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Research Article

The temporal abundance-distribution relationship in a global invader sheds light on species distribution mechanisms

Christine Ewers[1], Monika Normant-Saremba[2], Heleen Keirsebelik[3], Jonas Schoelynck[3]

1 Kiel University, Zoological Museum, Hegewischstrasse 3, 24105 Kiel, Germany
2 University of Gdańsk, Faculty of Oceanography and Geography, Department of Marine Ecology, Al. Marszałka Piłsudskiego 46, 81-378 Gdynia, Poland
3 University of Antwerp, ECOSPHERE Research Group, Universiteitsplein 1, 2610 Wilrijk, Belgium
Corresponding author: Christine Ewers (ewers-saucedo@zoolmuseum.uni-kiel.de)

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Abstract

The geographic expansion and abundance fluctuations of invasive species offer unprecedented insights to investigate potential mechanisms underlying the distribution-abundance relationship, one of the most universal patterns in community ecology. However, the abundance of invasive species is rarely documented in the needed detail. Data from historical records, scientific and popular literature, citizen science and expert interviews were synthesized to obtain insights into the long-term expansion and abundance cycles of the Chinese mitten crab, one of the world's 100 worst invasive species. Thus for the first time, global long-term data on population size fluctuations have been correlated with the global spatiotemporal invasion history of a non-native species. Geographic expansions and increases in abundance co-occurred in the 1930s and again since the 1990s in agreement with the distribution-abundance relationship. Furthermore, a regional case study for the German river Elbe indicates that increases in abundance may be driven by improved riverine water quality and rising sea surface temperatures. Environmental restoration and climate change therefore benefit this invasive species, and could lead to further geographic expansion and increases in abundance.

Key words: invasive species, geographic expansion, abundance, ecological principles, natural resource management, *Eriocheir sinensis*

Introduction

Humans have moved organisms around the globe for millennia, both accidentally and on purpose (Mack et al. 2000). In the last century, the number of non-native species (also referred to as alien or non-indigenous species) has increased rapidly, and today they represent one of the main drivers of global change (Crowl et al. 2008; Bailey et al. 2020). They alter ecosystems at an increasing rate as novel predators, competitors, and disease vectors, and can lead to significant economic costs (Carlton 1994; Lowe et al. 2000; Haubrock et al. 2021). The most detrimental non-native species (i.e., invasive species) tend to be those that are both locally abundant, easily dispersed, and capable of inhabiting a variety of ecosystems on a large geographic scale. Understanding what makes a species globally invasive is essential for the protection of biodiversity and the mitigation of global change.

Community ecology suggests that local abundance and geographic distribution of non-native species should be correlated. At least for native species and communities, local abundance and geographic distribution show a positive correlation (Miller and Wiegert 1989; Gaston 1996; Eriksson and Jakobsson 1998; Venier and Fahrig 1998; Granado-Lorencio et al. 2005; Borregaard and Rahbek 2010; Villa et al. 2019). This relationship is in fact so universal that it has been deemed one of the few "laws of ecology" (Lawton 1999). For non-native species, this relationship implies that highly abundant species are also widespread (Gaston 1999). This so-called 'double trouble' hypothesis, however, has not been confirmed empirically. Although it is generally acknowledged that the abundance of non-native species varies between localities (Veldtman et al. 2010; Leung et al. 2012; Bradley et al. 2018), temporal abundance data are not readily available for most non-native species (but see Hansen et al. 2013; Haubrock et al. 2022), preventing tests of this consequential relationship. More generally, non-native species would provide unprecedented model systems to understand the universal nature and causality between abundance and geographic expansion, which remains elusive for native species that have already spread throughout their habitat (Borregaard and Rahbek 2010). In particular, non-native species with several expansion cycles offer the singular opportunity to investigate the temporal sequence of abundance and geographic expansion, as well as explore the factors that drive these two aspects of invasions.

First discovered in Germany in 1912, the Chinese mitten crab *Eriocheir sinensis* (H. Milne-Edwards 1853) has spread rapidly throughout German, Dutch, Belgian, and French river systems, and reached the Baltic Sea (Panning and Peters 1933; AquaNIS 2015). The Chinese mitten crab is considered one of the world's worst 100 invasive species given its potential to negatively impact invaded ecosystems (Lowe et al. 2000), and has been listed as a species of EU concern sensu the EU regulation 1143/2014 on the prevention and management of the introduction and spread of invasive alien species (IAS) (European Commission 2016). Water temperature is thought to explain much of the present-day distribution of the Chinese mitten crab in the context of ecological niche models (Herborg et al. 2007; Zhang et al. 2019, 2020), as well as larval abundance (Anger 1991; Blumenshine et al. 2012). Further, periods of decline for Chinese mitten crab populations have been linked to poor riverine water quality and a resulting food shortage (Petermeier et al. 1996; Fladung 2000). The relevant link between riverine water quality, biodiversity and food availability has been shown for European river systems (Leitner et al. 2021). Additionally, higher water levels in rivers have been hypothesised to increase juvenile crab migration upstream (Fladung 2000), thus leading to higher abundance in years with high river water levels.

In the present study, the Chinese mitten crab is used as a model system to test the hypothesis that the temporal abundance-distribution relationship holds for non-native species. To do so, the geographic expansion of this species is correlated with regional increases in abundance. Furthermore, possible drivers of increasing abundance are investigated in the Elbe River, which is used due to the continuous presence of the Chinese mitten crab since its introduction to Europe (Panning and Peters 1933; Fladung 2000) and the availability of long-term data.

Methods

This study queried scientific literature, governmental reports, online databases for citizen science observations and natural history collection information, contacted researchers, natural resource managers and fishermen to obtain a detailed, up-to-date picture of regional invasion histories until the end of 2021. For identifying relevant scientific and grey literature, google scholar was searched with the terms "Eriocheir" or "mitten crab" in combination with "new record", "geographic expansion", "abundance" or "distribution". We collated data on a regional scale. Regions were defined as a major river system, its estuary and the marine/brackish coastal area the river drains into regardless of national borders. This definition of a region was driven by the life history of the Chinese mitten crab: juveniles and adults live in estuaries and rivers, with larvae developing in the estuaries and coastal areas around the mouths of these rivers (Panning and Peters 1933). In contrast, if crabs were predominantly found in coastal areas, then the region was defined by its national borders, as most data are reported at the national level. Overall, three aspects of the invasion history were considered: the current distribution of the Chinese mitten crab, the temporal sequence of geographic spread and changes in abundance over time.

Introduction history and current distribution

The year in which the Chinese mitten crab was first reported in a new region was extracted from the Online Information System on Aquatic Non-Indigenous and Cryptogenic Species (AquaNIS, http://www.corpi.ku.lt/databases/index.php/aquanis/). To identify additional new regional records and map the Chinese mitten crabs' current distribution, the scientific literature and the Global Biodiversity Information Facility (GBIF, www.gbif.org) were queried. In addition, the following databases were considered as they were not – or not completely – represented in GBIF: Invasive Species Northern Ireland (http://invasivespeciesireland.com), Mitten Crab Watch (http://mittencrabs.org.uk), Centre de Ressources Espèces exotiques envahissantes (http://especes-exotiques-envahissantes.fr), and the Smithsonian Environmental Research Center's National Estuarine and Marine Exotic Species Information System (https://invasions.si.edu/nemesis) (see Suppl. material 1 for a complete list).

Abundance fluctuations

Information on changes in abundance was extracted from scientific publications, reports of researchers, natural resource managers and interviews with fishermen. In particular, the year in which abundance began to increase or decrease was noted. This is a metric that is independent of the way crab abundance was estimated, e.g. catch per unit effort or number of crabs caught per day, and these measures are not comparable across studies.

Correlations between geographic expansion and abundance fluctuations

If the abundance-distribution relationship holds for non-native species, a significant, positive relationship between the number of regional expansion events and the number of regional increases in abundance is expected. All statistical analyses were carried out in the R statistical environment (R Core Team 2019). The years 2010 to present were omitted from the analysis, as new reports on range expansions and abundance fluctuations may not have been published yet (publication time lag) and may therefore be incomplete. We conducted a generalized linear model (GLM) between the annual number of geographic expansions and reported number of regional increases in abundance with a Poisson error distribution. This distribution is best suited to analyse count data.

Potential drivers of abundance fluctuations in the Elbe River

The Elbe River and associated estuarine ecosystem was used as a case study for the trends occurring in many other large waterways at a European and global scale (Cane et al. 1997; European Environment Agency 2012; Stets et al. 2012; Lopez et al. 2020), partly due to the impulse of the EU Water Framework Directive (2000/60/EG). Moreover, the first non-native discovery of the Chinese mitten crab was near the Elbe, and the Chinese mitten crab has been a continuous resident there since 1914 (Panning and Peters 1933; Fladung 2000). The Elbe is a 1164 km long river that springs in Czech Republic and flows through Germany before mouthing in the North Sea at the Dutch-German border. Taken together, this makes this large river system a core habitat for the invasive Chinese mitten crab. The port of Hamburg on the Elbe is one of the largest harbours worldwide and may therefore act as a dispersal hub. Long-term data for the Elbe River was collated to investigate three factors that may influence abundance and geographic expansion of the Chinese mitten crab: average annual oxygen concentration, an indicator of overall riverine water quality, from a station near Magdeburg (European Environment Agency 2012), average annual sea surface temperature (SST) from a near-shore North Sea station close to the Elbe Estuary (van Aken 2008; BNSC Uni Hamburg https://icdc.cen.uni-hamburg.de/, accessed Sept 17, 2020), average annual Elbe River water discharge at a station near Darchau (Klein et al. 2018; Fladung 2000). The abundance of the Chinese mitten crab in the Elbe River was categorised as high or low for each year from 1912 to 2021. Logistic regressions between each potential driver and the abundance were carried out. The potential drivers were not combined into a model as they were strongly correlated (Pearsons correlation coefficient > 0.7), and several tightly correlated variables within the same model can lead to erratic model outcomes, also known as collinearity.

Results

Introduction history and current distribution

Data were extracted from 28 reports and scientific articles, and six online databases. Detailed, referenced accounts of the introduction history and current distribution for each region are available in the Suppl. material 2, and a tabular view is available in Suppl. material 3. In summary, introductions to new regions occurred from 1912 to 1914 (Weser and Elbe Rivers in Germany), 1927 to 1935 (remaining North Sea region including the Scheldt River and several observations in Belgium and The Netherlands, and the Baltic Sea region), 1945 to 1959 (Seine, Loire and Gironde Rivers in France), 1970 to 1976 (Laurentian Great Lakes, Caspian Sea, Norway), and from the late 1980s onwards (Guadalquivir River in Spain, Tagus river in Portugal, Northern Dvina River in Russia, Danube River in Serbia, Romania and Ukraine, Hudson River in the USA, San Francisco Bay in the USA, and several observations in Scotland, Ireland, and Italy) (Suppl. materials 2, 3). The English Rivers Thames and Humber did not become colonised until the 1970s, despite two single specimens caught in 1935 and 1949 (Suppl. material 3). Curiously, few of the introductions of the late 1950s to 1970s became established in the long-term (only the Thames River and possibly the Seine and Loire Rivers) (Fig. 1). Until the end of 2021, the Chinese mitten crab has been observed in Europe in the North Sea area including the British Isles, Baltic Sea, East and West Atlantic, Mediterranean, Caspian Sea, Black Sea, and White Sea (Fig. 2). In North America, the crab occurred on both the west

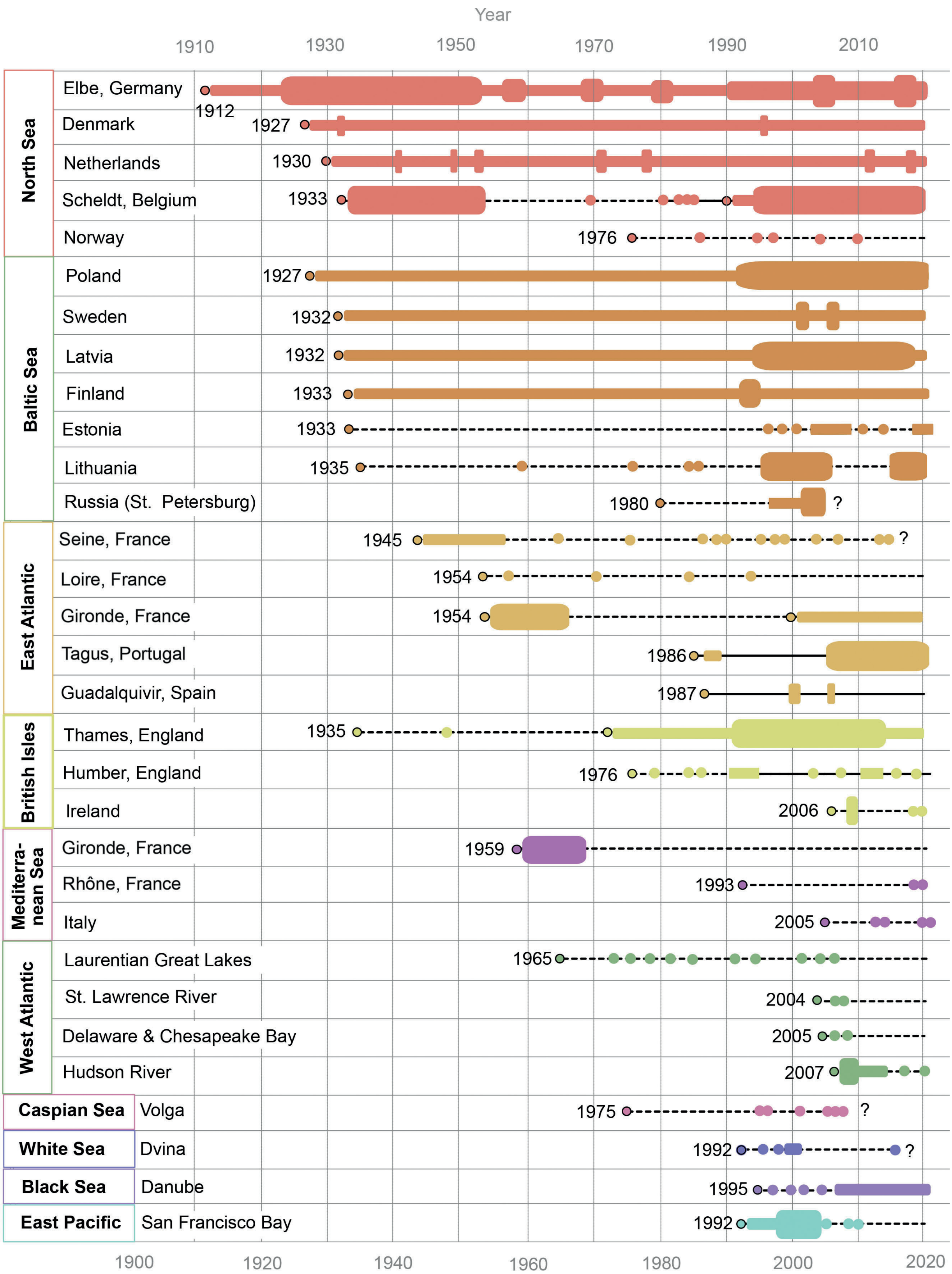

Figure 1. Temporal abundance data for the Chinese mitten crab by region. Regions are either major rivers and the coastal area they drain into, or countries if crabs are predominantly coastal or inhabit several small river systems. Black solid lines indicate the presence of the Chinese mitten crab but without knowledge of its abundance, dashed black lines indicate that the Chinese mitten crab has not been reported in the respective time frame. No line indicates a lack of data, which is highlighted by a question mark. Colored dots indicate single years with few recorded crabs, and thin colored lines indicate continuous annual records of few crabs. Thicker colored lines indicate an increase in abundance, as discussed in the Suppl. material 2.

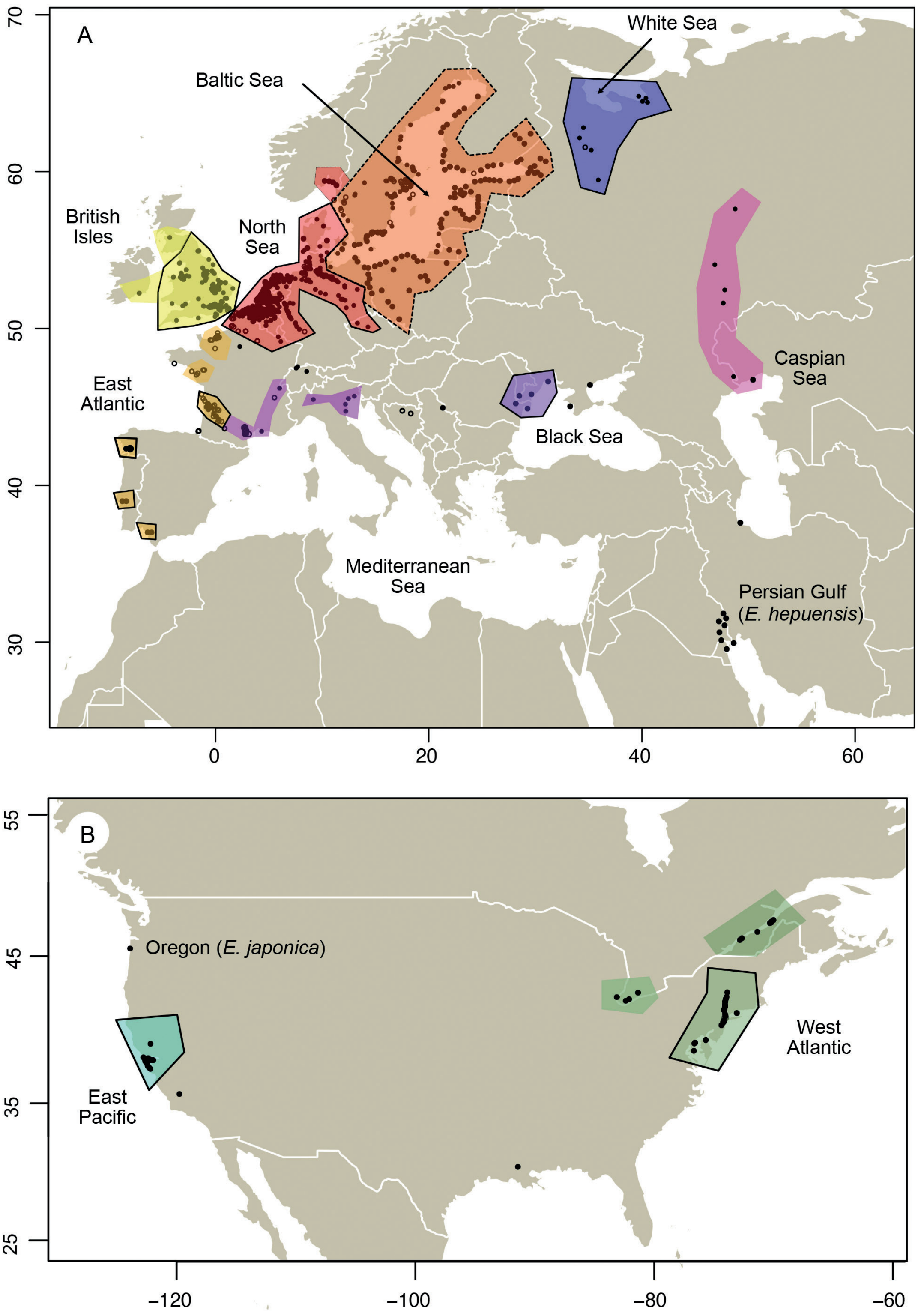

Figure 2. Non-native distribution of the Chinese mitten crab. Each dot is a record (GBIF.org 2021; Ojaveer et al. 2007; Shakirova et al. 2007; Dittel and Epifanio 2009; Veilleux and Lafontaine 2009; Petrescu et al. 2010; Naser et al. 2012). **A:** European distribution; **B:** North American distribution. Closed black dots: records of crabs collected after 2000 in GBIF and literature records, open dots: GBIF records prior to 2000. Colored areas are regions with abundant reports of the Chinese mitten crab shown in Figure 1 and detailed in the Suppl. material 2. The shape of the colored regions was chosen to include all reports from an area, but does not reflect the exact range of the Chinese mitten crab. Regions with a black outline represent established populations. The Baltic Sea region is a special case (dashed outline), as it is unclear if this region should be considered an independent population or if it is an extension of North Sea populations. Mitten crabs from the Persian Gulf are *Eriocheir hepuensis*. A single observation of *Eriocheir japonica* has been reported from the west coast of the United States in the state of Oregon.

and the east coast, as well as in the Laurentian Great Lakes (Fig. 2B). Single records for the Chinese mitten crab also exist from Japan (Suppl. material 2).

Fluctuations in abundance

Data were extracted from 14 reports and scientific articles and three online databases. In addition, three researchers and one fisherman were interviewed. Detailed, referenced accounts of abundance fluctuations for each region are available in Suppl. material 2, and a tabular view is available in Suppl. material 4. Overall, newly established populations followed different patterns of abundance fluctuations: the Chinese mitten crab in the Elbe had an initial boom with high abundance shortly after its establishment, followed by a phase of lower but persistent abundance (Suppl. material 2). At its peak abundance in the 1930s, over 100,000 crabs were trapped per day (Panning 1939). This pattern is the classical expectation for an invasive species (Boudouresque 1999; Gothland et al. 2014; Geburzi and McCarthy 2018). In the Scheldt, the Gironde, San Francisco Bay and the Hudson, initially abundant populations disappeared completely or were subsequently only found in coastal areas, recapitulating a boom-and-bust cycle (Fig. 1, Suppl. materials 2, 4). The rivers Scheldt and Gironde were re-colonised in 1990 and 2000, respectively. The Scheldt population is currently at a very high density, but the Gironde has remained at low density ever since (Suppl. material 2). Other populations (rivers Seine, Guadalquivir, Humber, Dvina, Danube, Thames) have been at low abundance throughout much of their invasion history (Suppl. material 2).

The relationship between abundance fluctuations and geographic expansion

At a global scale, increases in abundance of established populations occurred between 1924 and 1930 (rivers Elbe and Scheldt), and have been especially common since the 1990s (Baltic Sea countries, rivers Elbe, Thames and Scheldt) (Figs 1, 3B, Suppl. material 2). New regional records that resulted in established populations were most common between 1927 and 1935 and from the 1970s on. The annual number of reported geographic expansions explained the annual number of reported increases in abundance (p-value = 0.034, z-value = 2.119, df = 109), but not vice versa (p-value = 0.105, z-value = 1.622, df = 109).

At a regional level, within a river system or geographically close rivers, the temporal sequence of geographic expansion and abundance increases could be reconstructed in detail for two cases. The first appearance of the Chinese mitten crab in Europe in 1912 was an expansion from the native range. This initial expansion was likely facilitated by increased shipping activity, and especially increased trade with China between 1840 and 1950 (Fravel 2005). Following this initial introduction, the Chinese mitten crab increased in abundance in its non-native range in the Elbe and Weser Rivers (from 1924 on), followed by regional expansion in the 1930s (Peters and Panning 1933; Panning 1939; Panning 1952). This means that an increase in abundance was followed by geographic expansion. The more recent expansion throughout the United Kingdom also follows the same sequence: after the Chinese mitten crab became abundant in the Thames River starting in 1992 (Clark et al. 1998; Herborg et al. 2005), it spread further across Britain, reaching Scotland and neighboring Ireland in the 2000s (see Suppl. material 2 for detailed account). Therefore, our data show that the temporal sequence at the regional scale is: 1. introduction, 2. abundance increase, 3. geographic expansion.

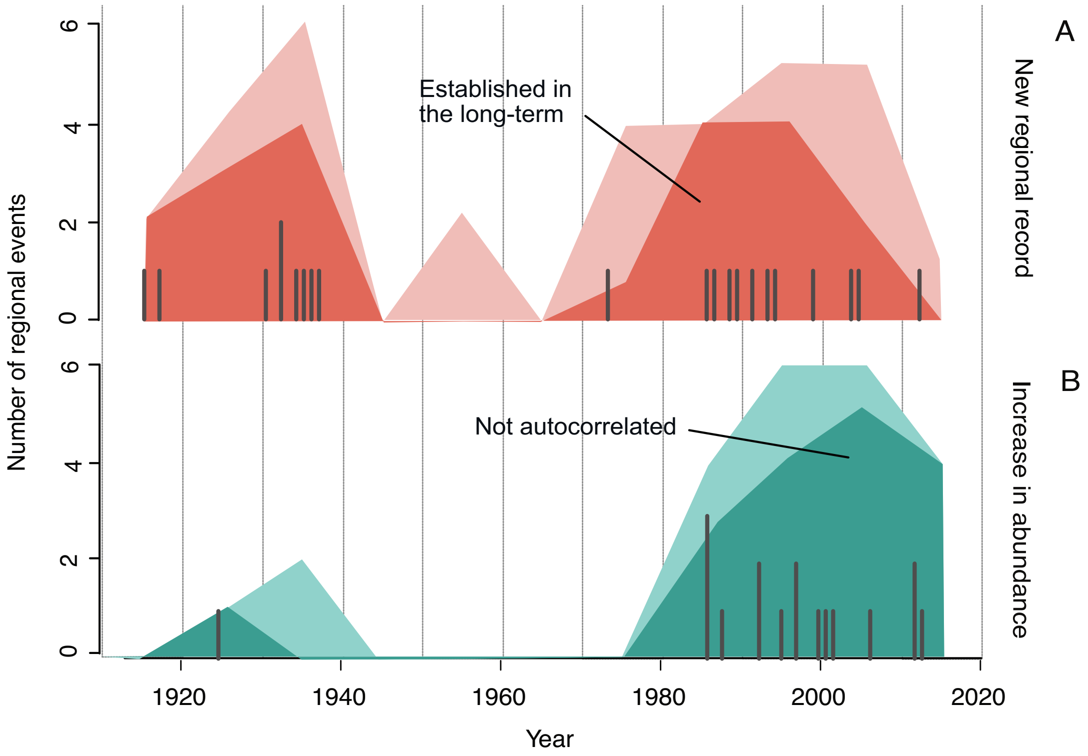

Figure 3. Temporal changes in Chinese mitten crab geographic expansion and increases in abundance. Black lines indicate the number of events per year, while the colored areas represent the same data collated by decade. **A:** The number of new regional records that were observed globally. Populations not established in the long-term either did not become established at all, or went locally extinct after a short boom phase; **B:** The number of observed regional increases in abundance. Autocorrelated increases are observed in a population that had been present in a region for less than ten years prior to the increase.

Potential drivers of abundance in the Elbe River

Oxygen concentration in the Elbe River was low in the 1950s and 1960s, and increased at the end of the 1980s (Fig. 4A), whereas SST peaked in the 1930s, and increased again since the end of the 1980s (Fig. 4B). River water discharge fluctuated throughout the last century, but no clear trends are recognisable (Fig. 4C). Crab abundance was generally low between 1955 to 1990, with a few short increases in abundance. This matched the oxygen content of the Elbe River and SST reasonably well. The binomial GLM models found significant positive relationships for both oxygen content (p-value = 0.0122, z-value = 2.506, df = 69) and SST (p-value = 0.000768, z-value = 3.364, df = 84), but not for riverine water discharge (p-value = 0.861, z-value = 0.176, df = 84) (Fig. 4D, F). In other words, crab abundance increased with increasing oxygen content and rising SST.

Discussion

For the first time, global long-term data on population size fluctuations have been correlated with the global spatiotemporal invasion history of a non-native species. This study shows that increases in population size coincided with geographic expansions of the invasive Chinese mitten crab. These findings are in accordance with one of the few "laws of ecology", the distribution-abundance relationship that has been shown to be near-universal for native species and communities (Miller and Wiegert 1989; Gaston 1996; Eriksson and Jakobsson 1998; Venier and Fahrig 1998; Lawton 1999; Granado-Lorencio et al. 2005; Borregaard and Rahbek 2010; Villa et al. 2019). In the following, the temporal pattern of geographic expan-

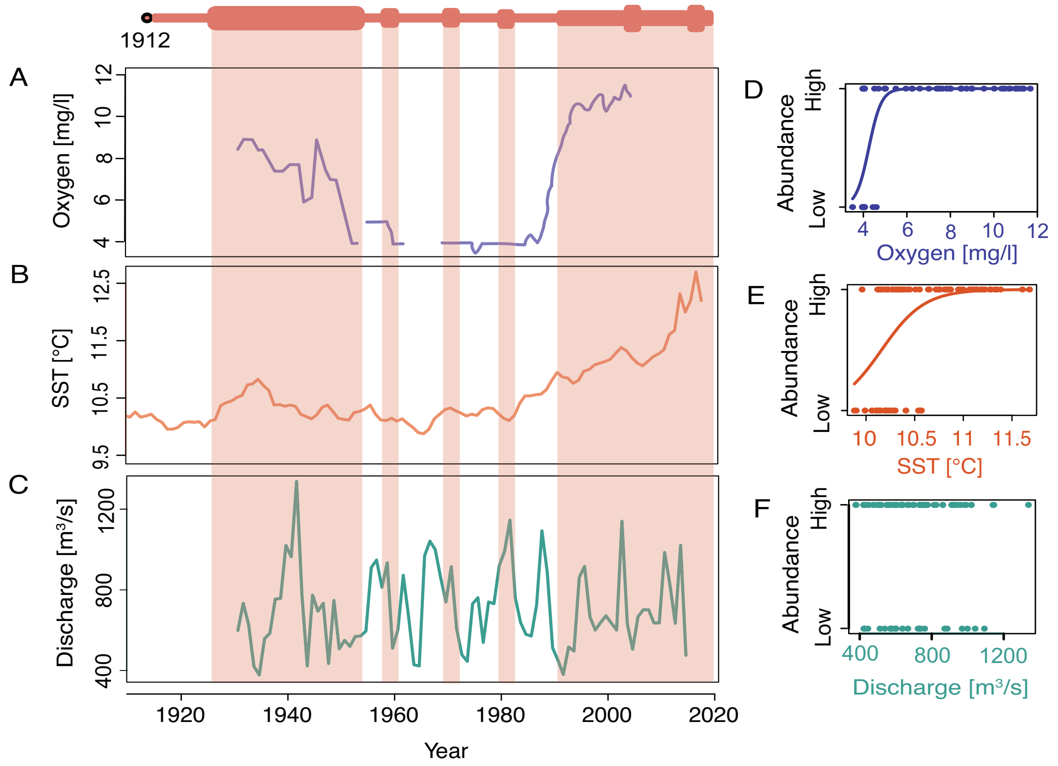

Figure 4. Possible drivers of abundance fluctuations of Chinese mitten crabs in the Elbe River and the adjacent coastal North Sea region. The top of the panel shows the abundance fluctuations for the Chinese mitten crab in the Elbe River (see Fig. 1). **A–C:** temporal changes in environmental variables that have been linked to Chinese mitten crab abundance. **A:** Mean annual riverine water quality, approximated by oxygen concentration in the Elbe River near the city of Magdeburg; **B:** Mean annual SST for the North Sea close to the mouth of the Elbe River; **C:** Annual riverine water discharge; **D–F:** results of logistic regressions. The predictive values (line) are drawn for all significant explanatory variables; **D:** oxygen content; **E:** SST; **F:** riverine water discharge. Abbreviations: SST = sea surface temperature.

sion and abundance will be discussed at different geographic and temporal scales, highlighting possible causal links. Furthermore, we assess as well as the potential environmental factors that may determine abundance.

The abundance-distribution relationship in the invasive Chinese mitten crab

The relationship between abundance increase and geographic expansion could be assessed at the regional and the global scale. At the regional scale within a river system or several proximate rivers, the temporal sequence of events appears to be: 1. introduction, 2. abundance increase, 3. geographic expansion. A probable cause of this sequence is that at times of high abundance, many individuals are available to disperse, resulting in high propagule pressure. Within a river system or between neighboring river systems, they can disperse naturally through larval dispersal and juvenile migration. Juveniles appear to migrate further upstream when densities are high, likely to avoid competition for resources (Fladung 2000). In these expansions, man-made channels play a significant role: crabs reached the Baltic Sea via the Kiel Canal (Panning and Peters 1933), the Maas river probably via the Albert canal (La Nation Belge 1-2-1939), the Saimaa Lake District via a channel that connects it to the eastern Gulf of Finland (Ojaveer et al. 2007), and lagoons along the Mediterranean coast via artificial channels (Petit and Mizoule 1973).

At a global scale, two concerted peaks of abundance increase and geographic expansion exist, one in the 1930s, and a second peak from the 1990s on. The statistical analysis indicated that geographic expansion drives the increase in abundance but not vice versa. Therefore, in the temporal sequence at the global scale abundance increase is preceded by geographic expansion. This is the opposite pattern to the sequence of events at the regional scale that was reconstructed descriptively, not statistically. The difference in scale between regional and global relationships itself may explain the differences in causality between increases in abundance and geographic spread. In local (nearby) systems, crabs may disperse more when abundance is high (thus abundance increase is followed by geographic expansion). At a global scale, however, natural dispersal capacity is limited in comparison to e.g. dispersal via shipping. Increases in abundance within regions then, may not lead to global scale expansion. On the other hand, global expansion via e.g. shipping lends itself to creating a new population whereby abundance will only increase if the introduction is successful.

Another possibility is that the second peak in abundance increase and geographic expansion were caused by a cryptic invasion of crabs with different ecological preferences. These crabs were able to establish populations in regions that could not be colonised by the non-native Chinese mitten crabs. In this case, the subsequent increase in abundance of already established populations would have been caused by an introduction wave of these "new" crabs. This hypothesis may be the case for the Belgian and Dutch population, where crabs are morphologically identical to Chinese mitten crab, but about two thirds carry Japanese mitten crab mitochondrial DNA (Hayer et al. 2019; Homberger et al. 2022). This indicates a cryptic invasion of the Japanese mitten crab with subsequent introgression, which could have altered their ecological tolerance (Homberger et al. 2022). But neither the German nor Portuguese population, which expanded and were newly founded at the end of the 1980s, respectively, show signs of a cryptic invasion of Japanese mitten crabs (Herborg et al. 2007; Hayer et al. 2019; Homberger et al. 2022). Unfortunately, no data on the detailed colonisation pathways of the Chinese mitten crab are available to test this hypothesis. Alternatively, but not exclusive to the cryptic invasion hypothesis, environmental conditions for the Chinese mitten crab improved at a global scale.

Environmental change and increasing abundance of the Chinese mitten crab

For four decades between 1940 and 1980, no increases in abundance were recorded, but a few geographic expansion attempts were noticed. None of them were successful, which may indicate that ecological conditions were not favourable for the establishment of Chinese mitten crabs. Such ecological mismatch is apparent for crabs found in the Laurentian Great Lakes and the Caspian Sea, where salinity is assumed too low for reproduction (Ricciardi 2006). Invasion attempts in Norway, Denmark and Japan may have been unsuccessful due to low temperatures (Anger 1990; Zhang et al. 2019, 2020).

In the late 1980s, the establishment of populations in Portugal and Spain marked the beginning increase of successful invasion attempts and increasing abundance across the non-native range of the Chinese mitten crab. Our case study in the Elbe River indicates that environmental change, i.e. an improvement of riverine water quality and rising sea surface temperatures, contributed to the increase of abundance of mitten crabs in this river. River quality improved in many parts of the world in the 1990s (Cane et al. 1997; European Environment Agency 2012; Stets et al. 2012; Lopez et al. 2020) Increasing SST is also a global phenomenon (Bulgin et al. 2022), whereby climate change may play a significant role in the current increase of abundance and geographic expansion of this highly invasive species.

In support of this hypothesis, ecological niche models for the Chinese mitten crab indicate that water temperature is the most important predictor of its present-day distribution (Herborg et al. 2007; Zhang et al. 2019, 2020). Thus this case study could hint at reasons for the global causes in the Chinese mitten crab invasion process: global-scale changes in the environmental conditions.

Increases in Chinese mitten crab abundance could also have been facilitated by other ecological factors, such as predator relief, lack of specific pathogens and parasites, decline of interspecific competition or the removal of migration obstacles, especially dams which have been hypothesized to limit the spread of the Chinese mitten crab in the Weser in the 1930s (Panning and Peters 1933). Macro-predators of juvenile and adult crabs include birds, fish, amphibians, and mammals including humans (Veldhuizen and Stanish 1999; Rudnick et al. 2003; Weber 2008; Bouma and Soes 2010), while larvae are likely eaten by any planktivore in the sea. Anthropogenic activities, for example overfishing of wild fish stocks, could also cause changes in predator pressure. Competitors of the Chinese mitten crab in freshwater are crayfish, which also burrow riverbanks, and have a similar food spectrum (Rosewarne et al. 2016), while in estuaries its competitors are other species of crabs, e.g., the green shore crab *Carcinus maenas* (Gilbey et al. 2008). Despite the fact that Chinese mitten crabs are threatened in their native range by many different viral and parasitic diseases (Cohen 2003; Li et al. 2011; Ding et al. 2017), invasive crabs carry few of them. The only known parasites of European populations are the microsporidian *Hepatospora eriocheir* (Stentiford et al. 2011) and the crayfish plague *Aphanomyces astaci* (Schrimpf et al. 2014).

Fishing and removal of crabs may play a particular role in preventing large-scale outbreaks of the Chinese mitten crab. In the 1930s, crabs were systematically caught and removed from German rivers draining into the North Sea (Panning 1952; Fladung 2000). Following these efforts, mass occurrences ceased. At a regional scale, fishing may therefore be a way to limit the negative impacts of the Chinese mitten crab that are mostly driven by mass occurrences.

Anthropogenic dispersal does not limit geographic expansion

The fact that introduction attempts have been reported throughout the introduction history of the Chinese mitten crab shows that propagule pressure must have been relatively high at all times. The implementation of vessel discharge regulations in North America in 2008 (U.S. Environmental Protection Agency 2013) and the Ballast Water Management Convention entry into force (IMO 2022) aim to reduce the propagule pressure of e.g. larval mitten crabs in ballast tanks. It will be very interesting to investigate future pattern of geographic expansion and if the spread of the Chinese mitten crab can be slowed down by these actions.

We would like to point out that especially in more recent times with increased globalisation, other routes of anthropogenic dispersal may become more important. Besides crabs moving coincidentally in ballast water or on the hulls of ships, active release of crabs may become a prevalent mode of anthropogenic dispersal, but only anecdotal data exist (Cohen and Carlton 1997; per. obs. H.K.). Due to its value as a delicacy for the Asian community, the Chinese mitten crab has been transported repeatedly alive across borders, both legally and illegally (Cohen and Carlton 1997; Ebersole 2020; Sessa et al. 2020). The USA seized more than 14,000 live crabs that were illegally shipped to the USA in 2019 (Fig. 5A). Subsequent release of imported live crabs may well have been the cause of the San Francisco Bay invasion, and the recent appearance of the Chinese mitten crab in Italy (Cohen and Carlton 1997; Crocetta et al. 2020).

Figure 5. Novel introduction pathway for the Chinese mitten crab related to human consumption. **A:** A fraction of the specimens seized during the operation "Hidden Mitten" of the US government; **B:** specimens sold at a market in the Netherlands in May 2021. Photo credits: **A:** U.S. Fish and Wildlife Service www.fws.gov/news/blog/index.cfm/2020/5/19/Invasion-of-the-Hairyclawed-Crustaceans-Mitten-crabs-Mitten-Crabs-Are-a-Delicacy-for-Destruction; **B:** Newspaper AD https://www.ad.nl/rotterdam/viskraam-verkoopt-levende-krabben-op-de-markt-dit-is-dierenleed~aaf3e234/.

The effect of fishing on crab dispersal has not been assessed thoroughly. Intentional fisheries for the Chinese mitten crab have become more common in the last decades, and are present at least in Germany, Portugal, and the Netherlands (van Overzee et al. 2011; Tsiamis et al. 2017; pers. comm. Filip Ribeiro and Paula Chainho [University of Lisbon] and pers. obs. by H.K. and C.E.) (Fig. 5B), but other countries are also considering it as a management tool (Clark 2011). This increased availability of crabs at markets may further increase the rate of active release into non-native habitats, a scenario proposed for the recent Italian introduction event (Crocetta et al. 2020). Taken together, this means that fishing could increase the anthropogenic dispersal of the Chinese mitten crab while reducing its local abundance.

Double trouble for the management of the Chinese mitten crab

Our study shows that increases in abundance correlate positively with geographic range expansions of the Chinese mitten crab across its non-native range. This means the double-trouble hypothesis (sensu Gaston 1990) holds in this globally invasive species. If this hypothesis holds for non-native species in general, some species may emerge as "super invaders" that expand across the globe at high densities, while others occur in low abundance at few non-native sites. At a regional scale, monitoring of the Chinese mitten crab should pay attention to increases in abundance, as they precede geographic expansion via natural dispersal. Unfortunately, despite being one of the most invasive aquatic species in the world, the Chinese mitten crab is still not included in continuous and comprehensive monitoring in many of the countries to which it has been introduced. On the other hand, long-term data on geographic expansion patterns and dynamics as well as current distribution of the species are the elements necessary to carry out a risk assessment which in turn is prerequisite to any control and management actions. By incorporating global data from scientific sources and citizens science together with information obtained from local stakeholders, our study provides a wider picture of the spatiotemporal fluctuations in the geographic expansion and abundance of the Chinese mitten crab and for this reason could be of high importance to various levels (national, international or regional) of decision-makers.

Conclusions

Using a long-term dataset of abundance changes and colonisation history, we were able to reveal at least two different mechanisms by which abundance and distribution are co-regulated. At a regional scale, newly established populations increase in abundance before they expand geographically. Regional introduction attempts have occurred in most decades, independent of the regional abundance of established populations that exist at that time globally. This suggests that the availability of human-mediated dispersal mechanisms does not limit the distribution of the Chinese mitten crab. What ultimately defines when and where new regions become invaded is likely governed by environmental suitability, which may have ameliorated at the beginning of the 1980s. A "window of opportunity" of improved climatic conditions, in combination with continuous anthropogenic dispersal, likely lead to the second invasion wave, which is still on-going. The recently implemented Ballast Water Management Convention and beginning European fisheries for exploiting the Chinese mitten crab may curb its abundance and geographic expansion, however, on-going monitoring will be required.

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Authors' contribution

Jonas Schoelynck and Christine Ewers developed the idea. Monika Normant-Saremba and Heleen Keirsebelik contributed much of the data. CE wrote the first draft of the manuscript. JS, MNS and HK revised the manuscript repeatedly, and wrote sections of the manuscript.

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Supplementary material 1

Experts and databases that were consulted (next to scientific literature) to extract first records and current distribution of *E. sinensis*

Authors: Christine Ewers, Monika Normant-Saremba, Heleen Keirsebelik, Jonas Schoelynck

Data type: occurrences, dates

Link: https://doi.org/10.3391/ai.2023.18.2.105548.suppl1

Supplementary material 2

Detailed regional accounts on the abundance and distribution of the Chinese mitten crab throughout its invasion history

Authors: Christine Ewers, Monika Normant-Saremba, Heleen Keirsebelik, Jonas Schoelynck
Data type: descriptive

Link: https://doi.org/10.3391/ai.2023.18.2.105548.suppl2

Supplementary material 3

Geographic spread and establishment of populations of *E. sinensis* summarized per region. 'Year' indicates the first record of *E. sinensis* in the region

Authors: Christine Ewers, Monika Normant-Saremba, Heleen Keirsebelik, Jonas Schoelynck
Data type: occurrences, dates

Link: https://doi.org/10.3391/ai.2023.18.2.105548.suppl3

Supplementary material 4

Fluctuations in abundance, i.e. increase or decrease, of *E. sinensis* summarized per region and the year in which the changes occurred

Authors: Christine Ewers, Monika Normant-Saremba, Heleen Keirsebelik, Jonas Schoelynck
Data type: occurrences, dates

Link: https://doi.org/10.3391/ai.2023.18.2.105548.suppl4