Unaided dispersal risk of *Magallana gigas* into and around the UK: combining particle tracking modelling and environmental suitability scoring

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Abstract Marine non-indigenous species are a significant threat to marine ecosystems with prevention of introduction and early detection considered to be the only effective management strategy. Knowledge of the unaided pathway has received relatively little attention, despite being integral to the implementation of robust monitoring and surveillance. Here, particle tracking modelling is combined with spatial analysis of environmental suitability, to highlight UK coastal areas at risk of introduction and spread of *Magallana gigas* by the unaided pathway. ‘Introduction into UK’ scenarios were based on spawning from the continental coast, Republic of Ireland, Channel Islands and Isle of Man and ‘spread within UK’ scenarios were based on spawning from known UK wild populations and

aquaculture sites. Artificial structures were included as spawning sites in an introduction scenario. The UK coast was scored, based on parameters influencing larval settlement, to reflect environmental suitability. Risk maps were produced to highlight areas of the UK coast at elevated risk of introduction and spread of *M. gigas* by the unaided pathway. This study highlights that introduction of *M. gigas* into UK waters via the unaided pathway is possible, with offshore structures increasing the potential geographical extent of introduction. Further, there is potential for substantial secondary spread from aquaculture sites and wild populations in the UK. The results of the study are considered in the context of national *M. gigas* management, whilst the approach is contextualised more broadly as a tool to further understanding of a little-known, yet significant pathway.

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Introduction

Effective prevention of non-indigenous species (NIS) introduction and spread requires a comprehensive understanding of introduction pathways, in addition to a robust framework that facilitates prioritisation of pathways for management. Pathway assessments are

crucial to understand the relative risk of different pathways, identify locations at high risk of introduction, inform risk based biosecurity and surveillance, and aid assessment of costs in order to inform management and policy decisions (e.g. Hulme et al. 2008; CBD 2014; Essl et al. 2015; Cassey et al. 2018). Pathway analysis has tended to focus a priori on key ‘deliberate’ and ‘accidental’ human-mediated pathways and associated vectors, given that mitigation to reduce associated risk is likely possible through targeted biosecurity efforts. Several studies have quantified pathway activity associated with a particular location (Tidbury et al. 2016), environment (Williams et al. 2013) or species group (Zenni 2014), with the aim of informing management. The unaided pathway (i.e. natural dispersal of a species after its initial introduction into another territory (Hulme et al. 2008)), has received comparatively little attention, likely due to impediments in understanding and managing this pathway (Hulme 2015). Further, difficulties in attributing introductions of NIS to the unaided pathway with certainty may result in poor documentation of the risk posed by this pathway and a likely underestimation of its importance in global assessments (Hulme et al. 2008; Essl et al. 2015). However, an understanding of the unaided pathway is vital to guide decisions on risk-based biosecurity and surveillance and in the prioritisation of species for management, with re-introduction risk and feasibility of pathway management being an important consideration in species management feasibility (Booy et al. 2017).

Species-pathway interactions are often complex, with several discrete introduction routes contributing to propagule pressure. The Pacific oyster, *Magallana gigas* (previously *Crassostrea gigas*), is one example of a widespread marine NIS for which management decisions are particularly challenging. *Magallana gigas* is native to warm temperate regions, specifically the Northwest Pacific and Sea of Japan (Herbert et al. 2016). However, the species has been introduced into more than 66 countries outside of its native range, mainly for aquaculture, with self-sustaining populations reported in at least 17 of these countries (Ruesink et al. 2005; Smaal et al. 2006; Cardoso et al. 2007; Wrange et al. 2010). In addition to aquaculture, its spread is associated with shipping (ballast water, hull fouling), and live trade (live seafood, bait) pathways (Herbert et al. 2012; d’Auriac et al. 2017).

Magallana gigas has a dispersive pelagic phase, typically lasting 2–4 weeks (Helm 2004) that comprises three temperature dependent pelagic larval stages of different durations (trochophore, veliger, pediveliger). The species is known to disperse via ocean currents, resulting in its spread over large areas (approx. 50 km) (Brandt et al. 2008). Hard substrate, such as rocks, man-made structures, small stones, or living or dead shells of other animals, is required for settlement (Kochmann et al. 2013). *Magallana gigas* has been shown to colonise wind farms in the North Sea (De Mesel et al. 2015) and such artificial structures have been suggested to act as potential ‘stepping stones’ in long distance dispersal of NIS (Coolen et al. 2020), possibly contributing to changes in distribution (Adams et al. 2014). Wild establishment in non-native ecosystems has likely been favoured by a lack of natural predators, beneficial species traits such as rapid growth, and rising air and sea temperatures due to global warming (see Troost 2010 for a review). Impacts in its non-native range may be in the form of ecological impacts, such as the displacement of native species and habitats through the formation of reef systems (Herbert et al. 2012), or socio-economic impacts, such as injuries caused by shells on leisure beaches and blockage of navigational channels for recreational vessels (Herbert et al. 2016).

In the UK *M. gigas* is an important aquaculture species, with an annual production of 1,200 tonnes and a value of £4,911,600 (Ellis et al. 2015). Despite assumptions that *M. gigas* would not establish in the wild in UK waters, self-sustaining populations are widely reported in the warmer waters of the South of England. However, only a few isolated populations are reported in the more northern and cooler waters (Natural England 2009; Herbert et al. 2012; Smith et al. 2015). Its commercial value yet ‘moderate’ risk as an invasive species (GB NNSS 2010; Copp et al. 2016), render policy decisions concerning *M. gigas* challenging and controversial (Herbert et al. 2016). Through altering species communities, wild settlement of *M. gigas* may change the condition of European marine sites that have been designated as protected under the Conservation of Habitats and Species Regulations 2010. Authorisation of new *M. gigas* aquaculture sites is therefore considered in the context of wild populations and their potential impacts. However, prohibition of aquaculture is only likely to be effective in reducing the risk of *M. gigas*

spread if effective management of all pathways is in place (Booy et al. 2017). A comprehensive evidence base from which to formulate management and policy decisions is therefore crucial. However, despite its potential role in the introduction and spread of *M. gigas* into and around the UK and implications for species management, understanding of the risk associated with the unaided pathway remains limited for this species.

The aim of this study was to apply particle tracking modelling, integrating hydrodynamics and biological behaviour of pelagic larvae, to gain insight into the potential dispersal of *M. gigas* into and within UK waters, via the unaided pathway, in order to inform its management. The risk of introduction into the UK was simulated based on spawning of larvae from populations outside the UK (continental coast (France, Belgium, Netherlands, Germany), Channel Islands, Isle of Man (IoM) and Republic of Ireland (RoI)) (Fig. 1), both with and without the inclusion of spawning from windfarms. Secondary spread was simulated based on spawning from locations where wild populations are recorded or aquaculture sites are registered in the UK. A worst-case scenario of unaided dispersal was modelled, to align with the precautionary principle outlined in the Convention on Biological Diversity (CBD). Results indicate that within one spawning season (i.e. 1 year), introduction of *M. gigas* into the UK from outside is possible, with offshore structures increasing the potential geographical extent of introduction on the south-east coast of England. Further, results indicate potential for secondary spread around the UK from known aquaculture sites and wild populations. These results are discussed in the context of *M. gigas* management in the UK and highlight the need to consider the unaided pathway for effective species control. Further, the importance of trans-boundary management of highly dispersive NIS is highlighted.

Methods

Magallana gigas distribution data

Colonisation of the continental coastline (France, Belgium, Netherlands, Germany) by *M. gigas* was assumed, guided by the precautionary principle of NIS management, known distribution records (GBIF 2019)

and discussion with experts (Arjan Gittenberger, pers. comm. 12th June 2019; Cécile Masse, pers. comm. 29th June 2019) (see Fig. 1).

Occurrence records of wild populations in the UK, RoI, Channel Islands and IoM were obtained from Marine Recorder v5 2020-02-06 (JNCC 2019). Records were assessed and verified based on discussion with experts and unverified records were discarded (see Fig. 1).

Data detailing the location of *M. gigas* aquaculture sites in England and Wales were obtained from the Fish Health Inspectorate (FHI) of the Centre for Environment, Fisheries and Aquaculture Science (Cefas), data from Scotland were obtained from Scottish Government (aquaculture.scotland.gov.uk), and data from Northern Ireland and RoI were collated from Department of Agriculture, Environment and Rural Affairs (DAERA). Data from the Channel Islands were obtained from the government of Jersey (<https://www.gov.je>). Aquaculture sites active within the last three years were used.

Wind farm locations (polygon boundaries) were taken from the OSPAR offshore renewables database from 2018 (https://odims.ospar.org/layers/geonode:ospar_offshore_renewables_2018_01_002/metadata_detail). Windfarms determined to be located within maximum dispersal distance from introduction origins (i.e. continental coast, Channel Islands, RoI, and IoM coastlines) based on initial particle tracking simulations, were considered colonised to simulate a worst-case scenario.

Hydrodynamic model

The hydrodynamic model Generalised Estuarine Transport Model, GETM v2.4, (www.getm.eu; Burchard et al. 2002) for the North Western European Shelf domain was run, at a three nautical mile resolution (Fig. 1) to provide the ocean current velocities and turbulence for the advection and diffusion of larvae. The model was run in 3D with 25 sigma layers distributed non-homogeneously and was forced by tidal constituents from TOPEX-POSEIDON (Le Provost et al. 1998) and full meteorological forcing from ECMWF ERA Interim reanalysis (Berrisford et al. 2011; Dee et al. 2011; www.ecmwf.int/en/research/climate-reanalysis/era-interim). 3D current velocities and vertical diffusivity variables were saved hourly to resolve the effect of tides. For more details and

Fig. 1 Bathymetric map of the model domain with release sites depicted for particle tracking scenarios. Spawning was assumed to occur from release sites for the purposes of modelling and is not based on records of actual spawning in these locations

validation refer to Van der Molen et al. (2016). Each scenario was run for 2013, 2014, and 2015 to include interannual variability.

Particle tracking model

The particle tracking model General Individual Transport Model, GITM 2.0, combines physical advection and diffusion with biological development and behaviour to allow particles to progress through defined development stages. It uses ocean currents from the hydrodynamic model for the advection and diffusion of eggs and larvae. This was done with the diffusive random walk from Visser (1997) to correct for spatially varying diffusivity. Horizontal diffusion is constant while the turbulence from GETM is used to infer vertical diffusion of particles. Vertical migration behaviours (neutrally buoyant, floating, sinking, diel migration, tidally cued migration) were defined for

each development stage (see Spawning and Larval Development). In order to reduce the number of particles required for a simulation, each particle represented a super-individual with a set amount of health, which is reduced over time according to a mortality rate or function. This is more computationally efficient than having particles subject to mortality at random according to a probability. Particle trajectory outputs from GITM were output into a netCDF file every 30 minutes. Both GETM and GITM were run on the High-Performance Computing cluster at the University of East Anglia (UEA).

Model Setup and scenarios

The hydrodynamic model GETM and the particle tracking model GITM were combined to allow dispersal of *M. gigas* larvae to be simulated. The domain of GETM was the north-eastern Atlantic

Ocean, encompassing areas of the Celtic Sea, English Channel, North Sea and southern Irish Sea. The GITM domain was limited to the continental shelf to reduce computational demands (see Fig. 1).

Four scenarios were simulated: (A) Spawning (i.e. particle release) from the continental coast (France, Belgium, Netherlands, Germany), RoI, Channel Islands and IoM (hereafter referred to as spawning from populations outside the UK); (B) As in A but including spawning from windfarms (C) Spawning from known aquaculture sites in the UK; (D) Spawning from wild populations in the UK (Fig. 1).

Under Scenario A, the continental coast was assumed to be colonised continuously; *M. gigas* is widespread across the continental coast (GBIF 2019) and suitable biotic and abiotic conditions are present for species establishment (Wrange et al. 2010). Spawning locations were defined as a 15 km buffer along the coastline from 47 to 54° N. Note that, particles were not released from locations east of the mouth of the River Elbe, Germany, as preliminary ocean current analysis indicated negligible risk of dispersal to the UK from these locations. Spawning from wild and aquaculture sites in the RoI, IoM and Channel Islands were also included under Scenario A (see Fig. 1).

Under scenario B, the potential contribution of offshore windfarms as stepping stones for the introduction of *M. gigas* was explored by adding spawning from windfarms (within maximum dispersal distance from introduction origins outlined in scenario A) to scenario A. Particles were released from 26 discrete areas in the North Sea, occupied by windfarms, with colonisation of *M. gigas* assumed at each of these sites.

For scenarios C and D, spawning from all known UK aquaculture sites and wild populations respectively was simulated.

Spawning sites across RoI, Channel Islands, IoM and UK related to model grid cells (5.5×5.5 km) within which the species is documented as present. For the continental coastal and windfarm polygons (Fig. 1) spawning sites related to 3×3 model grid cells (around 16.5 km spacing) given that the forcing fields vary smoothly between cells. An initial test showed that using a 5.5 km model grid for spawning sites combined with a 5 km wide coastal polygon along the continental coastline resulted in a patchier spawning distribution (when compared to a 16.5 km interval). Further analysis was undertaken for each

scenario to determine how many particle releases were necessary to meet the maximum dispersal. The number of particles released in each of the spawning seasons i.e. per year simulated, is listed in Table 1. The total number of particles released per spawning season i.e. year, under each scenario was the result of the number of release locations and the number of releases per day.

Spawning and larval development

Spawning in *M. gigas* occurs in response to environmental triggers once gonad maturation is reached, with a threshold temperature of 16 °C required (Rico-Villa et al. 2009; Dutertre et al. 2010; Kochmann 2012) to trigger spawning, in addition to other environmental cues (Bernard et al. 2016). Mann (1979) modelled this maturation period for larvae from Kent, UK, as 600-degree days above 10.55 °C. The onset of spawning in the present study was informed by the median maturation date (7th July) for the years 2013–2015 based on Mann (1979), and published literature that reports that spawning in *M. gigas* has been reported to occur as early as June–July in northern Europe (Lango-Reynoso et al. 2006). Since *M. gigas* is a broadcast spawner, spawning dates were randomly sampled from a normal distribution with mean 15th July and a standard deviation of four days. This meant that 95 % of the releases happened between the 7th and 22nd July. The relationship between *M. gigas* larval survival and temperature or salinity is not well known, thus the effect of these parameters on survival was not modelled. Changing the simulated spawning date, therefore, only affects the initial tidal and wind driven currents.

Larvae that reached land by diffusion were reflected back into the sea, so that no early settling/wastage occurred, and larvae remained in circulation, maximising the statistical power of the results (Van der Molen et al. 2015). A larval mortality value of 0.044 day^{-1} was taken from Galtsoff (1964, in Rumrill 1990). A constant larval mortality was incorporated into the model as a fractional reduction in health at every biological time step. Particle health was used to weight each particle when calculating settling probabilities i.e. the number of particles surviving to settlement stage and occurring in a 5 km grid cell.

Table 1 The number of *M. gigas* records, spawning locations and number of particles released

	Scenario	Total number of data records for <i>M. gigas</i>	Number of modelled spawning locations (5.5 × 5.5 km)	Number of released particles per spawning season i.e. year
Continental coastline	A, B	–	303	15,000
RoI, Channel Islands, IoM	A, B	214	45	7000
Windfarms	B	–	69	6100
Aquaculture UK	C	132	78	10,800
Wild UK	D	483	63	7800

The number of records is not stated for the continental coastline or windfarms as colonisation of the entire coastline, and all polygons with windfarms present, was assumed. Spawning locations (i.e. particle release sites) across RoI, Channel Islands, IoM and UK relate to model grid cells (5.5 × 5.5 km) within which the species is recorded. Spawning locations across the continental coastline and spawning sites across areas occupied by windfarms reflect points at 15 km intervals

Based on previous work (Coon et al. 1990; Collet et al. 1999; Troost 2010; Robins et al. 2017) biological development was split into three stages: Stage (1) trochophores (1.5 days); Stage (2) veligers (19.5 days) and Stage (3) pediveliger: competent larvae, capable of settling (7 days); modelled as in Robins et al. (2017). At 5 km resolution GETM does not allow representation of most estuaries and the intertidal area. It is considered that by the time the larvae reach the coastal grid cells of the model, they are at veliger stage (Stage 2), when larvae are capable of active swimming (Troost et al. 2008). Thus, the trochophore stage, is considered implicit in the model, and particles are released as veligers. It is assumed that particles released from estuaries and intertidal flats did not settle within these areas and continued to disperse as veligers. 19.5 days later these enter the settling stage and seven days after that are removed from the simulation (see Table 2).

Bivalve larvae are known to exhibit vertical migration in response to tidal movement, which is thought to enhance dispersal (Knights et al. 2006, Troost et al. 2008). For Stage 2 of the model this was represented by an upward migration during the rising tide and downward during the falling tide. The vertical velocities were set to 0.003 ms⁻¹ according to the swimming velocities seen in the laboratory by Newell et al. (2005) for *Crassostrea virginica* pediveligers. This is on the upper limit (0.001–0.003 ms⁻¹) of estimates for *Mytilus* spp. (James et al. 2019). During Stage 3, the larvae were competent to settle and swim towards the bed (Arakawa 1990). A speed of

0.01 ms⁻¹ was chosen to overcome vertical transport and diffusion and allow the particles to remain close to the seabed (see Table 2).

Larval dispersal and model outputs

Particle trajectories were plotted and used to calculate the number of particles in settling stage (Stage 3) for each 5 km grid cell. Each particle was weighted by its health value, which takes mortality into account. The number of particles in settling stage therefore decreased with time (as probability of death increases with time). The number of particles in settling stage for each 5 km grid cell was normalised across the model domain.

Environmental suitability scoring

Environmental data covering UK waters, defined by the UK EEZ, were obtained for the four significant parameters influencing settlement, survival, growth and development of *M. gigas* larvae (henceforth termed ‘settlement’), namely ocean temperature (SST) (Met Office Hadley centre EN4.2.0 ocean series), water salinity (Met Office Hadley centre EN4.2.0 ocean series), seabed substrate type (UKSea-Map 2018, JNCC), and ocean depth (EMODNet Bathymetry data portal (<https://emodnet.eu>)). Although local hydrodynamic conditions, e.g. wave action, impact the settlement of oyster larvae (Fuchs et al. 2015), they were not considered in this study due

Table 2 Summary of development stage parameterisation for *M. gigas*

	Pelagic larvae (veliger)	Settling larvae (pediveliger)
Duration	19.5 days	≤ 7 days (Coon et al. 1990)
Mortality	0.044 day ⁻¹ (Galtsoff 1964)	
Vertical migration	Tidal (North et al. 2008)	Attempt settling (Robins et al. 2017)
Vertical velocity	0.003 (-0.003) ms ⁻¹ (Newell et al. 2005)	Downward 0.01 (-0.01) ms ⁻¹ (present study)
Horizontal swimming	None	None

to a lack of high resolution, coastal hydrodynamic data for the entire study area. Environmental parameters and suitability ranges for *M. gigas* are summarised in Table 3. Environmental data processing was performed in R v.3.5.3 (R Core Team 2019) using the package raster (Hijmans 2019). UK waters were split into 10,892 grid cells (0.11° × 0.11°) and scored to reflect their suitability for *M. gigas* larval settlement. Grids with optimal, suboptimal and unsuitable *M. gigas* conditions were scored two, one and zero respectively for each environmental parameter. An overall score was generated by calculating the mean,

with any cell recording a zero score for any of the four parameters being assigned a value of 0. Environmental suitability scores were therefore either zero, or in a range between one; where all the environmental parameters were suboptimal and two, where all the environmental parameters were optimal.

Comparison of the environmental suitability scoring and the recorded *M. gigas* populations (wild and aquaculture) was used to validate the scoring methodology (see Fig. 3).

Table 3 *Magallana gigas* environmental suitability

Environmental parameters	Range/classification	Suitability classification	Reference
Temperature (°C)	0–3	Unsuitable	Mann et al. (1991), Ruiz et al. (1992), Kochmann (2012), Robins et al. (2017)
	3–16	Suboptimal	Mann et al. (1991), Ruiz et al. (1992), Kochmann (2012), Robins et al. (2017)
	16–35	Optimal	Mann et al. (1991), Ruiz et al. (1992), Castaños et al. (2009), Kochmann (2012), Robins et al. (2017)
Salinity (ppt)	0–11	Unsuitable	Mann et al. (1991), Ruiz et al. (1992), Kochmann (2012)
	11–34	Optimal	Mann et al. (1991), Ruiz et al. (1992), Kochmann (2012)
Depth (m)	> 40	Unsuitable	FAO (2016)
	0–40	Optimal	FAO (2016)
Substrate	Rock and hard	Optimal	Seafish (2019), FAO (2019)
	Coarse	Optimal	
	Mixed sediment	Optimal	
	Sandy Mud	Suboptimal	
	Sand	Suboptimal	
	Muddy sand	Suboptimal	
	Fine mud	Suboptimal	
	Seabed	Suboptimal	

For each environmental parameter the unsuitable, suboptimal (if appropriate) and optimal range (with respect to temperature, salinity and depth) and classification (with respect to substrate) is documented

Risk maps

Particle tracking outputs and environmental suitability scores were combined to create risk maps to indicate *M. gigas* introduction and spread risk in UK coastal waters. The risk map grid was based on ICES statistical rectangles split into sixteenths. Risk map grid cells were attributed a ‘dispersal’ score for each spawning scenario by summing maximum (across years 2013, 2014 and 2015) particle tracking scores (particles in settling stage (Stage 3)) falling within the cell. Similarly, risk map grid cells were attributed a ‘suitability’ score by summing environmental suitability scores (environmental suitability for larval settlement) falling within the cell. A suitability map was created. Cells with scores < 1, 1–2, 2–3, 3–4 and > 5 were categorised as ‘very low’, ‘low’, ‘moderate’, ‘high’ and ‘very high’ suitability, respectively. For each risk map grid cell, the larval dispersal score was multiplied by the suitability score to provide an estimated risk score. Risk scores were scaled between 0 and 100. Risk maps were produced by colour grading each cell to reflect the relative risk of introduction/spread of *M. gigas* into the cell. Cells with scores < 1, 1–5, 5–25, 25–50 and > 50 were categorised as ‘very low’, ‘low’, ‘moderate’, ‘high’ and ‘very high’ risk, respectively. The number of cells currently occupied by *M. gigas*, and for which dispersal to, and settlement in, is possible under each scenario was calculated. Figure 2 provides an illustration of the methodology implemented in this study.

Results

Environmental suitability

Coastal regions of England and Wales, below a latitude of 54° N (Fig. 3), had the greatest environmental (temperature, salinity, substrate and depth) suitability for larval settlement. Off-shore areas in the North Sea, the Strait of Dover and sections of the eastern Irish Sea also had high environmental suitability. Suitability was only moderate east of the IoM due to a seabed substrate of sandy mud (ICES sub-area VIIa; Table S1). Environmental suitability was generally lower in northern England and Scotland with small regions of higher suitability around the Western Isles, Moray Firth and around the Firth of Forth (ICES

sub-area IVa, IVb and VIa). In Northern Ireland, environmental suitability was highest on the south-eastern coast (ICES sub-area VIIa). Lower environmental suitability in the northern parts of the UK was driven largely by suboptimal temperatures for *M. gigas* settlement. Spatial heterogeneity in bathymetry and substrate also influenced environmental suitability, with salinity having comparatively little effect at the spatial scale considered. As such, although temperature is a major driver of environmental suitability, for an accurate assessment all environmental factors must be considered in combination.

Risk of introduction and secondary spread

Scenario A: spawning from populations outside the UK

Simulations and environmental suitability analyses suggest that dispersal and subsequent settling of *M. gigas* in the UK following spawning from the continental coast was possible (see Figs. 4, 5a). More specifically, *M. gigas* larvae may have dispersed into and subsequently settled within regions north of the Strait of Dover, and south of Lowestoft (ICES sub-area IVc), and isolated locations on the south coast of England (ICES sub-areas VIId) (see Figs. 4a, 5b). Locations at moderate to high relative risk of introduction were located on the south-east coast of England (see Fig. 5a). Particle trajectories suggested that potential source locations on the continent are predominantly on the north-east coast of France (see Fig. 4a).

Simulations indicated that introduction into UK waters was also possible following spawning in the IoM and RoI, with high to moderate risk of introduction in coastal waters south of the Channel of the River Esk (ICES sub-area VIIa) and south of Barra and Tiree (ICES sub-area VIa) (Figs. 4a, 5a). Dispersal into UK coastal waters following spawning from the Channel Islands was not observed (Fig. 4a).

Simulations indicated that introduction into 79 UK coastal grid cells was possible; 75 (95 %) of which were not occupied by aquaculture sites and 72 (91 %) of which were not occupied by wild populations of *M. gigas* (see Table 4; Fig. 5a).

Fig. 2 Summary of methods used in this study

Scenario B: spawning from wind farms in North Sea and populations outside of the UK

Inclusion of windfarms as spawning sites increased the geographical extent of the south-east coast of England into which dispersal was possible, specifically the Essex and Suffolk estuaries rather than just Kent (see Fig. 4b). Potential introduction into an additional 12 risk map grid cells was seen when spawning from windfarms was included (see Table 4; Fig. 5b).

Scenario C: spawning from aquaculture sites in the UK

Particle trajectories indicated that dispersal of larvae into the Sea of Hebrides, and around the Orkneys and Shetlands, Anglesey and the Severn Estuary was likely (Fig. 4c). However, given that environmental conditions are unfavorable due to suboptimal sea

temperatures in the region (Fig. 3), successful settlement, and risk of secondary spread into these locations is low to very low (Fig. 5c).

UK coastal areas at risk of secondary spread from active UK aquaculture sites were located on the south coast of England, around the Thames estuary, the Bristol Channel, the River Mersey, the east coast of Northern Ireland and the west coast of Scotland (ICES subregion IVc, VIIe, VIIf, VIIa and VIa) (See Fig. 5c). Locations at high risk of secondary spread occurred off the Dorset coast.

Potential secondary spread from UK aquaculture sites into 271 risk map grid cells was predicted, of which 232 (86 %) were outside locations where aquaculture sites are currently present and 241 (89 %) of which were outside locations where wild populations of *M. gigas* are present (Fig. 5c; Table 4).

Fig. 3 *Magallana gigas* environmental suitability based on ocean temperature, water salinity, seabed substrate type, and ocean depth. Environmental conditions were scored as either optimal or suboptimal for larval settlement and the suitability score was taken as the mean of these scores. Any area with an

environmental factor unsuitable for larval settlement was scored as unsuitable. Cells with scores < 1, 1–2, 2–3, 3–4 and > 5 were categorised as ‘very low’, ‘low’, ‘moderate’, ‘high’ and ‘very high’ suitability, respectively

Scenario D: spawning from wild populations in the UK

Risk of secondary spread from known established wild *M. gigas* populations in the UK was greatest along the south coast of England (ICES subregions IVc, VIId and VIIe) and around the Bristol Channel (VIIf) (see Fig. 5d). Locations at very high to high risk of secondary spread occurred around the Thames estuary, and off parts of the Dorset and West Sussex coast (see Fig. 5d). Locations at

low or very low risk of secondary spread occurred on the west coast of Scotland (ICES subregion VIa) and south of the channel of the River Esk (ICES subregion VIIa).

A total of 194 grid cells around the UK were at risk of potential introduction and settlement of larvae from spawning on wild sites in the UK. 166 (86%) risk cells occurred outside locations where aquaculture sites are currently present in the UK and 161 (83%) risk cells occurred in locations where wild populations of *M. gigas* are not currently present.

Fig. 5 Risk map illustrating the relative risk of **a** introduction from spawning of populations outside the UK **b** introduction from windfarm spawning and spawning of populations outside the UK **c** secondary spread from aquaculture spawning

d secondary spread from wild spawning. Cells with scores < 1, 1–5, 5–25, 25–50 and > 50 were categorised as ‘very low’, ‘low’, ‘moderate’, ‘high’ and ‘very high’ risk, respectively

Discussion

A comprehensive evidence base is vital to inform NIS management. Despite this, understanding of the importance of the unaided pathway in marine NIS introduction and spread remains limited for many species. Understanding all pathways and their

associated risk, in combination with assessment of the effectiveness of potential management actions, such as biosecurity measures, is required to determine the likely feasibility of NIS management. This study applies a particle tracking modelling approach, in combination with an environmental suitability assessment, to shed light on the potential for *M. gigas* to be

Table 4 The number of cells within which aquaculture sites and reported wild UK and RoI populations of *M. gigas* are located, in addition to the number of cells at risk of introduction under each scenario

Scenario	# cells occupied or 'at risk'	# cells outside those occupied by Aq sites	# cells outside those occupied by wild sites	# cells outside those occupied by Aq or wild sites
Current aquaculture (Aq) sites	74	NA	54	NA
Current wild sites	57	37	NA	NA
Current aquaculture AND wild sites	19	NA	NA	NA
Current aquaculture OR wild sites	110	NA	NA	NA
A. 'Introduction into UK' (not inc windfarm): France, Belgium, Netherlands, RoI, Channel Islands, IoM	79	75	72	69
B. Continent (inc windfarm spawning): France, Belgium, Netherlands, RoI, Channel Islands, IoM	91	83	79	74
C. Aquaculture spawning (UK)	271	232	241	216
D. Wild spawning (UK)	194	166	161	146
All spawning scenarios	353	312	317	290

introduced into UK coastal waters following natural dispersal from populations outside the UK (continental coast (France, Belgium, Netherlands, Germany), Republic of Ireland, Channel Islands and Isle of Man), and spread within UK coastal waters, following dispersal from known aquaculture sites and wild populations in the UK. The approach aimed to assess the overall risk of the unaided pathway for *M. gigas* at a national level, using a precautionary approach, and can be used, in combination with other sources of evidence, to inform national-level policy and management decisions for the species. However, further local-scale modelling will be required to inform site specific management of *M. gigas*, for example, with respect to understanding the likely contribution of aquaculture activity, relative to other pathways, to wild *M. gigas* population dynamics. The methodology and approach implemented in this study can be applied to other species with pelagic life stages, for different geographical areas and at different spatial resolutions in order to assess the risk of introduction and spread via the unaided pathway.

Unaided introduction into UK waters

With respect to informing national *M. gigas* management, a few key insights can be gained from this study. Firstly, in a single spawning season (one year), there is

potential for both introduction of *M. gigas* into UK coastal waters, and substantial secondary spread from where the species is currently known to occur within the UK. Secondly, offshore structures aid the dispersal of *M. gigas* and may increase the potential geographical area at risk of introduction. Management of the species, both in terms of restrictions on aquaculture sites and management of wild populations, should be considered in light of introduction risk via the unaided pathway from outside the UK, where *M. gigas* populations are not subject to UK jurisdiction and management. The outputs of the precautionary approach taken in this study indicate that, restricting further aquaculture and undertaking management of wild *M. gigas* populations on the south coast of England is unlikely to reduce its long-term distribution dramatically, since introduction events from populations on the continental coast, or from colonised artificial structures in the North Sea, may still occur. Simulations indicated that locations at highest risk of introduction and potential settlement were located on the south-east coast of England, with larval trajectories indicating that *M. gigas* introduction is most likely to occur from where populations have been reported on the north-east coast of France, south of Dunkirk (Dauvin et al. 2019). Herbert et al. (2012) consider cross-channel dispersal between Dover and Calais to occur only under exceptional hydrographic

conditions, attributing wild settlement in the south-east of the UK to the spread from aquaculture facilities in the region and/or from fouled boats and larvae within ballast water discharges. However, the results of the present study indicate that unaided introduction from populations off the north-east French coastline may be more common than previously considered. Spawning of *M. gigas* occurs in the warmer, summer months. During these months, thermal stratification occurs in the western channel and inhibits lateral exchange between the western and eastern channel. However, the central, eastern channel, Straits of Dover and south North Sea are all vertically mixed with exchange between them occurring freely. Salinity is lower and more variable where the Rhine discharges into the North Sea and this acts as a barrier to hydrological mixing. However, in the summer months this salinity barrier is reduced aiding dispersal across the straits of Dover (Pingree 1980; Otto et al. 1990).

Previous suggestions that genetically distinct wild populations on the south-west coast of the UK originated from natural dispersal from North Brittany (Lallias et al. 2015) seem unlikely based on the particle tracking simulations presented here, which indicate local larval retention on the north-west coast of France. This study presents outputs from models parameterised for three years. It may be possible that extreme conditions (e.g. relating to wind), not captured within these three years, could result in wider dispersal of *M. gigas* larvae. Further, the occurrence of artificial structures in the English Channel, such as Rampion Wind Farm, not accounted for in the present study, may aid dispersal from France.

This study also highlights that introduction into UK coastal waters south of the Channel of the River Esk and south of Barra and Tiree is possible from the IoM and RoI. Northwards spread of larvae from the south coast of Ireland to Northern Ireland was predicted in the present study, likely due to the prevailing currents in the area (Hill et al. 2008). This emphasises that dispersal is not bounded by political boundaries and highlights the need for communication and coordinated transboundary management of NIS (Hulme 2015). Under modelled conditions, populations of *M. gigas* around the Channel Islands did not disperse to and settle in the UK.

Hard substrate provided by artificial structures offers habitat for fouling species, in often otherwise unsuitable environments (Coolen et al. 2020).

Although representing only a small proportion of hard substrate within the marine and coastal environment, artificial structures often occur in locations where natural hard substrate is absent, providing vital 'stepping-stones' for fouling species and aiding larval dispersal and more broadly marine connectivity (Tidbury et al. 2020). Artificial hard substrate is becoming increasingly common in the marine environment. The offshore wind industry alone is rapidly expanding with as many as 2923 turbines already present in UK waters, and more in planning (The Crown Estate 2018). As such, future risk from the unaided pathway may increase, further emphasising the need for its consideration in management and policy decisions.

Unaided spread within UK waters

Results indicate low potential for *M. gigas* to spread northwards from the south-west and south-east coast of England via natural dispersal. This is perhaps intuitive given the general residual flow within the English Channel, mainly orientated to the east in the eastern channel and along the south coasts of England and to the west along the south-western coasts of England (Salomon and Breton 1993; Hill et al. 2008) i.e. remaining within the Celtic Sea rather than entering the Irish Sea. Particle tracking simulations indicated that larval transport from *M. gigas* populations located in the eastern English Channel was primarily to the north-east. From the coast of Devon and Cornwall, larval transport follows the coastal current around the coast (Hill et al. 2008). Similar patterns of larval dispersal were observed for *Pecten maximus* stocks (Nicolle et al. 2017). The spread northward in Scotland in the present study is entirely consistent with the general northwards current associated with the Scottish coastal current and flow regime around the UK in summer (Hill et al. 2008). However, risk in the region is low due to low environmental suitability for larval settlement attributed to suboptimal sea temperatures. The low number of established *M. gigas* wild populations off the Scottish coastline supports predictions of low environmental suitability.

The results from this study indicate potential for *M. gigas* to spread substantially within one spawning season. Although temperature is considered the main constraining factor for spread in the UK, our results suggest that it is the interplay between multiple

environmental suitability parameters and larval dispersal potential that drives distribution changes for this species. For example, reflecting all scenarios, *M. gigas* could occupy three times more UK coastal cells than currently occupied by known aquaculture sites and wild populations. However, given that a precautionary approach was adopted herein, it is more likely that gradual spread over multiple years will occur. Elsewhere in Europe, *M. gigas* rapid spread has been attributed to a combination of several factors, including increasing suitability of water temperature for natural recruitment and dispersal (Diederich 2005). Evidence to support this comes from several locations, including Denmark and Norway (Wrangé et al. 2010), France (Dutertre et al. 2010), Germany (Diederich 2005) and the Netherlands (Wehrmann et al. 2000). Other factors thought to contribute to rapid expansion include gregarious settlement of larvae, and attraction to conspecifics, which results in the rapid formation of reef systems (Diederich 2005; Troost 2010).

Management considerations

Outputs from this study suggest that large areas of the UK coast are not currently at risk of introduction or spread of *M. gigas* via the unaided pathway (e.g. risk score of zero). This broadly corresponds with the current UK distribution of *M. gigas*, with the species being notably absent from most of Scotland, Northern Ireland and the more northern parts of England. It could be argued that given the low suitability for *M. gigas* settlement in the cooler northern areas, authorisation of aquaculture sites would pose little risk. However, from a pathway perspective, prohibiting the authorisation of aquaculture sites in these locations would be more effective since introduction and spread from outside this area by the unaided pathway is unlikely.

Outputs from this study reflect one spawning season only. Also, and perhaps more crucial, this study does not consider anthropogenic vectors, such as hull fouling or ballast water exchange associated with shipping and boating, with associated activity likely to result in different patterns of risk (see Tidbury et al. 2016). For example, the presence of *M. gigas* within ports and harbours (e.g. in Southampton) that are some distance from aquaculture sites, suggests that pathways other than the unaided pathway play a role in *M. gigas* dispersal (Herbert et al. 2012; Smith et al. 2015).

Shipping (ballast water, hull fouling) pathways in particular have been highlighted as a potential route of unintentional *M. gigas* introduction. Consideration of the results from the present study in combination with relevant anthropogenic vector activity will be important to inform management. Effective control of established populations is difficult, with no successful population control approach known (Herbert et al. 2016) and spread from existing UK populations is further likely to limit the success of species controls implemented.

Modelling considerations

The accuracy of particle tracking model outputs and risk estimates in the present study is dependent on robust *M. gigas* distribution and abundance data, which are lacking at present (Herbert et al. 2012). Systematic monitoring for *M. gigas* around the UK to determine current distribution will be valuable. Outputs from this study are also impacted by a limited understanding of larval development and associated swimming behaviours, required for parameterisation (North et al. 2008; Robins et al. 2017). In the present study, *M. gigas* was assumed to exhibit upward migration during the rising tide and downward migration during the falling tide in line with observations for other bivalve species (Newell et al. 2005). A recent study (James et al. 2019) used observed vertical distributions of another bivalve species (*Mytilus* spp.) to infer the vertical swimming behaviour and concluded that an asymmetrical tidally driven migration where larvae swim up at the start of flood but start swimming downward at mid-flood was most appropriate. However, behaviour during ebb and low tide is not clear (James et al. 2019). The tidal behaviour used in the present study maximises dispersal and is therefore in line with the precautionary or worst-case scenario approach often used in NIS studies.

In this study larval settlement and therefore establishment risk was considered according to environmental suitability (with respect to temperature, salinity, ocean depth and substrate type). However, it is likely that factors not considered in the present study will influence establishment success. For example, nutrients, such as chlorophyll *a* and other resources are required for growth of *M. gigas*, with limitations on carrying capacity of wild populations in close proximity to aquaculture sites documented (Dame and

Prins 1997; Leguerrier et al. 2004; Forrest et al. 2009), potentially affecting population establishment and persistence (Teixeira Alves et al. in prep). Further, hydrodynamic conditions, such as from turbulence and waves, are known to influence larval settlement (Fuchs et al. 2015). Hydrodynamic connectivity is also known to be an important process in the recruitment of marine invertebrates, playing a key role in the biological and community spatial structure of coastal lagoons (Lagarde et al. 2019).

There is currently some uncertainty regarding the precise environmental conditions under which broadcast spawners such as *M. gigas* spawn in the field, with high interannual and geographic variation in spawning period reported (Bernard et al. 2016). For example, *M. gigas* spawning has been reported to occur as early as June–July (Lango-Reynoso et al. 2006) and as late as October in northern France (Pouvreau et al. 2016). Whilst altering the spawning period will affect larval dispersal due to differing tidal and wind conditions, previous studies suggest that effects on dispersal distance are unlikely to be significant (Robins et al. 2017). Further, for the purpose of the present study, all spawning sites were assumed to be reproductively active. Due to debate regarding whether *M. gigas* is currently able to develop and spawn at their northern boundary (60° N) (Thomas et al. 2016; Robins et al. 2017), the approach was precautionary, in line with NIS management, with climate change projections of warming seas likely resulting in favourable temperature conditions for spawning and settlement, and increased dispersal in the future, regardless (Diederich et al. 2005; Thomas et al. 2016; Rinde et al. 2017). Future changes to the marine environment, such as changes to ocean circulation patterns and sea temperature rises associated with climate change, may influence marine NIS introduction and spread risk. Here, the particle tracking model was run based on historic hydrodynamic conditions. While basing analyses on the maximum score across the three years is a worst-case scenario, it does not account for potential future projections under potential climate change scenarios. Extension of the study to account for changing conditions associated with climate change will be a valuable next step. Further, aquaculture practices, such as triploidy, practiced in France, (Normand et al. 2008), are likely to reduce the potential for dispersal from aquaculture sites,

indicating that results from this study may overestimate dispersal associated with aquaculture sites.

In addition, global socioeconomic changes, such as increased transport networks, changes in global trade routes, and increased artificial offshore substrate, may impact the importance of recognised pathways and vectors, and perhaps lead to the emergence of novel pathways and vectors. One example of this, is the recent recognition that marine litter is a NIS introduction vector, with hydrodynamic currents facilitating the short- and long-range dispersal of NIS on this vector (Rech et al. 2016). Fouling species, including *M. gigas*, have been reported rafting on anthropogenic litter pollution (Rech et al. 2018). Policy decisions should be made with full consideration of how future changes in the prevalence of existing and emerging pathways and vectors may influence the effectiveness of management actions in mitigating the risk of introduction and secondary spread.

While this study focuses on *M. gigas*, the unaided pathway is likely to be an important contributor to propagule pressure in ecologically similar species, with characteristic life-history traits of successful marine invaders often including high levels of fecundity, large numbers of propagules and long larval duration (from a few days to several months) (Cardecia et al. 2018). In the UK, other NIS with a long pelagic phase that may exhibit similar patterns of spread include *Amphibalanus amphitrite* (4–18 days; Anil et al. 1995) and *Crepidula fornicata* (14–21 days; Shanks 2009).

Conclusions

Modelling tools represent a powerful approach for furthering understanding and enhancing predictions of invasion risk. While for obvious reasons management of NIS is focussed on human mediated pathways, cost-effective management requires broad understanding and consideration of all relevant vectors and pathways, and transboundary management to ensure coordinated, effective mitigation. Further, understanding risk associated with the unaided pathway is likely to increase the probability of early detection, particularly when integrated with highly sensitive molecular detection techniques such as eDNA, and facilitate containment.

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Availability of data and material Request from authors.

Code availability (software application or custom code) GETM Model: <https://sourceforge.net/projects/getm/>, GITM: Request from authors, GITM postprocessing tools: <https://github.com/CefasRepRes/gitm-utils>.

Compliance with ethical standards

Conflict of interest The authors declare no competing financial interests.

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Consent to participate The authors declare they consent to participate.

Consent for publication The authors declare they consent for publication.

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