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Explosive demographic expansion by dreissenid bivalves as a possible result of astronomical forcing

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Abstract

Human induced range expansions of invasive dreissenid bivalves are of great concern. However, the underlying biological processes are only poorly understood, partly due to the lack of information on natural expansion events. Here we use the extinct bivalve species *Sinucongeria primiformis* as a model organism for testing natural (i.e. non-Anthropocene) blooms of dreissenid species in a lacustrine system of Lake Pannon during the Tortonian (~ 10.5 Myr; Late Miocene). 600 samples from a consecutive core were evaluated for the relative abundance of this pavement-forming mollusc, which cover about 8 millennia of Late Miocene time with a decadal resolution.

Our data indicate that the settlement by bivalves in the offshore environment was limited mainly by bottom water oxygenation, which follows predictable and repetitive patterns through time. These population fluctuations might be related to solar cycles: successful dreissenid settlement is re-occurring in a frequency known as the lower and upper Gleissberg cycles with a 50–80 and 90–120 yr period. These cycles appear to control regional wind patterns, which are directly linked to water mixing of the lake. This is modulated by the even more prominent 500 yr cycle, which seems to be the most important pacemaker for Lake Pannon hydrology.

1 Introduction

The range expansion of dreissenid bivalves is a potential threat to native fluvial and lacustrine ecosystems in Europe and North America. Massive settlement within few years as well as negative influence on power plant cooling systems and fish densities makes them also a socio-economic concern (Bij de Vaate et al., 2010). Problematic extant dreissenids are the Zebra Mussel *Dreissena polymorpha* (Pallas, 1771) and the Eastern European Quagga Mussel, *Dreissena (Pontodreissena) rostriformis bugensis* (Andrusov, 1897). *Dreissena polymorpha*, originated during the Pliocene in the Black Sea area (Babak, 1983), but spread within the last 200 yr throughout Europe due to

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artificial transcontinental waterways (Karatayev et al., 2007). Similarly, *Dreissena (Pon-*
tdreissena) rostriformis bugensis started to spread from its native range in the Don
 and Bug rivers (Orlova et al., 2004) and has already arrived in Central Europe and
 North America, where it starts to outcompete *Dreissena polymorpha* in some areas
 (Zhulidov et al., 2010; McMahon, 2011; Heiler et al., 2013). This species is geologi-
 cally very young with the oldest reliable records in the Late Pleistocene as described
 by Babak (1983). Recently, Wilke et al. (2010) documented that even the two endemic
 Carino Mussels (*Dreissena (Carinodreissena) presbensis*, Kobelt, 1915 and *D. (C.)*
blanci, Westerlund, 1890) – originally endemic to the Balkan lakes Ohrid/Prespa and
 Trichonis – started to rapidly invade artificial water bodies.

All these range expansions are happening within the Anthropocene (sensu Crutzen
 and Stoermer, 2000). The success of these dreissenids is usually attributed to human
 influence. Furthermore, the anthropogenic global warming is considered to positively
 affect the invasiveness of dreissenids (Schindler, 2001), although the connection re-
 mains vague.

In this study we used the bivalve species *Sinucongeria primiformis* (Papp, 1951)
 as a model organism for testing natural (i.e. non-Anthropocene) blooms of dreis-
 senid species. Specifically, we studied whether dreissenids have explosively taken over
 aquatic ecosystems in the past and analyse their connection with climate. The “natural
 laboratory” for this investigation is the ancient, long lived Lake Pannon, which provides
 an excellent fossil record.

2 Material and methods

2.1 Geological setting

The investigated bivalve assemblages lived in Lake Pannon, which covered the Pan-
 nonian Basin complex in Central and South-Eastern Europe during Late Miocene and
 Pliocene times (11.6 Myr to ~ 5.5 Myr). This lake formed a several hundred meters

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5 deep, long-lived, brackish and slightly alkaline lacustrine system (Magyar et al., 1999; Harzhauser et al., 2004; Piller et al., 2007; Harzhauser and Mandic, 2008). Lake Pannon is a textbook example for endemic evolution with spectacular radiations in many groups such as the melanopsid gastropods and dreissenid bivalves (e.g. Geary, 1990; Müller et al., 1999; Geary et al., 2002; Harzhauser and Mandic, 2008; Neubauer et al., 2013).

10 The studied samples derive from a drilled core in the opencast pit Hennersdorf south of Vienna, where offshore clays of Lake Pannon are exposed (Fig. 1). The mollusc fauna represents assemblages of the regional Pannonian stage, corresponding to the middle Tortonian (Magyar et al., 1999). Magnetostratigraphy allowed a correlation with the normal chron C5n (Magyar et al., 1999). Correlation with astronomically tuned well-logs in the Vienna Basin suggests an absolute age of 10.5–10.4 Myr for the section (Harzhauser et al., 2004; Lirer et al., 2009). These clay deposits are famous for its frequently occurring dreissenid-coquinas in the succession, which can be followed over large areas in the entire Vienna Basin pointing to major settlement events (Fig. 1b). This conspicuous succession of dreissenid coquinas was already recognised in the field by Harzhauser and Mandic (2004), who tentatively assigned the cyclicity to Milankovitch-forcing. Later, based on deep drillings in the Vienna Basin, Lirer et al. (2009) and Paulissen et al. (2011) showed that the sedimentation rates in the Vienna Basin during the Late Miocene were much higher, excluding the presence of several precession cycles in the about 20 m-thick succession of the clay pit. Based on cross-correlations with these astronomically tuned well-data, Kern et al. (2012) reinterpreted the section and proposed a sedimentation rate of ca. 10 mm per 13–14 yr. This study was performed on the same core that provided the herein studied mollusc samples. Kern et al. (2012, 2013) analysed a broad range of geophysical, geochemical and biological proxies, all of which exhibit a set of comparable cyclicities with similar frequencies.

25 The ratios of the frequency peaks correspond to the ratios between known solar cycles, allowing a tuning of the sedimentary record and a best-fit estimate of the sedimentation rate. The proposed age model for the core results in a resolution of roughly

13 yr per centimetre and a total of 8000 yr for the whole 6 m core. Palynological data of Kern et al. (2013) point to an at least warm-temperate climate with a mean annual temperature between 15.6 and 20.8 °C, with a cold season of 5.0–13.3 °C and a warm season range from 24.7 °C to 27.9 °C. The mean annual precipitation (MAP) was varying from ~ 820 mm up to ~ 1530 mm, displaying a clear seasonality with a wet phase of 204–236 mm and a dry phase of 9–24 mm per month.

2.2 Drilling and core handling

In November 2009 a 15 m-long core with a diameter of 15 cm was drilled at the Wienerberger AG clay pit Hennesdorf. The lowermost 6 m were taken without core-break. This is the most uniform part with respect to lithology (dark grey clay, low to absent bioturbation). Further analyses concentrated on this deepest segment (see Kern et al., 2012, 2013 for details and sampling protocol). After cutting the core into two halves, one half was sliced, following a strict 1 cm-sampling protocol. The samples were dried, weighed and treated with H₂O₂ before sieving with 125, 250 and 500 µm mesh-size sieves. As the bivalve shells were fragmented during washing, no individuals could be counted. Therefore, the abundance of bivalves was evaluated by using semi-quantitative categories: 0 = no fragments, 1 = rare fragments, 2 = frequent shell fragments, 3 = dense coquina layers with numerous fragments. Statistical analyses were performed first on these semiquantitative raw data, on a detrended data set and on a 3-point running mean data set (trend removed) – all with very similar results. To detect and describe cyclicities, the software PAST (Hammer et al., 2001) was used for Lomb–Scargle periodograms and REDFIT analysis (Schulz and Mudelsee, 2002) and the software Analy-Series (Paillard et al., 1996) for filtering. REDFIT is a program to remove unwanted red noise for the data set, which is a common problem for unevenly spaced time series due to sampling or changes in sedimentation rate. The Monte-Carlo method was applied to test a bias-corrected spectrum and only peaks above the 99 % confidence interval in the REDFIT spectrum were considered. Additionally, a wavelet analysis was performed to detect potential non-stationary periodicities.

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primiformis might represent an “explosive opportunist” sensu Levinton (1970) comparable to modern invasive *Dreissena* species. Shell cavities are commonly incrustated with pyrite (Fig. 1c), pointing to anoxia as a cause for their sudden death. Concluding, the pavements are interpreted to represent autochthonous in-situ census assemblages or “snapshots” sensu Kidwell (1998). No indication for transport or winnowing can be documented from the data.

4 Results

600 samples have been evaluated to document fluctuations in bivalve occurrence within the 6 m-long record (Fig. 2; Supplement 1). Distribution and abundance are clearly not uniform but characterised by an alternation of dense pavements and samples devoid of molluscs. There is a trend towards increasing dreissenid abundance with time from sample 1500 onwards (linear correlation $r = 0.57343$, $p < 0.001$). The lower part of the core reveals only infrequent intervals of settlement (samples 1540–1510, 1480–1460, 1380–1350) and few short settlement phases separated by long intervals of absence of any molluscs. From sample 1280 onwards, a phase of nearly continuous settlement starts, separated by short intervals of population breakdowns. The longer phases of settlement are also not uniform but exhibit a characteristic pattern. This starts with the presence of single shells, passing into moderately dense shell accumulations and culminating in extremely dense coquinas, followed by a gradual or sometimes abrupt decline. As several prominent cyclicities have already been detected for various biotic and abiotic proxies in the core by Kern et al. (2012, 2013), it might be expected that comparable periodicities influence the bivalve-signal.

Indeed, the spectral analyses of the raw data and of a 3-point-running-mean data set reveal several statistically significant peaks, passing the 99% confidence interval. The Lomb–Scargle periodogram shows a very prominent peak at 32.8–35.5 cm, a set of three peaks from 56.4 to 72.6 cm and a strong peak centred at 145 cm (Fig. 3a). A weaker peak appears at 100 cm only in the 3-point-running-mean data. The REDFIT

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analysis reveals three additional higher frequency peaks at 5.0–5.5, 7.5 and 10.8 cm (Fig. 3b). Increasing the number of segments in the REDFIT analysis reduces noise and then also confirms the dominant peak at 35–36 cm of the Lomb–Scargle periodogram, whilst high frequency cycles become less prominent (Fig. 4 right).

5 The wavelet analysis (Fig. 4) confirms the presence of the low-frequency signals especially in the upper half of the core, whereas the high-frequency cycles revealed by REDFIT form discrete bundles (e.g. between sample 1280–1200, 1120–1060).

The frequency-ratio between the significant peaks in the Lomb–Scargle periodogram calls for attention as the low frequency peaks might be only multiples of the prominent peak at 35.5 cm. Therefore, Gaussian filters were applied, centred at 10–11 cm, 33–36 cm, 57–73 cm and 145–150 cm (Fig. 5). The filtered data document that the higher frequency filter at 10–11 cm and 33–36 cm explain most of the observed fluctuations of the record. The fit is excellent especially in the upper half of the core, whilst in the lower part the filter coincides with the “signal-bundles” observed in the wavelets.

10 The low-frequency filter at 145–150 cm, in contrast, resolves especially the large scale pattern below sample 1050 but has a poor fit with the uppermost record. The filter spanning the triplet of peaks in the power spectra from 57 to 73 cm has lowest fit with the record below sample 1050 and only a moderately good fit above. Thus, tentatively we interpret this frequency band as harmonic of the higher frequency signals.

20 5 Discussion

The overall pattern describes a distinct amelioration of ecological conditions for dreissenid settlement from bottom to top. A similar trend is observed in the number of co-occurring ostracods, which are most abundant in the upper part of the core, whilst the lower half is characterised by long-lasting and severe population collapses, punctuated by short phases of ostracod settlement (Kern et al., 2012). This large-scale trend is explained by the fact that Lake Pannon changed from a transgressive phase into a high-stand phase with increasing bottom water oxygenation and a progradation of

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of the Gleissberg cycles and the 500 yr cycle, indicating that bottom water oxygenation was strongly influenced by these solar cycles.

This example shows that dreissenid bivalves may be pioneers, which quickly dominate aquatic ecosystems even in pre-Anthropocene records. The surprisingly strong influx of solar forcing on the success of the Miocene dreissenids might be an interesting and completely overlooked aspect for predicting the future population dynamics of extant dreissenids. To understand the success of extant *Dreissena* species in a larger context, analyses of Holocene lake records would be urgently needed. Such data could also help to identify and further quantify natural population fluctuations (“background noise”), often compounding human impact analyses. These analyses typically consider only short time periods and may thus not accurately differentiate between natural and anthropogenic factors.

Moreover, historical demographic data could also help to better understand the complex interplay of biotic and global abiotic factors triggering large-scale population expansions. This, in turn, may enable the improvement of existing invasion models, particularly in respect to niche opportunities and invasion dynamics.

Supplementary material related to this article is available online at:
**[http://www.biogeosciences-discuss.net/10/12009/2013/
bgd-10-12009-2013-supplement.pdf](http://www.biogeosciences-discuss.net/10/12009/2013/bgd-10-12009-2013-supplement.pdf)**

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References

Andrusov, N. I.: Fossile und lebende Dreissenidae Eurasiens, erstes Supplement, Trav. Soc. Nat. St. Petersburg, 29, 59–132, 1897.

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- Babak, E. V.: Pliotseno I Chevertichnye Dreissenid (*Dreissenidae*, *Bivalvia*) Evksinskogo Basseina [The Pliocene and Quarternary Dreissenidae of the Euxinian Basin], Tr. Paleontol. Inst., Akad. Nauka SSSR, 204, 1–104, 1983.
- Bij de Vaate, A., Rajagopal, S., and van der Velde, G.: The zebra mussel in Europe: summary and synthesis, in: The Zebra Mussel in Europe, edited by: van der Velde, G., Rajagopal, S., and Bij de Vaate, A., Backhuys Publishers, Leiden, 415–421, 2010.
- Crutzen, P. J. and Stoermer, E. F.: The “Anthropocene”, Global Change Newsletter, 41, 17–18, 2000.
- de Jager, C., Duhau, S., and van Geel, B.: Quantifying and specifying the solar influence on terrestrial surface temperature, J. Atmos. Sol.-Terr. Phy., 72, 926–937, 2010.
- Geary, D. H.: Patterns of evolutionary tempo and mode in the radiation of *Melanopsis* (Gastropoda: Melanopsidae), Paleobiology, 16, 492–511, 1990.
- Geary, D. H., Staley, A. W., Müller, P., and Magyar, I.: Iterative changes in Lake Pannon *Melanopsis* reflect a recurrent theme in gastropod morphological evolution, Paleobiology, 28, 208–221, 2002.
- Hammer, Ø., Harper, D. A. T., and Ryan, P. D.: PAST: Palaeontological Statistics Software package for education and data analysis, Palaeontol. Electron., 4, 1–9, 2001.
- Harzhauser, M. and Mandic, O.: The muddy bottom of Lake Pannon-a challenge for dreissenid settlement (Lake Miocene; Bivalva), Palaeogeogr. Palaeocl., 204, 331–352, 2004.
- Harzhauser, M. and Mandic, O.: Neogene lake systems in Central and South-Eastern Europe: faunal diversity, gradients and interrelations, Palaeogeogr. Palaeocl., 260, 417–434, 2008.
- Harzhauser, M. and Mandic, O.: Neogene dreissenids in Central Europe: evolutionary shifts and diversity changes, in: The Zebra Mussel in Europe, edited by: van der Velde, G., Rajagopal, S., and Bij de Vaate, A., Backhuys Publishers, Leiden, 11–28, 426–478, 2010.
- Harzhauser, M., Daxner-Höck, G., and Piller, W. E.: An integrated stratigraphy of the Pannonian (Late Miocene) in the Vienna Basin, Aust. J. Earth Sci., 95–96, 6–19, 2004.
- Harzhauser, M., Kern, A., Soliman, A., Minati, K., Piller, W. E., Danielopol, D. L., and Zuschin, M.: Centennial to decadal scale environmental shifts in and around Lake Pannon (Vienna Basin) related to a major Lake Miocene lake level rise, Palaeogeogr. Palaeocl., 270, 102–115, 2008.
- Heiler, K. C. M., Bij de Vaate, A., Ekschmitt, K., von Oheimb, P. V., Albrecht, C., and Wilke, T.: Reconstruction of the early invasion history of the quagga mussel (*Dreissena rostriformis bugensis*) in Western Europe, Aquat. Invasions, 8, 53–57, 2013.

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- Karatayev, A. Y., Padilla, D. K., Minchin, D., Boltovskoy, D., and Burlakova, L. E.: Changes in global economies and trade: the potential spread of exotic freshwater bivalves, *Biol. Invasions*, 9, 161–180, 2007.
- 5 Kern, A. K., Harzhauser, M., Piller, W. E., Mandic, O., and Soliman, A.: Strong evidence for the influence of solar cycles on a Late Miocene Lake system revealed by biotic and abiotic proxies, *Palaeogeogr. Palaeocl.*, 329–330, 124–136, 2012.
- Kern, A. K., Harzhauser, M., Soliman, A., Piller, W. E., and Mandic, O.: High-resolution analysis of Upper Miocene lake deposits: evidence for the influence of Gleissberg-band solar forcing, *Palaeogeogr. Palaeocl.*, 370, 176–183, 2013.
- 10 Kidwell, S. M.: Time-averaging in the marine fossil record: overview of strategies and uncertainties, *Geobios.*, 30, 977–995, 1998.
- Kobelt, W.: *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten von E. A. Rossmässler*, Neue Folge, Zwanzigster Band, 1–81, Kreidel, Wiesbaden, 1915.
- 15 Levinton, J. S.: The paleoecological significance of opportunistic species, *Lethaia*, 3, 69–78, 1970.
- Lirer, F., Harzhauser, M., Pelosi, N., Piller, W. E., Schmid, H. P., and Sprovieri, M.: Astronomically forced teleconnection between Paratethyan and Mediterranean sediments during the Middle and Late Miocene, *Palaeogeogr. Palaeocl.*, 275, 1–13, 2009.
- 20 Lörenthey, E.: Die pontische Fauna von Kurd im Comitate Tolna, *Földtani Közlöny, A Magyar Földtani Tarsulat Folyoirata*, 24, 148–161, 1894.
- Magyar, I., Geary, D. H., and Müller, P.: Integrated Paleogeographic evolution of the Late Miocene Lake Pannnon in Central Europe, *Palaeogeogr. Palaeocl.*, 147, 151–167, 1999.
- Marinescu, F. L.: Genre *Dreissenomya* Fuchs (Bivalvia, Heterodonta), *Inst. Géol. Géophy. Mém.*, 26, 75–118, 1977.
- 25 McMahan, R. F.: Quagga mussel (*Dreissena rostriformis bugensis*) population structure during the early invasion of Lakes Mead and Mohave January–March 2007, *Aquat. Invasions*, 6, 131–140, 2011.
- Müller, P., Geary, D. H., and Magyar, I.: The endemic molluscs of the Late Miocene Lake Pannon: their origin, evolution, and family-level taxonomy, *Lethaia*, 32, 47–60, 1999.
- 30 Neubauer, T. A., Harzhauser, M., and Kroh, A.: Phenotypic evolution in a fossil gastropod species lineage: evidence for adaptive radiation?, *Palaeogeogr. Palaeocl.*, 370, 117–126, 2013.

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- Ogurtsov, M. G., Nagovitsyn, Y. A., Kocharov, G. E., and Jungner, H.: Long-period cycles of the sun's activity recorded in direct solar data and proxies, *Sol. Phys.*, 211, 371–394, 2002.
- Orlova, M. I., Muirhead, J. R., Antonov, P. I., Scherbina, G. H., Starobogatov, Y. I., Biochino, G. I., Therriault, T. W., and Maclsaac, H. J.: Range expansion of quagga mussels *Dreissena rostriformis bugensis* in the Volga River and Caspian Sea basin, *Aquat. Ecol.*, 38, 561–573, 2004.
- Paillard, D., Labeyrie, L., and Yiou, P.: Macintosh program performs timeseries analysis, *Eos T. Am. Geophys. Un.*, 77, p. 379, 1996.
- Pallas, P. S.: *Reise durch verschiedene Provinzen des Russischen Reichs*, vol. 1, Kayserlichen Academie der Wissenschaften, St. Petersburg, 1–504, 1771.
- Papp, A.: *Das Pannon des Wiener Beckens*, *Mitt. Geol. Ges. Wien*, 39–41, 99–193, 1951.
- Paulissen, E., Luthi, S. M., Grunert, P., Ćorić, S., and Harzhauser, M.: Integrated high-resolution stratigraphy of a Middle to Late Miocene sedimentary sequence in the central part of the Vienna Basin, *Geol. Carpath.*, 62, 155–169, 2011.
- Piller, W. E., Harzhauser, M., and Mandic, O.: Miocene Central Paratethys stratigraphy – current status and further directions, *Stratigraphy*, 4, 71–88, 2007.
- Schindler, D. W.: The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium, *Can. J. Fish. Aquat. Sci.*, 58, 18–29, 2001.
- Schulz, M. and Mudelsee, M.: REDFIT: estimating red-noise spectra directly from unevenly spaced paleoclimatic time serie, *Comput. Geosci.*, 28, 421–426, 2002.
- Solanki, S. K., Usoskin, I. G., Kromber, B., Schüssler, M., and Beer, J.: Unusual activity of the Sun during recent decades compared to the previous 11,000 years, *Nature*, 431, 1084–1087, 2004.
- Westerlund, C. A.: *Katalog der in der paläarktischen Region lebenden Binnenconchylien*, Johansson, Karlshamn, 1–224, 1–128, 1–8, 1890.
- Wilke, T., Schultheiß, R., Albrecht, C., Bornmann, N., Trajanovski, S., and Kevrekidis, T.: Native *Dreissena* freshwater mussels in the Balkans: in and out of ancient lakes, *Biogeosciences*, 7, 3051–3065, doi:10.5194/bg-7-3051-2010, 2010.
- Zhulidov, A. V., Kozhara, A. V., Scherbina, G. H., Nalepa, T. F., Protasov, A., Afanasiev, S. A., Pryanichnikova, E. G., Zhulidov, D. A., Gurtovaya, T. Yu., and Pavlov, D. F.: Invasion history, distribution, and relative abundances of *Dreissena bugensis* in the old world: a synthesis of data, *Biol. Invasions*, 7, 1923–1940, 2010.

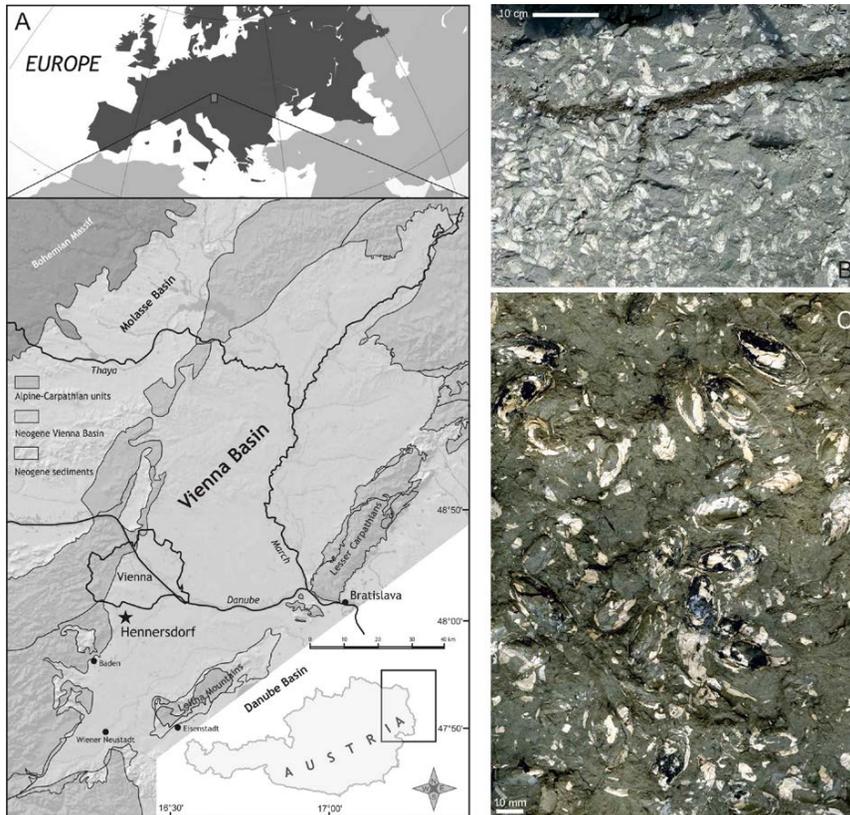


Fig. 1. (A) Geological map of the Vienna Basin showing the position of the investigated core at Hennersdorf. (B) A dreissenid pavement in the Hennersdorf pit during field work (with a fossil twig). This pavement can be followed over more than 400 m distance from the outcrop area. (C) Moderately dense coquina of *Sinucongeria primiformis*. The shells are articulated and the sediment fill of the valves is coated with pyrite indicating rather abrupt installation of dysoxic conditions killing off the population.

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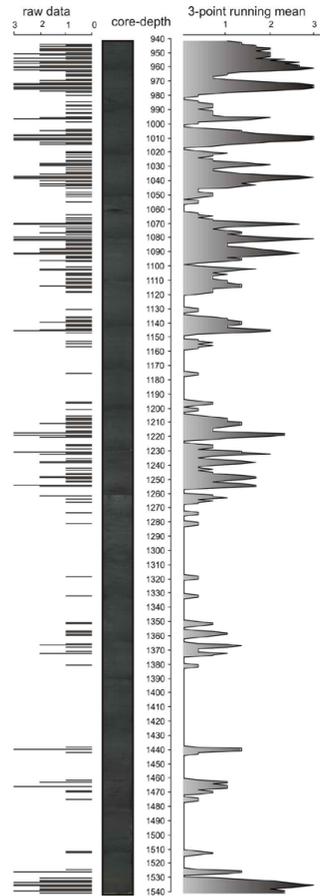


Fig. 2. Illustration of the core and relative dreissenid abundance indicated on a semi-quantitative scale (0 = no shells; 1 = rare debris or single shells; 2 = loose coquina; 3 = dense shell bed), left: raw data, right: 3-point-running mean; core depth in cm (corresponds to sample numbers 1540 to 940; = 600 samples).

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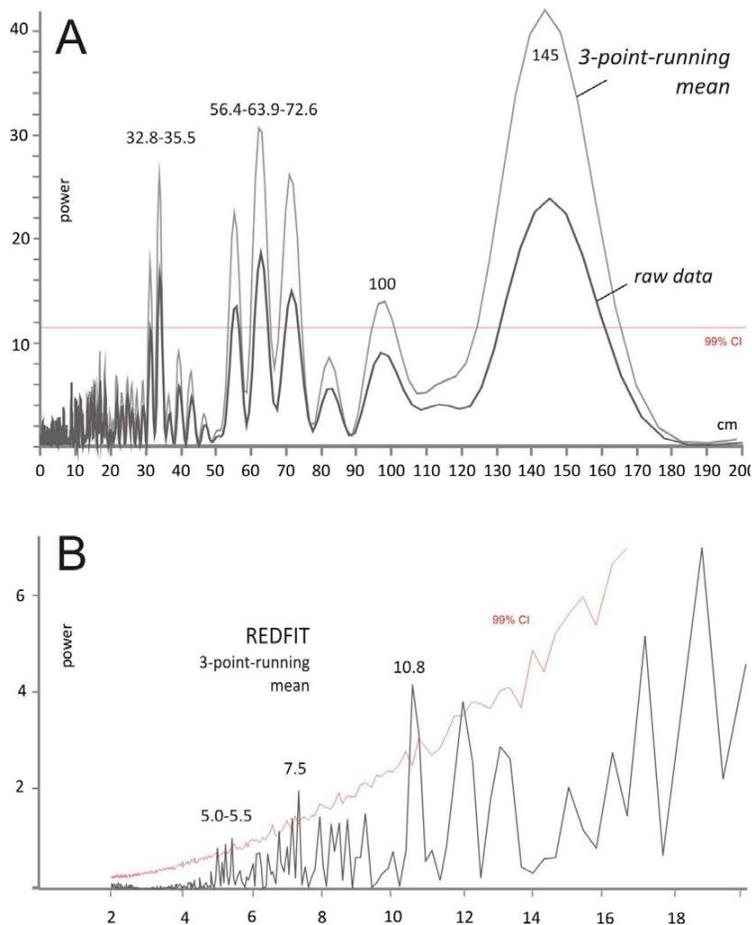


Fig. 3. Lomb–Scargle **(A)** and REDFIT **(B)** periodograms with indication of the 99 % confidence interval. Longer frequencies are better revealed in the power spectra, whilst short cyclicities are better supported by the REDFIT-analysis.

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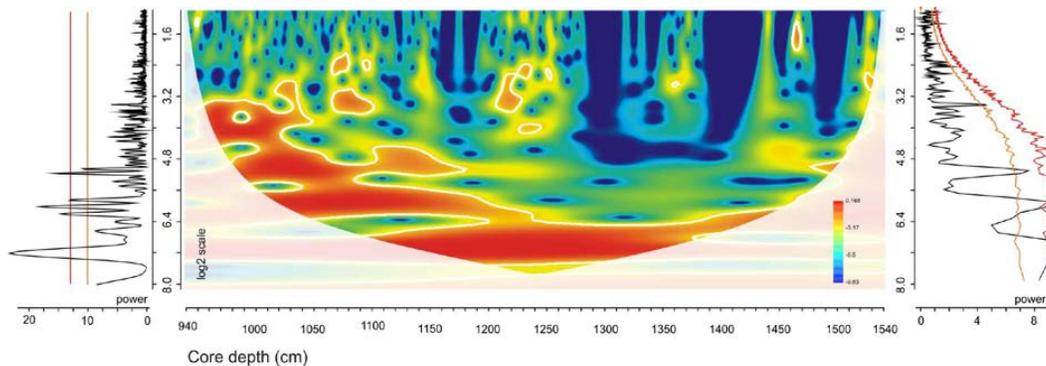


Fig. 4. Morlet wavelet power spectrum based on the 3-point-running mean data set (white line indicates significance level, $p = 0.05$). The Lomb–Scargle (left) and the REDFIT (right) periodograms are drawn along a log₂-scale for easier comparison of frequency peaks in the power spectra in Fig. 3 with the wavelet spectrum (orange and red lines = 95 % and 99 % confidence intervals).

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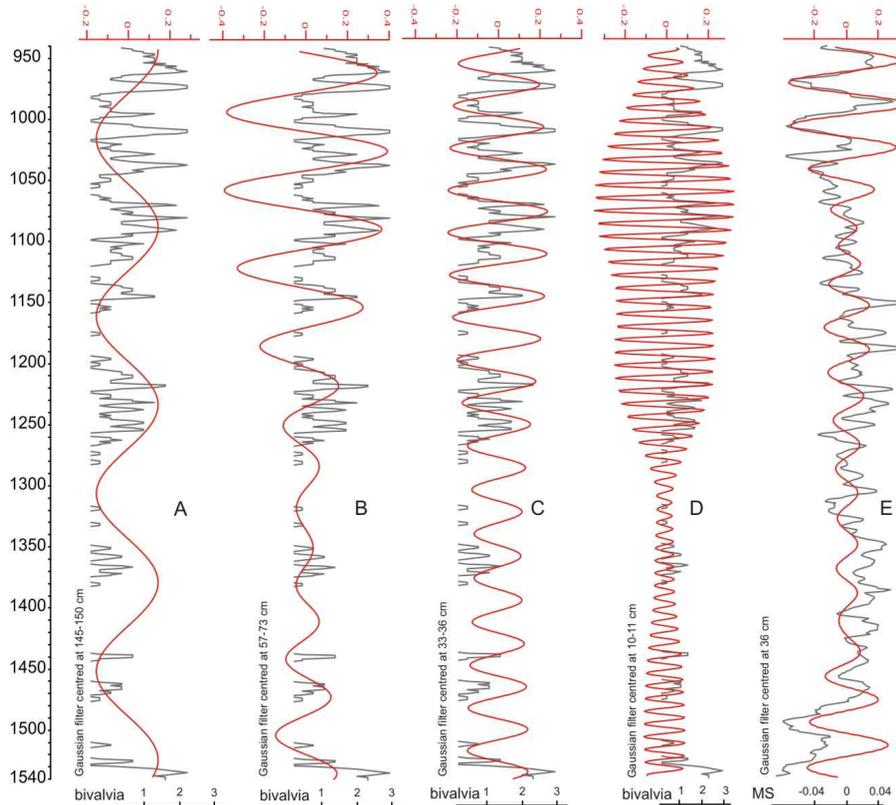


Fig. 5. Gaussian filters have been applied to the bivalve data according to the dominant periods revealed by the periodograms in Figs. 3 and 4. These filters are centered at 10–11 cm, 33–36 cm, 57–73 cm and 145–150 cm (**A–D**). The two high frequency filters explain most of the observed data. (**E**) shows magnetic susceptibility data from Kern et al. (2012). The Gaussian filter centered at 36 cm represents the hypothetical 500 yr cycle and is anticyclic compared with the bivalve record (**C**).