The distribution and spread of quagga mussels in perialpine lakes north of the Alps

Linda Haltiner, Hui Zhang, Orlane Anneville, Lukas de Ventura, Tyrell Deweber, John Hesselschwerdt, Michael Koss, Serena Rasconi, Karl-Otto Rothhaupt, Roland Schick, et al.

Research Article

The distribution and spread of quagga mussels in perialpine lakes north of the Alps

Linda Haltiner[1,2,*,+], Hui Zhang[3,+], Orlane Anneville[4], Lukas De Ventura[5], J Tyrell DeWeber[6], John Hesselschwerdt[7], Michael Koss[8], Serena Rasconi[4], Karl-Otto Rothhaupt[3], Roland Schick[9], Brigitte Schmidt[10], Piet Spaak[1,2], Petra Teiber-Siessegger[11], Martin Wessels[11], Markus Zeh[12] and Stuart R. Dennis[1]

[1]*Department of Aquatic Ecology at the Swiss Federal Institute for Environmental Sciences and Technology (Eawag), Überlandstrasse 133, 8600 Dübendorf, Switzerland*

[2]*Institute for Integrative Biology (IBZ) at the Federal Institute of Technology Zurich (ETHZ), Switzerland*

[3]*University of Konstanz, Limnological Institute, Mainaustrasse 252, 78464 Konstanz, Germany*

[4]*INRAE (National Research Institute for Agriculture, Food and Environment), University´ Savoie Mont Blanc, CARRTEL, 74200 Thonon-les-Bains, France*

[5]*Kanton Aargau, Departement Bau, Verkehr und Umwelt, Abteilung für Umwelt, Entfelderstrasse 22, 5001 Aarau, Switzerland*

[6]*LAZBW, Fischereiforschungsstelle Langenargen, Argenweg 50/1, 88085 Langenargen, Germany*

[7]*HYDRA, Büro Konstanz, Fürstenbergstrasse 25, 78467 Konstanz, Germany*

[8]*Zurich Water Supply, Hardhof 9, 8021 Zurich, Switzerland*

[9]*Zweckverband Bodensee-Wasserversorgung, Süssenmühle, 78354 Sipplingen, Germany*

[10]*Ville de Lausanne, Service de l'eau, Rue de Genève 36, CP 7416, 1002 Lausanne, Switzerland*

[11]*Institut für Seenforschung, Landesanstalt für Umwelt (LUBW), Argenweg 50/1, 88085 Langenargen, Germany*

[12]*Kanton Bern, Bündackerstrasse 44, 3047 Bremgarten, Switzerland*

[+]*Equal contribution*

**Corresponding author*

E-mail: linda.haltiner@eawag.ch

Citation: Haltiner L, Zhang H, Anneville O, De Ventura L, DeWeber JT, Hesselschwerdt J, Koss M, Rasconi S, Rothhaupt K-O, Schick R, Schmidt B, Spaak P, Teiber-Siessegger P, Wessels M, Zeh M, Dennis SR (2022) The distribution and spread of quagga mussels in perialpine lakes north of the Alps. *Aquatic Invasions* 17(2): 153–173, https://doi.org/10.3391/ai.2022.17.2.02

Received: 22 September 2021
Accepted: 19 January 2022
Published: 28 February 2022

Handling editor: Mikhail Son
Thematic editor: Elena Tricarico

Abstract

The dreissenids, quagga mussel *Dreissena bugensis* and zebra mussel *D. polymorpha,* are invasive freshwater mussels in Europe and North America. These species strongly impact aquatic ecosystems, such as the food web through their high abundance and filtration rate. They spread quickly within and between waterbodies, and have the ability to colonize various substrates and depths. The zebra mussel invaded and established in Swiss lakes in the 1960s, whereas the quagga mussel was not detected until 2014. We collected all available data from cantonal as well as local authorities and other institutions to describe the colonization pattern of quagga mussels in perialpine lakes north of the Alps. We also collected data regarding the distribution of larval stages of the mussels, the so-called veliger larvae. We observed that in lakes colonized by the quagga mussel, veligers are present the whole year round, whereas they are absent in winter in lakes with only zebra mussels. Additionally, we present detailed information about the invasion and colonization pattern of quagga mussels in Lake Constance. Quagga mussels colonized the lakeshore within a few years (~ 2016–2018), outcompeted zebra mussels, and have reached densities > 5000 ind. m^{-2} in the littoral zone, even at 80 m densities above 1000 ind. m^{-2} were found at some locations. At the end of the article, we discussed possibilities on how the spread of quagga mussels within and among northern perialpine lakes should be monitored and prevented in the future.

Key words: *Dreissena* density, *Dreissena bugensis*, veliger phenology, monitoring, Lake Constance, invasive species

Introduction

The quagga mussel, *Dreissena bugensis* (also described as *Dreissena rostriformis bugensis,* Andrusov, 1897; Wesselingh et al. 2019), and the zebra mussel *D. polymorpha* (Pallas, 1771) are amongst the most widespread and successful invasive species around the world (Lowe et al. 2000; Nalepa and Schloesser 2014). Originating in the Ponto-Caspian region, dreissenid mussels have colonized lakes and rivers across Europe and North America. In North America, both *Dreissena* species invaded near simultaneously in the late 1980s (Karatayev et al. 2015). In Europe, the zebra mussel invaded in the early 18th century (Bij de Vaate et al. 2002) and can now be found from Finland to Spain (Van der Velde et al. 2010). In contrast, the quagga mussel has only recently begun spreading in Western Europe with the first records from the mid-2000s (Bij de Vaate et al. 2014).

Dreissenids are considered ecosystem engineers because of their strong impacts on benthic habitats and resource availability for benthic and pelagic species (Crooks 2002; Karatayev et al. 2002; Gergs 2009). Dreissenid mussel beds change the substrate structure, which provide more colonization area for gastropods, amphipods and many other benthic taxa, however they have negative impacts on native bivalves through exploitative competition or biofouling (Mörtl and Rothhaupt 2003; Strayer and Malcom 2007, 2018). Their high filtration rate decreases the abundance of phytoplankton (Vanderploeg et al. 2010; Higgins et al. 2011), resulting in cascading effects on nutrient concentrations, water clarity, food competition with zooplankton, and increased macrophyte abundance (Zhu et al. 2006; Kissman et al. 2010; Higgins et al. 2011; Rowe et al. 2017). Dreissenids have positive effects on benthivorous fish in the littoral; however, they have negative effects on planktivorous fish (Higgins and Vander Zanden 2010). Colonies of dreissenids hinder some fishes, for example lake trout, with spawning. Dreissenids in shallow area are predated heavily by waterbirds which contributes to an increase in numbers of overwintering waterbirds and nutrient flows from waterbirds' feeding areas to resting areas (Werner et al. 2005). Furthermore, dreissenid mussels are also a source of major economic impact due to biofouling of water pipes and other infrastructure (Marsden and Lansky 2000; Connelly et al. 2007), damage to recreational and commercial boats, and overall negative effects on fisheries (Oreska and Aldridge 2011; Rudstam et al. 2016).

Quagga and zebra mussels share similar habitat requirements and dispersal ability. However, quagga mussels are typically found in waters where the zebra mussel has previously established. Both species produce planktonic larvae (veligers) that spread passively with prevailing currents (Churchill and Quigley 2018; Olson et al. 2018). Veligers may also be accidentally transported in wet conditions inside and outside boat hulls facilitating upstream and overland dispersal. Not only larvae disperse, as adult mussels can move short distances with their foot and attach to hard surfaces, including boat hulls with the byssal threads (Peyer et al. 2009). Similar to veliger transportation in ballast water, human mediated transport of adult mussels allows upstream and long-distance dispersal (Johnson et al. 2001; Leuven et al. 2009; De Ventura et al. 2016).

The differences in the environmental niche of quagga and zebra mussels suggest that quagga mussels may have larger ecosystem effects than those observed for zebra mussels (Karatayev et al. 2015). Zebra mussels tend to be restricted to shallower (less than 30 m) parts of lakes whereas quagga mussels can colonize much deeper. In North America, quagga mussels have been found at depths down to around 200m (Mills et al. 1993; Nalepa et al. 2014). Quagga mussels can also persist and reproduce at lower water temperatures (Roe and MacIsaac 1997), grow faster, and have a higher assimilation rate (Baldwin et al. 2002; Stoeckmann 2003). These factors combined allow quagga mussels to reproduce earlier and for a longer period of time throughout the year, which adds to the higher competitiveness of quagga mussels compared to zebra mussels (Ram et al. 2012; Marescaux et al. 2015; Hetherington et al. 2019). In some lakes, quagga mussels outcompeted zebra mussels due to various reasons not yet fully understood (Rudstam and Gandino 2020; Karatayev et al. 2021b). Further, a decrease in phytoplankton biomass and change in phytoplankton composition during spring were observed after quagga mussels replaced zebra mussels in Lake Michigan (Fahnenstiel et al. 2010).

A study reported that quagga mussels expanded from shallow to deep regions of a lake (Karatayev et al. 2021b). Thus, we expected perialpine lakes to be colonized first in the shallow, close to where they were first observed. Density and distribution of adult dreissenid mussels within a lake or riverbed may be extremely heterogenous (e.g. Patterson et al. 2005; Burlakova et al. 2006; Nalepa et al. 2010; Karatayev et al. 2014), as a result of multiple environmental factors like heterogenous substrates, hydrodynamics and oxygen concentration (Karatayev et al. 1998, 2018). The patchiness was found to be even higher recently after colonization and decreasing over time (Burlakova et al. 2006). Thus, we expected the distribution to be patchier in deeper areas. For perialpine lakes the patchiness or distribution is still unknown and so is the relation between patchiness and mussel abundance.

Veligers of the quagga mussel are present the whole year round in the water column in Lake Constance (IGKB Limnologischer Zustand des Bodensees 2018), which is in contrast to zebra mussel veligers that are only found in summer (Adrian et al. 2006). Although veligers of both mussel species cannot be differentiated by morphological traits, the sudden presence of veligers in colder months is indicative for quagga mussel's presence. Alternative molecular methods, e.g. environmental DNA, could be used to identify the species.

The invasion status and distribution of quagga mussels in Swiss lakes is not well understood. While there is a Swiss national monitoring program for water quality in surface waters (FOEN 1998, including plankton monitoring) there is no such program for the monitoring and management of invasive dreissenids. In general, cantons (Swiss districts) are responsible to monitor for and act against invasive species. Some local authorities have thus included monitoring for specific aquatic invasive species in their existing water quality monitoring programs, and the existing programs differ in frequency and the extent of monitoring. Moreover, most data have not previously been compiled into a single dataset and are not publicly available. Benthic monitoring is restricted to macrozoobenthos programs in shallow (1–5 meters), littoral regions of some lakes, without any systematic monitoring in deeper parts.

Here we present an overview of the current distribution of quagga mussels in northern perialpine lakes from Switzerland and Lake Constance. In order to better understand the status of the quagga mussel invasion and deduce its future invasion potential in Switzerland, we collated data from Swiss cantonal authorities and private companies to map the presence-absence of quagga mussels in Swiss rivers and lakes. We illustrated the speed of spread of quagga mussels from one or more sources to many important waterbodies in Switzerland. Since quagga mussels are found at greater depth than zebra mussels in North American lakes, we also examined the extend and speed of quagga mussel colonization, both vertically and horizontally, within Lake Constance in more detail. For this lake we expect to find more mussels in shallower areas and in the western part of the lake than in deeper areas and in the eastern part.

Since no monitoring program for quagga mussel has been developed in Switzerland yet, we investigated two patterns, which may be considered for the development of an adequate monitoring program:

a) The different seasonal distribution of quagga and zebra mussel veliger larvae in lakes, may offer the opportunity to detect the start of a quagga mussel invasion through changes of veliger abundances in regular plankton samples. We thus examined recent changes in the phenology and distribution of *Dreissena* veligers in lakes to investigate if veliger distribution is a reliable way to identify the presence of quagga mussels.

b) The patchiness of adult quagga mussels may have serious implications for early detection and monitoring of mussel abundances. We thus evaluated the patchiness and its relation to mussels' abundance in a case study in Lake Constance, expecting to find higher abundances with lower patchy mussel distribution.

With this article, we contribute to the general knowledge of the invasive potential of quagga mussels and provide a background for future monitoring strategies in perialpine lakes.

Table 1. Methods of monitoring *Dreissena* in benthic region.

Lake	Period	Frequency	Sites	Area/m^2	Depth	Sampling method	Source	Notes
Lake Constance	2004–2018	biannual	8–12	0.25	littoral	kicknet	HYDRA, annual LUBW, IGKB reports	semi quantitative sampling
	2010–2019	biannual	> 50		littoral	manual search	HYDRA, LUBW, IGKB reports	qualitative sampling
	2019	once	11	0.0225	littoral and depth down to 80 m	Ekman grab sampler	this study	depth monitoring
Lake Geneva	2009–2018	annual	2	0.3125–0.45	0–20 m	manual search	Kanton Vaud	
Lake Neuchâtel	2016–2017	annual	1	0.3125	0.5–13 m	manual search	Kanton Vaud	

Materials and methods

Dreissena *distribution in perialpine lakes north of the Alps*

We collected data about adult and larval dreissenids from cantonal authorities, environmental consulting companies and research institutes. The different regions of Switzerland survey and monitor quagga mussels in a variety of ways, usually as part of a broader river or lake monitoring program. Typical monitoring strategies fall into three main categories: littoral zone monitoring, plankton sampling and public reporting / citizen science.

Dreissena abundances in the littoral zone are regularly monitored in Lake Constance, Lake Geneva and Lake Neuchâtel by environmental consulting firms and local authorities in the framework of long-term water quality and macrozoobenthos monitoring programs (Table 1). Samples are typically taken at ~ 1 m depth using a combination of kicknet and quadrat sampling supplemented by manual searching. Lake Neuchâtel is sampled at a single site, and Lake Geneva at two sites. While the monitoring program at Lake Constance includes more than 50 stations around the lake (Supplementary material Table S1, http://www.neozoen-bodensee.de). This was possible because the International Commission of Lake Constance Water Conservation initiated a systematic monitoring of invasive invertebrates in the littoral zone around the lake in 2009 (Landesanstalt für Umweltschutz Baden-Württemberg 2005). Littoral samples are stored in ethanol, to facilitate species identification and counting in the laboratory. Littoral zone monitoring programs were initiated e.g. for Lake Geneva around 2010 and for Lake Neuchâtel in 2016, before the arrival of the quagga mussel. In other lakes dreissenid mussels are only monitored by manual searching and visual inspection of sites to confirm their presence in the littoral zone. Table 1 gives details about current monitoring efforts. This data allowed us to summarize presence – absence of quagga mussels as well as year of first discovery for each lake.

Local authorities sample regularly the zoo- and phytoplankton of lakes. In some of these samples also veliger larvae are counted. Although veliger larvae of quagga mussels cannot be discriminated from zebra mussel larvae, these larval samples can still help to identify quagga mussel invasions (see below).

The final source of collated information about the presence of quagga mussels in Swiss waterbodies comes from public reporting. This includes reports by fishermen about quagga mussels attached to their fishing nets, from researchers finding mussels attached to anchors after survey work, and from recreational and professional divers. With all this information, we produce a quagga mussel distribution map across Switzerland.

Veliger abundance and phenology in perialpine lakes north of the Alps

Time series of plankton samples from seven Swiss lakes were analysed to detect changes in abundance and presence of veligers. The resolution and length of each time series differs but are usually biweekly to monthly and began around 2010. Lake Zurich, where quagga mussels have not been found yet, has an exceptional time series dating back to 1982. Since 2018 samples from Lake Zurich are screened for zebra and quagga mussel veligers with a q-PCR taqman assay (target sequence: cytochrome-c-oxidase, subunit I, Table S2) modified by the Water Supply Zurich. Plankton samples in Swiss lakes are collected using nets of various mesh sizes between 41 and 212 µm, again varying by cantons. Historically, these plankton samples have been taken as integrated samples over the entire water column, but more recently, depth specific samples have been collected in some lakes. Usually, samples are preserved in Formalin or Lugol's solution and counted (ind.m^{-3}) under a (stereo) microscope. In addition to cantonal efforts, water providers have recently begun sampling plankton from their raw water inlet pipes specifically to detect the presence of veligers. Table 2 provides an overview of current veliger monitoring programs in Switzerland. For the seven lakes for which data about veliger larvae densities through time exists, we analysed the data using a generalized linear mixed model with year and lake interaction and site as random effect. We plotted for each year the number of months veliger larvae were observed, with the goal to investigate if veliger larvae appear earlier in the year in lakes where quagga mussels have been found (further details about the lake specific sampling is in the Supplementary material Appendix 1).

Lake Constance sampling – semi-quantitative littoral Dreissena *sampling*

The semi-quantitative sampling of Lake Constance was conducted by HYDRA AG (Germany) at 12 fixed sampling locations throughout the lake in the autumn of 2016–2019 as well as in the Rhine (after the outflow of Lower Lake Constance, Table S1). The total number of dreissenid mussels was determined for each site as well as the proportion quagga and zebra mussels (further details about the sampling is in the Appendix 1).

Table 2. Methods of monitoring *Dreissena* veligers in plankton samples.

Lake	Period	Frequency	Site	Depth (m)	Mesh size (μm)	Source	Notes
Lake Constance	2010–2019	biweekly	deepest (251m)	0–100	55	LUBW, IGKB reports	integrated sample
	2019	biweekly	deepest (251m)	0–200	55	LUBW, IGKB reports	depth profile
	2014–2019	weekly or biweekly	Sipplingen	60	41	Bodensee Wasserversorgung	inlet pipe
Lake Geneva	2006–2019	biweekly	deepest (309m)	0–50	64 or 212	OLA	
	2019–2020	monthly	St. Sulpice	50	41	Service de l'eau, Lausanne	inlet pipe
		monthly	Lutry	60	41	Service de l'eau, Lausanne	inlet pipe
Lake Neuchâtel	2001–2019	monthly	deepest (153m)	0–140	95	Kanton Neuchâtel	
Lake Biel	1999–2019	monthly	deepest (74m)	0–70	95	Kanton Bern	
Lake Thun	1999–2019	monthly	deepest (217m)	0–100	95	Kanton Bern	no evidence of quagga mussel
Lake Murten	2001–2019	monthly	deepest (45m)	0–40	95	Kanton Fribourg	
Lake Zurich	1982–2019	biweekly or monthly	Obersee Lachen	0–30	45	Water Supply Zurich	no evidence of quagga mussel
	1982–2019	biweekly or monthly	Lake Zurich, Thalwil	0–30	45	Water Supply Zurich	no evidence of quagga mussel
	1998–2020	monthly	Seewasserwerk Moos	30	95–100	Water Supply Zurich	inlet pipe
	1988–2020	monthly	Seewasserwerk Lengg	30	95–100	Water Supply Zurich	inlet pipe

*LUBW, State Institute for Environment Baden-Württemberg (LUBW, Landesanstalt für Umwelt Baden-Württemberg); *IGKB, International Commission for the Protection of Lake Constance (Internationale Gewässerschutzkommission für den Bodensee, IGKB); *OLA LAcs Observatory (OLA), Lake Geneva.

Lake Constance – depth Dreissena *sampling*

Sites close to the ones from the semi-quantitative littoral monitoring were also used to assess the distribution pattern in Lake Constance and its three different lake basins (Table S1). Samples were collected in August 2019 on 11 sites: 3 in Lower Lake Constance, 3 in Lake Überlingen and 5 in Upper Lake Constance (Table S1 and Figure S1). At each site we surveyed two transects approximately 500 m apart. The transects included three replicate Ekman grab samples (grab area 0.0225 m^2, Hydro-Bios, Germany) at 30 m, 60 m, and 80 m depth. In Lower Lake Constance, where it is much shallower, samples were taken at 10 m, and at the maximum depth at each site (20 or 45 m). We sieved the samples through a 2 mm sieve (Retsch, Germany) and live *Dreissena* were retained and preserved on site in 70% ethanol. Samples were later morphologically identified to species level (*D. polymorpha* or *D. bugensis)* and counted by HYDRA AG. We calculated site-specific mussel densities (per m^2) as the average number of mussels per species in each grab sample across both transects.

Quagga mussel density was analysed in detail at 7 stations in order to understand the vertical and horizontal colonization of Lake Constance. We excluded from analysis the Lower Lake Constance and the station "Wallhausen", because Lower Lake Constance is shallower compared to the rest of Lake Constance. In Wallhausen lake depth increases very fast

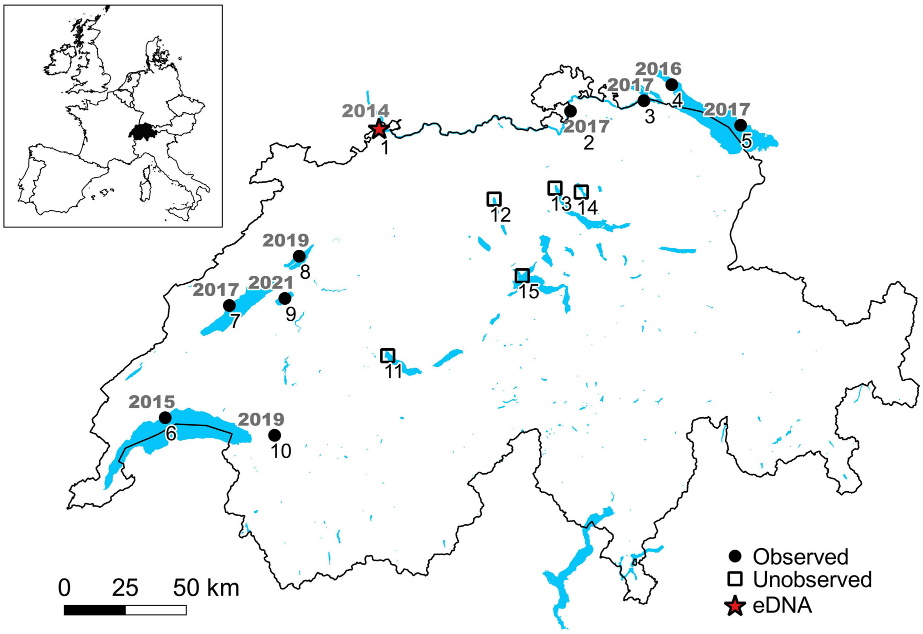

Figure 1. Current confirmed distribution of quagga mussels in Swiss lakes (filled points) and lakes where no quagga mussels could be found (empty squares). Years adjacent to symbols indicate the year of first discovery. Lakes without symbols have not been surveyed (Map: Swiss Federal Office of Topography). Numbers indicate lakes and sampling locations: 1: Rhine, Basel; 2: Rhine, Rheinau; 3: Lower Lake Constance, Stein am Rhein; 4: Lake Überlingen, Wallhausen; 5: Upper Lake Constance, Langenargen; 6: Lake Geneva; 7: Lake Neuchâtel; 8: Lake Biel; 9: Lake Murten; 10: Lake Hongrin; 11: Lake Thun; 12: Lake Hallwil; 13: Lake Zurich, Limmat; 14: Lake Greifen; 15: Lake Luzern.

from 5 m to 90 m along a cliff that cannot be sampled with a grabber. Mussel counts were analysed using zero inflated generalized linear models and a negative binomial distribution with depth as explanatory variable and site as random effect.

We also analysed quagga mussel patchiness, which is expected to be decreased with time since colonization. Therefore, we expected to find more variation in mussel densities in deep than shallow. Patchiness was calculated as the coefficient of variation (CV = standard deviation/mean), which is a measurement of variation of the quagga mussel abundance across three replicates per site and depth. We used a generalized linear model with a gaussian distribution to analyse the effect of depth on CV, with site as a random effect. Lake basin was dropped from the final model as no effect was observed. Differences associated with depth were confirmed using a Tukey Post Hoc test. We analysed if CV has an effect on mussel counts in a generalized linear model with a negative binomial distribution to account for overdispersion with site as random factor.

All statistical analyses were done using R (v3.5.2) (R Core Team 2018).

Results

Dreissena *distribution in perialpine lakes North of the Alps*

Figure 1 shows the current distribution of quagga mussels in Swiss lakes. First evidence of quagga mussels in Swiss waterways came from eDNA in the Rhine in Basel in 2014, although adults were not observed (De Ventura et al. 2017). In the following years quagga adults were found in Lake Geneva (2015), Lake Constance (2016), Lake Neuchâtel (2017), and more recently in Lake Hongrin (2019), Lake Biel (2019) and Lake Murten (2021). Quagga mussels were not found in Lake Greifen, Lake Thun, Lake Lucern, Lake Baldegg or Lake Zurich (status 03.2020). Many Swiss lakes are yet to be surveyed for quagga mussels.

Changes in veliger abundance and phenology

Compared to the period prior to the discovery of quagga mussels in Swiss lakes commencing in 2015, the number of months during which veligers can be found in plankton samples has increased in some lakes (glmm, year × lake interaction $F_{1,6} = 282.943$, $p < 0.0001$, Figures 2, 3). This is particularly evident in Lake Biel, Lake Constance, Lake Neuchâtel and Lake Geneva where veligers are now present for most of the year (Figure 2). In lakes where quagga mussels have not been found yet (e.g. Lake Zurich), this increase has not been observed (Figure 2). Furthermore, samples collected from the inlet pipes of water providers also show a recent increase in the abundance of veligers in lakes where quagga mussels are known to be present (Figure S2).

Lake Constance-semi-quantitative littoral Dreissena *sampling*

Figure 4 shows the change in distribution of quagga mussels in Lake Constance since 2016. After the first observation of quagga mussels in Lake Constance on 4 May 2016 by Patrick Steinmann in the western part of the lake (47°45′0.173″N; 9°7′51.982″E Lake Überlingen, Figure 4) quagga mussels spread very rapidly. By autumn 2016 they were found in Langenargen and at the eastern edge of the lake. During 2017 the quagga mussel colonized the entire lake including the Lower Lake Constance (Figure 4). While colonizing the lake, the quagga mussel almost entirely displaced the zebra mussel (Figure 5) in less than three years in most parts of the littoral zone.

Lake Constance-depth Dreissena *sampling*

Quagga mussels also colonized deeper parts of Lake Constance (Figure 6). Mussel densities often exceeded 5000 ind. m^{-2} in samples in 30 m depth (0–37’867 ind. m^{-2}) but were less abundant at deeper sites (0–8001 ind. m^{-2}, $\chi^2(2) = 107.06$, $p < 0.005$). One exception to this pattern was Wallhausen in Lake Überlingen (Figure 6h) which is an exceptional site due to a steep drop off which creates a cliff from 5 m to 90 m. Quagga mussel density did not differ between Upper Lake Constance (Figure 6a–e) and Lake Überlingen (Figure 6f–h, $\chi^2(1) = 0.09$, non-significant). In Lower Lake Constance (Figure 6i–k) we did not find high mussel densities deeper than 10 m.

The distribution of mussels is patchier at 60 m than at 30 m ($b = 0.64$, $t_7 = 2.47$, $p \leq 0.05$), but patchiness remains similar at 80 m and 30 m ($b = 0.44$,

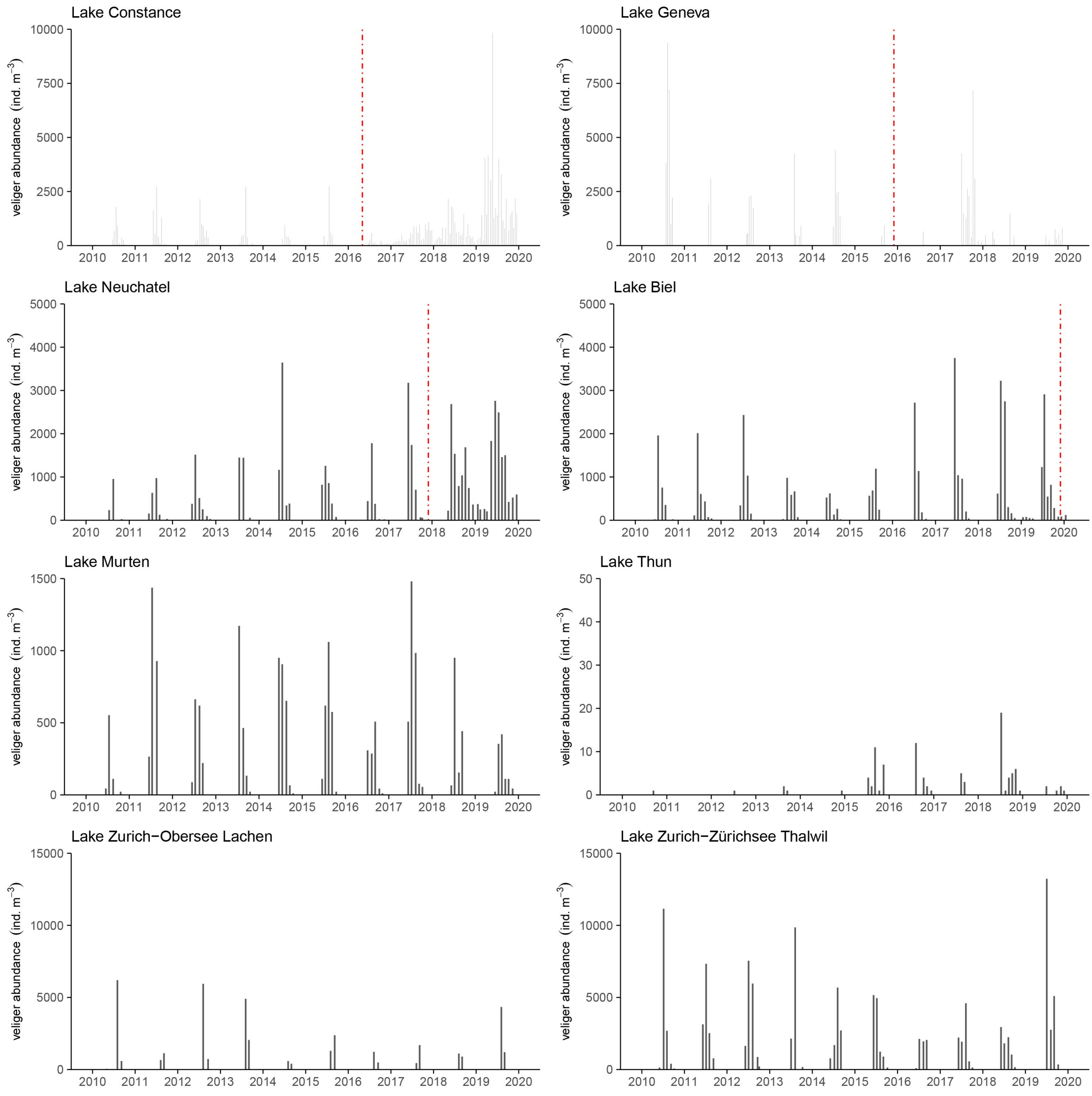

Figure 2. The seasonal distribution of *Dreissena* veligers in plankton samples in Swiss lakes. The dashed red line indicates the first record of adult quagga mussels for each lake. Note the different Y-axis scales; especially in Lake Thun veliger densities are very low.

t_7 = 1.37, non-significant). The coefficient of variation was higher at 60 m than at 30 m (Figure 6l) but did not differ between sites ($\chi^2(6)$ = 8.01, non-significant). In addition, the patchiness increased with lower mussel abundance (Figure S3, $b = -3.67$, $z = -5.88$, $p < 0.005$).

Discussion

Current status and speed of spread

The quagga mussel has invaded lakes and rivers in Europe and North America in the past 50 years. In Western Europe quagga mussels made their way up the Rhine as far as Karlsruhe by around 2006 (Heiler et al. 2013), but yet were not discovered in Lake Constance until early 2016.

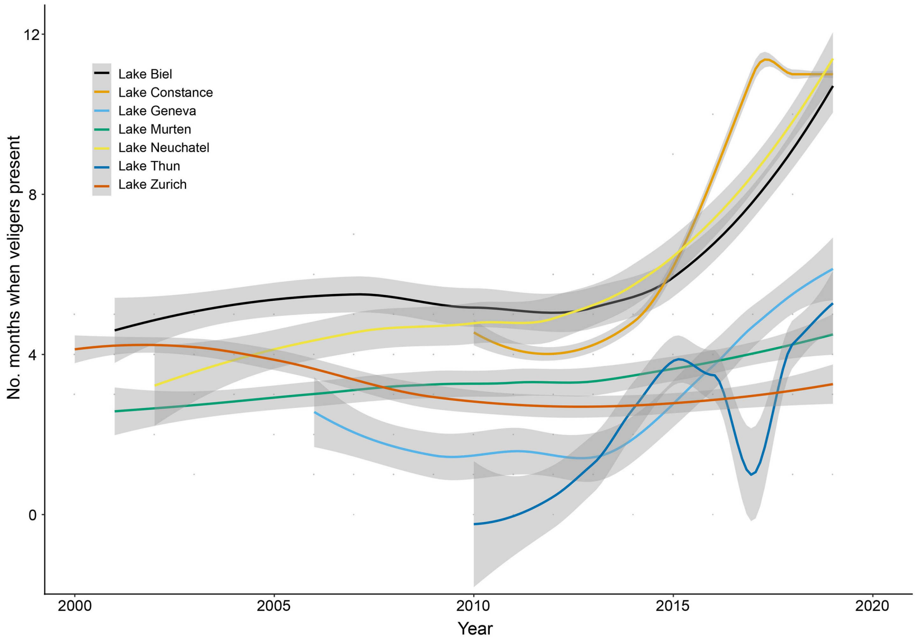

Figure 3. The number of months in each year that *Dreissena* veligers are observed in plankton samples, lines are Loess fits.

At around the same time quagga mussels were first found in Lake Geneva (2015) and soon after in other Swiss lakes (Figure 1). Given that, these lakes are often not connected via downstream water flow we must assume that human factors have been the main cause of this fast spread. One of the most likely factors is overland dispersal via recreational boat transport. De Ventura et al. (2016) interviewed boat owners in Switzerland and could distinguish main boat transport routes in Switzerland. Recently colonized lakes were identified as lakes with frequent boat transports. Comparable studies have been done in invaded lakes in the United States (Johnson et al. 2001), where the dynamics of quagga mussels colonization are similar (Mills et al. 1993; Karatayev et al. 2015). If private boats are the principal route of quagga mussels introductions, quagga mussels will spread if no measures, such as obligatory boat cleaning and information campaigns for boat owners, are taken. Although our data also shows that quagga mussels are not yet present in all Swiss lakes (Figure 1), the present pattern is very worrying and we must assume that quagga mussels will colonize more Swiss lakes in the near future especially those identified as hub lakes in De Ventura et al. (2016).

Only Lake Constance has been studied in sufficient detail to reconstruct the invasion pattern and spread of the quagga mussel within the lake. It took several years for quagga mussels to colonize Lake Constance after the first finding in the Rhine in Karlsruhe 2006 (Martens et al. 2009) and in Basel 2014 (De Ventura et al. 2017). Our analysis of the 2016–2019 dataset shows that within one year quagga mussels had spread from east to west, almost 50 kilometres (Figures 4, 5). Even more astonishing was the quick replacement of zebra mussels by quagga mussels in the littoral zone of Lake Constance. The replacement of zebra mussels by quagga mussels has also

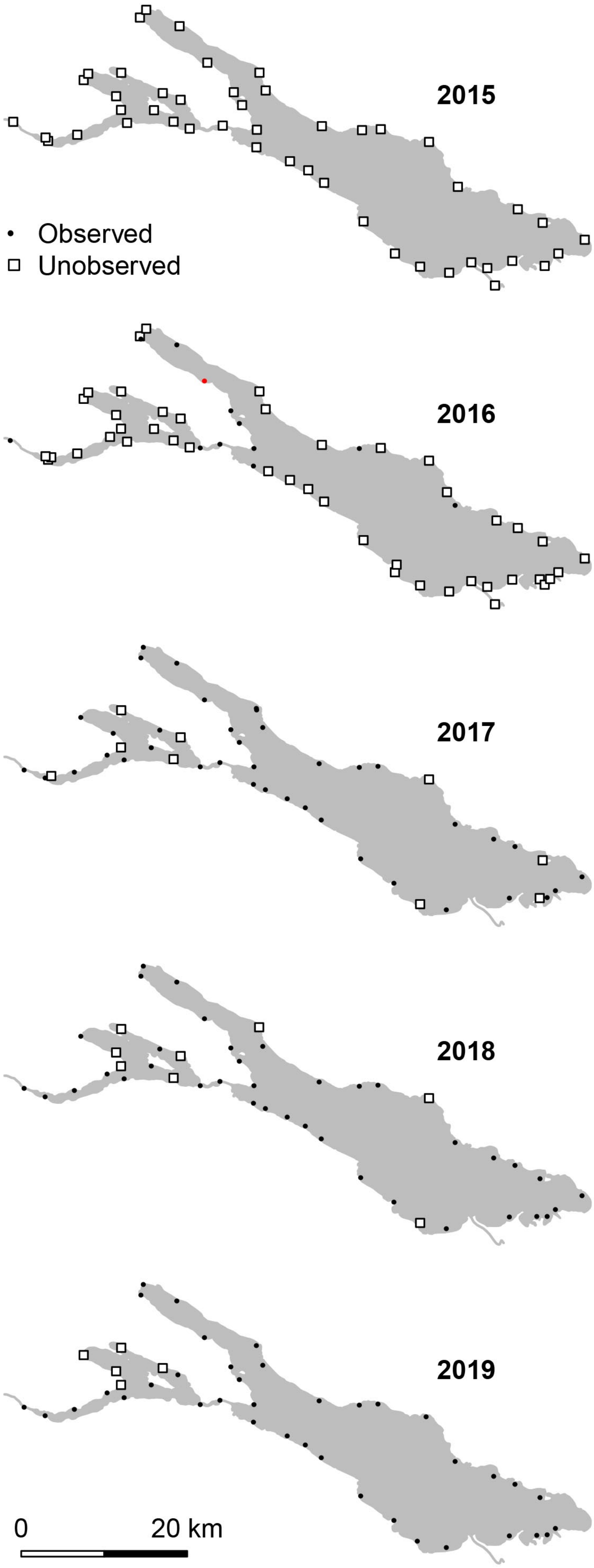

Figure 4. Distribution of quagga mussels (presence or absence) in Lake Constance since 2015 until 2019. In 2016 the station of first detection (Lake Überlingen, Wallhausen) is marked in red.

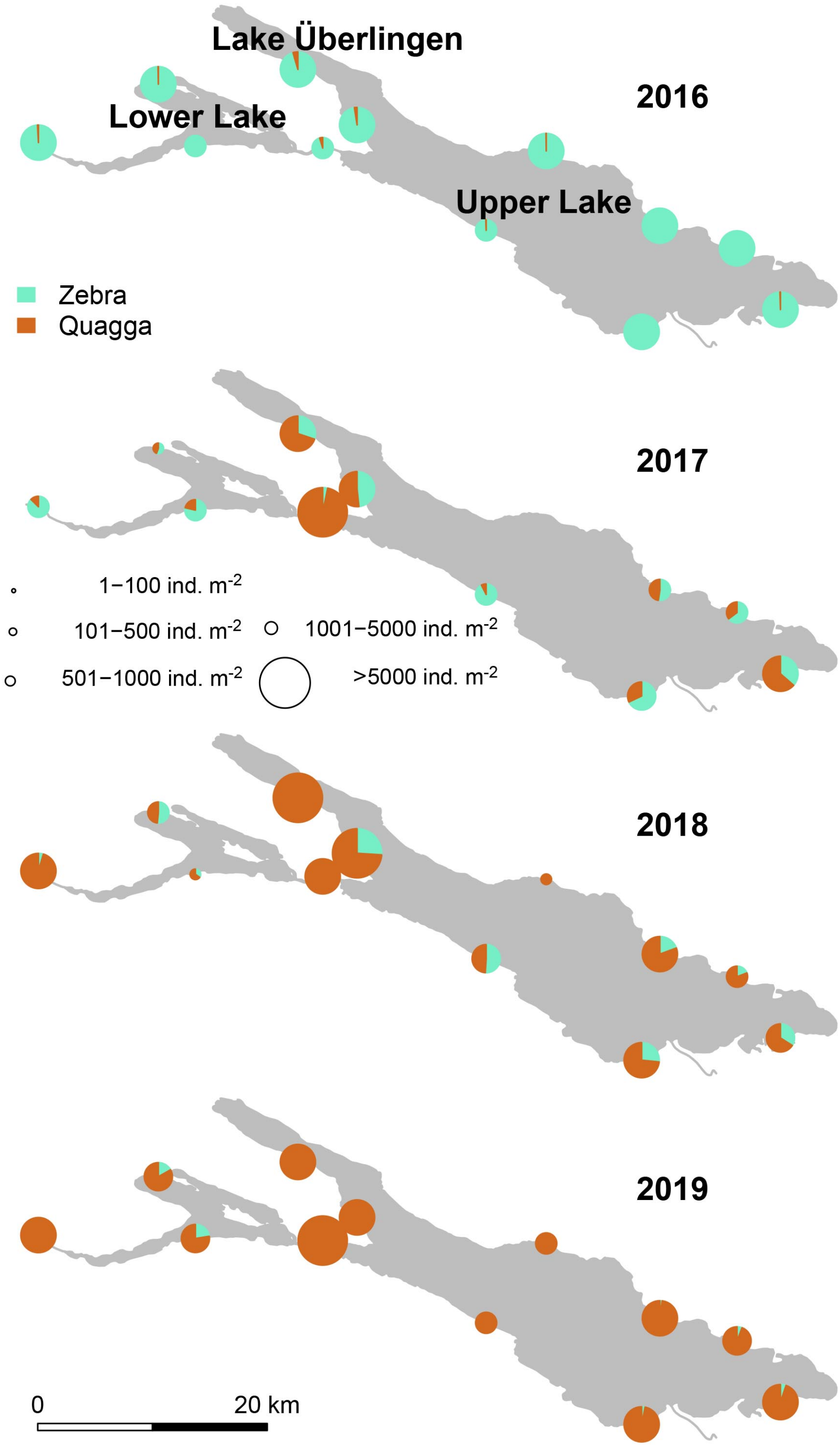

Figure 5. Quantitative estimates of the relative abundance of quagga (brown) and zebra (green) mussels in Lake Constance. The size of the pie chart represents the number of mussels found per square meter at each sampling site.

been observed in several North American lakes. Most of these lakes are larger and have other lake characteristics, replacement times are difficult to compare, it ranged from 4 to 13 years for quagga mussels to replace zebra mussels (Karatayev et al. 2015, 2021b). It is assumed that quagga outcompetes

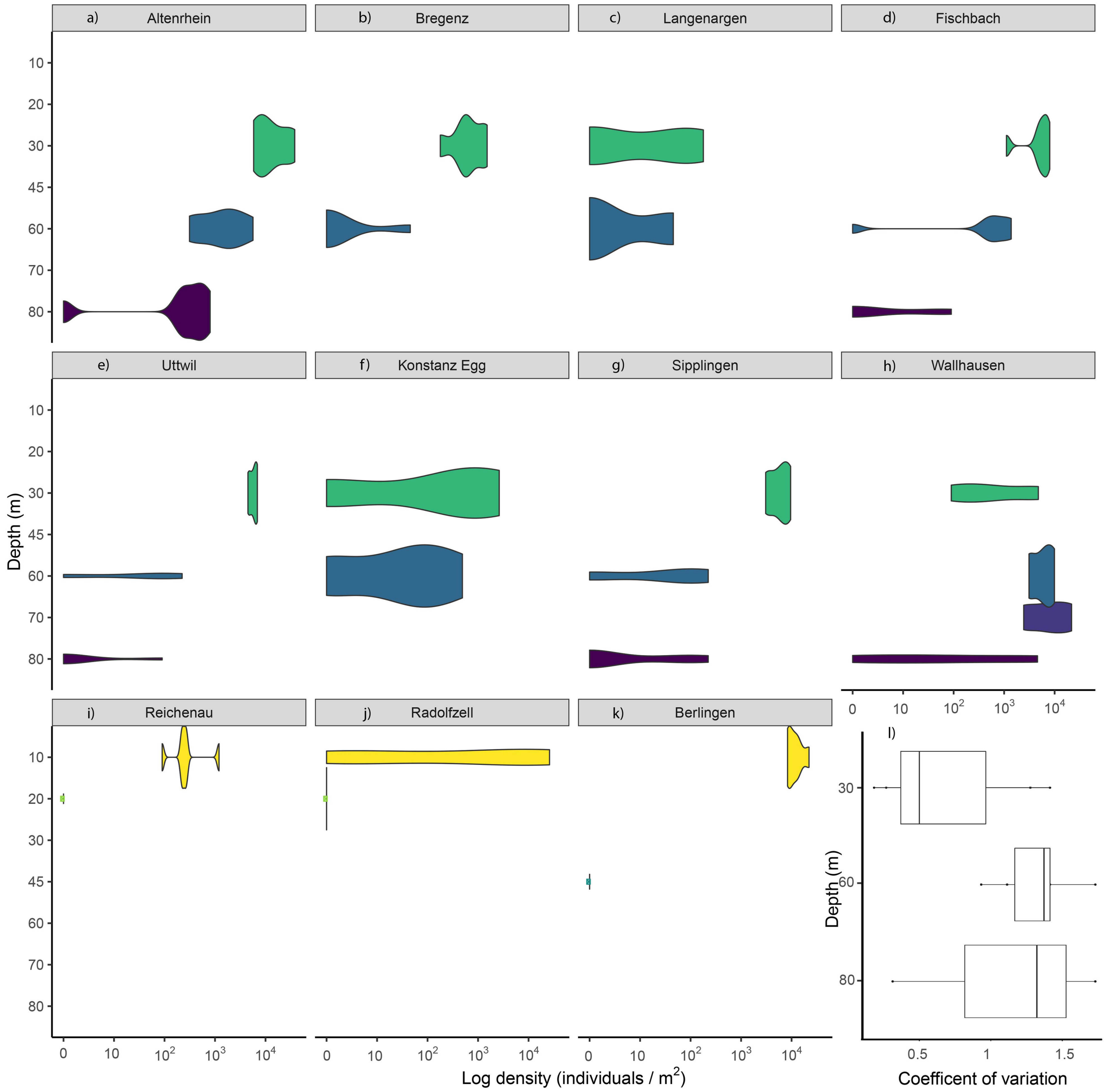

Figure 6. Quagga mussel densities (on log scale) over depth at 11 sites around Lake Constance. Quagga mussels were more abundant at 30m than at deeper depths in Upper Lake Constance (panels a–e) and in Lake Überlingen (f–h). In Lower Lake Constance quagga mussel was rarely found deeper than 10 m (i–k). Colours get darker as depth increases. Variability between samples (coefficient of variation) increased with increasing depth (l).

zebra mussels because they have a longer reproductive season, can live on softer substrate than the zebra mussel and are more efficient suspension feeders (reviewed in Karatayev et al. 2015).

Prior to this study, the macrozoobenthos of any Swiss lakes have not been examined systematically any deeper than the littoral zone. Our data of Lake Constance, shows that quagga mussels have colonized the lake to at least the deepest sampling points (> 80 m depth). However, anecdotal data (anchoring ropes, sediment sample campaigns) show that quagga mussels can be found up to the maximum depth at 251 m. This is again consistent with the pattern in North America where quagga mussels can be found in lakes at all depths at high densities. A prime example is Lake Michigan which is 100 times larger than Lake Constance, where quagga mussels dominate the sediments of the whole lake at all depth (Nalepa et al. 2020) and have changed the ecosystem significantly (mussels density reach 2,700 ind.m^{-2} in depth > 90 m) (e.g. Rowe et al. 2017). Baldwin et al. (2002) suggested that quagga mussel might grow better than zebra mussels in lakes where food levels are naturally low, which would support our observations in Lake Constance considered as an oligotrophic lake. Furthermore, a recent study of Karatayev et al. (2021b) analysing all published studies on quagga mussel invasions in the Great Lakes suggests that colonization speed and ecosystem-effects as observed in North America could be expected in Swiss lakes as well. Therefore, we expect that the increasing quagga mussel population in Lake Constance further will impact the ecosystem. However, future work (including size structures and growth rates to follow detailed population fluctuations) is required to validate these assumptions with more detailed quagga mussel distribution data from other Swiss lakes.

Monitoring quagga mussels within and among lakes

Monitoring of adult quagga mussel populations is a complex problem, and multiple approaches have been employed, each of which faces some limitation. Kick nets and snorkelling sample only a very small portion of the lake perimeter, the littoral zone (0–5 m), and grab samples in deeper water can easily miss colonies of mussels due to their patchy distribution. Our results imply that sites with lower mussel abundance the distribution is patchier, which would be true in a very recent invasion. Reliable estimates of mussel presence and density at those sites require that the sampling effort be increased. While dredges/sledges are effective sampling devices even at sites with a patchy mussel distribution, they are however particularly destructive of benthic habitats. Video analysis is an attractive non-destructive alternative which can handle the heterogenous mussel distribution but cannot detect mussels covered in soft sediment and is limited in turbid water (Karatayev et al. 2018, 2021a; Wick et al. 2020). Further, if physical samples are also required (e.g. for morphological or genetic studies), traditional sampling techniques are still needed in addition to video. Therefore, a combination of video and grab samples as recently shown for Lake Erie (Karatayev et al. 2021a) seems to be a suitable method to monitor the spread of quagga mussels in deep lakes like Lake Constance and Lake Geneva. Although this method is useful to follow the spread and speed of an invasion within a lake, it is not suitable to detect the first occurrence of quagga mussels in a lake.

A promising alternative to surveying and sampling adults is to target the dispersing larvae (veligers) in the water column. The advantage of veliger sampling is that a very large volume can be examined using a plankton trawl, which can even be combined with regular plankton sampling. For the comparison of distribution and patterns among lakes, it is less important that sampling methods (e.g. plankton net size) are identical across lakes, as long as methods stay the same within a lake over time. Manual identification and counting of veligers requires resources and expertise, moreover zebra and quagga mussel larvae still cannot be distinguished by morphological traits. With molecular detection using PCR or qPCR the identification is possible however (e.g. Frischer et al. 2002, Water Supply Zurich, Table S2). *Dreissena* veligers have previously been detected using specific primers in concentrated plankton samples, Frischer et al. (2002) could detect a single zebra mussel veliger in 67 m^3 of water. Moreover, De Ventura et al. (2017) and Blackman et al. (2020b) detected quagga mussels, veligers as well as adults, in water samples using eDNA. Species specific primers for quagga mussel have been developed and are used in flowing waters, where they outperform standard techniques (Blackman et al. 2020a, b). Indeed, the Water Supply Zurich has its routine using molecular tools for this purpose (Table S2) with negative results up to now in Lake Zurich. A criticism of molecular detection methods for *Dreissena* veligers is that there is little correlation between the number of veligers and the size of the adult population (Strayer et al. 2019). For early or rapid detection purposes we do not consider this to be problematic. Regardless of the size of the breeding population, the presence of veligers confirms that adults are established and reproducing.

In addition, when molecular methods are not available, veliger larvae sampling can still give information about the presence of quagga mussels in a lake as our study shows. The distribution of veliger larvae in plankton samples through the year (Figure 2 and Figure S2) gives information about the possible presence of quagga mussels. The presence of veliger larvae in late autumn, winter, or early spring is a strong indication for the colonization of a lake by quagga mussels and was significantly correlated (Figure 3).

Outlook: The need for a coordinated approach

This study clearly shows that quagga mussels have the potential to become established at high densities in perialpine lakes throughout north of the Alps. Given the potential effects on ecosystems and their services, a coherent monitoring and management strategy is urgently needed to better describe and control its distribution and spread with the aim to prevent colonization of lakes as long as possible. While monitoring of plankton can in some cases be used to track quagga mussel invasion (via the veligers) as described here, in other lakes this monitoring needs to be initiated and will require additional resources and potentially training. However, it is clear that when larvae are observed during colder months, quagga mussels have invaded a lake with significant densities.

At the scale of Switzerland, the present ad hoc nature of lake monitoring does not allow a full understanding of the dynamics of quagga mussel invasions or for the preparation of mitigation strategies to protect ecosystems and infrastructures. Another challenge is the fact that Switzerland shares large lakes with its neighbours (e.g. Lake Constance with Austria and Germany, Lake Geneva with France and Lake Maggiore with Italy). A coordinated national and international program monitoring quagga mussels would help to provide the needed information and make international management possible. In Lake Constance this international quagga mussel research started some years ago within the project SeeWandel (www.seewandel.org).

A promising avenue that could reduce the amount of resources and/or training required to detect quagga mussel veligers would be to analyse plankton samples directly with molecular methods for the presence of quagga mussels. We have seen (Figure 2) that quagga mussel veligers are present in the water column during most months of the year, whereas veligers of zebra mussel are present only in the warmer months. The presence of only quagga mussel veligers in colder months could be leveraged by annual sampling of lakes in winter. If veligers are found, it would be a strong indicator of the presence of an established breeding population of adults.

However, while monitoring veliger larvae is a good method to see if quagga mussels have invaded a lake, a detailed monitoring strategy is also needed for larger and deeper lakes. Until now, we do not know if the quagga mussel will spread in perialpine lakes at the same speed and with the same intensity as in the Great Lakes. We propose a combination of video and grab sampling, as Karatayev et al. (2021a) did in Lake Erie, to monitor the spread of quagga mussels within lakes such as Lake Constance and Lake Geneva to make better predictions of the ecosystem consequences. Furthermore, the ecosystems' own biotic resistance provided by diverse communities and the abiotic heterogeneity will lighten the impact of quagga mussel invasions on ecosystem stability (Carlsson et al. 2011; Ricciardi et al. 2013).

To limit the spread of quagga mussels, it is required to identify dispersal pathways and take action to reduce the likelihood of introduction. Such actions include informing the public about risks of mussel invasion, mandatory cleaning of watercraft and control measures. It would be most successful if such measurements were coordinated across cantons and countries. Preventions of invasions will be most helpful from both ecological and economic perspectives. Therefore, we think an important research topic is the strengthening of native ecosystems against invasive species. Diversification of habitats and strengthening of local species and populations might help to slow down or prevent the success of invasive species. Further research as well as coordinated monitoring strategies will be necessary to determine if management interventions can be effective for limiting the spread of quagga mussels and other invasive species in perialpine lakes.

Acknowledgements

We thank Vinzenz Maurer, AWA Bern and Heidi Berner, Lenzburg for veliger data of Lakes Neuchâtel, Biel, Thun and Murten. Veliger data for Lake Geneva was provided by OLA (Observatory on LAkes), © OLA-IS, AnaEE-France, INRAE Thonon-les-Bains, CIPEL for IS OLA Data, https://doi.org/10.15454/VBWYWG. The data about quagga mussel presence in Lake Murten was provided by Ivan Leo (IB-Murten). We thank two anonymous reviewers for their thorough and insightful comments.

Funding declaration

This work was supported in part by the grant "SeeWandel: Life in Lake Constance – the past, present and future" within the framework of the Interreg V programme "Alpenrhein-Bodensee-Hochrhein (Germany / Austria / Switzerland / Liechtenstein)" which funds are provided by the European Regional Development Fund as well as the Swiss Confederation and cantons. The work received further financial support from Eawag (Eawag Discretionary Funds 2018-2022). Hui Zhang received funding from the China Scholarship Council. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Authors' contribution

LH, SRD and PS devised the main conceptual ideas and proof outline. LH and SRD designed the details of the study. LH, OA, SR, JH, MK, RS, BS, PTS, MZ collected and provided the data for this study. LH, HZ, SRD and JTDW analysed the data and produced the figures. LH, HZ and SRD interpreted the results. LH, HZ, SRD wrote the original draft with help of PS. All authors commented and approved the final draft.

Data repository

All raw data underlying this article is available under following DOI: https://doi.org/10.25678/00052E

References

Adrian R, Wilhelm S, Gerten D (2006) Life-history traits of lake plankton species may govern their phenological response to climate warming. *Global Change Biology* 12: 652–661, https://doi.org/10.1111/j.1365-2486.2006.01125.x

Baldwin BS, Mayer MS, Dayton J, Pau N, Mendilla J, Sullivan M, Moore A, Ma A, Mills EL (2002) Comparative growth and feeding in zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*): Implications for North American lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 680–694, https://doi.org/10.1139/f02-043

Bij de Vaate A, Jazdzewski K, Ketelaars HA, Gollasch S, Velde G Van der (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1159–1174, https://doi.org/10.1139/f02-098

Bij de Vaate A, Velde G Van der, Leuven RSWE, Heiler KCM (2014) Spread of the Quagga Mussel (*Dreissena rostriformis bugensis*) in Western Europe. In: Nalepa TF, Schloesser D (eds), Quagga and Zebra Mussels: Biology, Impact and Control. 2 ed. CRC Press, Taylor & Francis Group, Boca Raton, London, New York, pp 83–92, https://doi.org/10.1201/b15437-11

Blackman RC, Benucci M, Donnelly RC, Hänfling B, Harper LR, Sellers GS, Handley LL (2020a) Simple, sensitive and species-specific assays for detecting quagga and zebra mussels (*Dreissena rostriformis bugensis* and *D. polymorpha*) using environmental DNA. *Management of Biological Invasions* 11: 218–236, https://doi.org/10.3391/mbi.2020.11.2.04

Blackman RC, Ling KKS, Harper LR, Shum P, Hänfling B, Lawson-Handley L (2020b) Environmental DNA consistently outperforms established methods for detection of quagga mussels, *Dreissena rostriformis bugensis* in flowing water. *Ecology and Evolution* 10: 13248–13259, https://doi.org/10.1101/2020.01.07.890731

Burlakova LE, Karatayev AY, Padilla DK (2006) Changes in the distribution and abundance of *Dreissena polymorpha* within lakes through time. *Hydrobiologia* 571: 133–146, https://doi.org/10.1007/s10750-006-0234-9

Carlsson NOL, Bustamante H, Strayer DL, Pace ML (2011) Biotic resistance on the increase: Native predators structure invasive zebra mussel populations. *Freshwater Biology* 56: 1630–1637, https://doi.org/10.1111/j.1365-2427.2011.02602.x

Churchill CJ, Quigley DP (2018) Downstream dispersal of zebra mussels (*Dreissena polymorpha*) under different flow conditions in a coupled lake-stream ecosystem. *Biological Invasions* 20: 1113–1127, https://doi.org/10.1007/s10530-017-1613-z

Connelly NA, O'Neill CR, Knuth BA, Brown TL (2007) Economic impacts of zebra mussels on drinking water treatment and electric power generation facilities. *Environmental Management* 40: 105–112, https://doi.org/10.1007/s00267-006-0296-5

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97: 153–166, https://doi.org/10.1034/j.1600-0706.2002.970201.x

De Ventura L, Weissert N, Tobias R, Kopp K, Jokela J (2016) Overland transport of recreational boats as a spreading vector of zebra mussel *Dreissena polymorpha*. *Biological Invasions* 18: 1451–1466, https://doi.org/10.1007/s10530-016-1094-5

De Ventura L, Kopp K, Seppälä K, Jokela J (2017) Tracing the quagga mussel invasion along the Rhine river system using eDNA markers: early detection and surveillance of invasive zebra and quagga mussels. *Management of Biological Invasions* 8: 101–112, https://doi.org/10.3391/mbi.2017.8.1.10

Fahnenstiel G, Pothoven S, Vanderploeg H, Klarer D, Nalepa T, Scavia D (2010) Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. *Journal of Great Lakes Research* 36: 20–29, https://doi.org/10.1016/j.jglr.2010.03.009

FOEN (1998) Federal Office for the Environment - Waters Protection Ordiance https://www.admin.ch/opc/en/classified-compilation/19983281/index.html#app2 (accessed 23 September 2021)

Frischer ME, Hansen AS, Wyllie JA, Wimbush J, Murray J, Nierzwicki-Bauer SA (2002) Specific amplification of the 18S rRNA gene as a method to detect zebra mussel (*Dreissena polymorpha*) larvae in plankton samples. *Hydrobiologia* 487: 33–44, https://doi.org/10.1023/A:1022971918673

Gergs R (2009) *Dreissena polymorpha* in Lake Constance: An example of a keystone engineer? University of Konstanz, 118 pp

Heiler KCM, Bij de Vaate A, Ekschmitt K, Oheimb PV von, Albrecht C, Wilke T (2013) Reconstruction of the early invasion history of the quagga mussel (*Dreissena rostriformis bugensis*) in Western Europe. *Aquatic Invasions* 8: 53–57, https://doi.org/10.3391/ai.2013.8.1.06

Hetherington AL, Rudstam LG, Schneider RL, Holeck KT, Hotaling CW, Cooper JE, Jackson JR (2019) Invader invaded: population dynamics of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) in polymictic Oneida Lake, NY, USA (1992-2013). *Biological Invasions* 21: 1529–1544, https://doi.org/10.1007/s10530-019-01914-0

Higgins SN, Vander Zanden MJ (2010) What a difference a species makes a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs* 80: 179–196, https://doi.org/10.1890/09-1249.1

Higgins SN, Vander Zanden MJ, Joppa LN, Vadeboncoeur Y (2011) The effect of dreissenid invasions on chlorophyll and the chlorophyll: total phosphorus ratio in north-temperate lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 319–329, https://doi.org/10.1139/F10-134

IGKB Limnologischer Zustand Des Bodensees (2018) Jahresbericht 2016/2017 Nr. 42. https://www.igkb.org/oeffentlichkeitsarbeit/limnologischer-zustand-des-sees-gruene-berichte/

Johnson LE, Ricciardi A, Carlton JT, Applications E, Dec N (2001) Overland dispersal of aquatic invasive apecies: a risk assessment of transient recreational boating. *Ecological Applications* 11: 1789–1799, https://doi.org/10.1890/1051-0761(2001)011[1789:ODOAIS]2.0.CO;2

Karatayev A, Burlakova ILE, Padilla DK (1998) Physical factors that limit the distribution and abundance of *Dreissena polymorpha* (Pall.). *Journal of Shellfish Research* 17(4): 1219–1235

Karatayev AY, Burlakova LE, Padilla DK (2002) Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. In: Leppäkoski E, Gollasch S, Olenin S (eds), Invasive Aquatic Species of Europe. Distribution, Impacts and Management. Springer, pp 433–446, https://doi.org/10.1007/978-94-015-9956-6_43

Karatayev AY, Burlakova LE, Pennuto C, Ciborowski J, Karatayev VA, Juette P, Clapsadl M (2014) Twenty five years of changes in *Dreissena* spp. populations in Lake Erie. *Journal of Great Lakes Research* 40: 550–559, https://doi.org/10.1016/j.jglr.2014.04.010

Karatayev AY, Burlakova LE, Padilla DK (2015) Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. *Hydrobiologia* 746: 97–112, https://doi.org/10.1007/s10750-014-1901-x

Karatayev AY, Mehler K, Burlakova LE, Hinchey EK, Warren GJ (2018) Benthic video image analysis facilitates monitoring of *Dreissena* populations across spatial scales. *Journal of Great Lakes Research* 44: 629–638, https://doi.org/10.1016/j.jglr.2018.05.003

Karatayev AY, Burlakova LE, Mehler K, Hinchey EK, Wick M, Bakowska M, Mrozinska N (2021a) Rapid assessment of *Dreissena* population in Lake Erie using underwater videography. *Hydrobiologia* 848: 2421–2436, https://doi.org/10.1007/s10750-020-04481-x

Karatayev AY, Karatayev VA, Burlakova LE, Mehler K, Rowe MD, Elgin AK, Nalepa TF (2021b) Lake morphometry determines *Dreissena* invasion dynamics. *Biological Invasions* 23: 2489–2514, https://doi.org/10.1007/s10530-021-02518-3

Kissman CEH, Knoll LB, Sarnelle O (2010) Dreissenid mussels (*Dreissena polymorpha* and *Dreissena rostriformis bugensis*) reduce microzooplankton and macrozooplankton biomass in thermally stratified lakes. *Limnology and Oceanography* 55: 1851–1859, https://doi.org/10.4319/lo.2010.55.5.1851

Landesanstalt für Umweltschutz Baden-Württemberg (2005) Wirbellose Neozoen Im Bodensee. https://pudi.lubw.de/detailseite/-/publication/30466

Leuven REW, Velde G, Baijens I, Snijders J, Zwart C, Lenders HJR, bij de Vaate A (2009) The river Rhine: a global highway for dispersal of aquatic invasive species. *Biological Invasions* 11: 1989–2008, https://doi.org/10.1007/s10530-009-9491-7

Lowe S, Browne M, Boudjelas S, Poorter M De (2000) 100 of the world's worst invasive alien species. A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12 pp, https://doi.org/10.1614/WT-04-126.1

Marescaux J, Boets P, Lorquet J, Sablon R, Doninck K Van, Beisel JN (2015) Sympatric *Dreissena* species in the Meuse River: towards a dominance shift from zebra to quagga mussels. *Aquatic Invasions* 10: 287–298, https://doi.org/10.3391/ai.2015.10.3.04

Marsden JE, Lansky DM (2000) Substrate selection by settling zebra mussels, *Dreissena polymorpha*, relative to material, texture, orientation, and sunlight. *Canadian Journal of Zoology* 78: 787–793, https://doi.org/10.1139/z00-004

Martens A, Grabow K, Schoolmann G (2009) Die Quagga-Muschel *Dreissena rostriformis bugensis* am Oberrhein: der Beginn einer Invasion. Annual Assemply of the German Limnological Society (DGL) 2008. Konstanz, 8 pp

Mills EL, Dermott RM, Roseman EF, Dustin D, Mellina E, Conn DB, Spidle AP (1993) Colonization, ecology, and population structure of the "Quagga" mussel (Bivalvia: Dreissenidae) in the lower Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2305–2314, https://doi.org/10.1139/f93-255

Mörtl M, Rothhaupt KO (2003) Effects of adult *Dreissena polymorpha* on settling juveniles and associated macroinvertebrates. *International Review of Hydrobiology* 88: 561–569, https://doi.org/10.1002/iroh.200310640

Nalepa TF, Schloesser DW (eds) (2014) Quagga and zebra mussel: biology, impacts, and control, 2nd ed. CRC Press, 779 pp, https://doi.org/10.1201/b15437

Nalepa TF, Fanslow DL, Pothoven SA (2010) Recent changes in density, biomass, recruitment, size structure, and nutritional state of *Dreissena populations* in southern Lake Michigan. *Journal of Great Lakes Research* 36: 5–19, https://doi.org/10.1016/j.jglr.2010.03.013

Nalepa TF, Fanslow DL, Lang GA, Mabrey K, Rowe M (2014) Lake-wide benthic surveys in Lake Michigan in 1994-95, 2000, 2005, and 2010: Abundances of the amphipod *Diporeia* spp. and abundances and biomass of the mussels *Dreissena polymorpha* and *Dreissena rostriformis bugensis*. *NOAA Technical Memorandum GLERL* 164: 1–21

Nalepa TF, Burlakova LE, Elgin AK, Karatayev AY (2020) Abundance and biomass of benthic macroinvertebrates in Lake Michigan in 2015, with a summary of temporal trends. *NOAA Technical Memorandum GLERL* 175: 1–41

Olson J, Robertson JJ, Swannack TM, McMahon RF, Nowlin WH, Schwalb AN (2018) Dispersal of zebra mussels (*Dreissena polymorpha*) downstream of an invaded reservoir. *Aquatic Invasions* 13: 199–209, https://doi.org/10.3391/ai.2018.13.2.02

Oreska MPJ, Aldridge DC (2011) Estimating the financial costs of freshwater invasive species in Great Britain: a standardized approach to invasive species costing. *Biological Invasions* 13: 305–319, https://doi.org/10.1007/s10530-010-9807-7

Patterson MWR, Ciborowski JJH, Barton DR (2005) The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. *Journal of Great Lakes Research* 31: 223–237, https://doi.org/10.1016/S0380-1330(05)70316-6

Peyer SM, McCarthy AJ, Lee CE (2009) Zebra mussels anchor byssal threads faster and tighter than quagga mussels in flow. *Journal of Experimental Biology* 212: 2027–2036, https://doi.org/10.1242/jeb.028688

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ram JL, Karim AS, Banno F, Kashian DR (2012) Invading the invaders: Reproductive and other mechanisms mediating the displacement of zebra mussels by quagga mussels. *Invertebrate Reproduction and Development* 56: 21–32, https://doi.org/10.1080/07924259.2011.588015

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83: 263–282, https://doi.org/10.1890/13-0183.1

Roe SL, MacIsaac HJ (1997) Deepwater population structure and reproductive state of quagga mussels (*Dreissena bugensis*) in Lake Erie. *Canadian Journal of Fisheries and Aquatic Science* 54: 2428–2433, https://doi.org/10.1139/f97-151

Rowe MD, Anderson EJ, Vanderploeg HA, Pothoven SA, Elgin AK, Wang J, Yousef F (2017) Influence of invasive quagga mussels, phosphorus loads, and climate on spatial and temporal patterns of productivity in Lake Michigan: A biophysical modeling study. *Limnology and Oceanography* 62: 2629–2649, https://doi.org/10.1002/lno.10595

Rudstam LG, Gandino CJ (2020) Zebra or quagga mussel dominance depends on trade-offs between growth and defense - Field support from Onondaga Lake, NY. *PLoS ONE* 15: 1–17, https://doi.org/10.1371/journal.pone.0235387

Rudstam LG, Jackson JR, Hetherington AL (2016) Concluding remarks: Forecasting the future of Oneida Lake and its fishery in an era of climate change and biological invasions. In: Rudstam LG, Mills EL, Jackson JR, Stewart DJ (eds), Oneida Lake: Long-Term Dynamics of a Managed Ecosystem and Its Fisheries. American Fisheries Society, Bethesda, NY, pp 525–540, https://doi.org/10.47886/9781934874431.ch24

Stoeckmann A (2003) Physiological energetics of Lake Erie dreissenid mussels: a basis for the displacement of *Dreissena polymorpha* by *Dreissena bugensis*. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 126–134, https://doi.org/10.1139/f03-005

Strayer DL, Malcom HM (2007) Effects of zebra mussels (*Dreissena polymorpha*) on native bivalves : the beginning of the end or the end of the beginning? *Journal of the North American Benthological Society* 26: 111–122, https://doi.org/10.1899/0887-3593(2007)26[111:EOZMDP]2.0.CO;2

Strayer DL, Malcom HM (2018) Long-term responses of native bivalves (Unionidae and Sphaeriidae) to a *Dreissena* invasion. *Freshwater Science* 37: 697–711, https://doi.org/10.1086/700571

Strayer DL, Adamovich BV, Adrian R, Aldridge DC, Balogh C, Burlakova LE, Fried-Petersen HB, G.-Tóth L, Hetherington AL, Jones TS, Karatayev AY, Madill JB, Makarevich OA, Marsden JE, Martel AL, Minchin D, Nalepa TF, Noordhuis R, Robinson TJ, Rudstam LG, Schwalb AN, Smith DR, Steinman AD, Jeschke JM (2019) Long-term population dynamics of dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*): a cross-system analysis. *Ecosphere* 10: e02701, https://doi.org/10.1002/ecs2.2701

Van der Velde G, Rajagopal S, Bij de Vaate A (eds) (2010) The zebra mussel in Europe. Backhuys Publishers, Leiden, 500 pp

Vanderploeg HA, Liebig JR, Nalepa TF, Fahnenstiel GL, Pothoven SA (2010) *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. *Journal of Great Lakes Research* 36: 50–59, https://doi.org/10.1016/j.jglr.2010.04.005

Werner S, Mörtl M, Bauer HG, Rothhaupt KO (2005) Strong impact of wintering waterbirds on zebra mussel (*Dreissena polymorpha*) populations at Lake Constance, Germany. *Freshwater Biology* 50: 1412–1426, https://doi.org/10.1111/j.1365-2427.2005.01411.x

Wesselingh FP, Neubauer TA, Anistratenko VV, Vinarski MV, Yanina T, Poorten JJ ter, Kijashko P, Albrecht C, Anistratenko OY, D'Hont A, Frolov P, Gándara AM, Gittenberger A, Gogaladze A, Karpinsky M, Lattuada M, Popa L, Sands AF, Velde S van de, Vandendorpe J, Wilke T (2019) Mollusc species from the Pontocaspian region - an expert opinion list. *ZooKeys* 827: 31–124, https://doi.org/10.3897/zookeys.827.31365

Wick MJ, Angradi TR, Pawlowski MB, Bolgrien D, Debbout R, Launspach J, Nord M (2020) Deep lake explorer: A web application for crowdsourcing the classification of benthic underwater video from the Laurentian Great Lakes. *Journal of Great Lakes Research* 46: 1469–1478, https://doi.org/10.1016/j.jglr.2020.07.009

Zhu B, Fitzgerald DG, Mayer CM, Rudstam LG, Mills EL (2006) Alteration of ecosystem function by zebra mussels in Oneida Lake: Impacts on submerged macrophytes. *Ecosystems* 9: 1017–1028, https://doi.org/10.1007/s10021-005-0049-y

Supplementary material

The following supplementary material is available for this article:

Appendix 1. Method Details.
Table S1. Sampling sites in Lake Constance for *Dreissena* in benthic region. Depth sampling sites LC: letters correspond to sites in Figure 6 and S1.
Table S2. qPCR primers according to Bronnenhuber and Wilson (2013) and De Ventura et al. (2017) modified for TaqMan assay.
Figure S1. The map shows the locations of the depth sampling in Lake Constance from Table S1. Letters correspond to the sites in Figure 6 and Table S1 a) Altenrhein b) Bregenz c) Langenargen d) Fischbach e) Uttwil f) Konstanz Egg g)Sipplingen h) Wallhausen i) Reichenau j) Radolfzell k) Berlingen.
Figure S2. The seasonal abundance of veliger larvae in inlet pipes of drinking water plants at Lake Constance (Sipplingen), Lake Geneva (St Suplice and Lutry) and Lake Zurich (Moos and Lengg).
Figure S3. Relationship between quagga mussel abundance and the coefficient of variation. The blue line represents the linear model with 95% confidence interval in grey.

This material is available as part of online article from:
http://www.reabic.net/aquaticinvasions/2022/Supplements/AI_2022_Haltiner_etal_Appendix.pdf
http://www.reabic.net/aquaticinvasions/2022/Supplements/AI_2022_Haltiner_etal_SupplementaryTables.xlsx
http://www.reabic.net/aquaticinvasions/2022/Supplements/AI_2022_Haltiner_etal_SupplementaryFigures.pdf