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Science paper or big data? Assessing invasion dynamics using observational data

Charlotte H. Clubley [a,*], Louise B. Firth [a], Louisa E. Wood [b], David T. Bilton [a,c], Tiago A.M. Silva [d], Antony M. Knights [a]

[a] *School of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, United Kingdom*
[b] *Centre for Blue Governance, Department of Economics and Finance, University of Portsmouth, Portsmouth, Hampshire PO1 3DE, United Kingdom*
[c] *Department of Zoology, University of Johannesburg, PO Box 524, Auckland Park, Johannesburg 2006, South Africa*
[d] *Lowestoft Laboratory, Centre for Environment, Fisheries and Aquaculture Science, NR33 0HT Lowestoft, United Kingdom*
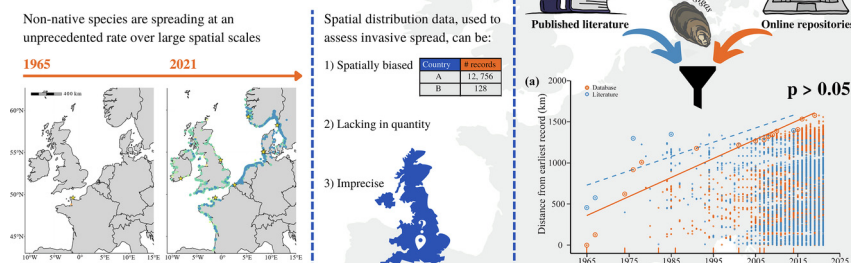
HIGHLIGHTS

- Improving predictions of invasive spread is fundamental to effective management.
- We compare 'big data' against published literature to quantify invasion dynamics.
- Both data forms yielded similar predictions despite major disparity in first record.
- Expansion was characterised by a combination of short- and long-range 'jumps'.
- This framework enables critical evaluation of invasion using diverse data sources.

GRAPHICAL ABSTRACT

ABSTRACT

Non-native species are spreading at an unprecedented rate over large spatial scales, with global environmental change and growth in commerce providing novel opportunities for range expansion. Assessing the pattern and rate of spread is key to the development of strategies for safeguarding against future invasions and efficiently managing existing ones. Such assessments often depend on spatial distribution data from online repositories, which can be spatially biased, imprecise, and lacking in quantity. Here, the influence of disparities between occurrence records from online data repositories and what is known of the invasion history from peer-reviewed published literature on non-native species range expansion was evaluated using 6693 records of the Pacific oyster, *Magallana gigas* (Thunberg, 1793), spanning 56 years of its invasion in Europe. Two measures of spread were calculated: maximum rate of spread (distance from introduction site over time) and accumulated area (spatial expansion). Results suggest that despite discrepancies between online and peer-reviewed data sources, including a paucity of records from the early invasion history in online repositories, the use of either source does not result in significantly different estimates of spread. Our study significantly improves our understanding of the European distribution of *M. gigas* and suggests that a combination of short- and long-range dispersal drives range expansions. More widely, our approach provides a framework for comparison of online occurrence records and invasion histories as documented in the peer-reviewed literature, allowing critical evaluation of both data sources and improving our understanding of invasion dynamics significantly.

1. Introduction

The causative factors shaping the geographical distribution of animals have long been of fundamental interest to biologists (Brown et al., 1996;

* Corresponding author at: 618 Davy Building, University of Plymouth, Drake Circus, Plymouth PL4 8AA, United Kingdom.
E-mail address: charlotte.clubley@postgrad.plymouth.ac.uk (C.H. Clubley).
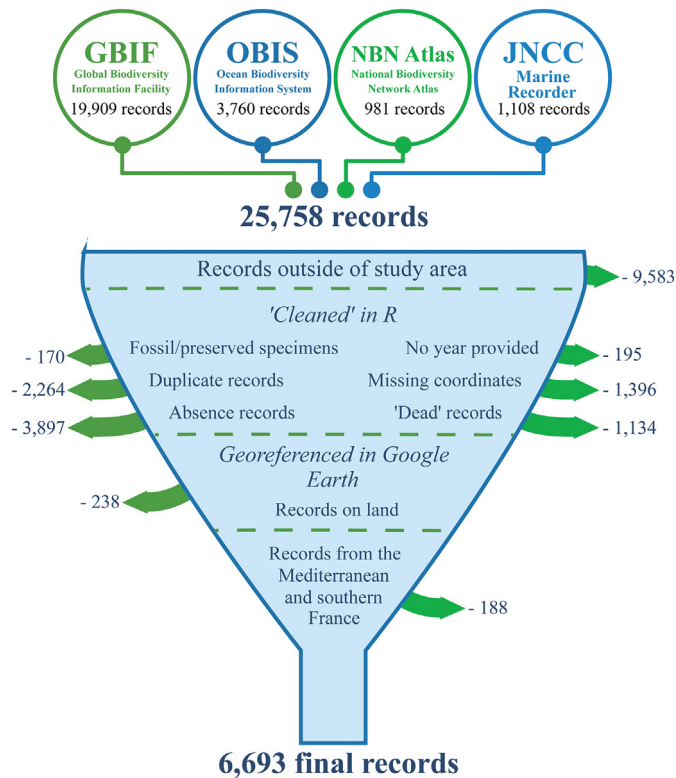
Fig. 1. Steps taken in the download and cleaning of *Magallana gigas* occurrence data from online data repositories, including the number of records removed at each step.

the relative importance of long-distance and local dispersal in shaping species ranges during invasions (Pyšek and Hulme, 2005).

Estimates of the rate of spread of NNS depend on information on the spatial distribution of the species over time. The quantity and quality of these data, however, influence the accuracy of estimates of spread (Hastings et al., 2005). Online data repositories, such as the Global Biodiversity Information Facility (GBIF, 2021) or Ocean Biodiversity Information System (OBIS, 2021), can be fragmented and spatially biased in their representation of species distributions (Firth et al., 2021a; Kochmann et al., 2013; Rotenberry and Balasubramaniam, 2020). In the case of NNS that have been deliberately introduced, despite there often being detailed accounts of early introduction history in both peer-reviewed and grey literature (Seebens et al., 2017), this is often not captured in online databases (Ma et al., 2021), in part due to the large quantity of records in these databases stemming from public observations through portals such as iNaturalist, many of which were not created until the 2000s and so contain a disproportionate amount of records from more recent years. There do exist databases where early invasion history is the focus of records, such as the Alien Species First Record Database (Seebens et al., 2017) or AquaNIS (http://www.corpi.ku.lt/databases/index.php/aquanis/), however in these cases only a single record from each country is provided. As numerous scientists, particularly modellers, rely heavily on online data repositories, many interpretations of the spread of NNS should be regarded with caution when used to inform species management. Problems of this nature have been demonstrated in the case of endangered species management, where the accuracy of uncleaned GBIF data in predicting IUCN threat categories of plant groups was substantially lower than when manual cleaning was applied to the same data (Panter et al., 2020).

One species for which there are detailed accounts of the early introduction history in the peer-reviewed literature is the Pacific oyster, *Magallana gigas*, which was initially introduced to its non-native range for aquaculture multiple times following the decline of the native oyster (*Ostrea edulis*, Linnaeus, 1758) (Herbert et al., 2012). Since its introduction it has expanded rapidly and is now considered to be established across much of its non-native range (McAfee and Connell, 2021), with populations formed across the majority of the world's seas, including many European coastlines (Ewers-Saucedo et al., 2020). Despite its success as a NNS and the potentially negative impacts it may have on recipient habitats (Herbert et al., 2016; Miossec et al., 2009; Ruesink et al., 2005), *M. gigas* remains the most widely farmed oyster globally (Jones et al., 2013; Troost, 2010).

Here we compare the year and location of the first record of *M. gigas* from nine countries across two data sources: a database constructed from occurrence records obtained from online data repositories and the peer-reviewed literature, to (1) identify any discrepancies in the timing and location of invasion events between the two data sources, and (2) determine whether such discrepancies in documented invasion history lead to differences in rate of spread estimates. Additionally, we further apply the database data to examine the invasion dynamics of *M. gigas* in its non-native European range. This approach provides a means of comparing data sources as references for introduction and spatio-temporal spread of NNS, and the implications of any differences identified by this comparison for NNS science and policy, as well as adding to a rich body of literature on the distribution and rate of spread of *M. gigas* in its non-native range.

2. Methods

2.1. Compiling the database of occurrence records

A database of *M. gigas* occurrence records in its introduced European range was compiled in July 2021 using four online repositories: Global Biodiversity Information Facility (GBIF, 2021), Ocean Biodiversity Information System (OBIS, 2021), NBN Atlas (National Biodiversity Atlas (NBN)

Darlington, 1957; Gaston, 2003; Kirkpatrick and Barton, 1997; Parmesan et al., 2005; Rotenberry and Balasubramaniam, 2020) and are of particular importance to non-native species (NNS), where an understanding of range dynamics may inform management and predictions of ongoing ecosystem change (Pyšek et al., 2020; Seebens et al., 2021a). In the Anthropocene, global environmental change coupled with exponential growth in trade and transport provide novel opportunities for the introduction of NNS to sites beyond their natural capabilities, in ways that the recent biota has not previously experienced during its evolutionary history (Mack et al., 2000; Seebens et al., 2021a; Thomas et al., 2016; Wilson et al., 2009). Whilst this may lead to increased movement of NNS across the globe, establishment of populations and subsequent secondary spread is required for individual NNS to succeed within new distributional limits (Seebens et al., 2021b). Understanding patterns of secondary spread of NNS during the invasion process is a key objective in invasion biology (Arim et al., 2006; Seebens et al., 2021b), particularly as this may assist in the prediction and management or prevention of future invasions (Evans and Gregoire, 2007; Mack et al., 2000; Tobin et al., 2015). With >800 NNS in European seas (Montes Vilanova, 2020), such management strategies will not only be invaluable to safeguarding against future invasions but also to efficiently managing existing ones.

When evaluating NNS spread on scales as large as the European seas, a single measure of spread is unlikely to capture all patterns, including the coalescing of populations established across multiple introduction sites and patterns of dispersal at fine spatial scales. Employment of a combination of spread measures, ideally both linear and non-linear, which document patterns in species expansion over time is likely to generate an improved understanding of species spread (Gilbert and Liebhold, 2010; Liang et al., 2019; Mineur et al., 2010). Furthermore, exploring the spatio-temporal dynamics of NNS spread at a variety of spatial scales is crucial if we are to understand

Fig. 2. Decadal spread of *Magallana gigas* in its introduced European range, depicted using occurrence records amalgamated from online repositories (GBIF, OBIS, NBN Atlas, Marine Recorder). Maps show the distribution in the (a) 1960s, (b) 1970s, (c) 1980s, (d) 1990s, (e) 2000s, (f) 2010s, and (g) 2020 – July 2021. Points are coloured by decade. Stars represent the location of the first record in the database for each country.
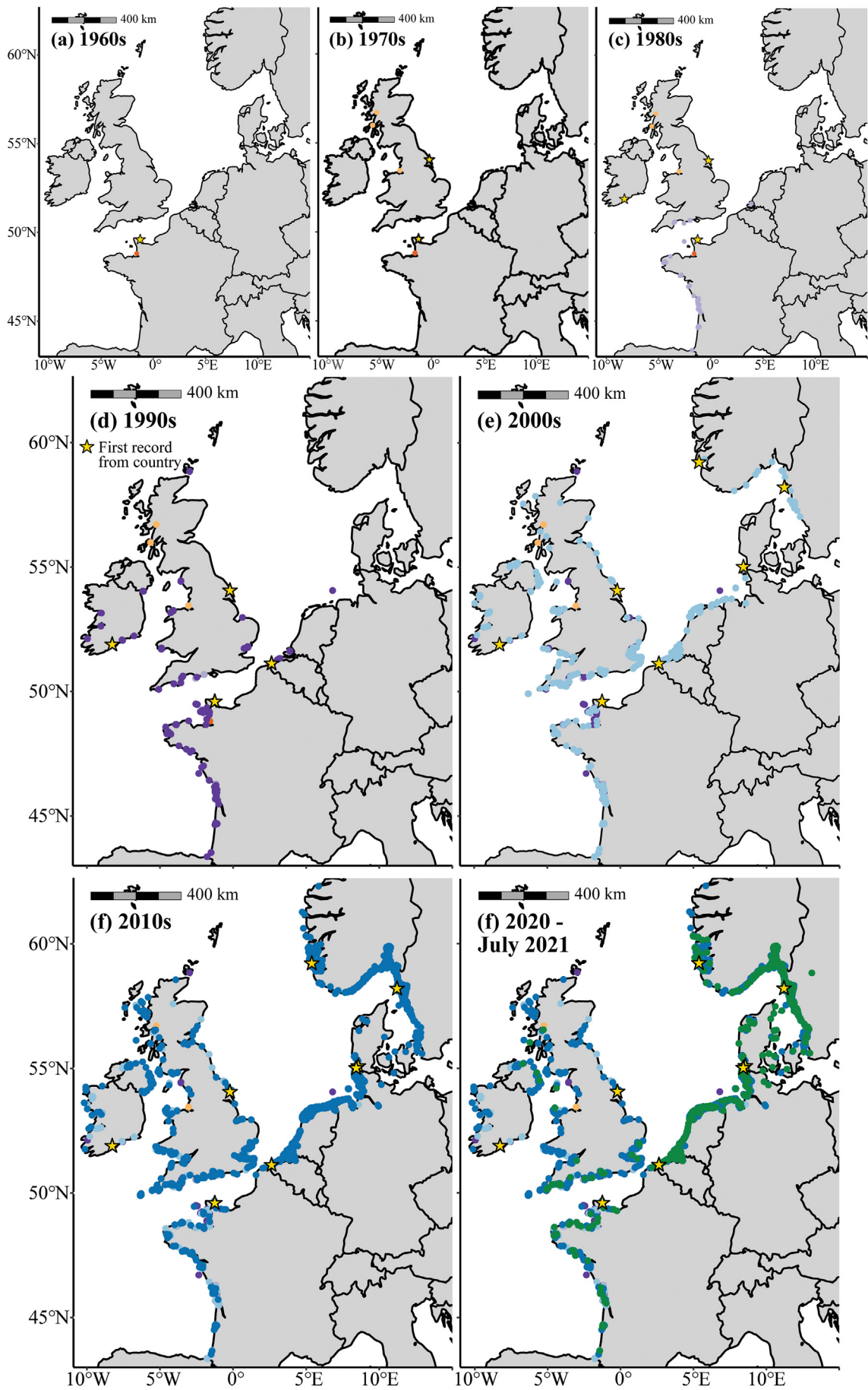
Atlas occurrence download, 2021) and the Joint Nature Conservation Committee's (JNCC) Marine Recorder (Marine Recorder, 2021) (Fig. 1). GBIF and OBIS provide data on the global distribution of species, whilst NBN Atlas and Marine Recorder are specific to the United Kingdom and Ireland. Together, these data cover a spatial extent of 28°N – 63°N, 15°W – 24°E. Absence (species not observed) records were only available for the United Kingdom and Ireland, so were not included in the final database. Where records were reported alongside a link to an online record, the online record was searched for any additional information linked to the species occurrence.

The database was uploaded into R, version 4.1.0 (R Core Team (2021)), and 'cleaned' to remove any records without coordinates, duplicate records, records from fossil and preserved specimens, and records with no associated year. Remaining records were spatially mapped using a water bathymetry raster of the study area taken from MARSPEC (Sbrocco and Barber, 2013) with a 100 m buffer added to account for low resolution in coastal areas. If a record did not overlap this raster, it was initially flagged as being 'on land' and was then georeferenced in Google Earth Pro (2015). A two-step process for identifying records on land was required as some records, particularly those in the Norwegian Fjords, were flagged even with the addition of a buffer (likely due to the resolution of the raster layer used). If a record was on land it was removed from the database, otherwise it was retained.

Individual database records included the status of each oyster observation as alive, dead, or unknown. Here, only alive or unknown records were retained to avoid the possibility of false presences caused by the inclusion of dead individuals. Unknown records were retained under the precautionary approach of the Convention on Biological Diversity (2016). Upon examination of the resulting data, records from countries bordering the Mediterranean Sea and from Portugal were scarce (n = 58, from six countries (Croatia, Greece, Italy, Portugal, Slovenia and Spain); n = 96 from southern France), and so the data were further reduced to cover only western and northern Europe (extent: 43°N – 63°N, 14°W – 11°E; Fig. 2) as a paucity in records meant meaningful spread estimates could not be calculated. The process for compiling records of occurrence is summarised in Fig. 1.

2.2. Comparison of invasion histories: literature vs. database

To compare the invasion history of M. gigas as reflected by the database data with what is known about its invasion history, the engines Web of Science and Google Scholar were searched for published peer-reviewed scientific literature referencing the year and location of the first record of M. gigas in each country within the study area. Where possible, references were followed until the source of the original record was located. Records pertaining to the Portuguese oyster, Crassostrea angulata – considered a potential subspecies of M. gigas (Wang et al., 2010) – were not considered in this process due to genetic differences identified between the two species (Gagnaire et al., 2018). Approximate coordinates for these locations were taken from Google Earth Pro (2015) as the closest area of coastline to the named location. This resulted in nine sets of years and coordinates, one for each country within the study area.

The locations of the first records from the database and those obtained from the peer-reviewed literature were compared by calculating the 'seaway distance' (the shortest path length between points when travelling over water) between the two locations. Seaway distance was calculated using the 'shortestPath' function from the 'gdistance' package in R (van Etten, 2017), and constrained to allow 'travel' over the ocean cells of a transition layer built using the MARSPEC bathymetry raster.

2.2.1. Estimating rates of spread

Following Mineur et al. (2010), we used the maximum rate of spread (hereafter max-spread), a spatially explicit measure, to compare spread estimates between data sources. Max-spread was calculated by first computing the seaway distance of records of M. gigas from each year to a reference point representing the first record of M. gigas in the study area, after which distances were filtered to include only those representing an increase on the previous maximum distance. Linear regression was then used to visualise spread over time, from which the coefficients were used to estimate max-spread, quantified as $km\ y^{-1}$. Max-spread was calculated twice, using the location of the first record from (i) the database (Saint-Vaast-la-Hougue, France), and (ii) the searched peer-reviewed literature (Oosterschelde estuary, the Netherlands, Table 1) as the reference location. In both instances database records were used to calculate distances from the reference point due to a lack of temporal data from the literature. An F-test was used to test for differences in the slopes of max-spread estimates calculated using either data source as a reference location.

As many of the records within the database derive from citizen science projects or grey-literature reports, sampling is not systematic. For instance, repeat sampling of locations does not occur, meaning that it can be difficult to distinguish true range contraction or expansion on a local scale. By considering only increases in the maximum distance, the dependent variable is constrained and it is assumed that each record represents a population that survived to the following year, regardless of a lack of systematic repeat sampling (Mineur et al., 2010). Although this assumption follows the precautionary principle (Convention on Biological Diversity, 2016), it results in increased probability of Type-I error. To account for this, a null model was simulated to estimate the probability of Type-I error at eight different levels of α (Table S1). A distance (km) value for each year from 1965 to 2021 (one distance per year) was randomly generated using the mean (661 km) and standard deviation (406) of the distances of each occurrence record to the first temporal record in the database calculated across all years. A regression was then run using only those distances representing an increase on the previous maximum, as in the methods described above. This was repeated 1000 times for each of the eight levels of α, and the percentage of simulations that yielded a significant result was used to indicate the percentage likelihood of Type-I error at that α level (Table S1). Based on these null models an alpha value of p = 0.001 was

Table 1
The year of the first record of *Magallana gigas* from countries in northern and western Europe, determined by searching the peer-reviewed literature, and the year of the first record in the database amalgamated from GBIF, OBIS, NBN Atlas and Marine Recorder. * Indicates a gap of >10 years between the first record from the literature and the first record from the database.

Country	Peer-reviewed literature			Database	
	Year	Location	Reference	Year	Location
The Netherlands	1964	Oosterschelde estuary	Dolmer et al. (2014); Troost (2010); Wolff (2005); Wolff and Reise (2002)	1982*	Zierikzee
Ireland	1965	Cork Harbour and Dungarvan	Martínez-García et al. (2021); Steele and Mulcahy (1999)	1986*	Rossleague, County Cork
United Kingdom	1965	Conwy, Wales	Humphreys et al. (2014); Utting and Spencer (1992); Wolff and Reise (2002)	1974	Wilsthorpe, Bridlington, Yorkshire
France	1966	Bay of Marennes-Oléron	Goulletquer et al. (2002); Grizel and Heral (1991); Wolff and Reise (2002)	1965	Saint-Vaast-la-Hougue
Belgium	1969	Sluice Dock, Oostende	Kerckhof et al. (2007); Troost (2010)	1995*	Koksijde
Germany	1971	Sylt	Troost (2010); Wolff and Reise (2002)	2006*	List
Denmark	1972	Limfjorden	Dolmer et al. (2014); Jensen and Knudsen (2005); Troost (2010)	2014*	Havneby, Rømø
Sweden	1973	Stromstad, northern Bohuslan	Dolmer et al. (2014); Troost (2010)	2007*	Skagerrak
Norway	1979	Vallersund, Espevik and Oygarden	Gederaas et al. (2012); Troost (2010); Wrange et al. (2010)	2001*	Bokn Municipality, Bokn

adopted as using lower (i.e. more conservative) values did not substantially reduce the likelihood of Type-I error.

As well as pan-European, transboundary (i.e. across national borders – all records from the database) measures, max-spread was also calculated separately for each country within the study area by filtering the database to records solely from that territory. In the case of the United Kingdom, excluding Northern Ireland (NI) from mainland UK did not produce significant differences in spread estimates, so all data for NI were retained.

2.3. Assessing invasion dynamics using online database records

The invasion dynamics of *M. gigas* in its non-native range were further examined using only the database data due to a lack of temporal data in the peer-reviewed literature. To visualise the spread of *M. gigas* in its introduced range over time, database records were first separated into subsets by decade, then mapped to show geographical spread relative to the earliest record in the database – an observation at Saint-Vaast-la-Hougue, on the Atlantic coast of France in 1965 (Fig. 2). The seaway distance was calculated for the two most distant records from each year in the database as an indication of the total range size of the species at that time.

To examine the increase in the total area occupied by *M. gigas* in its introduced range over time, a spatial polygon grid with 0.5° ($\sim$50 $\times$ 50 km) resolution was superimposed over the sea area and the total number of polygons containing at least one spatial point record of *M. gigas* each year since the first record in the database (1965) was determined. To account for the lack of systematic repeat sampling, we assumed that once a polygon was 'occupied' it remained occupied for all subsequent years. As for max-spread, the accumulation of grid polygons was calculated at both the transboundary and within-country level.

3. Results

At the transboundary (international) level, max-spread significantly increased over time when calculated using the first record in the database as a reference point, with a rate of spread of 23.1 km y^{-1} $\pm$ 2.7 ($F_{1, 13} = 71.71$, $p < 0.001$, $R^2_{adj} = 0.83$; Fig. 3). The maximum distance of database records from the first record in the database increased 15 times over the 56-year

period (Fig. 3), these increases corresponding with increases in the range size of *M. gigas* (Fig. 4a). In contrast to when using the database data, calculation of max-spread using the peer-reviewed literature introduction location led to a non-significant fit of max-spread over time ($F_{1, 3} = 3.98$, $p > 0.05$, $R^2_{adj} = 0.43$; Fig. 3). This is unsurprising, however, given the low number of increases in maximum distance (n = 5) included in the model in contrast to the number included in that constructed using the database reference (n = 15). In the database data, the first record of *M. gigas* is in northern France, whilst the first in the peer-reviewed literature is from the Oosterschelde estuary in the Netherlands (Table 1; these locations are 456.6 km distant). However, comparison of slopes revealed no significant differences in overall rates of spread ($F_{16, 17} = 0.75$, $p > 0.05$, Table 2) when either location was used to calculate transboundary max-spread.

Individual country max-spread values appear to be idiosyncratic for calculations using both data sources, with no consistent, general pattern emerging across territories (Table 2, Fig. S1). Differences in the location of the first record from the database and from the peer-reviewed literature varied among countries. There was <50 km distance between the two locations for the Netherlands, Belgium, Germany and Ireland, but >50 km for Denmark, France, Norway, Sweden and the United Kingdom (Fig. 5). However, similar to transboundary spread, there was generally no significant difference between max-spread slopes constructed using the different locations at a country level (Table 2, Fig. S1). Of the seven countries where it was possible to compare differences between slopes (the Netherlands and United Kingdom were excluded due to too few increases in maximum distance from one or both of the reference locations), the only country with a significant difference in max-spread between using the database or literature data as a reference location was France ($F_{8, 9} = 13.14$, $p < 0.05$, Table 2). For France, max-spread significantly increased over time when using the first record from the database as a reference ($F_{1, 4} = 16.54$, $p < 0.05$, Table 2, Fig. S1) and showed a rapid increase from 1965 to 1985, following which there were no further increases in the maximum distance from the reference location. Conversely, increases in the maximum distance from the literature-based reference location were more evenly spread across time, and resulted in a non-significant fit for max-spread ($F_{1, 4} = 3.001$, $p > 0.05$, Table 2, Fig. S1). Of the seven countries where slope comparison was possible, France was the country with
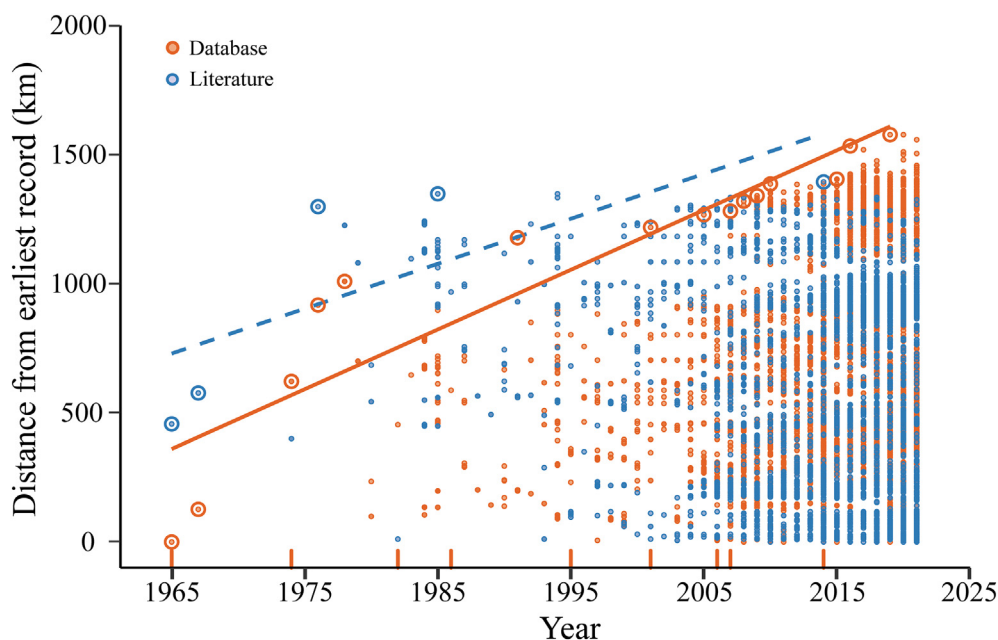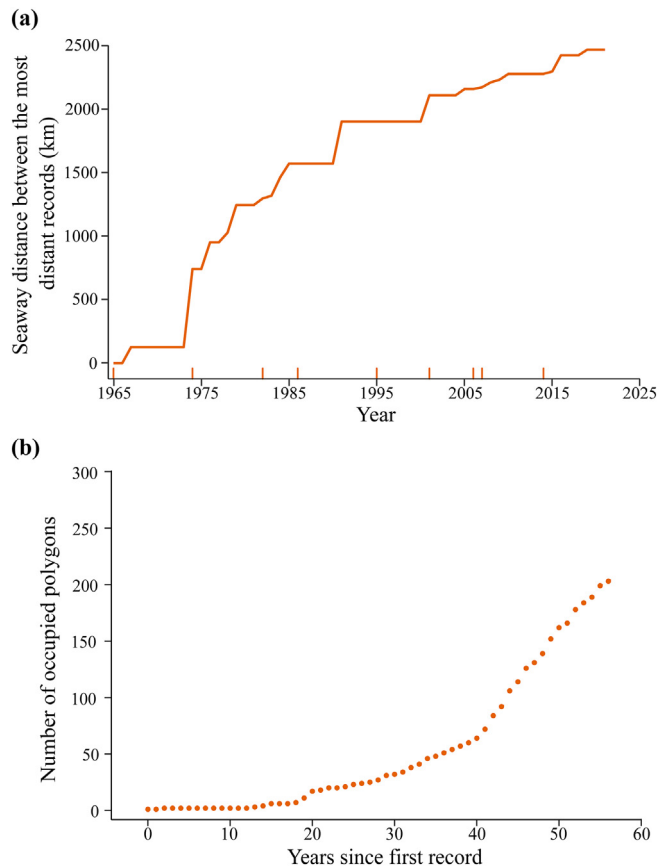

Fig. 3. Seaway distance (km) of records of *Magallana gigas* from a reference point representing either the first record in the database (Saint-Vaast-la-Hougue, France, 1965) or the first record based on the peer-reviewed literature (Oosterschelde estuary, the Netherlands, 1964). Lines show the outputs of two linear models calculated using only new maximum distances (circled) from the reference point. The dashed line indicates linear regression fit was not significant. Rugs along the x-axis show the year of the first record in the database from each country in the study area.

(a)

(b)

Fig. 4. Spread metrics calculated using occurrence records of *Magallana gigas* from the database only. (a) Cumulative increases in the seaway distance (km) between the two most distant records recorded each year. Rugs along the x-axis show the year of the first record in the database from each country in the study area. (b) The cumulative accumulation of occupied grid polygons within the introduced range since the first record in 1965.

the greatest distance between the first record from the database and from the literature (683.6 km distant, Fig. 5), which may account for the observed difference.

Altogether, there were disparities between the year of the first record of *M. gigas* from the peer-reviewed literature and the first record from the database. At the level of the entire introduced area (transboundary), the year of the first record in the database (1965) was only one year following the year of the first record from the peer-reviewed literature (1964), and so at this scale the database data reflects the literature relatively well (Table 1). At the country scale, the differences between the two years are generally much greater ($\geq$ nine years difference), with the exception of France where the year of first record in the database precedes the year of first record in the literature (Table 1).

Increases in the overall range size of *M. gigas* were calculated using the database data only, and were characterised by large infrequent jumps in the 10 years immediately following the first record (1965–1975), with the largest increase of the entire invasion period, 613.3 km, occurring from 1973 to 1974; corresponding with the first record in the database of *M. gigas* in the United Kingdom in Wilsthorpe, Bridlington, Yorkshire (Fig. 4a). Following this there were frequent (every 1–3 years) yet smaller increases for the next 10 years (1975–1985), with an average increase in distance of 118 km. The subsequent 20 years (1985–2005) showed a pattern of infrequent increases (6, 10 and 4 years apart), after which increases occurred once every 1–5 years from 2005 to 2021 (Fig. 4a). Increases in range were reflected in an increase in the number of polygons occupied over time (Fig. 4b). However, increases in maximum distance from the location of the first record in the database in early years (for example the increase from 1974 to 1975,

Fig. 4a) are not reflected in a similarly large increase in the number of occupied polygons (Fig. 4b), suggesting a change in the range size of *M. gigas* does not always indicate a marked increase in numbers of individuals.

When considering the accumulation of grid polygons at the within-country level, the total number of occupied polygons in Belgium appears to have stabilised over the last 12 years (2010 − 2021) suggesting the country is approaching or has indeed already reached the occupation of all available polygons (Fig. S1). This is mirrored in distribution maps (Fig. 2), where the majority of Belgium's short coastline (~65 km) appears occupied. Germany and Sweden show similar patterns in the accumulation of polygons, whereby there is an initial rapid accumulation for a period of around five years followed by a more gradual increase (Fig. S1). However, distribution gaps show that, unlike Belgium, there are apparently unoccupied areas along the eastern coasts of these countries in the Baltic Sea (Fig. 2).

4. Discussion

The distribution and spatial spread of species has been studied for many decades (Elton, 1927; Ma et al., 2021) and remains of immense scientific interest, particularly in the context of non-native species (NNS). Our analysis of the spread of the Pacific oyster, *Magallana gigas*, in its introduced European range demonstrates how a database compiled from occurrence records available through online data repositories can be used to confidently predict the past spread of a NNS. Using two metrics of spread, maximum rate of spread (max-spread) and the accumulation of grid polygons, we demonstrate that at the transboundary (international) level, rate of spread of *M. gigas* has significantly increased since its introduction to Europe in the 1960s, and that discrepancy between the database data and the invasion history of *M. gigas* documented in the peer-reviewed literature does not significantly impact estimations of spread.

4.1. Comparison of rate of spread estimates from two data sources

The accuracy of any measurement of species spread is clearly dependent on the availability of robust information on their past and present distributions (Pagad et al., 2018), which often comes from online data repositories, such as those used in the present study. However, these data sources can be spatially biased, imprecise and lacking in quantity (King et al., 2021; Rotenberry and Balasubramaniam, 2020; Wood et al., 2021). In the case of *M. gigas*, the early introduction history of the species is well-detailed as it was deliberately introduced to its non-native range for aquaculture before escaping into the wild. Therefore, information on the timing and location of introduction events is relatively easily found and is supported by the increase in global efforts to produce databases with first record dates for NNS (e.g. AquaNIS or the Alien Species First Records database (Seebens et al., 2017)). However, this information does not often extend beyond the very first record of a species, and so there remains a reliance on data repositories for records of species occurrence across the entire invasion timeline. Here we have demonstrated that first records and early invasion history of *M. gigas* is fairly poorly reflected in online data repositories of occurrence records (despite being listed as one of the 100 worst alien species in Europe (Herbert et al., 2016; Vilà et al., 2009) and being keenly monitored by a range of countries), with disparities in invasion timing and location and a general paucity of early occurrence records. Nevertheless, when calculated using either the location of the first record from the database or from the peer-reviewed literature, transboundary max-spread estimates for *M. gigas* do not differ significantly. Given the high dependency of NNS science on these online databases (see GBIF Secretariat (2019) for examples of published literature using GBIF data records - >1750 peer-reviewed publications as of 2016 (Anderson et al., 2016)) this is promising; however *M. gigas* is a conspicuous species that is relatively easy to locate and identify. Future studies on less conspicuous NNS would be well-placed to compare online data repositories with the published introduction history of the species to determine whether this remains the case across species.

At a country level, the same was true with the exception of France, where max-spread estimates were significantly different when calculated

Table 2

Comparison of p-values, rate of spread and R^2_{adj} from models using either the first record from the database or the peer-reviewed literature as a reference point for maximum rate of spread model fitting. The final column shows the p-value result of an F-test comparing the two model slopes (where it was possible to fit two models). Grey cells indicate a model could not be fit due to insufficient data points.

Country	Database			Literature			Slope comparison P-value
	P-value	Rate (km y⁻¹)	R^2_{adj}	P-value	Rate (km y⁻¹)	R^2_{adj}	
All	1.19×10^{-6}	23.123 (± 2.731)	0.8347	0.14	17.384 (± 8.715)	0.4268	0.4004
Belgium	0.03926	3.996 (± 0.816)	0.8845	0.3193	2.706 (± 1.483)	0.5377	0.4593
Denmark	0.06305	255.06 (± 67.27)	0.8168	0.184	50.59 (± 15.02)	0.8379	0.08343
France	0.01526	37.717 (± 9.274)	0.7566	0.1582	5.281 (± 3.048)	0.2858	0.006504
Germany	0.1139	27.78 (± 13.77)	0.3804	0.1626	22.27 (± 13.6)	0.2187	0.7835
Ireland	0.03468	22.334 (± 6.064)	0.7585	0.03409	21.891 (± 5.904)	0.7612	0.96
The Netherlands							
Norway	0.01261	30.51 (± 7.09)	0.778	0.01479	32.35 (± 7.88)	0.7602	0.8669
Sweden	0.004559	19.825 (± 4.064)	0.7917	0.004128	19.612 (± 3.928)	0.7996	0.9707
United Kingdom	0.261	236.8 (± 103)	0.682				

using either reference location. This is likely due to the large distance between the two locations when compared to other countries where slope comparison was possible, and may also in part be due to poor reflection of the early invasion history of *M. gigas* in France within the database. France was the only country where the first record in the database preceded the year of the first record from the literature, and therefore it is possible
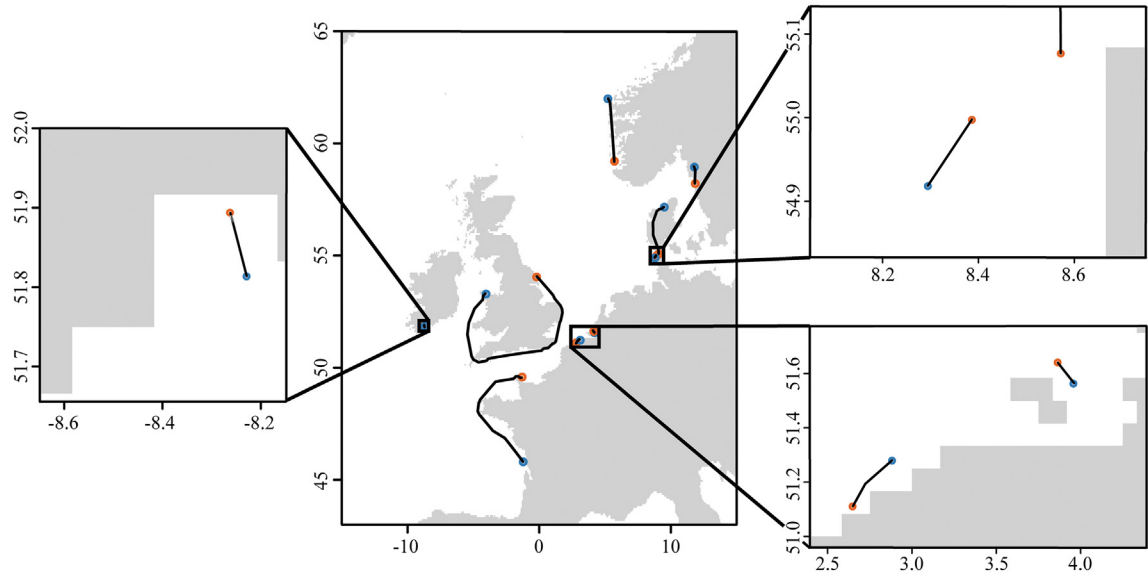
Fig. 5. The shortest path seaway distance between the first record from the database (orange) and from the peer-reviewed literature (blue) for each country. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that the database record from 1965 was misidentified. This may obscure the accuracy of the database data in reflecting the early invasion history in France and be the cause of disparity in max-spread estimates. On the whole, whilst country-level analysis of max-spread is valuable as historically this is the scale at which decisions regarding NNS policy are made (Gallardo et al., 2016), in the case of *M. gigas* there are many countries where there are too few records available to predict max-spread with any real accuracy. For all countries, the max-spread p-value was greater than the alpha value of 0.001 chosen after running the null model, indicating a high degree of Type-I error. Therefore, whilst country-level analysis is useful for examining fine-scale patterns of spread encapsulated within the transboundary spread, individual country max-spread estimates must be interpreted with caution.

4.2. The rate of spread of Pacific oysters in Europe

Our analysis of *M. gigas* invasion dynamics using only the database data adds significantly to our understanding of its spread through Europe since first introduction (Jones et al., 2013; King et al., 2021; McAfee and Connell, 2021). At the transboundary level, max-spread estimates calculated using the first record from the database suggest that *M. gigas* has spread at a rate of 23.1 km y^{-1} ± 2.7 – providing a singular estimate of rate of spread over the 56-year period captured by the database (1965 – July 2021). Calculation of max-spread represents advancements of the range edges of the species by including only increases on a previous maximum distance from an initial record. Past studies enumerating the spread of *M. gigas* have resulted in greater spread rates than calculated here, as these studies included the entire range of the species in spread calculations. For example McAfee and Connell (2021), averaged the spatial extent of *M. gigas* by the number of years since initial introduction to produce an estimated global spread rate of 1009 km by 2010. Here, by using only increases in the maximum distance from a reference point representing the initial introduction location of the species to calculate a max-spread value and coupling this with calculations of the area occupied by the species using a spatial polygon method, we are able to visualise fine-scale patterns in the invasion history of *M. gigas*, and therefore gain a better understanding of the process of invasion, including both multiple introduction events and movement as an invasion front from a single localised introduction (Mineur et al., 2010). Such an approach is particularly valuable for studying invasion dynamics across contiguous seascapes (Ma et al., 2021) such as that of north-west Europe (excluding the islands of Ireland and Britain).

Increases in the maximum distance of records of *M. gigas* from the database reference location, used to calculate max-spread, were characterised by large increases in the early years of invasion. Increases such as these are not necessarily beyond the natural dispersal potential of *M. gigas*, which has a planktonic larval duration (PLD) of 2–4 weeks (Herbert et al., 2012; Robins et al., 2017) allowing for rare long distance dispersal events (Melo et al., 2010). However, on at least one occasion, an increase in distance was associated with the first record of *M. gigas* in a new country, and so may be a direct result of movement of the species for aquaculture, though anthropogenic movement such as this has been shown to not significantly impact our ability to reconstruct species invasion (Hudson et al., 2022). As a commercially important species, *M. gigas* has undergone multiple introductions via anthropogenic movement (Troost, 2010), with at least 27 countries farming *M. gigas* in 2015 (McAfee and Connell, 2021), and movements of this kind have been shown to facilitate secondary spread and genetic admixture of NNS (Elton, 1958; Hudson et al., 2020; Wilson et al., 2009). Deliberate introductions to areas at great distance from pre-existing populations, leading to what appear to be saltatory jumps in distribution, give rise to a pattern of spread known as 'jump' (Tobin et al., 2015) or 'extra-range' (Wilson et al., 2009) dispersal (Prentis et al., 2008; Rius et al., 2014). In the case of *M. gigas*, when considering both transboundary max-spread and the accumulation of polygons concurrently this pattern becomes clear as large increases in maximum distance in the early years of invasion are not reflected in comparable increases in the number of polygons 'occupied' by the species.

The transboundary accumulation of polygons shows an apparent exponential increase, and begins to visibly accelerate from around 1985 onwards (20 years since the first record), at which point some of the greatest increases in *M. gigas*' range had already occurred. This delay in the accumulation of occupied polygons suggests coalescence of populations of *M. gigas* established by jump dispersal and those moving forward as an invasion front from the first record. Shigesada et al. (1995) termed this spread pattern 'stratified dispersal' – where short- and long-range dispersal occur simultaneously – and this seems the most likely pattern of spread for *M. gigas* in its introduced European range. Without the use of both spread metrics this pattern would be lost, and our understanding of patterns in NNS spread, essential for designing effective management actions (Arim et al., 2006; Evans and Gregoire, 2007; Mineur et al., 2010), is obscured. By coupling dispersal models with these rate of spread measures and records of introductions for aquaculture, the relative importance of short- and long-range dispersal events to the overall rate of species spread could begin to be understood. Even further, the addition of genetic techniques such as high throughput sequencing could reveal the importance of multiple introduction events to the invasion history of a species (Hudson et al., 2022).

A lag phase preceding exponential growth is typical of patterns of NNS invasion (Arim et al., 2006; Mack et al., 2000), however when using data from online data repositories the lack of systematic sampling and the ad-hoc nature of occurrence records can make it difficult to distinguish whether there is a true lag or rather just a lack of sufficient sampling (Herbert et al., 2012). Whilst progress is being made towards collating NNS distribution data that should reduce uncertainties of this kind (see, for example, the Global Register of Introduced and Invasive Species (GRIIS - Pagad et al. (2018))) this aspect should clearly be considered in future use of online data repositories for occurrence records.

4.2.1. Boundaries to present, and likelihood of future, spread of Magallana gigas
Max-spread analysis using the database data demonstrates that *M. gigas* has spread at a significant rate through its introduced European range, whilst the accumulation of polygons shows an exponential-style increase in the occupied area of *M. gigas*, with no evidence of saturation. Comparatively, a number of other NNS introduced during the same period (between 1950 and 2000) have not spread beyond a single region (Seebens et al., 2021b). This would suggest that the species is likely to continue to spread in future years. Indeed, the poleward-most record within the database dates from 2016, and the easternmost record as recently as March 2021, indicating that recent spread continues to extend the range boundaries of *M. gigas*. Despite potentially unfavourable environmental conditions at range limits (Ma et al., 2021), Jones et al. (2013) predict that by 2050 the range of *M. gigas* could extend as far as the eastern Norwegian Sea and the Faroe Islands. At present, *M. gigas* is limited in the north by cool temperatures (Diederich et al., 2005; Robins et al., 2017; Troost, 2010). However, in Norway the accumulation of polygons shows a pattern of exponential increase and there was a significant increase in max-spread. Given a continued increase in warm summers it therefore seems highly likely there will be further poleward advancement of *M. gigas* (Jones et al., 2013; Reise et al., 2017). Whilst in the present study not much can be said of southern spread due to a paucity of records in the database from Mediterranean countries, it is thought that warmer temperatures are limiting and that the species is already living close to its thermal limits in the Adriatic (Bertolini et al., 2021).

The relationship between *M. gigas* and salinity is not well-understood (Wood et al., 2021), however the species is thought to be limited by conditions below 20 PSU (Ewers-Saucedo et al., 2020; Wrange et al., 2010). As of 2020, the easternmost occurrence of *M. gigas* was Isefjorden, Denmark in the Belt Sea, and the Baltic Sea was thought to be impermeable to further spread due to low salinity conditions (Ewers-Saucedo et al., 2020). This is reflected in patterns in spread in Germany and Sweden, where the accumulation of polygons first increased rapidly, before slowing as polygons on the western coasts become increasingly occupied. However, in the case of Germany this appears set to change as a marked increase in distance, seen in calculations of max-spread in 2019, corresponds to the first record of

M. gigas from eastern Germany in the Baltic Sea proper (Ewers-Saucedo et al., 2020). It has been proposed that the cryptogenic common shipworm (*Teredo navalis* (Linnaeus, 1758)), also limited by salinity, may be actively adapting to the low salinity conditions in the Baltic Sea (Borges et al., 2014), and it is possible that something similar may happen with *M. gigas* in the future. Further investigations of salinity tolerance in the species would prove illuminating. Here we have demonstrated that whilst using spread metrics to calculate transboundary spread across a wider region is invaluable (Hulme, 2015), without considering spread within each individual country these fine-scale patterns are lost, and thus it is useful to consider spread of NNS over multiple spatial scales.

4.3. Conclusion

In conclusion, the use of multiple metrics for assessing spread of NNS provides a much-improved view of patterns of invasion and allows characterisation of fine-scale patterns of spread. Using this approach we demonstrate that with the assistance of multiple introductions *M. gigas* has spread rapidly throughout its introduced European range over the past 56 years and given ongoing climate change coupled with adaptation of the species itself, is likely to continue to spread having not yet apparently entered a phase of saturation. Eradication of *M. gigas* in Europe is almost certainly impossible (Herbert et al., 2016), but better understanding its potential future spread, and the rate at which this may occur, is clearly of both scientific and practical interest (Arim et al., 2006; Evans and Gregoire, 2007; Molnar et al., 2008). Additionally, this understanding could lead to improved management plans for other NNS in the early stages of invasion that have similar life history to *M. gigas*, contributing to the prevention of further invasion and prioritisation of management effort to high-risk species. In the case of *M. gigas*, any disparities in the detail of early invasion history between online data repositories and the published literature do not result in significantly different spread estimates. However, when studying NNS spread, care should be taken to ensure that such repositories are cleaned or indeed enhanced through systematic curation of records (e.g. Curd et al. (2020), Firth et al. (2021a), Firth et al. (2021b)) prior to use. In cases where the early introduction history is well-documented, as it is for *M. gigas*, comparison with literature-based invasion history provides an invaluable opportunity to critique the accuracy of online data repository records and improve the quality of distributional data.

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CRediT authorship contribution statement

Charlotte H. Clubley: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – Original, Writing – Review & Editing, Visualization.
Louise B. Firth: Conceptualization, Methodology, Writing – Review & Editing.
Louisa E. Wood: Conceptualization, Writing – Review & Editing.
David T. Bilton: Writing – Review & Editing.
Tiago A. M. Silva: Writing – Review & Editing.
Antony M. Knights: Conceptualization, Methodology, Writing – Review & Editing.

Data availability

The data used are available to download from freely avalable online repositories as indicated in the research paper. Code is available at https://github.com/cclubley/Assessing-invasion-dynamics.

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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