelletti et al. 2009; Ciutti and Cappelletti 2009), Sinanodonta woodiana (Lea, 1834) (Cappelletti et al. 2009) and more recently, *Corbicula leana* Prime, 1867 and *Corbicula largillierti* (Philippi, 1844) (Lopez-Soriano et al. 2018), which have formed extensive deposits of dead shells along the shores. Another notable Ponto-Caspian invasive species, *Dikerogammarus villosus* (Sowinsky, 1894), was recorded in Lake Garda in 2003, displacing the indigenous *Echinogammarus stammeri* (Karaman, 1931) from the littoral zones (Casellato et al. 2006, 2008) and later expanding to depths of up to 100 m (Marchi et al. 2014).

The discovery of *D. bugensis* in Lake Garda in 2022 marked the first observation of this species in Italy and in water bodies south of the Alps (Salmaso et al. 2022) while its discovery in Lake Ledro in 2023 represents the second occurrence. However, this new invasion seems to follow a different pattern of colonization compared to zebra mussels, characterized by higher densities and preference for soft substrates at greater depths. Since Lake Garda does not have direct connections (such as rivers or canals) to water bodies already colonized by *D. bugensis*, the introduction of quagga mussels is likely linked to human activity.

It may have been unintentionally facilitated by recreational boating and fishing gear, as has been suggested for other invasions in Lake Garda (Ciutti et al. 2011; Salmaso et al. 2022). A similar hypothesis has been proposed for the rapid spread of quagga mussels from Lake Geneva to other Swiss lakes (Haltiner et al. 2024), as this bivalve is highly resilient, capable of surviving air movement speeds up to 50 km/h for over 18 h and can spread via boat hulls (Collas et al. 2021). Lake Garda is one of the most popular tourist destinations in Italy, attracting approximately 25 million overnight stays in 2024, predominantly from international visitors, especially Germans (~ 12 million). Many of these tourists engage in water sports such as swimming, sailing, surfing, and recreational boating and, in 2023 the lake hosted up to 90 national and international regattas. Given the high boating activity, it is highly probable that the introduction of non-native species in Lake Garda was facilitated by the transport of infested recreational boats. Therefore, it is crucial to implement biosecurity measures, such as the "Check, Clean, Dry Protocol," (Di Vittorio et al. 2012; Anderson et al. 2015; Carnevali et al. 2018) and raise awareness among boat owners about the risk of invasive species spread to and from the lake basin.

## Conclusion

The discovery of *D. bugensis* in Lake Garda represents the first record of a naturalized population of this species in lakes south of the Alps. Three years after its introduction, the quagga mussel had successfully colonized the entire lake, spreading to both the littoral and sublittoral zone. Its numbers have increased over time, and it has spread into deeper areas. This ongoing invasion highlights the adaptability of this species and suggests that further spread is inevitable. Lake Garda, with several invasive species, has become a European hotspot for xenodiversity. It not only serves as an entry point for invasive species, largely driven by recreational boating and aquatic sports, but also acts as a source for unintentional spread to other water bodies, as evidenced by the detection of *D. bugensis* in nearby Lake Ledro. Given the ecological importance of Lake Garda and its role in local tourism and economies, the protection of its biodiversity is crucial. Since eradication of dreissenids and other invasive species is not feasible, preventing further invasions through constant monitoring, management strategies, and biosecurity measures remains the best approach to mitigate ecological damage and preserve the integrity of the lake.

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## Declarations

**Conflict of interest** The authors declare no conflict of interest.

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**Consent to Participate** Not applicable.

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