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To be alive or not to be alive: Radiocarbon data provide new perspective on species diversity in the Caspian Sea

Catharina Clewing¹  | Christian Albrecht¹  | Vitaliy V. Anistratenko²  |
Olga Yu. Anistratenko²  | Thomas Wilke¹ 

¹Department of Animal Ecology and Systematics, Justus Liebig University Giessen, Giessen, Germany

²Department of Invertebrate Fauna and Systematics, Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine

Correspondence

Catharina Clewing, Department of Animal Ecology and Systematics, Justus Liebig University Giessen, Heinrich-Buff-Ring 26 (IFZ), 35392 Giessen, Germany.
Email: catharina.clewing@allzool.bio.uni-giessen.de

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Abstract

1. The Caspian Sea is undergoing a severe biodiversity crisis. However, estimates of current extinction rates are difficult to obtain due to the lack of reliable pre-Anthropocene baseline data. For example, because the majority of endemic gastropod species was described from “fresh looking” shells, it remains unclear which species still existed prior to the Anthropocene.
2. This study therefore used the species-rich microgastropod family Hydrobiidae to assess the extent to which endemic species were collected alive during the Anthropocene. Literature and database searches were performed. In addition, ¹⁴C dating was conducted on “fresh looking” shells collected in the Caspian Sea during the last 150 years.
3. The literature review revealed that 75% of the “recent” species are only known from empty shells and 25% were recorded with a soft body. The ¹⁴C data showed that all “recent” specimens examined had an age between 1624 cal BC and 1888 cal AD. Two species studied predate the beginning of the Anthropocene. Two other species potentially or likely existed during the Anthropocene. This suggests that the number of endemic species still present at the beginning of the Anthropocene is lower than previously thought.
4. The data also suggest that there was a substantial loss of species between the late 18th century and the 1950s and that only two endemic hydrobiid species have recently been found alive. These findings further contribute to the notion of a severe biodiversity crisis in the Caspian Sea.
5. For accurate estimates of current extinction rates of Caspian Sea gastropods, pre-Anthropocene biodiversity data need to be further corroborated. Particularly, studies are required to clarify the taxonomic status of the dubious taxa and a possible “collection crisis” in the Caspian Sea due to decreasing sampling efforts in recent decades. In addition, comprehensive IUCN assessments are urgently required.

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KEYWORDS

ancient lake, Anthropocene, biodiversity crisis, extinction, Hydrobiidae, taxonomy

1 | INTRODUCTION

The increasing rate of extinctions in the Anthropocene, caused by various stressors and impacts such as habitat modification, climate change, pollution, and the introduction of invasive species, has led to biodiversity crises in many parts of the world (Johnson et al., 2017). Biodiversity loss is particularly critical for ecosystems that are highly vulnerable to anthropogenic impacts and/or for those with high degrees of endemism. A prime example of a biodiversity crisis is the ancient Caspian Sea, the largest inland water body on Earth with a strong north–south salinity gradient (Kostianoy & Kosarev, 2005). It harbours a unique continental aquatic biodiversity in several higher taxa (Bogutskaya et al., 2013; Copilas-Ciocianu & Sidorov, 2022), with molluscs being particularly diverse and rich in endemic species (99 species in total, 86 endemic species; Wesselingh et al., 2019).

Today, many of these formerly abundant endemic species are in severe decline or at risk of extinction. They suffer greatly from deliberately or unintentionally introduced species, chemical pollution, habitat destruction, and oil industry disturbance (Grigorovich et al., 2003; Lattuada et al., 2019, 2020; Shiganova et al., 2023). This has been exemplified by the formerly common endemic bivalve species *Dreissena elata* and *Dreissena caspia*, which disappeared in the mid-20th century (Kosarev & Yablonskaya, 1994). These facts and the lack of recent records for most endemic Caspian species (Wesselingh et al., 2019) indicate an ongoing biodiversity crisis. However, the extent of the Anthropocene biodiversity crisis is difficult to determine, in part because of the lack of reliable baseline data on the number of pre-Anthropocene endemic mollusc species in the Caspian Sea.

The majority of endemic gastropod species in the Caspian Sea has been described from shells (Vinarski & Kantor, 2016). Many of them look “fresh,” but their actual age has never been critically evaluated. The preservation or degree of dissolution of shells in aquatic ecosystems depends on a variety of processes and conditions operating at different scales (Cohen, 2003; Cummins, 1994). While some taphonomic processes, such as cementation and encrustation, can increase the preservation potential of shells, other processes are destructive and cause the loss of shelly material (Olszewski, 2004). Water chemistry, composition of the lake sediments, intrinsic shell properties (e.g., shell size, thickness, and mineralogy), and the burial depth are some of the key factors mentioned (Cohen, 2003). Therefore, it often remains unclear whether “fresh looking” shells represent living or (sub)fossil taxa.

In the present study, we used the most species-rich group of molluscs in the Caspian Sea—the microgastropod family Hydrobiidae (see Wesselingh et al., 2019)—as a model taxon. Our general goal was to assess the degree to which putatively recent endemic species were collected alive during the Anthropocene (here considered as the

period since the beginning of industrialization in the late 18th century sensu Waters & Turner, 2022; see also Perkins, 2023). Specifically, we (i) used current and historical literature records to assess the number of endemics that were either found alive or whose shells were reported to contain (parts of) the soft body and (ii) applied radiocarbon (¹⁴C) dating to “fresh looking” hydrobiid shells collected in the Caspian Sea over the past 150 years. By identifying species falsely assumed to have lived during the Anthropocene, we will help quantify the contribution of this temporal bias to the ongoing biodiversity crisis in the Caspian Sea and thereby strengthen the credibility of claims by scientists around the world of an unprecedented biodiversity loss in the Caspian Sea (Dumont, 1995; Wesselingh et al., 2019; Zonn, 2001).

2 | MATERIAL AND METHODS

2.1 | Biodiversity assessment

The microgastropod family Hydrobiidae (superfamily Truncatelloidea), characterized by a shell size of 0.5–15 mm, represents one of the most diverse gastropod groups with 900–1200 valid species (Delicado et al., 2023). They inhabit a wide range of freshwater ecosystems (e.g., springs, streams, and lakes) but are also found in coastal marine and brackish waters (Barnes, 1999; Bodon et al., 2001; Hershler, 1994; Wilke & Delicado, 2019). Numerous hydrobiid species seem to be narrow-range endemics (Wilke & Delicado, 2019). Especially ancient lakes such as the Caspian Sea (Wesselingh et al., 2019) exhibit a high degree of endemism.

To gain a more comprehensive understanding of which endemic hydrobiid species have been described or at least reported alive in the Caspian Sea, we extracted information for each recent species from the scientific literature and databases on (i) soft body and radula, if available, (ii) date of last mentioned record alive, (iii) taxonomic status (i.e., accepted, uncertain, or synonymized), and (iv) conservation status (based on the IUCN Red List).

2.2 | ¹⁴C dating

The criteria for the selection of the species to be examined were as follows: (i) species that are endemic to the Caspian Sea, (ii) species that have only been described from shells and have never been found alive, and (iii) the shells must not represent type material. On this basis, we selected the following four species: *Andrusovia dybowskii* Brusina, 1903 (location CS01; Figure 1), *Clathrocaspia brotzkajae* (Starobogatov, 1992) (location CS02), *Laevicaspia sieversii* (Clessin, 1887) (location CS03), and *Turricaspia eburnea* (Logvinenko &

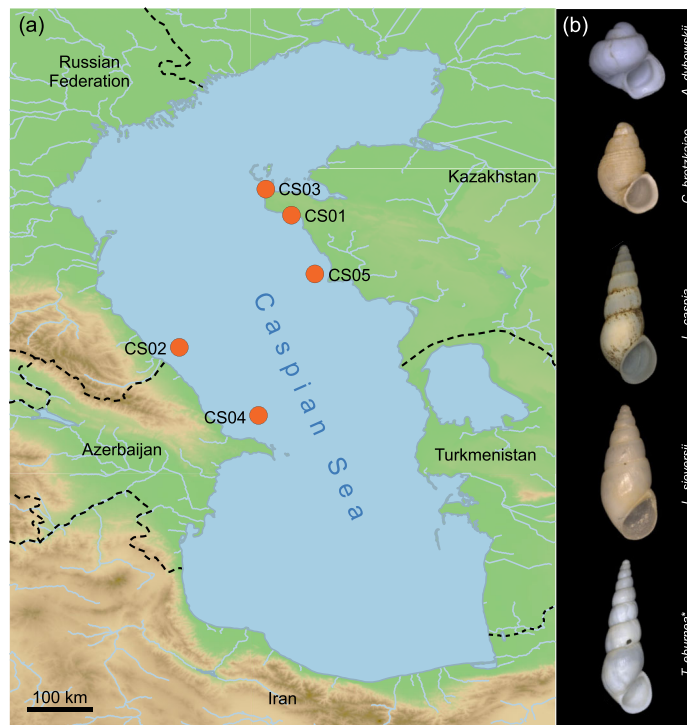


FIGURE 1 (a) Locations (orange dots: CS01 – CS05) of all Caspian Sea gastropods used for ^{14}C dating in the present study. (b) Shell images of the five endemic hydrobiid species analysed: *Andrusovia dybowskii* (shell height = 1.2 mm), *Clathrocaspia brotzkajae* (shell height = 2.2 mm), *Laevicaspia caspia* (shell height = 12.4 mm), *Laevicaspia sieversii* (shell height = 4.1 mm), and *Turricaspia eburnea** (shell height = 13.6 mm). The map was created in QGIS3 and the SRTM 90 m digital elevation data were downloaded from <http://srtm.csi.cgiar.org>.

Starobogatov, 1969) (location CS04). In addition, the shell of one *Laevicaspia caspia* (Eichwald, 1838) specimen that was collected alive (location CS05; previously used for phylogenomic analyses in Clewing et al., 2022) was chosen to test which calibration curve is most suitable for the raw ^{14}C data from the Caspian Sea.

For the dating, complete shells were subjected to accelerator mass spectrometry (AMS) method at the Poznań Radiocarbon Laboratory in Poland (<https://radiocarbon.pl/en>). To obtain accurate AMS ^{14}C measurements, a total shell mass of about 20 mg is recommended. If samples fell below this mass, individuals from the same population were pooled. This was necessary for *A. dybowskii*, *C. brotzkajae*, and *L. sieversii* where 16, 5, and 2 specimens, respectively, were pooled.

The program OxCal (version 4.4; Ramsey, 2009) was used to convert ^{14}C ages to calendar years (cal). To determine the best-fit calibration curve for the Caspian Sea material, the following two curves were used to calibrate the living material of *L. caspia* collected in 1876: (i) the atmospheric curve for the northern Hemisphere, IntCal20 (Reimer et al., 2020); and (ii) the marine curve, Marine20 (Heaton et al., 2020), representing a modelled global ocean average. The curve closest to the actual collection date of *L. caspia* was selected as the best-fit calibration curve. For the marine calibration,

local variations in ^{14}C concentration had to be taken into account. Therefore, ΔR values and associated uncertainties for four sites in the Caspian Sea region (see Table S2) were taken from the Marine Reservoir Database (Reimer & Reimer, 2001), resulting in an average ΔR of -163 ± 19 .

3 | RESULTS

3.1 | Biodiversity assessment

Information on 60 endemic hydrobiid species of the Caspian Sea is listed in Table S1. Of these, seven species (*Andrusovia andrusvi*, *Andrusovia brusinai*, *Andrusovia marina*, *Ulskia behningi*, *Ulskia derzhavini*, *Turricaspia eucalia*, and *Turricaspia ptychophora*) were recently considered to be junior synonyms (Anistratenko et al., 2019, 2021). Of the remaining 53 species, 30 (57%) likely represent valid species and 23 (43%) species whose taxonomic status is considered as uncertain (marked with asterisk throughout this study); 40 (75%) of the 53 species are only known from empty shells, and 13 species (25%) were ever recorded alive or with a soft body inside the shell (see Figure 2 and Table S1). Of these latter 13 species, only two

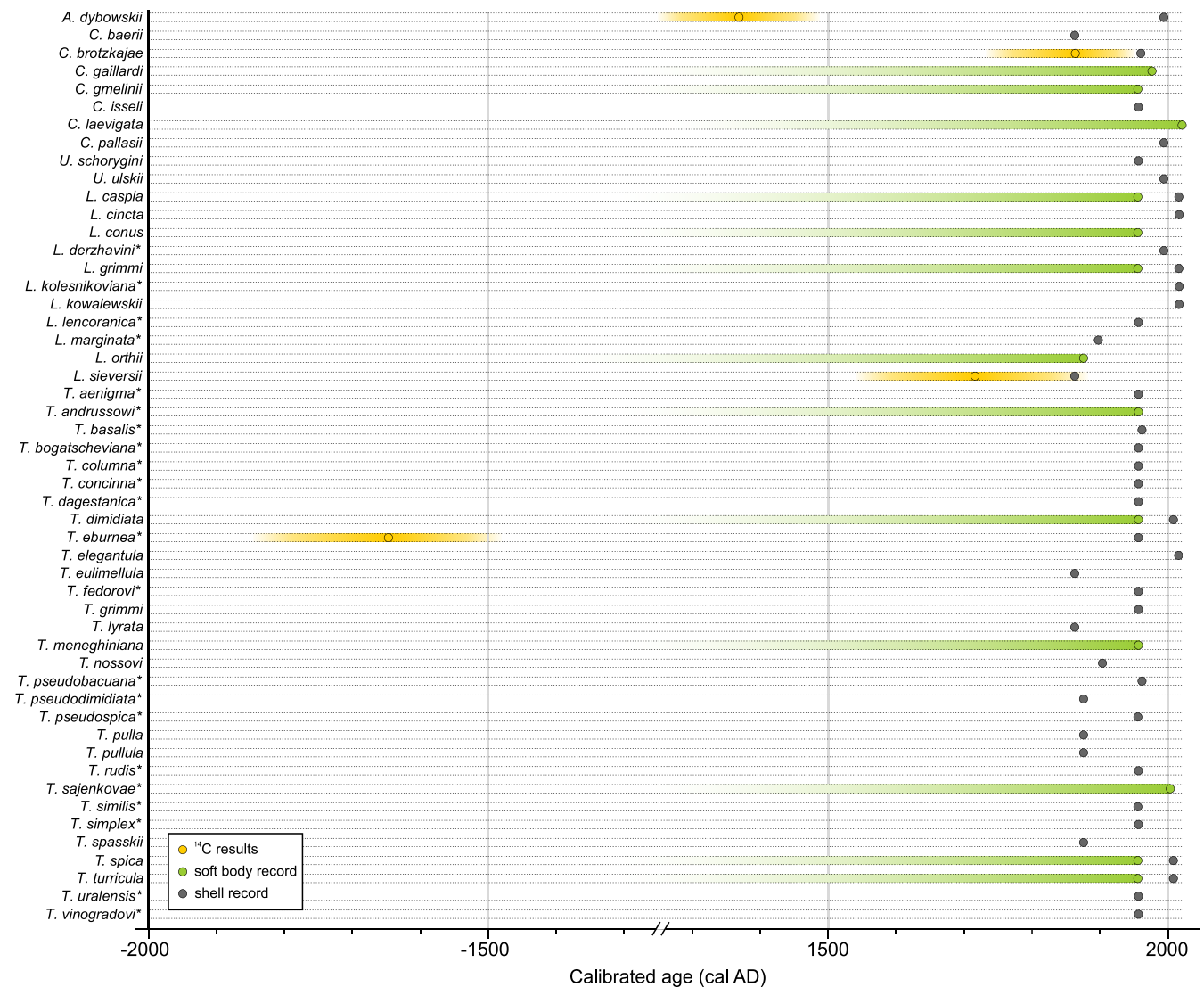


FIGURE 2 Summary plot showing the results of the biodiversity assessment (grey and green dots) and the calibrated shell ages based on the ¹⁴C dating (yellow dots). Species names for which the taxonomic status is currently uncertain are marked with an asterisk. Genus abbreviations: A. = Andrusovia, C. = Clathrocaspia, L. = Laevicaspia, T. = Turricaspia.

species were found alive within the last 20 years. The remaining 11 species were (last) found alive between 1876 and 1977 (for more details, see Table S1). Five of these latter species have recently (since 2008) been found as shells: *L. caspia*, *Laevicaspia grimmi*, *Turricaspia dimidiata*, *Turricaspia spica*, and *Turricaspia turricula* (for details see Figure 2 and Table S1).

Only 17 of 53 hydrobiid species (32%) endemic to the Caspian Sea were assessed in the IUCN Red List. Of these, 16 species are categorized as DD (i.e., data deficient) and the remaining as LC (least concern; see Table S1).

3.2 | ¹⁴C ages

The comparison of the two calibration approaches for *L. caspia* (collected alive in 1876) using either the IntCal20 curve

(mean = 1460 cal AD, range = 1421–1615 cal AD; see Figure S1) or the Marine20 curve (mean = 1877 cal AD, range = 1728–1953 cal AD; see Figure S2) indicated that the latter seems to be better suited for the Caspian taxa, because it is congruent with the time of collection. By applying this calibration curve to the remaining ¹⁴C ages (see Table 1), we obtained the following ages: (1) *A. dybowskii*, collected in 2017, was dated to the year 1382 (range: 1272–1500 cal AD); (2) *C. brotzkajae*, collected in 1960, was dated to the year 1888 (range: 1744–1953 cal AD); (3) *L. sieversij*, collected in 2017, was dated to the year 1733 (range: 1553–1905 cal AD), and (4) *T. eburnea**, collected in 1957, was dated to 1624 cal BC (range: 1801–1454 cal BC). In summary (Figure 2), all shells examined here came from individuals that had long been dead at the time of collection (i.e., collection year minus mean ¹⁴C age = 635 years for (1), 72 years for (2), 284 years for (3), and 3581 years for (4)).

TABLE 1 Information on location and ^{14}C dating results of all analysed specimens.

Species	Voucher no.	State	Collection year	Location	Coordinates	^{14}C age (BP)	Calibrated age (cal AD)	
							From	to
<i>Andrusovia dybowskii</i>	UGSB 27112	Shell	2017	Caspian Sea, offshore, Kazakhstan, CS01	44.24470°N 50.66580°E	985 ± 35	1272–1500	1382
<i>Clathrocaspia brotzkajae</i>	UGSB 26460	Shell	1960	Caspian Sea, offshore, Russian Federation, CS02	42.07500°N 48.82500°E	410 ± 30	1744–1953	1888
<i>Laevicaspia caspia</i>	UGSB 26462	Whole animal	1876	Caspian Sea, off the eastern coast of Kazakhstan, CS05	43.28000°N 51.05000°E	435 ± 30	1728–1953	1877
<i>Laevicaspia sieversii</i>	UGSB 26461	Shell	2017	Caspian Sea, off Bautino Bay, Kazakhstan, CS03	44.67250°N 50.24540°E	600 ± 30	1553–1905	1733
<i>Turricaspia eburnea</i>	UGSB 26458	Shell	1957	Caspian Sea, off Apsheron Peninsula, CS04	40.95833°N 50.12500°E	3640 ± 30	–1801 to –1454	–1624

4 | DISCUSSION

In order to assess the extent of the Anthropocene biodiversity crisis in the Caspian Sea, unbiased baseline data on the number of pre-Anthropocene endemic species are required. The current study therefore aimed to assess the extent to which presumably recent microgastropod species were actually collected alive during the Anthropocene.

Our literature review showed that 75% of the “recent” species are known only from shells and 25% were recorded with a soft body (Figure 2; Table S1). Furthermore, our ^{14}C data for “fresh looking” shells collected in the Caspian Sea over the last 150 years revealed that all specimens examined had a calibrated age between 1624 cal BC and 1888 cal AD. Given the relatively high SD in our analyses (see Section 3), two of the four species studied (i.e., *A. dybowskii* and *T. eburnea**) clearly predate the onset of the Anthropocene, which arguably began in the late 18th century (Perkins, 2023; Waters & Turner, 2022), one species (*L. sieversii*) may have still been alive during the early Anthropocene, and one species (*C. brotzkajae*) likely existed during much of the Anthropocene.

Of course, the ^{14}C ages alone cannot prove that these four species were already extinct at the time of their description. However, considering all available data (Figure 2), there is evidence of a temporal biodiversity bias, as at least some of the “recent” gastropod specimens were long dead at the time of collection. Furthermore, the literature searches revealed that despite recent efforts to disentangle the complex taxonomy of Caspian Sea hydrobiid gastropods (e.g., Anistratenko et al., 2019, 2021; Neubauer et al., 2018; Wesselingh et al., 2019), nearly 50% of taxa remain dubious, further complicating the generation of reliable baseline data on endemic biodiversity.

In spite of these taxonomic obstacles, our study further contributes to the notion of a severe biodiversity crisis in the Caspian Sea. Our data show that only two endemic hydrobiid species have been found alive in the last two decades, namely, *Clathrocaspia laevigata* and *Turricaspia sajenkova*, the latter being an uncertain taxon (see Table S1 for details). Furthermore, the timeline in Figure 2 indicates that between the beginning of the Anthropocene (late 18th century) and the 1950s, there was a considerable loss of species that cannot be explained by taxonomic uncertainties alone. The timeline of extinction roughly coincides with the period of increasing industrialization and chemical pollution in the Caspian Sea region (Lattuada et al., 2019). For example, the first onshore oil well was drilled near Baku (Azerbaijan) in 1848 and the development of offshore oil fields began in 1949 (Zhiltsov et al., 2016). Moreover, the invasion of nonnative species into the Caspian Sea has peaked in parallel, with a variety of negative effects on the native fauna (Shiganova et al., 2023). Unfortunately, the severe loss of hydrobiid species is not yet reflected in the current IUCN assessment, as no endemic hydrobiid species in the Caspian Sea is listed as threatened or extinct (see Table S1).

In conclusion, the current study provides a wealth of evidence for a temporal biodiversity bias in Caspian Sea microgastropods,

suggesting that the number of endemic species still present at the beginning of the Anthropocene is lower than previously thought. At the same time, there is overwhelming evidence of a considerable loss of endemic species over the last 150 years, supporting the notion of a Caspian Sea biodiversity crisis.

However, for accurate estimates of current extinction rates of Caspian Sea endemic gastropods, pre-Anthropocene biodiversity data need to be further corroborated. In particular, further systematic studies are needed to clarify the taxonomic status of the dubious taxa listed in Table S1. This could be achieved, for example, by historical DNA (e.g., Clewing et al., 2022) or proteomic fingerprinting studies of museum specimens (e.g., Wilke et al., 2020). In addition, there may be a “collection crisis” in the Caspian Sea, which could lead to an overestimation of extinction rates. After the collapse of the former Soviet Union and the political changes in the former Eastern Bloc countries, fieldwork in the Caspian Sea region entered a crisis. Many positions in local museums were cut, field stations were closed, and research vessels decommissioned. The fact that numerous species have not been recorded in the last 20 years may therefore be partly related to the sharp decline in sampling effort and the loss of taxonomic expertise. Future studies could therefore use, for example, ignorance maps (Ruete, 2015) to assess the potential bias in sampling effort across the Caspian Sea region.

Despite these limitations and knowledge gaps, we believe that our collection information and ^{14}C data provide a new perspective on endemic species diversity in the Caspian Sea because, to paraphrase William Shakespeare, the question of “to be alive or not to be alive” is crucial to obtaining reliable pre-Anthropocene baselines. This may apply not only to molluscs but also to other shell-bearing endemic species in the Caspian Sea—the world's largest inland water body, which is currently undergoing a catastrophic environmental crisis (Prange et al., 2020).

AUTHOR CONTRIBUTIONS

Catharina Clewing: Writing—original draft (lead); formal analysis (lead); writing—review and editing (equal). **Christian Albrecht:** Conceptualization (supporting); funding acquisition (supporting); writing—review and editing (equal). **Vitaly Anistratenko:** Resources (lead); validation (lead). **Olga Anistratenko:** Resources (supporting); validation (supporting). **Thomas Wilke:** Conceptualization (lead); funding acquisition (lead); writing—review and editing (equal). All authors critically revised the methodology and contributed to writing and drafting the article.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The results are reproducible from data and cited references presented in the article or supporting information tables.

ORCID

Catharina Clewing  <https://orcid.org/0000-0001-7974-5037>

Christian Albrecht  <https://orcid.org/0000-0002-1490-1825>

Vitaliy V. Anistratenko  <https://orcid.org/0000-0003-0832-7625>

Olga Yu. Anistratenko  <https://orcid.org/0000-0002-5270-7900>

Thomas Wilke  <https://orcid.org/0000-0001-8263-7758>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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