Signs of the times: Isotopic signature changes in several fish species following invasion of Lake Constance by quagga mussels

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ABSTRACT

Since the arrival of the invasive quagga mussels *Dreissena rostriformis bugensis* in Lake Constance, significant changes in the zooplankton and benthic invertebrate community were observed. Five years later the quagga mussel has become the dominating species of the benthic community. Its effects on other components of the food web, especially those at higher trophic levels such as fish, remain unclear around the world. To evaluate the actual impact of quaggas on the local food web of Lake Constance, the stable isotope compositions of pelagic whitefish and different benthic fish species from before and after the quagga invasion were compared. A significant increase in $\delta^{13}C$ was detected in pelagic whitefish one year after the establishment of the quagga mussel in the lake. This change was most likely the consequence of an increase in benthic-derived nearshore primary production and a shift towards more littoral feeding, than a change in dietary composition. Stomach content analysis of contemporary samples revealed that pelagic whitefish (*Coregonus wartmanni*) still feed exclusively on pelagic zooplankton. In contrast, benthic whitefish (*Coregonus macrophthalmus*), roach (*Rutilus rutilus*) and tench (*Tinca tinca*) show today high levels of quagga consumption. However, this behaviour alone could not explain the observed differences in $\delta^{15}N$ from periods before and after the quagga invasion. The results suggest that energy sources and pathways have changed considerably for both pelagic and benthic dwelling fish species in Lake Constance following the establishment of quaggas.

Introduction

Non-native species have established populations in a wide variety of aquatic ecosystems worldwide (Molnar et al., 2008; Pimentel et al., 2001; Toussaint et al., 2016), and many of these invasions have resulted in severe impacts on native species and systems (Chucholl, 2016; Kakareko et al., 2013; Keller et al., 2011; Moore et al., 2019). Given the ongoing climate crisis and the continuation of global trade and travel, the problems presented by invasive non-native species seem set to worsen (Karatayev et al., 2007; Peeler et al., 2011; Rahel and Olden, 2008).

The quagga mussel *Dreissena rostriformis bugensis* is considered as one of the most problematic freshwater invaders (Karatayev et al., 2015, 2005). The species is native to fresh and brackish waters of the Caspian and Black Sea but is now widespread in the whole Northern hemisphere (Karatayev et al., 2007). Quagga mussels compete for space and food resources with most native invertebrates resulting in decreased diversity, density, and biomass (McNickle et al., 2006) and drive system-wide change via their highly effective suspension feeding strategy, which often results in increased water clarity and light penetration and concomitant declines in phytoplankton, seston, and organic matter in the water column (Higgins and Vander Zanden, 2010; Pothoven and Fahnenstiel, 2013; Strayer and Malcom, 2018). As a consequence of reduced abundance of phytoplankton and hence also of zooplankton, zooplanktivorous fish are thought to be negatively impacted by quagga mussels invasion (Karatayev et al., 2015). A notable example is that of the lake whitefish *Coregonus clupeaformis*, which following invasion of quagga mussels are forced by reduced availability of their main prey item, the amphipod *Diporeia* spp, to switch to eating the mussels themselves, leading to deterioration in condition, slower growth and reduced abundance (Hoyle et al., 2008; Madenjian et al., 2015, 2010; Rennie et al., 2009). On the other hand, many different fish species are adapted to feed on

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Dreissena spp. (Molloy et al., 1997). Furthermore, the increase in benthic invertebrate biomass typically observed after a quagga invasion is often followed by an increase in biomass of benthivorous fish in the littoral zone (Higgins and Vander Zanden, 2010; Karatayev et al., 2015).

The extent to which quagga mussels impact higher tropic levels remains debatable. This is especially true in areas were quaggas potentially affect the production of economically important fish stocks (Bunnell et al., 2014; He et al., 2015; Riley and Dunlop, 2016). For example in North America, a number of studies alluded to potential shifts in energy pathways between invasive quaggas and fish populations (Rennie et al., 2009; Turschak et al., 2014), but direct comparisons between post- and pre-invasion scenarios are scarce. However a large study explored links between quaggas and resource use by the benthivorous lake whitefish *Coregonus clupeaformis* using stable isotopes ratios (δ^{15}N and δ^{13}C) determined from archived scale samples collected from many different lakes before and after the mussels arrived (Fera et al., 2017). The authors showed that δ^{13}C of this keystone native fish species increased following the mussel invasion. Trends in δ^{15}N were less clear but generally showed a decline in most lakes after the establishment of the mussel (Fera et al., 2017). This result provided important support for the theory that fundamental energy pathways are changed following quagga invasion.

The present study was conducted in Lake Constance, the second largest lake in Central Europe. Here, the presence of quagga mussels was first reported in 2016 (Hydra, 2021). Since then, the species has spread rapidly. Quaggas are now hyperabundant and a dominant feature of the benthic community lake-wide, occurring in densities of more than 2,000 individuals per square meter (personal communications T. Basen) on sandy bottoms down to 40 m depth and on stones and rocks as deep as 100 m, with further records even in the deepest parts of the lake at 250 m (Hydra, 2021). Quagga mussels are today the dominant members of the bivalve community, having almost completely displaced the previously abundant non-native zebra mussel *Dreissena polymorpha* (Pallas 1771) (Hydra, 2021), introduced in the mid-1960 s (Cleven and Frenzel, 1993; Werner et al., 2005). Currently, zebra mussels are hard to detect and occur isolated only in some shallower parts of the lake (T. Basen, per. comm.). The extent to which quagga mussels impact the fundamental energy pathways within the lake remains unknown, but results from elsewhere suggest that zooplankton density in the pelagic zone will have decreased due to the filtration by the quaggas while production in the littoral zone will have increased (Evans et al., 2011; Fahnenstiel et al., 2010; Vanderploeg et al., 2010). It is hypothesised that recent declines in both growth rates and catches (Rösch et al., 2018) of the most commercially important fish species in Lake Constance, the pelagic feeding whitefish *Coregonus wartmanni* (Bloch 1784) (Baer et al., 2022, 2017) may be a result of the species being forced to feed more in littoral waters. A similar shift was previously documented for the sister species *C. clupeaformis* in the Great Lakes (Rennie et al., 2009). If this is the case, pelagic whitefish might be expected to show an increase in δ^{13}C after quagga invasion, because primary producers of shallow waters are more enriched in δ^{13}C than those living in pelagic zone (Fera et al., 2017; Rennie et al., 2009; Vander Zanden and Rasmussen, 1999). Furthermore, it is hypothesised that a fundamental shift in energy pathways similar to that outlined above has taken place post-invasion for many other fish taxa. To test both hypotheses, the present study compares the δ^{15}N and δ^{13}C values from pelagic feeding whitefish and benthic species of different feeding guilds before and after the invasion of the quagga mussel in Lake Constance. Further analyses of stomach contents, isotopic niche overlap of the different feeding guilds, and isotopic composition of energetic baseline organisms (mussels and snails) were used to interpret the results. Those have implications beyond Lake Constance and may inform responses in other large lakes in Central Europe facing invasion by quagga mussels.

Material and methods

Approval by a review board institution or ethics committee for procedures undertaken in the present study was not necessary because all fish were caught under permission granted by the local fisheries administration (Regierungspräsidium Tübingen) by licenced personnel. All captured species were handled according to the German Animal Protection Law (§ 4) and the ordinance on slaughter and killing of animals (Tierschutzschlachtverordnung § 13).

Sampling

Lake Constance is situated between Austria, Germany and Switzerland (Fig. 1) and is part of the Rhine drainage basin. It has a total surface area of 536 km^2, including a 472 km^2 large, deep, oligotrophic Upper Lake (ULC) and a 63 km^2 large, shallower, mesotrophic Lower Lake (LLC). The lake has undergone intensive re-oligotrophication between 1990 and 2010 (Baer et al., 2017; Stich and Brinker, 2010), and its fish community comprises a minimum of 30 species (Eckmann and Rösch, 1998) of which about 10 are targeted by the fishery (Rösch, 2014). Of these, whitefish (*Coregonus* spp.) make up the economically most important catch (Baer et al., 2017).

Before the quagga invasion took place, no specific monitoring of quaggas and their influence on the fish community was conducted. However, in two different scientific studies tissue samples from a variety of fish species were taken and stored before the quagga invasion took place. Due to this fortunate circumstance it was possible to get some tissue samples from eight different fish species of the pre-quagga period. Therefore, the present study focused on the following fish species from five different feeding guilds: 1) zooplanktivorous pelagic whitefish from ULC; 2) benthivorous whitefish (*Coregonus macrophthalmus* Nüsslin 1882) from ULC, plus bleak (*Alburnus alburnus* L.), roach (*Rutilus rutilus* L.) and tench (*Tinca tinca* L.) from both lakes; 3) benthi-zooplanktivorous benthic whitefish (*Coregonus* spp.) from LLC; 4) herbivorous rudd (*Scardinius erythrophthalmus* L.) from ULC and 5) piscivorous pike (*Esox lucius* L.) from both lakes.

In a study analysing the energy content of whitefish, pelagic whitefish of ULC were sampled from July to September every year from 2014 to 2020, using drifting gill nets. For each year, tissue samples were prepared for analysis by oven-drying at around 60 °C for 48 h and grinding to fine powder. These powders were stored in vacuum-insulated plastic bags for later analysis. From ten powders per year; we used sub-samples for our analysis (n = 70). The seven other fish species were sampled during two surveys looking for the overall composition and changes in the local fish community: 1) an intensive four week fishing campaign in both parts of the lake in September 2014 (Alexander et al., 2015) and 2) an additional survey in August and September 2020, again covering both parts of the lake. All fish were caught using benthic gill nets in the littoral zone and euthanized with an overdose of clove oil (1 mL L^{-1}) and a gill cut. In 2014, (hereafter called "prequagga" period), samples of the white muscle of the seven additional species were stored in a freezer at − 20 °C for further analysis. Those samples were used to compare their stable isotope contents with samples taken in 2020 (hereafter called "post-quagga" period). The samples of 2020 were stored until stable isotope analysis in the same way as the samples from 2014. Preliminary studies (Baer et al., 2022) identified benthic whitefish, roach, and tench as "quagga consumers" and pelagic
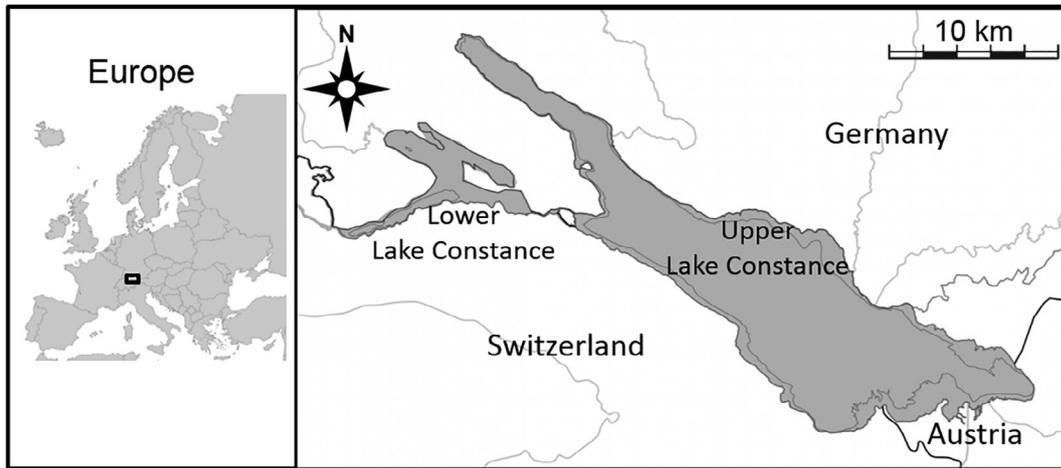
Fig. 1. Location of Lake Constance in Europe (left side, black square) and the position of Upper and Lower Lake Constance (right side).

whitefish, rudd, pike, and bleak as "non-quagga consumers" (Table 1).

All fish were measured and weighed wet shortly after capture to the nearest millimetre total length (TL) and gram. In the above-mentioned survey of benthivorous species in 2014, no stomach content analysis was conducted. During the sampling of pelagic whitefish between 2014 and 2019, stomachs were opened in irregular intervals and the food components were macroscopically identified (R. Rösch, personal communication). To get a deeper insight into the actual, post-quagga diet composition, in total 345 fish were caught in 2020 and used for stomach content analysis (Table 1). In each, an abdominal incision was made with small scissors and the digestive tract (stomach and intestine) was removed, separated from other visceral organs and remains and stored in methylated ethanol (70 %). Digestive tracts were dried with tissue paper and weighed to the nearest 0.01 g on a micro-balance, opened by a longitudinal slit so that food items could be carefully pushed out into a glass frame. The empty digestive tract was reweighed. Food items were identified and counted under a binocular (Zeiss Stemi 508, Carl Zeiss Microscopy GmbH, Jena, Germany), using ten-fold magnification, following the procedure described in (Brandner et al., 2013). Due to the fact that shell fragments from zebra mussels could be much easier identified correctly than those from quaggas (Beggel et al., 2015), it was especially examined for fragments with the typical features of *D.*

polymorpha, *i.e.* the arched and flattened ventral surface of the shell and the sharp angled transition of the ventral and dorsal surface. If none of those were found, in the next step fragments with the typical features of quaggas were sought. If no discrimination was possible (<5% of all stomachs with mussels), the fragments were defined as pieces from *Dreissena* spp. Because more than 90 % of all consumed dreissenids were categorized as quagga mussels (although the protocol favoured the classification as zebra mussel) and that zebra mussels were rare in the lake in 2020, all found dreissenids were assigned to quagga mussels. The food items were categorized as follows: 1) quagga mussels, 2) Asian clam (*Corbicula fluminea*), 3) snails (*Lymnea stagnalis, Bithynia tentaculata, Viviparus viviparus*), 4) benthic macroinvertebrates (*Gammarus* spp. and larvae, pupae and adults of different insect species), 5) pelagic zooplankton (*Bosmina*, Copepoda, *Daphnia/Diaphanosoma*), 6) aquatic plants (remains of submerged macrophytes), 7) fish (*Perca fluviatilis*, Cyprinidae). For each analysed digestive tract, the observed food categories were weighed as a group to the nearest 0.01 g and the proportion of food in each category was calculated by wet weight (%W).

Preliminary studies showed that benthic whitefish, roach, and tench consume large quantities of quagga mussels and several species of snail (Baer et al., 2022). To compare the isotopic value in the source and the consumer and to discuss the possibility that a switch from snail to mussel feeding could be responsible for

Table 1

Relative proportions of different food categories by wet weight (%W ± standard deviation SD) in the diets of seven different fish species from Upper (ULC) and Lower (LLC) Lake Constance.

Species	Lake (sample size)	%W (±SD)						
		Quagga mussel	Asian clam	Snails	Benthic macroinvertebrates	Pelagic zooplankton	Aquatic plants	Fish
Benthic whitefish	ULC (76)	14 (±31)	1 (±6)	1 (±7)	43 (±40)	39 (±48)	2 (±13)	0 (±0)
	LLC (55)	7 (±24)	6 (±17)	0 (±2)	29 (±41)	57 (±49)	0 (±1)	0 (±0)
Pelagic whitefish	ULC (10)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	100	0 (±0)	0 (±0)
	LLC	–	–	–	–	–	–	–
Roach	ULC (66)	81 (±35)	0 (±0)	5 (±19)	6 (±18)	0 (±0)	7 (±23)	0 (±0)
	LLC (55)	61 (±47)	15 (±34)	23 (±44)	0 (±0)	0 (±0)	2 (±6)	0 (±0)
Tench	ULC (30)	23 (±41)	0 (±2)	60 (±46)	15 (±13)	0 (±0)	25 (±6)	0 (±2)
	LLC (10)	43 (±46)	0 (±0)	25 (±42)	32 (±45)	0 (±0)	0 (±1)	0 (±0)
Bleak	ULC (19)	0 (±0)	0 (±0)	0 (±0)	66 (±16)	34 (±11)	0 (±0)	0 (±0)
	LLC (20)	0 (±0)	0 (±0)	0 (±0)	59 (±10)	41 (±13)	0 (±0)	0 (±0)
Rudd	ULC (11)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	100	0 (±0)
	LLC	–	–	–	–	–	–	–
Pike	ULC (18)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	100
	LLC (15)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	0 (±0)	100

changes in the isotopic composition, the common pond snail *Lymnea stagnalis* (L.) (n = 20) and the faucet snail *Bithynia tentaculata* (L.) (n = 10) were additionally collected from the littoral of ULC in August 2020. The widespread freshwater snail *Viviparus viviparus* (L.) was collected by snorkelling in LLC in September 2020 (n = 20), and quagga mussels were collected from piles at depth of 0.5 – 2 m in both parts of the lake (n = 100 each lake). Soft tissue excised from snails and mussels was frozen at − 20 °C until further stable isotope analysis.

A total of 401 samples of white muscle tissues were taken from fish captured in ULC and LLC before (2014) and after (2020) the quagga invasion (Table 2). In 2020, samples were taken from fish used for stomach content analysis.

For benthic whitefish (here: *Coregonus macrophthalmus* from ULC and *Coregonus* spp. from LLC) and roach, both known to be potential quagga consumers (Baer et al., 2022), post-invasion samples for stable isotope analysis were taken from fish with and without mussels in the digestive tract. This was done to test whether changes in isotope values could be associated with quagga consumption or to indicate specialist quagga feeding by single individuals. Therefore, tissues samples from ULC included 11 benthic whitefish and 25 roach with mussels in the stomachs and 7 whitefish and 9 roach without mussels in the stomachs. For LLC the corresponding numbers were 5 whitefish and 4 roach with mussels and 15 whitefish and 16 roach without mussels in the stomachs.

Stable isotope analysis

Samples of mussels, snails and fish were prepared for analysis via freeze drying at − 50 °C and pressurization at < 1 mbar, then ground to homogenous powder using a mixer mill. Sample powder (0.3 – 0.4 mg) was weighed into tin capsules and combusted in an isotope ratio mass spectrometer (Delta plus, Finnigan MAT, MasCom GmbH, Bremen, Germany), interfaced (viaConFlo II, Finnigan MAT, MasCom GmbH, Bremen, Germany) with an elemental analyser (EA 1108, CarloErba, Thermo Fisher SCIENTIFIC, Milan, Italy). Because the mean C:N values (±SD) of all fish samples were below 3.5, lipid extraction of fish muscle tissue was not conducted (Matthews et al., 2010; Skinner et al., 2016). Measurements are reported in δ-notation ($\delta^{13}C$, $\delta^{15}N$) in parts per thousand deviations (‰), where $\delta = 1000 \times (Rsample/Rstandard – 1)$ relative to the Pee Dee Belemnite (PDB) standard for carbon and atmospheric N_2 for nitrogen. Finely ground animal horn (keratin) was used as laboratory standard for every 10 unknowns in sequence. Replicate assays of internal laboratory standards indicated measurement errors (SD) of ± 0.05 % and 0.15 % for $\delta^{13}C$ and $\delta^{15}N$ respectively.

When comparing organic materials from different sampling years, the Suess effect has to be considered (Verburg, 2007), taking into account changes in $\delta^{13}C$ in any carbon reservoir resulting from anthropogenic release of CO_2 to the atmosphere (Keeling, 1979; Verburg, 2007). To this end, atmospheric CO_2 data measured at

Mauna Loa by the Scripps CO_2 program (Keeling and Keeling, 2017) was used, in which mean annual $\delta^{13}C$ of atmospheric CO_2, linearly increased by 0.0281‰ per year between 1994 and 2020 ($r^2 = 0.9877$; n = 27). Thus to account for the Suess effect and make the data comparable, 0.0281‰ was added to the $\delta^{13}C$ values for each year of pelagic whitefish data and 0.169‰ (=6 × 0.0281) was added to the 2020 data of all other analyzed species.

Statistical analysis

Temporal trends in the stable isotope ratios of pelagic whitefish (sampled yearly from 2014 to 2020) were investigated using a segmented least squares linear regression (*i.e.*, "breakpoint analysis") to identify potential breakpoints in the slopes of $\delta^{15}N$ and $\delta^{13}C$ through time, and test their temporal relationship with quagga establishment in ULC during 2016. The statistical significance of the breakpoint was set at $P < 0.05$ and tested by respective confidence values.

To test the effects on $\delta^{15}N$ and $\delta^{13}C$ values of quagga consumers (benthic whitefish, roach, and tench) and non-quagga consumers (bleak, rudd, and pike) sampled before (2014) and after (2020) quagga invasion in both parts of the lake (ULC and LLC) the following general linear model (GLM) (Sachs, 1997) was used:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \gamma_k + \delta_{ijkl} \tag{1}$$

where Y_{ijkl} is the $\delta^{15}N$ (or $\delta^{13}C$) value of muscle tissue; μ is the overall mean, α_i denotes feeding behaviour (quagga consumer, non-quagga consumer), β_j is period (2014 and 2020), $(\alpha\beta)_{ij}$ is the interaction between feeding behaviour and period, γ_k represents lake (LLC and ULC), and δ_{ijkl} is the random residual error. Single outliers were excluded from the dataset (selection criterion: more than eight times standard deviation). Student-t tests were used for *post hoc* comparisons between period, feeding behaviour, and lake.

To test whether quaggas found in the digestive tracts of roach and benthic whitefish could be related to highly specialized quagga feeding of single individuals, the following GLM was used:

$$Y_{ijklm} = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\beta)_{ij} + (\gamma\beta)_{jk} + \delta_{ijklm} \tag{2}$$

where Y_{ijklm} is the $\delta^{15}N$ (or $\delta^{13}C$) value of muscle tissue in roach and benthic whitefish; μ is the overall mean, α_i denotes quagga presence in the digestive tract (yes/no), β_j is length (TL in cm), γ_k represents lake (LLC and ULC), $(\alpha\beta)_{ij}$ is the interaction between quaggas in the digestive tracts and TL, $(\gamma\beta)_{jk}$ is the interaction between TL and lake, and δ_{ijklm} is the random residual error. Student-t tests were used for *post hoc* comparison between lake and quagga presence or absence the digestive tracts (yes *vs.* no).

Data from all examined fish species from both lakes and for both periods (before and after quagga invasion, and for ULC pelagic whitefish sampled in 2014 and 2020) were pooled according to feeding guild (benthivorous, zooplanktivorous, benthi-zooplanktivorous, herbivorous, and piscivorous) in order

Table 2
Species, total length (TL) range, and number of fish used for stable isotope analysis (before and after the quagga invasion) from Upper (ULC) and Lower (LLC) Lake Constance.

Species	Quagga consumer?	Min.–max. TL in cm	Samples (n) before quagga invasion		Samples (n) after quagga invasion	
			ULC	LLC	ULC	LLC
Benthic whitefish	Yes	26 – 61	3	5	21	20
Pelagic whitefish	No	17 – 40	30	–	40	–
Roach	Yes	9 – 37	17	6	34	20
Tench	Yes	14 – 53	15	8	19	20
Bleak	No	5 – 16	15	9	19	20
Rudd	No	5 – 30	7	–	12	–
Pike	No	23 – 60	16	12	18	15
total			**103**	**40**	**163**	**95**

to calculate the standard ellipse area corrected for small samples (SEA$_c$). The SEA$_c$ represents the core isotopic niche of each guild after factoring in maximum likelihood, similar to a two-dimensional measurement of standard deviation, and is drawn from around 40 % of data (Jackson et al., 2011). The isotopic niche overlap of the different feeding guilds was subsequently calculated as a proportion of the sum of the non-overlapping area of SEA$_c$s. All analyses were performed with help of the SIBER package (Stable Isotope Bayesian Ellipses in R, v. 2.15; (Jackson et al., 2011)) in R (v. 4.04, (R Core Team, 2020)).

All other statistics were run on JMP Pro 16.1 (64 bit, SAS Institute).

Results

Stomach content

In both lakes, the highest proportions of quaggas by weight were found in the digestive tract of roach (Table 1), in which species all other food categories appeared of minor importance (Table 1). Quaggas were also consumed by tench and benthic whitefish, but in smaller amounts (Table 1). For tench, snails were of much greater importance than mussels, making up nearly 60% of all tench prey in ULC. The tench in LLC also ate far more snails and other benthic macroinvertebrates than mussels (including both quagga and Asian clam). For benthic whitefish in both lakes the food category with the highest %W-values in the digestive tracts was benthic macroinvertebrates, especially gammarids (Table 1), while the diet of bleak was dominated by insect pupae (Table 1). Pelagic whitefish fed exclusively on zooplankton, rudd on aquatic plants and pike solely on fish (Table 1).

Breakpoint analysis of pelagic whitefish

In the segmented regression analysis for pelagic whitefish sampled yearly between 2014 and 2020, a significant breakpoint was detected in the slope of δ^{13}C values in 2017, one year after the establishment of the quagga mussel in the lake (Fig. 2). Values of δ^{15}N on the other hand remained relatively consistent between pre- and post-quagga periods (Fig. 2).

δ^{15}N and δ^{13}C values before and after quagga establishment for other fish species

For all other analyzed fish species, clear differences were observed in δ^{15}N between the periods with and without quaggas. In benthic whitefish in both lakes δ^{15}N values increased between 2014 and 2020 (Fig. 3), while for roach the δ^{15}N values decreased from 2014 to 2020 (Fig. 3). In tench differences in δ^{15}N were only observed for fish from LLC (Fig. 3). Bleak exhibited lower δ^{15}N values in 2020 than in 2014 in both lakes, similar to rudd, which was only available for ULC (Fig. 3). For pike in both lakes, δ^{15}N increased between 2014 and 2020 (Fig. 3). These observations were corroborated by the GLM for δ^{15}N (r^2 $_{adjusted}$ = 0.31, n = 346, P < 0.0001), indicating that period and lake both had a highly significant impact on the outcome of the model (P < 0.0001). Overall δ^{15}N-values recorded from LLC fish were significantly larger than those from ULC (t-test, α < 0.05) while in both lakes values were significantly lower in the post- quagga invasion period (2020) than they had been pre-invasion (2014) (t-test, α < 0.05). Neither feeding behaviour (quagga consumption or non-quagga consumption) nor the interaction of feeding behaviour and period had an impact on the outcome of the model.

Compared to δ^{15}N, the changes observed in δ^{13}C between the pre- and post-quagga periods among the sampled fish species were small (Fig. 3), a result underlined by the outcome of the GLM for δ^{13}C (r^2 $_{adjusted}$ = 0.50, n = 346, P < 0.0001) in which period had no impact on the output of the model (P < 0.05) and according to the profiler only a small effect strength in the interaction leading to a marginal overall impact on the model output. In contrast, feeding behaviour was highly influential on the outcome of the model (P < 0.0001). Lake had also a significant influence (P = 0.002). *Post hoc* comparisons revealed that non-quagga consumers showed significantly higher δ^{13}C values than quagga consumers (t-test, α < 0.05) and δ^{13}C values in LLC were significantly higher than in ULC (t-test, α < 0.05).

Stable isotope values of mussels and snails

Quagga mussels and snails exhibited highly divergent stable isotope values in both lakes (Table 3). δ^{15}N values of quaggas were
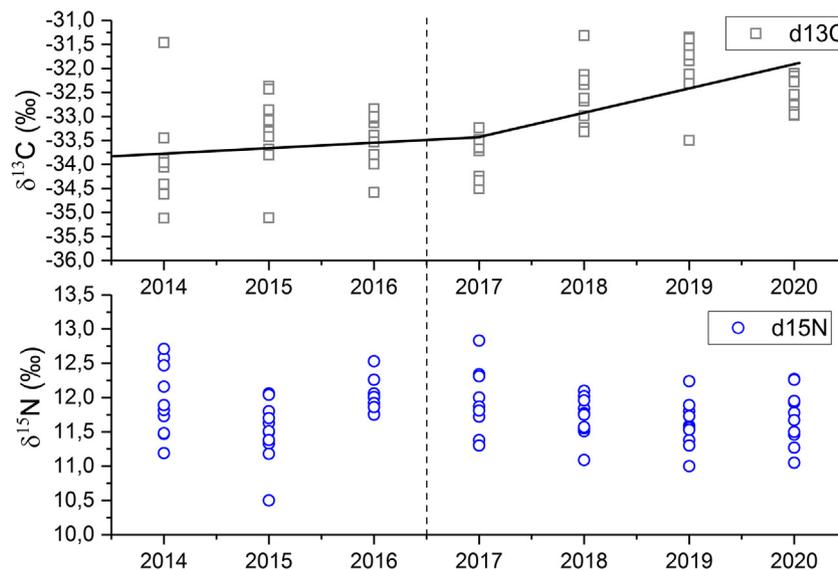

Fig. 2. Breakpoint regression for δ^{13}C of pelagic whitefish with regression line (top), showing no significant breakpoints for δ^{15}N (below). Vertical dashed line depicts the period of dreissenid establishment (between 2016/2017). Points represent individual measurements, δ^{13}C was adjusted for the Suess effect (reference year 2016).
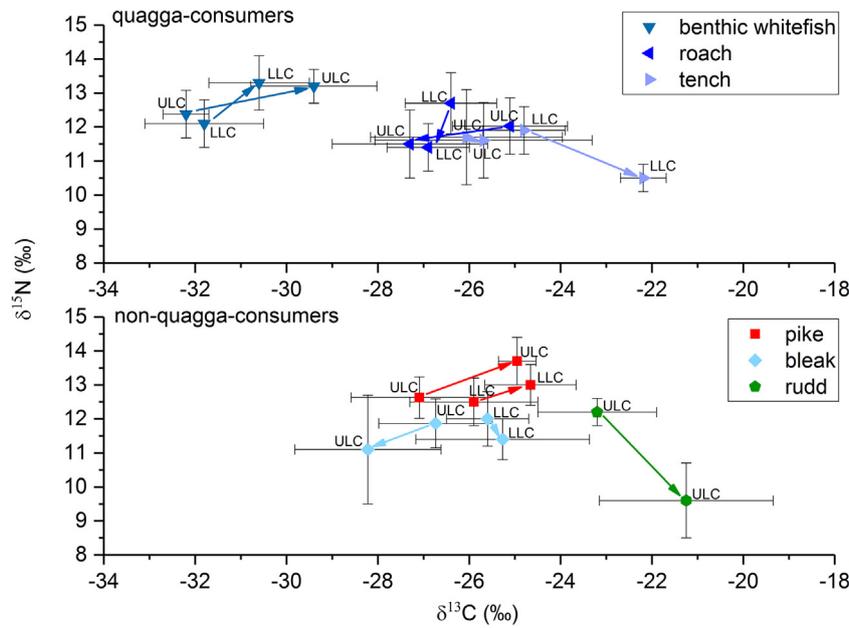
Fig. 3. Shifts in the mean $\delta^{15}N$ and $\delta^{13}C$ values with standard deviation for six different fish species in Upper Lake Constance (ULC) and Lower Lake Constance (LLC), arrows represent the direction of change from the period before invasion (2014) to the period of establishment of quagga mussels in both lakes (2020). Fish species are divided into quagga-consumers (above) and non-quagga-consumers (below), $\delta^{13}C$ was adjusted for the Suess effect (reference year 2016).

Table 3
$\delta^{15}N$ and $\delta^{13}C$ values with standard deviation (±SD) of quagga mussels and three species of snail present in Upper (ULC) and Lower (LLC) Lake Constance sampled in 2020, $\delta^{13}C$ was adjusted for the Suess effect (reference year 2016).

Species	Lake	Sample size	$\delta^{15}N$ ± SD	$\delta^{13}C$ ± SD
Dreissena rostriformis bugensis	ULC	100	5.6 ± 0.1	−30.1 ± 0.3
Lymnea stagnalis	ULC	20	11.5 ± 0.4	−30.7 ± 0.8
Bithynia tentaculata	ULC	10	6.9 ± 0.2	−24.3 ± 0.9
Dreissena rostriformis bugensis	LLC	100	8.6 ± 0.2	−30.2 ± 0.5
Viviparus viviparus	LLC	20	9.7 ± 0.5	−23.4 ± 1.1

lower than those of snails and only the great pond snail *Lymnea stagnalis* exhibited a $\delta^{13}C$ value as low as that of quaggas (Table 3).

Specialized quagga feeding

The GLM showed that presence or absence of quaggas in the digestive tracts of benthic whitefish had no impact on the outcomes for either the $\delta^{13}C$ model (r^2 $_{adjusted}$ = 0.22, n = 38, *P* = 0.02) or the $\delta^{15}N$ model (r^2 $_{adjusted}$ = 0.14, n = 38, *P* = 0.02). Furthermore, there was no significant effect of the other tested parameters (length, lake or the interaction of length with lake or quagga consumption) on stable isotopes in benthic whitefish. The $\delta^{13}C$ model for roach (r^2 $_{adjusted}$ = 0.39, n = 54, *P* < 0.0001) showed comparable results, with no influence of quagga presence in the digestive tract on outcomes and no impact of lake (ULC or LLC), interaction of length with lake or quagga-consuming tendency. However, there was a significant positive influence of total length of this species on $\delta^{13}C$ (*P* < 0.05). The GLM for $\delta^{15}N$ (r^2 $_{adjusted}$ = 0.15, n = 54, *P* = 0.02) showed a positive correlation between total length of roach in LLC and $\delta^{15}N$ and a significant influence of the interaction between total length and lake (*P* = 0.04). As for all other models the remaining parameters showed no impact on roach model (*P* greater than 0.05).

Isotopic niche overlap

Fig. 4 displays core isotopic niches of each feeding guild before and after the quagga invasion of Lake Constance. In ULC during the

pre-quagga period, the standard ellipse area corrected for small samples (SEAc) ranged from 1.6 for zooplanktivorous fish to 6.6 for benthivorous species while in LLC the range was 2.7 for piscivorous to 3.3 for benthi-zooplanktivorous whitefish (Fig. 4). Post-invasion, in 2020, the margin of SEAc values was higher, ranging in ULC from 2.0 for piscivorous species to 7.8 for benthivorous and in LLC from 2.0 for piscivorous to 5.1 in benthivorous fish. Pre-invasion niche overlaps observed between benthivorous and piscivorous fish amounted to 19.1% in ULC and 51.2% in LLC (Fig. 4), but by 2020 no such overlaps were apparent in either ULC or in LLC despite the larger standard ellipse areas (Fig. 4).

Discussion

The data presented here corroborates the first hypothesis, that following quagga mussel invasion the pelagic living whitefish *Coregonus wartmanni* in ULC has been forced into littoral waters, comparable to its sister species *C. clupeaformis* in the Great Lakes (Rennie et al., 2009). This change is evidenced by the break point analysis and an enrichment of $\delta^{13}C$ in pelagic whitefish shortly (one year) after the mussel invasion. It is well established that primary producers in shallow waters are enriched in $\delta^{13}C$ relative to those in deeper waters (Fahnenstiel et al., 2010; Vander Zanden and Rasmussen, 1999; Vanderploeg et al., 2010) and this general trend seems also to hold for higher trophic levels (Fera et al., 2017). Therefore, the $\delta^{13}C$ value of a consumer can serve as an indicator of feeding location, whereby higher $\delta^{13}C$ values point to a greater importance of nearshore sources (Rennie et al., 2009).
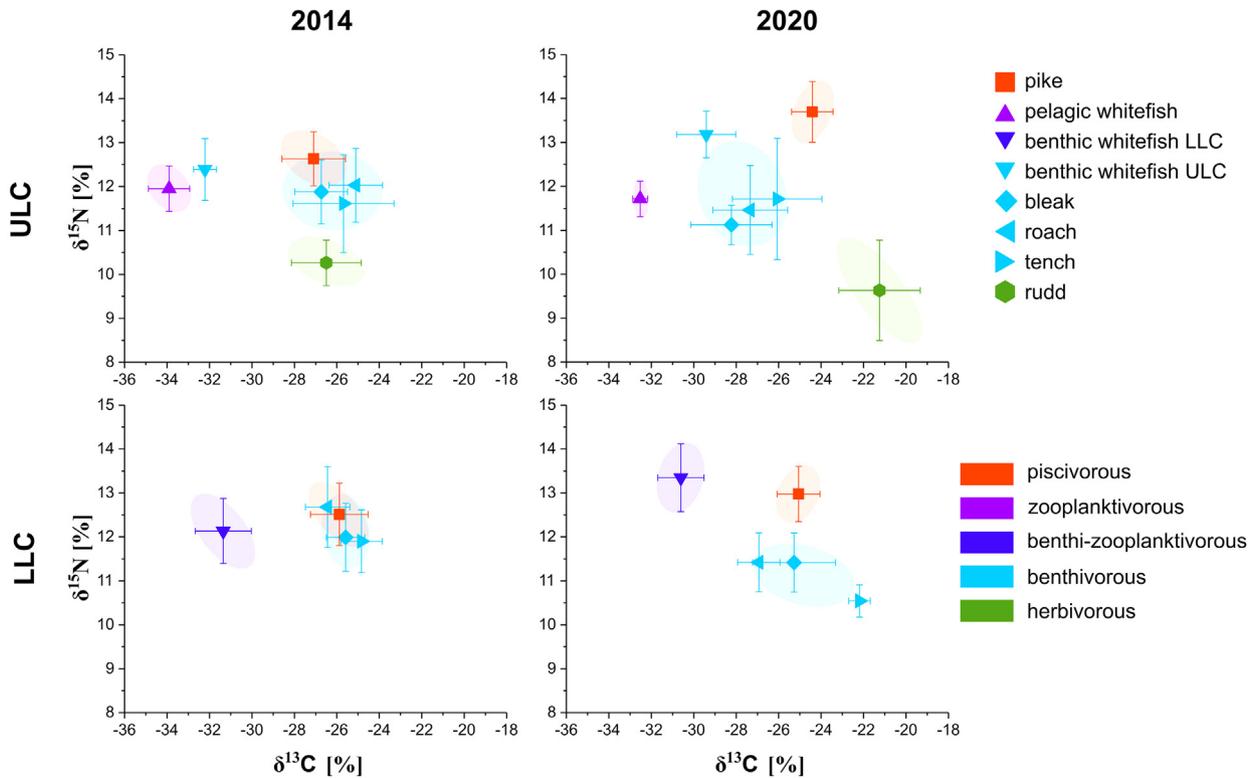
Fig. 4. $\delta^{15}N$ versus $\delta^{13}C$ bi-plot showing the mean isotope values of different fish species in Upper (ULC) and Lower (LLC) Lake Constance before and after quagga mussel invasion (2014 and 2020 respectively). Horizontal and vertical bars represent ± SD of total pooled data. The standard ellipse areas (SEAc) represent the core isotopic niches for each feeding guild (comprising ~ 40 % of the data; Jackson et al., 2011), $\delta^{13}C$ was adjusted for the Suess effect (reference year 2016).

Interestingly in ULC, there is no evidence that pelagic whitefish have changed their foraging habits to favor benthic organisms. The stomach analyses reported here reveal no macrozoobenthic content and suggest that pelagic zooplankton continue to dominate the diet, as it has for decades (Eckmann and Rösch, 1998). One possible explanation for the observed increase in $\delta^{13}C$ in pelagic whitefish is an overall shift in energy pathways in ULC whereby the entire lake system, including pelagic zooplankton, is now more driven by benthic primary production. This shift in energy production from the open pelagic to the benthic region is called benthification (Mayer et al., 2014) and was also documented after the invasion of the quagga mussel in Lake Simcoe, Canada, (Rennie et al., 2013). Thus, changes in the stable isotope pattern of analyzed fish may be part of an increasing $\delta^{13}C$ across both primary and secondary nearshore consumers. If this is the case, a profound shift in the source of carbon at the base of the food web could be responsible for the observed changes (Rennie et al., 2013) rather than a change in diet composition. Future studies analyzing benthic and pelagic samples from different biota and from different depths in Lake Constance will be required to further develop this hypothesis, and sediment samples from periods before and after quagga invasion may help to resolve historic and existing energy pathways.

The profound changes in $\delta^{13}C$ of pelagic whitefish observed here also corroborate the second hypothesis of the present study, that sources of energy, and thus energy pathways, have changed considerably in Lake Constance since the establishment of quaggas. This change is supported by the elimination of pre-invasion isotopic niche overlaps between benthivorous and piscivorous feeding guilds previously (before quagga invasion) amounting to 19% and 51% niche overlaps in ULC and LLC respectively.

On first view it is surprising that no changes were observed in $\delta^{15}N$ of pelagic whitefish between pre- and post-quagga periods. However, this is consistent with results from other large lakes where hyperabundant quaggas are associated with greatly altered energy pathways. For example in Lake Huron whitefish exhibited large changes in $\delta^{13}C$ after quagga invasion, but no or only slightly (dependent on sampling site) changes in $\delta^{15}N$ (Fera et al., 2017). Meanwhile the model for $\delta^{15}N$ revealed that in Upper and Lower Lake Constance the occurrence of quaggas significantly changed the isotopic values of other analyzed fish species. Highly variable shifts in $\delta^{15}N$ across taxa like in Lake Constance have also been observed in other lakes (Rennie et al., 2013; Turschak et al., 2014). For herbivorous rudd in Upper Lake Constance, the observed shift may be associated with changes in the submerged macrophytes community following quagga invasion (Geisler et al., 2016; Zhu et al., 2006). For roach, tench, bleak, and benthic whitefish the variations in the isotopic signature may be associated with changes in the benthic macrozoobenthos community, because aggregations of quaggas (druses) rapidly develop into three-dimensional reef-like structures that provide shelter and food for invertebrates, thereby boosting diversity and species interactions (Karatayev et al., 2015; Umek et al., 2010). Such changes at the base of the food web could easily influence consumers at higher trophic levels, such as piscivorous fish (Turschak and Bootsma, 2015) and thus account for large difference in the $\delta^{15}N$ value of piscivorous pike in Lake Constance before and after quagga invasion. While it is possible that overarching impacts, such as watershed influences from sewage or agricultural inputs or an increase in N-fixers (*i.e.,* cyanobacteria) among the algal community (Rennie et al., 2013) might cause to decline the $\delta^{15}N$ value of fishes, there is no evidence that such impacts exist on a large scale and hence cannot explain different directional shifts observed here. Indeed,

there appears to be no single explanation for the variable changes in the $\delta^{15}N$ values of different endemic fish species. Additional work is required to determine the causes for varying $\delta^{15}N$ values in particular benthic fish species in Lake Constance.

Meanwhile the changes in the isotopic signature of endemic benthivorous fish species in Lake Constance point to a general change in feeding behavior. Before quagga mussel invasion, mussels were only rarely found in benthivorous whitefish, and only a few individual mussels when mussels were found (R. Rösch, unpublished data). In recent years, more than 1000 quaggas can be found in large benthic whitefish (data not shown). Furthermore, the $\delta^{13}C$ model reveals that quagga consumers exhibit significantly lower $\delta^{13}C$ values than non-quagga consumers and that the interaction of feeding behaviour and period had a significant impact. The analyses of stomach contents revealed that roach in both lakes and tench in LLC consume large quantities of quagga mussels. Roach are opportunistic feeders (Nahon et al., 2020), and appear to have switched from their previously preferred diet of zooplankton and insect larvae (Hölker and Breckling, 2001; Persson, 1987) in response to this new, superabundant food source. A similar opportunistic switch could be assumed for tench in LLC (Boedeltje et al., 2019). Nevertheless, other interpretations are possible, given the isotopic values of several other potential diet components. For example, zooplankton and insect larvae also differ significantly from dreissenids (Verstijnen et al., 2019), and highly divergent values are to be expected between quagga consumers and non-quagga-consumers. Furthermore, snail species commonly found in the digestive tracts of roach and tench in this study, such as the very abundant *Bithynia tentaculata* in ULC or *Viviparus viviparus* in LLC, exhibit considerably higher $\delta^{13}C$ values than quaggas. The conclusion that observed changes in $\delta^{13}C$ in roach and tench reflect a shift away from previously high levels of snail consumption is supported by stomach content analysis from tench; in tench from ULC, the diet comprised 60 % snails and 23 % quaggas, while those from LLC consumed fewer snails (25 % of diet) and more quaggas (43 % of the diet). This difference alone could be the explanation for the differences in stable isotope signatures between tench from the two lakes.

While stomach content analysis reveals that some roach and whitefish in Lake Constance do consume mussels, the instantaneous presence or absence of quaggas in the digestive tract was not reflected in the $\delta^{15}N$ or $\delta^{13}C$ archived in the tissue of analysed individuals. Furthermore, there was no evidence that some individuals became specialists on mussel feeding while others preferred a different diet. However, in the case of roach, there is a clear positive correlation between body size (length) and both $\delta^{13}C$ and $\delta^{15}N$, suggesting that mussel predation may be length-dependent in this species. This result confirms the findings of previous authors suggesting that gape size, the dimensions of pharyngeal teeth and chewing ability limit the range of quagga sizes available to roach (Nagelkerke and Sibbing, 1996; Sibbing, 1988) but contradicts another study in Lake Constance (Baer et al., 2022) where no correlation was observed between total length and mussel consumption by roach. Additional studies are needed to evaluate the importance of roach length for mussel consumption.

Despite the distinct changes in the energy pathways indicated by stable isotope composition, the overall impact of quagga invasion on the commercially important whitefish seems to be of minor significance. The high proportions of either zooplankton or benthic macroinvertebrates in the digestive tracts of Lake Constance whitefish suggest that adequate food remained available at the time of sampling and that whitefish have not thus far been forced to supplement their usual diet with quaggas (Pothoven et al., 2001; Pothoven and Madenjian, 2008). However, if the filtration of quaggas does decrease zooplankton density in Lake Constance in the future (Karatayev et al., 2015), forcing whitefish

to begin targeting quaggas as prey, the impact on growth and recruitment could be severe (Hoyle et al., 2008; Rennie et al., 2009) because of the relatively low caloric value and high handling cost of consuming mussels (Baer et al., 2022; Nagelkerke and Sibbing, 1996).

Conclusion

The present study highlights pronounced changes in energetic pathways in a large aquatic ecosystem, Lake Constance, following invasion of quagga mussel. For pelagic whitefish, observed increases in stable isotope values are most likely the result of increasing benthic-derived nearshore primary production and feeding closer to shore, rather than a change in dietary composition. In contrast, other fish species including benthic whitefish, roach and tench, showed marked qualitative changes in feeding behaviour and now rely on quagga mussels for at least part of their diet. This novel food source in combination with likely changes in the benthic macrozoobenthos and submerged macrophytes community appears to be driving changes in the isotopic composition of the fish community in Lake Constance. It is likely that similar changes will occur in other large lakes in Central Europe facing invasion by quagga mussels.

CRediT authorship contribution statement

Jan Baer: Formal analysis, Data curation, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. **Christina Spiessl:** Formal analysis, Data curation, Software, Investigation. **Karl Auerswald:** Validation, Visualization, Writing – review & editing. **Juergen Geist:** Validation, Visualization, Writing – review & editing. **Alexander Brinker:** Formal analysis, Project administration, Resources, Software, Supervision, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Alexander, T.J., Vonlanthen, P., Périat, G., Eckmann, R., Raymond, J.C., Degiorgi, F., Seehausen, O., 2015. Artenvielfalt und Zusammensetzung der Fischpopulation im Bodensee. Eawag, Kastanienbaum.

Baer, J., DeWeber, J.T., Rösch, R., Brinker, A., 2021a. Aquaculture of coregonid species — Quo vadis? Ann. Zool. Fennici. 58, 307–318. https://doi.org/10.5735/086.058.0414.

Baer, J., Eckmann, R., Rösch, R., Arlinghaus, R., Brinker, A., 2017. Managing Upper Lake Constance fishery in a multi-sector policy landscape: beneficiary and victim of a century of anthropogenic trophic change, in: Song, A.M., Bower, S.D., Onyango, P., Cooke, S.J., Chuenpagdee, R. (Eds.), Inter-Sectoral Governance of Inland Fisheries. TBTI Publication Series, E-01/2017. Too Big To Ignore-WorldFish, St. John's, Canada, pp. 32–47.

Baer, J., Spiessl, C., Brinker, A., 2022. Size matters? Species- and size-specific fish predation on recently established invasive quagga mussels *Dreissena*

rostriformis bugensis Andrusov 1897 in a large, deep oligotrophic lake. J. Fish Biol.. https://doi.org/10.1111/jfb.15043.

Beggel, S., Cerwenka, A., Brandner, J., Geist, J., 2015. Shell morphological versus genetic identification of quagga mussel (*Dreissena bugensis*) and zebra mussel (*Dreissena polymorpha*). Aquat. Invasions 10 (1), 93–99. https://doi.org/10.3391/ai10.3391/ai.2015.10.110.3391/ai.2015.10.1.09.

Boedeltje, D.B., Barbiero, R.P., Schaap, M., Sollman, P., de Vos, M., Lenssen, J.P.M., Verberk, W.C.E.P., 2019. Plant dispersal in a temperate stream by fish species with contrasting feeding habits: The role of plant traits, fish diet, season, and propagule availability. Front. Ecol. Evol. 7, 54. https://doi.org/10.3389/fevo.2019.00054.

Brandner, J., Auerswald, K., Cerwenka, A.F., Schliewen, U.K., Geist, J., 2013. Comparative feeding ecology of invasive Ponto-Caspian gobies. Hydrobiologia 703 (1), 113–131. https://doi.org/10.1007/s10750-012-1349-9.

Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., Weidel, B.C., 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-Up and Top-Down regulation. BioScience 64, 26–39. https://doi.org/10.1093/biosci/bit001.

Chucholl, C., 2016. The bad and the super-bad: prioritising the threat of six invasive alien to three imperilled native crayfishes. Biol. Invasions 18, 1967–1988. https://doi.org/10.1007/s10530-016-1141-2.

Cleven, E.J., Frenzel, P., 1993. Population-dynamics and production of *Dreissena polymorpha* (Pallas) in River Seerhein, the outlet of Lake Constance (Obersee). Arch Hydrobiol. 127, 395–407.

Eckmann, R., Rösch, R., 1998. Lake Constance fisheries and fish ecology. Advanc. Limnol. 53, 285–301.

Evans, M.A., Fahnenstiel, G., Scavia, D., 2011. Incidental oligotrophication of North American Great Lakes. Environ. Sci. Technol. 45 (8), 3297–3303. https://doi.org/10.1021/es103892w.

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. J. Great Lakes Res. 36, 20–29. https://doi.org/10.1016/j.jglr.2010.03.009.

Fera, S.A., Rennie, M.D., Dunlop, E.S., 2017. Broad shifts in the resource use of a commercially harvested fish following the invasion of dreissenid mussels. Ecology 98 (6), 1681–1692. https://doi.org/10.1002/ecy.1836.

Geisler, M.E., Rennie, M.D., Gillis, D.M., Higgins, S.N., 2016. A predictive model for water clarity following dreissenid invasion. Biol. Invasions 18 (7), 1989–2006. https://doi.org/10.1007/s10530-016-1146-x.

He, J.X., Bence, J.R., Madenjian, C.P., Pothoven, S.A., Dobiesz, N.E., Fielder, D.G., Johnson, J.E., Ebener, M.P., Cottrill, R.A., Mohr, L.C., Koproski, S.R., 2015. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. Can. J. Fish. Aquat. Sci. 72 (1), 7–23. https://doi.org/10.1139/cjfas-2014-0161.

Higgins, S.N., Zanden, M.J.V., 2010. What a difference a species makes: a meta–analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. 80 (2), 179–196. https://doi.org/10.1890/09-1249.1.

Hölker, F., Breckling, B., 2001. An individual-based approach to depict the influence of the feeding strategy on the population structure of roach (*Rutilus rutilus* L.). Limnologica 31 (1), 69–78. https://doi.org/10.1016/S0075-9511(01)80051-7.

Hoyle, J.A., Bowlby, J.N., Morrison, B.J., 2008. Lake whitefish and walleye population responses to dreissenid mussel invasion in eastern Lake Ontario. Aquat Ecosyst Health Manag 11, 403–411. https://doi.org/10.1080/14634980802530392.

Hydra, 2021. Aktuelles | Aquatische Neozoen im Bodensee [WWW Document]. Aquatische Neozoen im Bodensee. URL http://www.neozoen-bodensee.de/aktuelles (accessed 3.11.21).

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

Kakareko, T., Kobak, J., Grabowska, J., Jermacz, Ł., Przybylski, M., Poznańska, M., Pietraszewski, D., Copp, G.H., 2013. Competitive interactions for food resources between invasive racer goby *Babka gymnotrachelus* and native European bullhead *Cottus gobio*. Biol. Invasions 15 (11), 2519–2530. https://doi.org/10.1007/s10530-013-0470-7.

Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 2015. Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. Hydrobiologia 746 (1), 97–112. https://doi.org/10.1007/s10750-014-1901-x.

Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 2005. Contrasting distribution and impacts of two freshwater exotic suspension feeders, *Dreissena polymorpha* and *Corbicula fluminea*, in: Dame, R.F., Olenin, S. (Eds.), The comparative roles of suspension-feeders in ecosystems: Proceedings of the NATO Advanced Research Workshop on the comparative roles of suspension-feeders in ecosystems. Nida, Lithuania 4–9 October 2003. Springer Netherlands, Dordrecht, pp. 239–262. https://doi.org/10.1007/1-4020-3030-4_14.

Karatayev, A.Y., Padilla, D.K., Minchin, D., Boltovskoy, D., Burlakova, L.E., 2007. Changes in global economies and trade: the potential spread of exotic freshwater bivalves. Biol. Invasions 9 (2), 161–180. https://doi.org/10.1007/s10530-006-9013-9.

Keeling, C.D., 1979. The Suess effect: 13Carbon-14Carbon interrelations. Environ. Int. 2 (4-6), 229–300. https://doi.org/10.1016/0160-4120(79)90005-9.

Keeling, R.F., Keeling, C.D., 2017. Atmospheric Monthly In Situ CO2 Data - Mauna Loa Observatory, Hawaii. In Scripps CO2 Program Data. UC San Diego Library

Digital Collections [WWW Document]. URL https://doi.org/10.6075/J08W3BHW (accessed 7.1.21).

Keller, R.P., Geist, J., Jeschke, J.M., Kühn, I., 2011. Invasive species in Europe: ecology, status, and policy. Environ. Sci. Eur. 23, 23. https://doi.org/10.1186/2190-4715-23-23.

Madenjian, C.P., Bunnell, D.B., Warner, D.M., Pothoven, S.A., Fahnenstiel, G.L., Nalepa, T.F., Vanderploeg, H.A., Tsehaye, I., Claramunt, R.M., Clark, R.D., 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: A synthesis. J. Great Lakes Res. 41, 217–231. https://doi.org/10.1016/j.jglr.2015.08.009.

Madenjian, C.P., Pothoven, S.A., Schneeberger, P.J., Ebener, M.P., Mohr, L.C., Nalepa, T.F., Bence, J.R., 2010. Dreissenid mussels are not a "dead end" in Great Lakes food webs. J. Great Lakes Res. 36, 73–77. https://doi.org/10.1016/j.jglr.2009.09.001.

Matthews, B., Marchinko, K.B., Bolnick, D.I., Mazumder, A., 2010. Specialization of trophic position and habitat use by sticklebacks in an adaptive radiation. Ecology 91 (4), 1025–1034. https://doi.org/10.1890/09-0235.1.

Mayer, C.M., Burlakova, L.E., Eklöv, P., Fitzgerald, D., Karatayev, A.Y., Ludsin, S.A., Millard, S., Mills, E.L., Ostapenya, A.P., Rudstam, L.G., Zhu, B., Zhukova, T.V., 2014. Benthification of freshwater lakes - exotic mussels turning ecosystems upside down. In: Nalepa, T.F., Schloesser, D.W. (Eds.), Quagga and Zebra Mussels: Biology, Impacts, and Control. CRC Press, Boca Raton, FL., pp. 575–585.

McNickle, G.G., Rennie, M.D., Gary Sprules, W., 2006. Changes in benthic invertebrate communities of South Bay, Lake Huron following invasion by zebra mussels (*Dreissena polymorpha*), and potential effects on Lake Whitefish (*Coregonus clupeaformis*) Diet and Growth. J. Great Lakes Res. 32, 180–193. https://doi.org/10.3394/0380-1330(2006)32[180:CIBICO]2.0.CO;2.

Molloy, D.P., Karatayev, A.Y., Burlakova, L.E., Kurandina, D.P., Laruelle, F., 1997. Natural enemies of zebra mussels: Predators, parasites, and ecological competitors. Rev. Fish. Sci. 5 (1), 27–97. https://doi.org/10.1080/10641269709388593.

Molnar, J.L., Gamboa, R.L., Revenga, C., Spalding, M.D., 2008. Assessing the global threat of invasive species to marine biodiversity. Front. Ecol. Environ. 6 (9), 485–492. https://doi.org/10.1890/070064.

Moore, T.P., Collier, K.J., Duggan, I.C., 2019. Interactions between *Unionida* and non-native species: A global meta-analysis. Aquat Conserv 29 (9), 1438–1451. https://doi.org/10.1002/aqc.v29.910.1002/aqc.3040.

Nagelkerke, LAJ, Sibbing, F.A., 1996. Efficiency of feeding on zebra mussel (*Dreissena polymorpha*) by common bream (*Abramis brama*), white bream (*Blicca bjoerkna*), and roach (*Rutilus rutilus*): the effects of morphology and behavior. Can. J. Fish. Aquat. Sci. 53 (12), 2847–2861. https://doi.org/10.1139/f96-229.

Nahon, S., Roussel, J.-M., Jaeger, C., Menniti, C., Kerhervé, P., Mortillaro, J.-M., Aubin, J., 2020. Characterization of trophic niche partitioning between carp (*Cyprinus carpio*) and roach (*Rutilus rutilus*) in experimental polyculture ponds using carbon (δ13C) and nitrogen (δ15N) stable isotopes. Aquaculture 522, 735162. https://doi.org/10.1016/j.aquaculture.2020.735162.

Peeler, E.J., Oidtmann, B.C., Midtlyng, P.J., Miossec, L., Gozlan, R.E., 2011. Non-native aquatic animals introductions have driven disease emergence in Europe. Biol. Invasions 13 (6), 1291–1303. https://doi.org/10.1007/s10530-010-9890-9.

Persson, L., 1987. Effects of habitat and season on competitive interactions between roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*). Oecologia 73 (2), 170–177. https://doi.org/10.1007/BF00377504.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., Tsomondo, T., 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agric. Ecosyst. Environ. 84 (1), 1–20. https://doi.org/10.1016/S0167-8809(00)00178-X.

Pothoven, S.A., Fahnenstiel, G.L., 2013. Recent change in summer chlorophyll a dynamics of southeastern Lake Michigan. J. Great Lakes Res. 39 (2), 287–294. https://doi.org/10.1016/j.jglr.2013.02.005.

Pothoven, S.A., Madenjian, C.P., 2008. Changes in consumption by alewives and lake whitefish after dreissenid mussel invasions in Lakes Michigan and Huron. N Am J Fish Manag 28 (1), 308–320. https://doi.org/10.1577/M07-022.1.

Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J., Brandt, S.B., 2001. Changes in diet and body condition of Lake Whitefish in Southern Lake Michigan associated with changes in benthos. N Am J Fish Manag 21, 876–883. https://doi.org/10.1577/1548-8675(2001)021<0876:CIDABC>2.0.CO;2.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahel, F.J., Olden, J.D., 2008. Assessing the effects of climate change on aquatic invasive species. Conserv. Biol. 22 (3), 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x.

Rennie, M.D., Evans, D.O., Young, J.D., 2013. Increased dependence on nearshore benthic resources in the Lake Simcoe ecosystem after dreissenid invasion. Inland Waters 3, 297–310. https://doi.org/10.5268/IW-3.2.540.

Rennie, M.D., Sprules, W.G., Johnson, T.B., 2009. Resource switching in fish following a major food web disruption. Oecologia 159 (4), 789–802. https://doi.org/10.1007/s00442-008-1271-z.

Riley, S.C., Dunlop, E.S., 2016. Misapplied survey data and model uncertainty result in incorrect conclusions about the role of predation on alewife population dynamics in Lake Huron: a comment on. Can. J. Fish. Aquat. Sci. 73 (5), 860–864. https://doi.org/10.1139/cjfas-2015-0237.

Rösch, R., 2014. Lake Constance fish and fisheries, in: Welcomme, R.L., Valbo-Jorgensen, J., Walls, A.S. (Eds.), Inland fisheries evolution and management - Case studies from four continents, FAO Fisheries and Aquaculture Technical Paper. Rome, FAO, pp. 21–32.

Rösch, R., Baer, J., Brinker, A., 2018. Impact of the invasive three-spined stickleback (*Gasterosteus aculeatus*) on relative abundance and growth of native pelagic whitefish (*Coregonus wartmanni*) in Upper Lake Constance. Hydrobiologia 824 (1), 243–254. https://doi.org/10.1007/s10750-017-3479-6.

Sachs, L. (Ed.), 1997. Angewandte Statistik. Springer Berlin Heidelberg, Berlin, Heidelberg.

Sibbing, F.A., 1988. Specializations and limitations in the utilization of food resources by the carp, Cyprinus carpio: a study of oral food processing. Environ Biol Fish 22, 161–178. https://doi.org/10.1007/BF00005379.

Skinner, M.M., Martin, A.A., Moore, B.C., 2016. Is lipid correction necessary in the stable isotope analysis of fish tissues? Rapid Commun. Mass Spectrom. 30 (7), 881–889. https://doi.org/10.1002/rcm.7480.

Stich, H.B., Brinker, A., 2010. Oligotrophication outweighs effects of global warming in a large, deep, stratified lake ecosystem. Glob Chang Biol 16, 877–888. https://doi.org/10.1111/j.1365-2486.2009.02005.x.

Strayer, D.L., Malcom, H.M., 2018. Long-term responses of native bivalves (*Unionidae* and *Sphaeriidae*) to a Dreissena invasion. Freshw Sci 37 (4), 697–711. https://doi.org/10.1086/700571.

Toussaint, A., Beauchard, O., Oberdorff, T., Brosse, S., Villéger, S., 2016. Worldwide freshwater fish homogenization is driven by a few widespread non-native species. Biol. Invasions 18 (5), 1295–1304. https://doi.org/10.1007/s10530-016-1067-8.

Turschak, B.A., Bootsma, H.A., 2015. Lake Michigan trophic structure as revealed by stable C and N isotopes. J. Great Lakes Res. 41, 185–196. https://doi.org/10.1016/j.jglr.2015.04.004.

Turschak, B.A., Bunnell, D., Czesny, S., Höök, T.O., Janssen, J., Warner, D., Bootsma, H.A., 2014. Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. Ecology 95 (5), 1243–1252. https://doi.org/10.1890/13-0329.1.

Umek, J., Chandra, S., Rosen, M., Wittmann, M., Sullivan, J., Orsak, E., 2010. Importance of benthic production to fish populations in Lake Mead prior to the establishment of quagga mussels. Lake Reserv Manag 26 (4), 293–305. https://doi.org/10.1080/07438141.2010.541328.

Vander Zanden, M.J., Rasmussen, J.B., 1999. Primary consumer δ 13C and δ 15N and the trophic position of aquatic consumers. Ecology 80 (4), 1395–1404.

Vanderploeg, H.A., Liebig, J.R., Nalepa, T.F., Fahnenstiel, G.L., Pothoven, S.A., 2010. Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan. J. Great Lakes Res. 36, 50–59. https://doi.org/10.1016/j.jglr.2010.04.005.

Verburg, P., 2007. The need to correct for the Suess effect in the application of δ13C in sediment of autotrophic Lake Tanganyika, as a productivity proxy in the Anthropocene. J. Paleolimnol. 37 (4), 591–602. https://doi.org/10.1007/s10933-006-9056-z.

Verstijnen, Y.J.M., Lucassen, E.C.H.E.T., Gaag, M. van der, Wagenvoort, A.J., Castelijns, H., Ketelaars, H.A.M., Velde, G. van der, Smolders, A.J.P., 2019. Trophic relationships in Dutch reservoirs recently invaded by Ponto-Caspian species: insights from fish trends and stable isotope analysis. Aquat Invasions 14, 280–298.

Werner, S., Mörtl, M., Bauer, H.G., Rothhaupt, K.O., 2005. Strong impact of wintering waterbirds on zebra mussel (*Dreissena polymorpha*) populations at Lake Constance, Germany. Freshwater Biol 50 (8), 1412–1426. https://doi.org/10.1111/j.1365-2427.2005.01411.x.

Zhu, B., Fitzgerald, D.G., Mayer, C.M., Rudstam, L.G., Mills, E.L., 2006. Alteration of ecosystem function by zebra mussels in Oneida Lake: Impacts on submerged macrophytes. Ecosystems 9 (6), 1017–1028. https://doi.org/10.1007/s10021-005-0049-y.