Running title

Restricting UK aquaculture does not suppress spread of the Pacific oyster

Title

Evaluating the net impacts of a naturalised non-native species and attempts to control its spread in the UK: Addressing the oyster in the room

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Abstract

The Pacific oyster (*Magallana* (*Crassostrea*) *gigas*) was introduced to UK waters in the mid-20th century and accounts for >95% of UK oyster production. Recently, its nonnative origin has led landowners and policymakers to consider limits on UK oyster aquaculture operations. *M. gigas* is ecologically naturalised in the UK, with multiple records of populations originating from wild sources, including from outside the UK, with France and the Netherlands treating *M. gigas* as a legally naturalised species. The naturalised status is justified, potentially simplifies regulation and enables aquaculture production to provide nutritious and sustainable food while supporting employment. The presence of *M. gigas* can have positive environmental impacts by improving water quality, diversifying the seascape and providing living breakwaters for contemporary coastal defence. Positive effects of non-native species are notably missing from habitat-regulation assessments. While acknowledging the important role of non-native species in biodiversity loss, the potential negative effects of *M. gigas* have not universally materialised and efforts to reduce its wider spread in England will fundamentally fail due to natural spread across Europe and the UK from substantive larval connectivity. UK policy on *M. gigas* should be revised to reflect the socioeconomic benefits of Pacific oysters to shellfish production and the evaluation of the legally prescribed ecological status of protected sites requires updating. Location-specific management interventions should consider a *dynamic* ecological status that focuses on ecological function, the provision of services and the realised impacts of non-native species instead of a rigid focus on the identity of a species.

Key words: Pacific oyster, *Magallana* (*Crassostrea*) *gigas*, aquaculture, naturalisation, invasive non-native species (INNS), novel ecosystems

1. Introduction

Since its introduction to United Kingdom and European waters, the Pacific oyster (*Magallana* (*Crassostrea*) *gigas*) has become vitally important to a fishery that dates back millennia. Historically, the industry was wholly reliant on the native Flat or European oyster (*Ostrea edulis*; Thurstan et al., 2024). However, the *O. edulis* population was decimated during the late 19th and early 20th centuries by a combination of overexploitation, poor fishery practices, pathogen introductions, habitat loss and pollution (zu Ermgassen et al., 2023a). *M. gigas*, a non-native species originating from Japan and South-East Asia, was identified as a suitable replacement species and, following the development of bio-secure hatchery protocols, with support of various government agencies at that time, was introduced to fisheries in the UK in 1965 (Herbert et al., 2012; Utting and Spencer, 1992). This strategy to boost shellfish aquaculture included the introduction of other non-native shellfish species, for example the Manila clam (*Ruditapes philippinarum*), and was also adopted for *M. gigas* elsewhere, including in Canada in the 1920s and 1930s, Ireland in the late 1960s and France throughout the 1970s (Lallias et al., 2015). It is notable that UK wild fisheries for Manila clam are increasing as they respond positively to European climate warming, with some given sustainable certification status (Marine Stewardship Council, 2023). The original licences for commercial use of many of these non-native shellfish including *M. gigas* were granted based on the belief that UK water temperatures were too low for these species to reproduce and naturalise. However, this has since proved not to be the case, with *M. gigas* now regularly spawning in UK and other European waters resulting in a spreading wild population (King et al., 2021).

UK oyster production relies on *M. gigas* for >95% of its landings and supported 142 full-time equivalent jobs in 2017 (Syvret et al., 2021). These jobs are often in rural coastal communities where secure employment is scarce and therefore relatively more important (McDowell and Bonner-Thompson, 2020). A recent fisheries statistical report documents that the UK aquaculture production for *M. gigas* was 2564 tonnes in 2022 with an estimated value close to £10 million (Cefas, 2024). Valuation of the full UK *M. gigas* supply chain suggests that its production was worth over £13 million to the UK economy in 2011/12, since when landings have more than trebled from 754 tonnes (Cefas, 2024; Humphreys et al., 2014).

The UK *M. gigas* production is smaller than in some other European countries, with France producing an average of ca. 80,000 tonnes annually between 2011 and 2020 (EUMOFA, 2022). It therefore represents an opportunity for expansion in the UK, with substantial socioeconomic potential for rural and coastal communities, as well as the prospect of increased domestic production of a sustainable and high-quality food perceived by consumers as a healthy source of protein with low industrial input that contributes to the blue economy (Domech et al., 2025).

The nonnative origin of *M. gigas*, their potential impact on coastal ecosystems and their ability to breed in the temperate waters of Northern Europe, have raised several ecological and policy concerns in the UK and its European neighbours (see review by Herbert et al., 2016; Moehler et al., 2011). These concerns centre around their abilities as ecosystem engineers to alter habitats including the transformation of mudflats to oyster reefs, the perceived interference with restoration efforts of native *O. edulis*, competition with other aquaculture species and their settlement on maritime infrastructure (Herbert et al., 2016; Martinez-Garcia et al., 2022; Morgan et al., 2021). Specifically, the concern is whether aquaculture represents a source of further spread of this species in the United Kingdom (Lallias et al., 2015; Morgan et al., 2021), and whether regulatory limits to the aquaculture of *M. gigas* would therefore limit that spread. Because of this concern, calls are being made to limit the expansion, or continuation, of the aquaculture of this species in some areas due to an assumption that current industry activity is the source of free-living dispersing oyster larvae, and that the perceived risks of *M. gigas* aquaculture are being realised.

The debate around the future of UK oyster production was intensified in early 2023 by the decision of the Duchy of Cornwall, a private landowner that leases foreshore and riverbed areas to oyster growers in the South-West of England (the counties of Devon and Cornwall), that they would be ‘phasing out’ *M. gigas* production in their waters (BBC, 2023). This was motivated in response to the complex regulatory framework that requires habitats-regulation assessments to test if shellfish aquaculture activities could significantly harm the designated features of European Marine Sites (Conservation of Habitats and Species Regulations 2017; GB Government, 2017). Although the source of *M. gigas* spread into local environments was not evidenced, a legal landscape that provides opportunity for costly litigation against landowners that permit farming of *M. gigas* is leading to a change in leasing behaviour. Concurrent statements by the UK Department for Environment, Food and Rural Affairs (DEFRA) that they were ‘considering control measures’ on new *M. gigas* aquaculture licences north of the 52 °N parallel – a line connecting the towns of Fishguard and Felixstowe – to limit the spread of this species have further added to the concerns of the aquaculture industry (BBC, 2023; House of Commons Debate, 2023; McGowan, 2024). This ’red line‘ proposal applies to England despite the fact that oyster farms are already positioned north of this line in England, and in Wales and Scotland where different regulation exists. There has also been increased media coverage at some sites with varying colonisation of *M. gigas*, some where there does appear to be substantial habitat change and others not, and this has attracted volunteer programs to cull *M. gigas* colonising intertidal habitats due to perceived effects on coastal access, wildlife, tourism and pet dogs (BBC, 2021).

Here, we examine the evidence for the realised costs of *M. gigas* aquaculture and naturalisation on natural habitats and protected areas. We critically review the likely success of any efforts to slow-down or reverse the spread of this species via controls on aquaculture. We examine mitigations for aquaculture activity, including the likely impact on spread of the *apparent* request by regulators that producers switch to 'Triploid' oysters. We discuss potential benefits of naturalised populations of this species to a contemporary coastal European landscape. We present results of a survey of Oyster producers in Essex regarding the meaning of *M. gigas* production to them, and what alternatives exist if they were to lose the rights to farm these bivalves. Finally, we discuss the challenges of the regulatory landscape in the UK, specifically the Conservation of Habitats and Species Regulations 2017 (GB Government, 2017), in how it interacts with aquaculture and the highly dynamic and modified European coastal landscape experiencing climate change. We received and refer in the text to feedback that was invited from UK stakeholders on a draft version of this paper (Shakspeare et al., 2024), including from oyster producers, shellfish industry representatives, conservation groups, landowners, local governments (i.e. council representatives), employees of statutory agencies linked to DEFRA and scientists. We used this information to present a balanced view on the current issues surrounding the naturalisation of *M. gigas* in the UK. We will document the current challenges faced by *M. gigas* producers and regulators of protected sites in the UK, examining three areas: (i) the current status of *M. gigas* around the UK and European coasts, (ii) the impacts of this non-native species and potential mitigation strategies, and (iii) the likely impacts of climate and coastal change on *M. gigas* in the UK.

2. Naturalisation and dispersal of *M. gigas* from aquaculture sites

M. gigas occurs extensively throughout Europe and is now distributed from Norway in the north to Cyprus in the south (Hansen et al., 2023). Within the UK, the species can be found as far north as the Shetland Islands, although the greatest numbers are found along the South-West and South-East coastlines (McKnight, 2009; Morgan et al., 2021; Shelmerdine et al., 2017; Syvret et al., 2008). Spread from introduced populations has occurred throughout the European range of *M. gigas*, with wild populations now established in Denmark's Wadden Sea, around the Spanish, French, and UK Atlantic coasts and throughout the Mediterranean Sea (Clubley et al., 2023; Des et al., 2022; reviewed in Hansen et al., 2023).

Despite the granting of a General Licence in 1982 that allowed the release of *M. gigas* into UK waters, the species is still classified as an invasive, nonnative species in the UK under the terms of current legislation (Wildlife and Countryside Act, 1981). This is in contrast to the approach of other European countries, with the species listed as 'not of concern' by the European Union (European Commission: Directorate-General for Environment, 2023). In France, *M. gigas* is treated as sufficiently low risk that it is considered fully compatible with farming operations in Special Areas of Conservation (e.g. Natura 2000 network of nature protection areas). In Germany, *M. gigas* introduced for aquaculture is treated as exempt from EU invasive-species regulations (Haubrock et al., 2023). In the Netherlands, after unsuccessful attempts to control its spread, the presence of *M. gigas* is accepted as irreversible, and farming operations are allowed to continue (Syvret et al., 2021). Additionally in the Netherlands, *M. gigas* and its shell substrate are provided to encourage settlement of live *M. gigas*, and deployment of *M. gigas* can be integrated as nature-based alternatives to hard-engineered structures for coastal defence (Fivash et al., 2021).

While there is little doubt that the initial introduction of *M. gigas* to UK waters was from human activity with the aim of supporting economic growth of oyster production, the current contribution of UK-cultured *M. gigas* to the spread of the species is less clear. Observations of wild oysters without a clear link to current local aquaculture sources have been made from the south coast of England to the Shetland Isles (Shelmerdine et al., 2017). In Northern Ireland, wild *M. gigas* populations are genetically uncoupled from local aquaculture activities (Kochmann et al., 2012). Along the coasts of South-West England and South Wales, populations of wild *M. gigas* are genetically more closely related to French and Spanish populations than to UK hatchery stock (Lallias et al., 2015). Mills (2016) demonstrates that the population established in Southampton Water is genetically independent from any extant oyster aquaculture operation in the UK and appears to be self-sustaining. The introductory pathway of these oysters is not fully understood, but could include remnants of historical oyster introductions, illegal seed importation, transport of attached oysters on boat hulls and/or of planktonic larvae with ballast water. It is also likely – given other known large-scale marine plankton connectivity across and throughout the Channel and into the North and Celtic Seas (for example, eggs and larvae dispersal of Sea bass (*Dicentrarchus labrax*): Beraud et al., 2018; Graham et al., 2023) – that natural dispersal from already established naturalised reefs and substantial aquaculture holdings in continental Europe plays a substantial role.

Despite recent rhetoric in the national press and from some UK government communications about the role of aquaculture as a source of colonisation of *M. gigas*, the official UK risk assessment states that the spread of this species is primarily from extant wild populations, rather than aquaculture operations (GB Non-native Species Secretariat, 2010). Claims we received in feedback from local conservation groups in the South-West of England that shellfish farms are the source of local reef establishment are therefore not as well supported by the current evidence as they could be. It should be noted that the two genetic studies introduced above compare contemporary aquaculture stock with what might be naturalised populations that could have been originally established via shellfish-trade movements.

Although it is possible for there to be links between contemporary aquaculture activities and establishment of local populations, the typical harvesting of *M. gigas* for consumption at relatively small size may stifle development of a sufficient number of reproductive females since their life-history usually follows a protandrous hermaphrodite development where the probability of reproductive females and contributions to population fecundity increases with age. However, simultaneous hermaphroditism and self-fertilisation are possible and could facilitate recruitment from aquaculture into dispersed ‘wild’ oyster populations (Mills, 2016). Given all this evidence, restrictions on aquaculture activities are unlikely to result in a sufficiently substantial reduction of the spread of this species but would cause detrimental socioeconomic effects on coastal communities via the loss of employment and income from damage to aquaculture activity and weakened sector growth.

3. Impacts and potential mitigations

M. gigas is often referred to as an 'ecosystem engineer' (Troost, 2010). Ecosystem engineers are organisms that modify, maintain and/or create habitat (Alper, 1998). The potential ecological impacts of this species were comprehensively reviewed by Herbert et al. (2016) and Martinez Garcia et al. (2022), concluding that *M. gigas* can alter diversity, community structure and ecosystem processes. Further concerns have been raised about the habitat-restructuring capacity of this species, including competition with native bivalves, loss of wading-bird habitat and reduction of the appeal of coastal areas to leisure users (Des et al., 2022; Martinez-Garcia et al., 2022). Here, we examine the extent of these negative effects that have emerged in the UK since the species' introduction in the 1960s. We also examine the potential for positive effects of habitats engineered by Pacific oysters.

Native, wild and naturalised non-native and cultured bivalve populations all deliver a wide range of ecosystem service provisions, as reviewed by van der Schatte Olivier et al. (2020). This includes benefits from an increasing *M. gigas* population. These services include, but are not limited to, water quality improvement and water-column nitrogen removal (Clements and Comeau, 2019), habitat provision (Martinez-Garcia et al., 2022), carbon sequestration (Filgueira et al., 2015) and pathogen removal (van der Schatte Olivier et al., 2020).

3.1. Interactions with native Flat oysters (*O. edulis*)

Extensive work by Zwerschke et al. (2020, 2016, 2018a) at an experimental site in Strangford Lough, Ireland, and at monitoring sites throughout Europe consistently shows that there is very little difference between *O. edulis* and *M. gigas* reefs in terms of associated ecological community assemblage, biodiversity and nutrient cycling. Furthermore, Zwerschke et al. (2016, 2018a) suggest that *M. gigas* may compensate for the loss of ecosystem services previously provided by *O. edulis*, a species that formed extensive reefs along much of the UK coastline in the late 19th century (Olsen, 1883; Thurstan et al., 2024). Guy et al. (2018) assessed the epibiota on the shells (>50 mm length) of sympatric populations of *M. gigas* and *O. edulis* in Strangford Lough, finding similar species richness of epibionts on *M. gigas* (51 species, 30 of which are exclusive to their shells, n = 17) and *O. edulis* (48 species, 27 exclusive, n = 17). The most frequent epibionts on both species are barnacles (*Elminius modestus*) and Blue mussels (*Mytilus edulis*). Per individual, *O. edulis* carried significantly more epibionts (12.6 ± 0.78) than *M. gigas* (8.4 ± 0.97), possibly because of the higher age of *O. edulis* (4.4 ± 0.2 years) in comparison to the younger *M. gigas* (3.5 ± 0.2 years).

It has also been suggested that the presence of *M. gigas* may have facilitated the return of *O. edulis* along the Dutch North-Sea coast (Christianen et al., 2018), with evidence of similar facilitation of *O. edulis* recruitment onto an established *M. gigas* reef in the River Crouch, Essex, UK (Lown, 2019). International capacity for Flat oyster production for food or restorative aquaculture is notably restricted due to unpredictability of *O. edulis* seed production and resulting inability to consistently meet customer demands (zu Ermgassen et al., 2023b). Likewise, feedback we have received widely acknowledges that facilitation of *O. edulis* restoration is subsidised by the sales of *M. gigas* production (see Section 3.6.2) and occurs via hatchery production, restorative aquaculture and extensive mariculture. Hence, suppression of a thriving *M. gigas* business would likely stifle efforts that support Flat oyster recovery in several UK and European regions.

There has been reasonable concern that, where introduced *M. gigas* and native *O. edulis* co-occur, the faster growth and potential for rapid reproduction of *M. gigas* could result in the native species being outcompeted (Zwerschke et al., 2018b). Likewise the UK non-native organism risk-assessment scheme (GB Non-Native Speceis Secretariat, 2010) suggests that *M. gigas* could outcompete the native oyster but fails to provide scientific evidence for this claim. Experimental approaches by Zwerschke et al. (2018c) found that there are conditions in which *M. gigas* has direct negative competitive effects on *O. edulis*, specifically in subtidal habitats. It was also found that the competitive interaction between the two species was context dependent, and sometimes positive, with evidence of niche partitioning. Based on the support of a range of other species, and both spatial and niche partitioning, the potential for excessive negative interactions between Pacific and Flat oysters or net negative outcomes of Pacific oyster establishment seem small. However, there is also the potential for indirect interactions between these two species via their effects on predators and disease.

Oysters suffer from various microbial and viral infections that can increase their mortality resulting in density-dependent limitation. This suggests that a high density of oysters in a population increases their rate of infection which can slow or terminate population growth (Cranfield et al., 2005; Doonan et al., 1994). *Bonamia ostreae* is a protistan parasite that can lead to bonamiosis disease and high mortality in *O. edulis* which may weaken their competitiveness relative to *M. gigas* (Engelsma et al., 2010). This host specificity of bonamiosis possibly contributed to the success of *M. gigas* in European oyster aquaculture that was decimated by the emergence of this disease in *O. edulis* in the late 1970s (Peeler et al., 2010). Likewise, the host specificity underpins the policy position in both the UK and EU that *M. gigas* is not recognised as a carrier or transmitter of bonamiosis (both from *B. ostreae* and *B. exitiosa*). However, evidence is emerging that a high density of *M. gigas* as well as a wide range of other co-occurring native non-shellfish species (e.g. brittlestars) could be carriers of *Bonamia* (Lynch et al., 2010, 2007). Counter intuitively, co-culturing of the two oyster species has been suggested to reduce infection in *O. edulis* in some cases (le Bec et al., 1991). Bonamiosis is an extremely persistent disease, and areas are considered ‘*Bonamia* positive’ for substantial periods of time due to the parasite persisting in a range of host species and in the environment (Sas et al., 2020). While more information on the interaction is required, it is certainly unclear and unlikely that the presence of *M. gigas* in coastal estuaries will limit recovery of *O. edulis* via amplifying bonamiosis relative to the many other factors which facilitate this disease in the natural environment.

Ostreid herpes viruses (OsHV) infect different hosts and can result in mass-mortalities of *M. gigas*, particularly in their larvae and juveniles (<18 months). Whereas *O. edulis* has historically been thought to be unaffected by OsHV (Segarra et al., 2010), several studies have found that larvae or young juveniles may be infected and suffer high mortality in hatcheries (Renault et al., 2000). For example, experimental infection of *O. edulis* by direct intramuscular injection of viral particles from the OsHV-1 µvar strain resulted in 25% mortality within 10 d (Lopez Sanmartin et al., 2016). This suggests that a large population of OsHV-carrying *M. gigas* could increase infection of juvenile *O. edulis*. However, neither study demonstrates that infection could occur in the wild via exposure between these two species and, given the reasonable spatial and niche separation between these species, field conditions for co-infection will be substantially different to experimental tank studies.

Current guidance by the British Government states that *M. gigas* is not a vector for *Bonamia* spp. transmission and lists *M. gigas* as the only species susceptible to ostreid herpesvirus (OsHV-1 µvar) infection (GB Government, 2024). Other stressors including water temperature and presence of *Vibrio* bacteria can affect infectivity, and this adds to the already complex infection biology of shellfish. The epidemiology of bonamiosis and OsHV infection warrants further field-based research to disentangle the interactions between *M. gigas* and *O. edulis*.

3.2. Interactions with other habitat types and protected areas

Since 2010, England introduced various Marine Protected Areas (MPA: 178 sites covering 51% of inshore waters), some of which received further protection as Marine Conservation

Zones (MCZ: 91 sites within existing MPA) and Special Areas of Conservation (SAC: 116 sites within existing MPA). We received feedback from regulators that the threat of *M. gigas* on ecological status of protected areas, their habitat and features must be taken seriously. They highlighted that four MPA are considered to be in 'unfavourable ecological status' due to effects of *M. gigas* colonisation (*Fal and Helford SAC; Plymouth Sound and Estuaries SAC; Dart Estuary MCZ; Thanet Coast SAC*). For example, within the *Thanet Coast SAC*, protected Ross Worm (*Sabellaria spinulosa*) reefs have been damaged and displaced by *M. gigas* (McKnight, 2009; McKnight and Chudleigh, 2015). Notably these four SAC are all coastal areas of the English Channel and represent a small fraction of the total special and protected marine areas on the UK coast in this same area: there are 37 Marine Conservation Zones that are in contact with the intertidal between Porthgwarra in Cornwall and Whitstable in Kent, and many more SACs. Across all areas, the majority of surveys of coastal areas finding very low densities of *M. gigas* present (e.g. sites within *Plymouth Sound and Estuaries SAC* in 2014: average densities 0 to 0.18 oysters per m^2; Russell, 2019). However, within each site, small and enclosed areas have reached abundances that could be considered habitat-changing *M. gigas* reef (e.g. >5 oysters per m^2 and some sites greater than 100 oysters per m^2 in the River Yealm estuary). Hence, the effects of *M. gigas* colonisation are likely to be variable both between and within sites.

Concerns have been raised about Pacific oyster spread in the intertidal zone where European seagrasses such as Dwarf eelgrass (*Nanozostera* (*Zostera*) *noltei*) were once extensive around the UK and European coasts (Green et al., 2021). Seagrasses are recognised for their ability to provide multiple ecosystem functions and services, such as carbon sequestration and fish-nursery habitats, and therefore there has been concern that potential effects of Pacific oyster encroachment may weaken these important ecosystem services (Morgan et al., 2021). The evidence that eelgrass, especially *N. noltei*, delivers carbon sequestration or biodiversity benefits is currently weak. This is certainly the case relative to the better evidenced effects of shellfish aggregations to provide habitats that enhance biodiversity, and filter sediment and nutrients from seawater (Bazterrica et al., 2022; Zwerschke et al., 2020, 2016). Comparing shellfish versus seagrass is not useful or appropriate, as they have the potential for positive interactions, with oysters improving water quality and light availability for these true plants (Gagnon et al., 2020). We also received feedback that Pacific oyster reefs could displace eelgrasses or require removal prior to eelgrass restoration. This is of particular concern to conservation groups in South-West England since mitigation by removal of *M. gigas* is difficult without concurrent damage to the seagrass beds themselves (Morgan et al., 2021). More generally, Smith et al. (2018) find that long-line *M. gigas* aquaculture in Japan has no effect on subtidal eelgrass morphology, bed density or biomass but affects their epibiont composition. Kelly and Volpe (2007) report negative effects on Common eelgrass (*Zostera marina*) transplants below *M. gigas* reefs compared to controls, and they attribute this to sediment sulphide toxicity to eelgrass caused by Pacific oyster reef establishment. The authors note that *M. gigas* and *Z. marina* coexist via spatial separation, with oysters in the higher intertidal and *Z. marina* in the low intertidal and subtidal but they raise a concern about the effects of possible extensive spreading of Pacific oysters. As has been highlighted elsewhere, despite their presence in Europe since the 1960s, few cases of extensive spread have occurred with examples outside the Wadden sea including restricted settlements (Drinkwaard, 1999; Herbert et al., 2016; Holm et al., 2015). It is notable that several examples of localised oyster reefs were successfully mitigated; this includes in Brightlingsea, Essex (e.g. Herbert et al., 2018) and in the South-West of England via volunteer culls (e.g. *Fal and Helford SAC*; Morgan et al., 2021). In the Greater Thames (UK) where there has been such high potential for spread of Pacific oysters from naturalised reefs and their aquaculture, such expansive spread of Pacific oyster reefs is rare unless specifically encouraged by landowners. In the Blackwater estuary, part of the Greater Thames, there are several extant areas of Pacific oyster reef establishment – at Bradwell (relatively large reef area), at West Mersea (moderate size reef areas) and Tollesbury (relatively small reef area). Historically there was reef establishment at Thurslet creek (Goldhanger) but this is now much lower density, with harvest-pressure and oyster diseases proposed as potential causes. There are also many smaller outcrops of wild naturalised Pacific oysters at most creek edges surrounding West Mersea, but otherwise the estuary remains a mixed sediment and mud-dominated landscape. The only site of extensive seagrasses left in the Blackwater is at St Lawrence Bay, it having been lost from Osea Island, the outer estuary and Colne Point (Gardiner et al., 2024). Notably none of these sites have Pacific oyster reef establishment and conflicts with shellfish have never been linked to these seagrass losses. Likewise, despite the recorded historical losses, Dwarf eelgrass (*N. noltei*) is found across the upper intertidal of the northern Thames outer coastline (e.g. at Foulness) and is restricted by water quality and competing seaweeds while, again, competition with shellfish has not been highlighted (Richard and Quijón, 2023). Largely then, we may conclude that the evidence that *M. gigas* is a threat to seagrasses or its restoration is weak but also site-specific, where spatially constrained estuaries in the South-West of England will experience more conflicts. Furthermore, while we find the evidence for conflicts between seagrasses and naturalised populations of Pacific oysters weak, it is possible that under future climate and management scenarios, novel ecosystems including non-native shellfish such as *M. gigas* could have negative effects on native species such as Dwarf eelgrass (Richardson and Ricciardi, 2013).

Beyond the concerns of competition with native species such as seagrasses, some research suggests biodiversity gains after the establishment of *M. gigas*. Bazterrica et al. (2022) surveyed well established (~30-year-old) introduced *M. gigas* reefs in the Argentinian South Atlantic, comparing the macrofaunal community with that found in vegetated and soft sediments in the locality. The authors find significantly higher macrofaunal diversity associated with *M. gigas* reefs, particularly during the summer months. Hansen et al. (2023) report that, in European waters, the presence of *M. gigas* is likely to lead to equal or higher biodiversity than beds of native bivalves, for example, Blue mussel (*M. edulis*). Similar patterns are observed in Sweden, where the presence of *M. gigas* leads to greater abundance of associated organisms than the native *M. edulis* (Hollander et al., 2015).

However, in several cases the biodiversity gains associated with new *M. gigas* reef habitat result in part from the presence of other nonnative species that have arrived independently, including various amphipods, decapods and copepods, some of which have potentially negative effects on the native fauna (Bazterrica et al., 2022; Holmes and Minchin, 1995).

On UK coasts and in the Wadden Sea, this biodiversity gain is achieved without native-species displacement and can provide substantial areas of habitat for a range of native species (Markert et al., 2010; Martinez-Garcia et al., 2022; Troost, 2010). This is not to say that more biodiversity is necessarily better, however, in most cases and in our own experience, *M. gigas* reefs harbour similar species to that found in other native shellfish habitats but more of them due to the more rugose three-dimensional habitat that they engineer (McGinley, 2023). This was particularly the case following coastal heatwaves where the higher profile of *M. gigas*-shell reefs appeared to better protect animals using the reef from desiccation during low tides than did *O. edulis*-shell reefs (McGinley, 2023).

3.3. Effects on ecosystems and their function

Mudflats are important coastal habitats that support high densities of infauna and provide a wide range of ecosystem services (Barbier et al., 2011). Evaluation of the impact of *M. gigas* on the Wadden Sea, a notable mudflat dominated seascape, suggests that while the non-native species has affected some habitat types, species and interactions (see sections 3.2 and 3.4), the species has not impacted on the area’s overall level of ecosystem-service provision (Gutow and Buschbaum, 2019). Reddin et al. (2022) show that the colonisation of mudflats by *M. gigas* in the Bay of Bourgneuf, France, resulted in increased numbers of predatory crabs. In turn these crabs reduced grazer density, resulting in a significant increase in the levels of plant material stored in the mud. The authors suggest that increased presence of *M. gigas* in the region could result in large-scale shifts in trophic energy flows via supporting increased crab populations, but they also noted the effects were constrained to within 50-65 m of the edge of an oyster reef.

M. gigas can also impact ecosystem dynamics via their filter-feeding behaviours, through both competition for food resources and by consuming planktonic larvae, which is most significant at reef margins (Joyce, 2019; Martinez-Garcia et al., 2022; Troost, 2010). Dense aggregations of *M. gigas*, and the locally concentrated waste they produce, can have a substantial impact on the biogeochemistry and microbial ecology of sediment and pore water that alters ecosystem function (Green et al., 2012). However, where competition for space between *O. edulis* and *M. gigas* may occur, there is no difference in important ecosystem functions including nutrient cycling and associated infaunal biodiversity (Zwerschke et al., 2020).

3.4. Effects on birds

Two possible consequences of the presence of *M. gigas* on coastal bird populations are documented: *M. gigas* may convert existing habitats such as sand- or mudflats to an oyster reef or outcompete native species including *M. edulis*. Both may affect the abundance, diversity and accessibility of prey to birds in intertidal habitats. Perceived risk to foraging birds of non-native mudflat-colonising species is not new, with similar concerns also raised about cord grass (*Spartina* spp.) and excessive seaweed growth. However, the realised impact of *M. gigas* on birds that use coastal areas is uncertain. Markert et al. (2013) found that foraging by Herring gull (*Larus argentatus*) in the German Wadden Sea is hampered by *M. gigas* reefs. Contrastingly, Waser et al. (2016) suggest that *L. argentatus* were unaffected by higher *M. gigas* densities, but that four out of 22 examined species, Eurasian oystercatcher (*Haematopus ostralegus*), Common gull (*Larus canus*), Red knot (*Calidris canutus*) and Dunlin (*Calidris alpina*) were lower in abundance when *M. gigas* densities were the highest. In the case of the Dutch Wadden Sea, Waser et al. (2016) conclude that, whilst the impacts of *M. gigas* are substantial, it is likely that the disturbance resulting from efforts to remove or limit the spread of *M. gigas* would do substantially more harm than good to the avian diversity of the area. Additionally, research on the utilisation of intertidal habitats by foraging shorebirds in Delaware Bay (USA) suggests that the feeding rates are unaffected by the presence of oyster aquaculture (Maslo et al., 2020).

The Dutch Wadden Sea is a large intertidal habitat, supporting up to 12 million birds, many of which utilise *M. edulis* as a food source (Waser et al., 2016). Throughout the Wadden Sea, *M. gigas* has spread into areas historically dominated by *M. edulis* beds. Displacement of *M. edulis*, as well as wider impacts on the infaunal organisms predated on by resident and migratory birds is therefore a potentially significant concern. However, in many cases, the two species co-exist (Dolmer et al., 2014) and *M. gigas* can provide opportunities for the recovery of desired *M. edulis* and facilitate their settlement with numbers stabilising in under 10 years (Guy et al., 2018; Markert et al., 2010; OSPAR, 2023; Schmidt et al., 2008; Troost, 2010). It should also be noted that the decline of mussel beds is not unique to the Wadden Sea, with declines noted across the Atlantic region and attributed to a wide range of factors including climate change and nutrient enrichment (Baden et al., 2021; Nehls et al., 2006). In such scenarios other shellfish may not be displacing mussels but replacing them.

M. gigas and *M. edulis* reefs are associated with similar infaunal communities, with greater abundances associated with *M. gigas* (Hollander et al., 2015). Therefore, foraging birds could be better supported in areas where Pacific oyster reefs replace mussel beds, unless changes in reef structure decrease foraging success independent of prey availability. Few studies have addressed the realised effects of *M. gigas* reefs on foraging for birds relative to mussels, or the foraging potential for birds of oyster reefs that are harvested for food production or disrupted to minimise their spread. A study in Essex, UK, found large-sized invertebrate prey for three common estuary birds was at significantly higher abundance in *M. gigas* reefs and at sites where the reef had been dredged to remove live oyster biomass than in adjacent mudflats (Herbert et al., 2018). While mudflats covered larger areas and hosted more birds in total, foraging success and feeding rates were higher for oystercatchers

(*Haematopus ostralegus*) and curlew (*Numenius arquata*) on the *M. gigas*-associated habitats (Herbert et al., 2018). In the *Blackwater Estuary Special Protection Area* in Essex for example, curlew counts maintain a relatively stable medium-term trend, with a long-term trend that is similar to the national picture (Caulfield et al., 2025). This is despite the aforementioned expansion of rock oyster habitats at this and surrounding sites since the 1960s (see Section 2). Further scrutiny of bird count data such as the Wetland Bird Survey may provide a route to risk assessment of *M. gigas* for the capacity of protected areas to provision internationally important populations of wintering European birds. A key take-home message is that shellfish habitats, such as intact *M. gigas* intertidal reefs and areas managed by occasional removal of *M. gigas*, can, and often do, contribute to the rich mosaic of estuarine habitats that create foraging opportunities for diverse wildlife.

3.5. Effects on recreational activities

One complaint about establishing Pacific oyster populations and reefs that has received little academic research attention is the effect on recreation. We have found no research projects published on this topic but received feedback that Pacific oysters interfere with water sports including sailing and walking on coasts (see Morgan et al., 2021). A specific complaint we received was about pet/domestic dogs, that they would cut their feet when free ranging on sites of Pacific oyster establishment. One site that was discussed was a significant distance from the shore and accessed at low tide. The welfare of domestic dogs should be taken into account but it should also be noted that dogs should not be free ranging on coasts and estuaries, the majority of which are protected areas for birds including Special Areas of Conservation (SAC), Special Protection Areas (SPA), Sites or Areas of Special Scientific Interest (SSSI/ASSI), unless signage specifically invites them to do so. This is specifically the case when shellfish beds, native, non-native, cultured or wild, are noted foraging areas for wintering and summering waterbirds of conservation concern including Ringed plover (*Charadrius hiaticula*), oystercatcher (*Haematopus ostralegus*) and curlew (*Numenius arquata*).

A second complaint was about humans cutting feet and legs on Pacific oysters while undertaking water sports or swimming. This complaint came from the South-West of England, but historically the same complaints have been made in Essex (UK) at Brightlingsea (Herbert et al., 2012) and West Mersea (personal communications) where calls for mitigation ensued (see section 3.7). Further research on the potential for Pacific oyster establishment to negatively affect livelihoods, recreation and tourism is clearly overdue. This should include approaches to understand mitigation and adaptation to live in highly modified coastal landscapes, including changes brought about by Pacific oysters, which are now an inevitable consequence of climate change.

3.6. Effects on Socioeconomics

As introduced earlier, oyster production in the UK is highly dependent on *M. gigas* and supports a significant number of coastal jobs (Syvret et al., 2021). These jobs provide secure income where employment is often scarce (McDowell and Bonner-Thompson, 2020). We sought feedback from the shellfish aquaculture sector in North Essex on the importance of *M. gigas* to their businesses and from anyone nationally to understand their views on the economics and employment benefits of Pacific oyster aquaculture. First, we sent a survey to known shellfish and seafood producers and sales businesses associated with the Colne and Blackwater estuaries in Essex in 2023 (see Online Resource 1). Secondly, we received four responses from our general call for feedback on an earlier draft of this paper where the subjects of employment or economy were raised.

3.6.1. Shellfish business survey

Of the eight businesses we sent the survey to and referred to as ‘Fisheries A-H’, we received a response from five of which four were completed fully (Fisheries A, D, F, G). The businesses ranged in their dependency on shellfish vs other seafood capture or sales, and specifically ranged from 15% to 100% dependency on Pacific oyster as a percentage of total turnover. Likewise, there was high variation in the abundance of Pacific oysters that were farmed or harvested per year – ranging from hundreds of thousands to several million across 2018-2023 (Fig. 1). Three of the five had very high dependency on Pacific oysters of 90 to 100%. Business annual turnover ranged from £100,000 to £3 million, and number of employees per business from 1 to 31. Turnover and employment fluctuated substantially between years, largely due to the 2020 pandemic, but employment was positively related to turnover (Fig. 2).

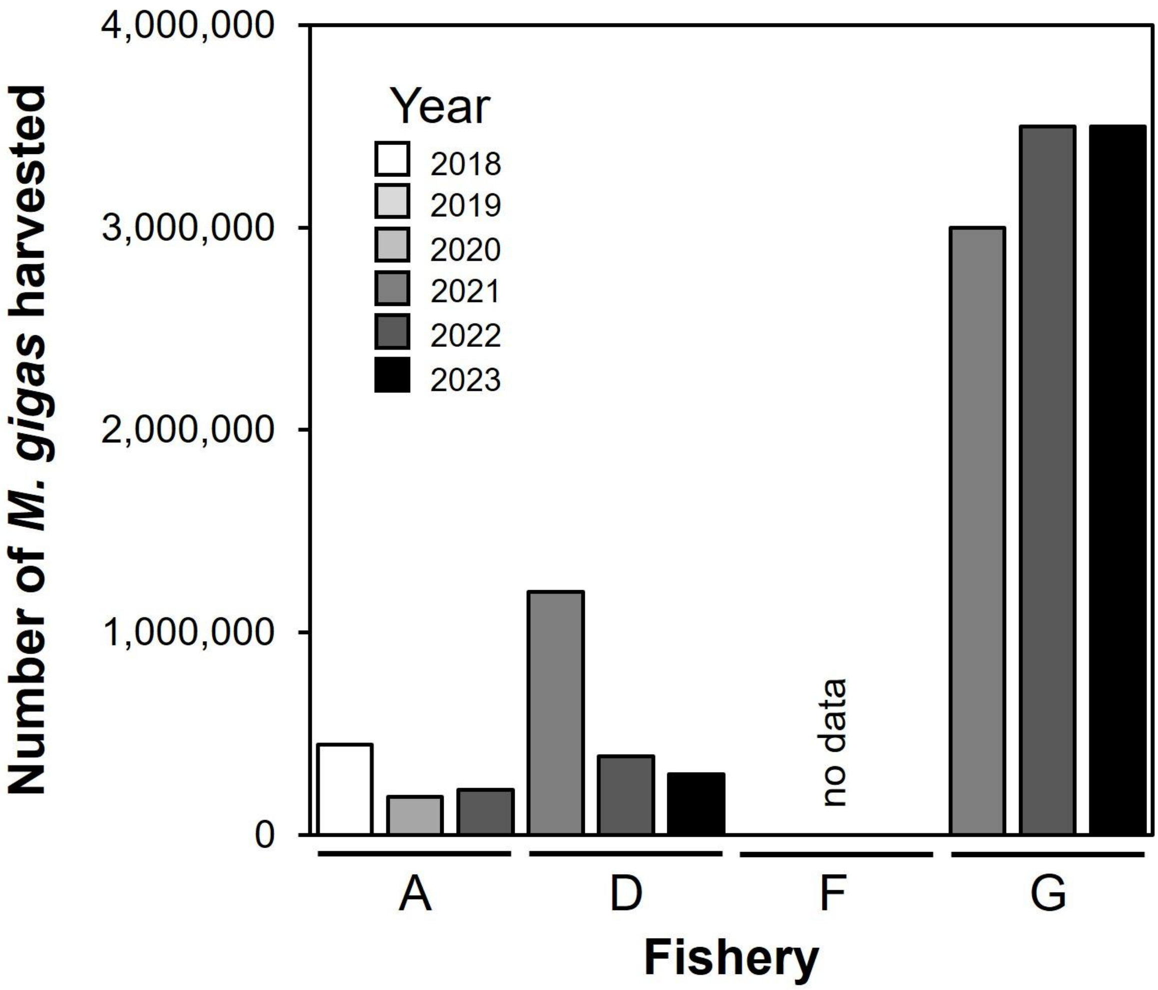

Fig. 1. Numbers of Pacific oysters harvested annually from across four aquaculture businesses in North Essex that provided an answer to this question. Greyscale in columns indicates the year of harvest

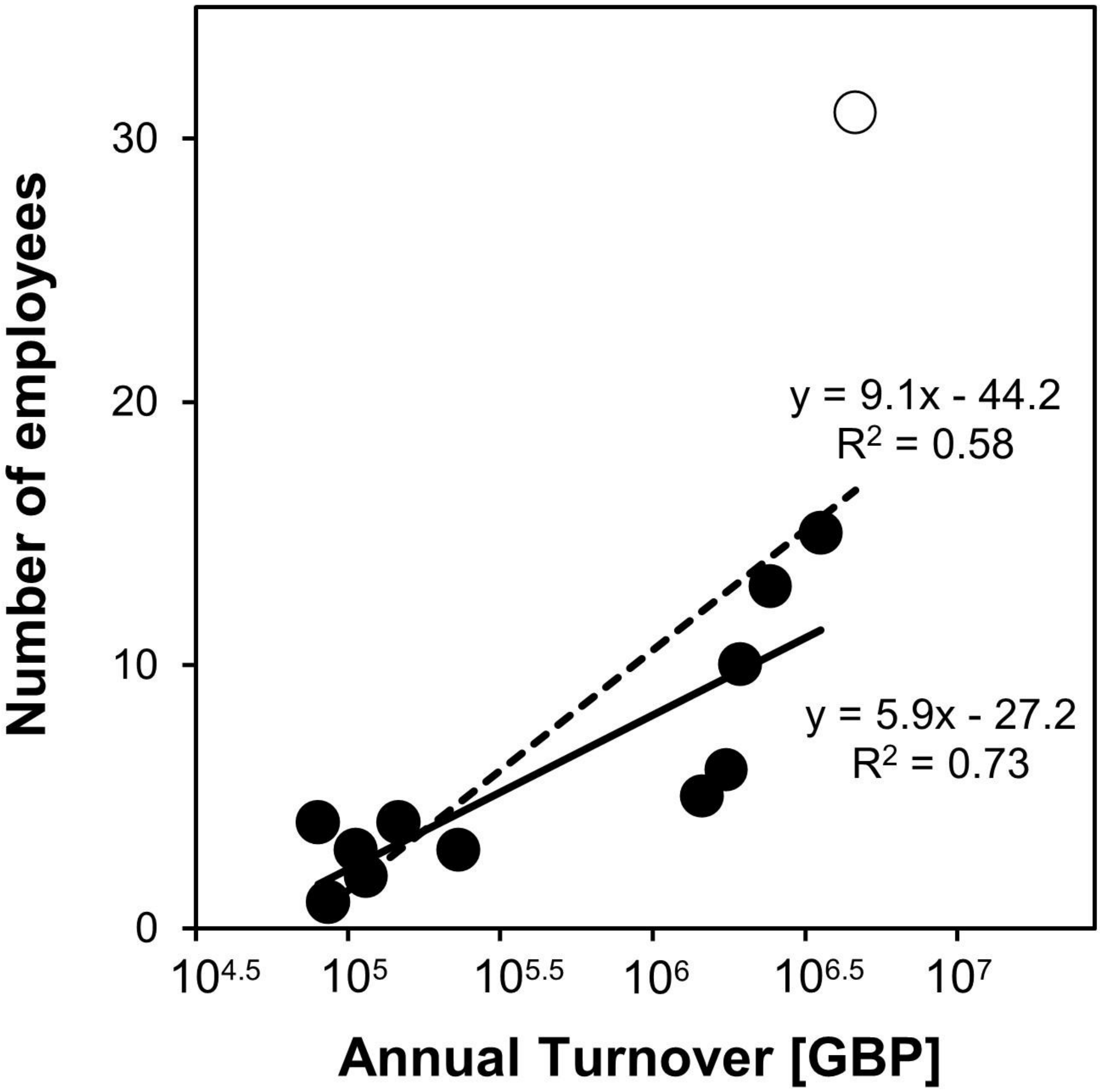

Fig. 2. The relationship between employee numbers and the annual turnover of the fisheries surveyed. Linear regression fitted including the outlier (○) showing a linear regression coefficient (R^2) of 0.58 (dashed line). Linear regression fitted excluding the outlier had an R^2 of 0.73 (solid line). Each dot represents a turnover~employment relationship each year

In addition to quantitative information, we asked shellfish businesses for their experiences with farming and harvesting Pacific oysters, whether they could find alternatives to Pacific oyster farming such as Flat oysters (Question 1), whether there had been any changes in abundance in wild Pacific oysters locally (Question 2), whether there were any local conflicts between Pacific oysters and the communities they live in (Question 3) and how they could help mitigating those conflicts (Question 4). Finally, we asked about employment, specifically the average age of employees and the hope for younger people gaining employment in the sector (Question 5).

Here, we summarise the responses to our questions:

Question 1: Every fishery surveyed stated that if cultivation and farming of *M. gigas* were banned, they could not recoup their losses and make the same income by farming solely native species. Fisheries B and G mentioned that Blue mussel (*M. edulis*) would not be a viable native species option as the area is unsuitable for their cultivation. All respondents agreed that Flat oysters (*O. edulis*) would not be viable economically and present a high risk in terms of cultivation. Fishery A stated that slow growth rates and high costs are their issue with growing *O. edulis*. Fishery B claimed that rising summer temperatures in local creeks and the continued presence of disease makes *O. edulis* too high a risk for commercial cultivation. Fishery G said the inability to grow large numbers of this species make them unsuitable while Fishery D responded that, in the past, *O. edulis* trade has been lost due to the lack of access to wild stock.

Question 2: Three out of five respondents said they saw a decrease in the abundance of wild *M. gigas* in their local area in comparison to ten years ago with one respondent putting this down to harvesting. One respondent mentioned the role of oyster herpes virus in the past, preventing recovery of an area known for Pacific oysters after it had been heavily harvested.

Question 3: All five respondents did not believe that wild *M. gigas* have caused any problems for themselves or heard of them causing problems for anyone else locally.

Question 4: Three fisheries felt that, should the government ask for the removal of *M. gigas* from their local areas, they would only participate in removal activities if they were able to keep the *M. gigas* harvested for future financial gain, and, in one case, included a monetary incentive as well. Fishery B, the only sole trader surveyed, believed that no naturalised *M. gigas* should be removed and that the industry instead needed investment to grow.

Question 5: There was a wide variety of ages working at all the fisheries, and businesses were asked about concerns around future recruitment. Fishery B was a sole trader, hence, a single employee, Fishery D was a small family-run company also with a single employee. Fishery A had the largest employee age range of 25-65 years, but they said that they are struggling to recruit new staff to the business. Fishery G had a smaller age range and younger workforce of 20-45 years old and were not worried about future recruitment.

3.6.2. Feedback on economics and employment from general call

Of the responses we received from our general call for feedback on an earlier draft of this manuscript, four responses provided information on their experience or opinion on the role of *M. gigas* in coastal employment or economics. Three of the responses were from shellfish producers; one in Wales, one in North-West England and the other in South-West England. The first was a shellfish grower that specialises in both Flat oyster production for marine restoration projects as well as *M. gigas* for human consumption. They described their ability to produce small bespoke orders of Flat oyster for restorative aquaculture as fully dependent on their income from *M. gigas* farming. The second was a shellfish hatchery which helped to produce many of the restoration aquaculture production orders for Flat oyster in the UK. They attest that the hatchery industry would collapse if it were not for *M. gigas* production and say that orders for Flat oyster or other species could not fill the socioeconomic role of Pacific oyster production in the UK.

The third and fourth responses we received were from a coastal consortium and an oysterman in the South-West of England, that could be characterised as having a negative opinion of *M. gigas* and its aquaculture. The consortium described employment in the shellfish sector as ‘*poor’*, ‘*low skilled*’ and ‘*minimum wage*’. Separate to the consortium, the oysterman told us low wages were ‘*due to poor management and longwinded regulatory policies*’, limiting the success of both Pacific oyster and other shellfish aquaculture. The consortium suggested that shellfish aquaculture employment was not what their region needed, as cost of living was too high. It is not our experience that wages in shellfish aquaculture are dissimilar to other fishing industries that span across a broad salary range, but it is recognised that the low yield or value of shellfish from wild stocks can mean low incomes. Despite the consortium’s negative response on employment linked to Pacific oysters, the same group suggested that employment linked to Flat oysters should be championed. Specifically, they said the Flat oyster fishery should be ‘*given every opportunity to flourish*’. Oystermen nationally have told us of the greater challenges of basing a viable household income on solely Flat oysters compared to Pacific oysters. This feedback is seen in our survey results of those working with both Flat and Pacific oysters in Essex, as well as feedback we have obtained from North-West England, Wales, and South-West England where there is a dedicated Flat oyster fishery based on natural recruitment. Feedback from the oysterman suggested that now that *M. gigas* is established, were they able to utilise the ‘naturalised' Pacific oysters more effectively alongside their traditional Flat-oyster fishery, this would be a valuable diversification of their income.

Finally, the South-West England consortium suggested more should be done to investigate the potential negative effects of Pacific oyster spread on tourism revenue, with references to water sports, sailing and coastal tourism. The oysterman somewhat agreed saying they had also heard complaints that naturalised and large Pacific oyster reefs affect tourism and access to the shoreline. Besides the risks associated with sharp shell materials (see Section 3.5), it is not fully clear how Pacific oysters could have significant negative effects on coastal tourism, and no evidence for effects on tourism revenue has been provided in responses, and nor could we find any. However, in some areas of Europe the role of oyster production in attracting tourists is positive (e.g. Cancale, France and Mersea Island, Essex), but these are managed aquaculture and not wild populations. Clearly more research on people's experiences and effects on tourism revenue with the contemporary and ongoing ecological naturalisation of Pacific oysters in the UK is required.

3.7. Effectiveness of mitigation strategies to minimise the spread of *M. gigas*

There have been concerted efforts in some areas to eradicate established wild *M. gigas* settlements. These include destruction of individuals by 'hammering', removal by dredging or smothering of reefs with sediment. McKnight and Chudleigh (2015) report on attempts to remove *M. gigas* from substrate including chalk reef in a small section (1000 m^2) of the intertidal in the *Thanet Coast SAC* by hammering. The project utilised 235 hours of volunteer labour over a year, removing 34,333 oysters and resulting in considerable reduction in oyster numbers. This did not remove recruited oysters from other nearby sections of coast, or from the upper subtidal. Notably this removal is to protect a key protected marine feature in a section of coastline, and to reduce the abundance of the organism close to where it could recruit into another protected site, Pegwell Bay. This is a high energy open sand and mud-dominated site, but with considerable abundance of dead shell material in the form of cockle shell; whether it is as vulnerable to the establishment of *M gigas* as the chalk cliffs remains untested. Guy and Roberts (2010) utilised a similar methodology in Strangford Lough to similar effect. We received feedback that hammering has been used effectively in the River Helford estuary (Devon, UK), with management of *M. gigas* numbers rather than their eradication being the intended objective. However, large-scale trials in The Netherlands were unsuccessful with resulting damage to protected sites deemed unjustified (Herbert et al., 2016). Further feedback raised concerns that hammering during the summer months could release fertile eggs and sperm which may facilitate the dispersal of *M. gigas*. Overall, where this species is causing localised conflict, for example with habitat or species-specific conservation objectives or more aesthetic priorities (e.g. water sports or dog walking; see Section 3.5), localised campaigns to reduce the coverage of Pacific oysters on intertidal habitats appear to provide effective mitigation against the formation of naturalised reefs.

In contrast to the examples from hard-substrate environments above, reef-establishment on soft substrates is often easier to manage. After concerns were raised by waterway users, a naturally established *M. gigas* reef in Brightlingsea Harbour (Essex, UK) was dredged to remove the risks associated with sharp shell edges and return the area into a mudflat (Herbert et al., 2016). As a result of this operation, much of this site could currently be described as a managed intertidal mixed sediment and, while *M. gigas* persist in the area, there are no extensive intertidal reefs. This example, in which a local oyster fisherman was able to harvest commercially from an *M. gigas* population that was of concern to waterway users, illustrates a 'win-win' situation creating benefits to multiple coastal stakeholders while demonstrating the ease with which oyster reefs established on mudflats could be managed and safely brought into food production. Ongoing oyster harvest operations by the aquaculture industry are, in fact, uniquely placed to provide such a service in locations where such management is deemed necessary. For example, managing the establishment of Pacific oysters on the beachfront at Southend (Essex, UK) on the Thames estuary, Southend-on-Sea City Council encourages oyster businesses to register for permits to harvest the shellfish by hand which minimises adverse effects from established oyster reefs on beach users (Southend-on-Sea City Council, 2024). However, local rules prevent oystermen from landing and processing *M. gigas* in some areas (e.g. Fal), hampering effective management of spreading wild populations.

Smothering of oyster reefs has also been attempted as a means of control. This process involves the dumping of large quantities of dredged sediment (a layer of >0.2 m thickness) onto a reef (Hansen et al., 2023). In theory, this method will choke and starve the oysters, although full mortality is unlikely to be achieved given the depths of mud in which *M. gigas* can be found in some areas such as the River Colne (Essex, UK). Both smothering and dredging of a reef involve the disturbance of substantial areas and volumes of sediment, which can negatively impact local benthic community structure, and water and sediment quality (Newell et al., 1998; Schaffner, 2010). Because they are labour intensive, efforts are limited in scale, therefore relying on volunteer labour or require substantial additional funding. Furthermore, given that the underlying factors that encouraged settlement are not substantially altered, efforts will likely need to be repeated regularly to ensure that the areas remain free from a developing *M. gigas* reef.

The inherent practicality of eradication efforts is also questionable. Cassini (2020) suggests that, outside of isolated small-island environments, it is rarely possible to remove a species from an ecosystem. The interconnected nature of marine systems only adds to this challenge (Teixeira Alves and Tidbury, 2022). The dispersal patterns of *M. gigas* around Europe demonstrate that long-range dispersal has occurred regularly since its introduction (Clubley et al., 2023). Modelling of multi-generational dispersal in *M. gigas* suggests three distinct clusters connecting UK populations across (i) the southern North Sea, (ii) the western and (iii) eastern areas of the English Channel, that demonstrates connection can occur between UK coastal sites (Clubley et al., 2024). However, long-range dispersal between mainland Europe and the UK in the southern North Sea was substantially higher compared with dispersal between UK coastal sites. Lallias et al. (2015) found that there are a substantial number of wild and established *M. gigas* populations around the UK coast with closer genetic links to French than UK hatcheries and *M. gigas* without obvious links to local aquaculture activities are present at various locations ranging from Southampton to the Shetland Isles (Kochmann et al., 2012; Mills, 2016; Shelmerdine et al., 2017). It is important to note that one large female *M. gigas* can release in excess of 50 million externally fertilised eggs per spawning and that, based on harvesting data, French oyster populations alone are likely producing one to two orders of magnitude larger propagule sizes than much smaller populations in the UK. Several modelling studies converge on the same result, that the species has a high probability for rapid and successful long-range dispersal (Teixeira Alves and Tidbury, 2022). This outcome is independent of current UK aquaculture activities and is possibly aided by settlement on existing offshore installations including nautical markers, oil and gas platforms or windfarms across the southern North Sea that provide a ‘stepping stone’ for their dispersal (Clubley et al., 2023; Wood et al., 2021).

Prevention or slowing further spread instead of costly removal post-settlement is obviously preferred and it has been suggested this is possible using ‘triploid’ oysters in aquaculture. Unfertile triploid oysters are obtained in hatcheries by crossing female diploid oysters (2n) with male tetraploid oysters (4n) (Hansen et al., 2023). This is often suggested as a strategy in which the reproductive potential and, hence, spread of oysters from controlled aquaculture facilities into the wild can be minimised (Nell, 2002). However, the process is not completely effective because some individuals remain fertile or can revert to a fertile state (Syvret et al., 2008), but the risk of unwanted reproductive capacity is considered extremely low (Methratta et al., 2013) with numbers of resulting fertile female diploid oysters calculated at 0.0001 to 0.016% of the triploid population (Ward et al., 2022). Additionally, the use of triploid seed in aquaculture can come with some challenges, including those presented in feedback to us from producers of increased mortality, changeable product quality and confusion with the customer base that they are genetically modified products. Triploids could be accepted as a suitable mitigation in those areas without current established wild *M. gigas* populations, where they can minimise but not eliminate risks of establishing wild populations from aquaculture sources. Aquaculture industry feedback, both direct to us and communicated publicly, is the perception that Natural England, a UK Government statutory agency, are now mandating the use of triploid oysters for new aquaculture licences or applications for expansion of aquaculture activities north of the 52°N line. While we have heard representatives speak of “disappointment” about the lack of uptake of triploids, they have stated to us that there is no mandate for the use of triploid Pacific oysters. Noting their repeated commitment to view any aquaculture applications on a site-by-site basis, and to provide conservation advice accordingly, we received feedback that Natural England’s position can be summarised as the use of triploid *M. gigas* within England reduces the risk of adverse effects on protected features of the Marine Protected Area network when compared with the use of diploids grown within aquaculture operations.

We have concerns about regulatory overreach on the use of triploids industry-wide in order to limit the spread of *M. gigas* when UK aquaculture and local dispersal connectivity appear to represent a relatively low source of the reproductive capacity for spread in the UK. A shift to use of triploids in southern UK below the 52 parallel, as well as in Scotland, France and the Netherlands would be necessary for such actions to be effective at limiting spread to sites in northern England. There is the possibility for such regulatory actions to increase the time to colonisation of naturalised *M. gigas* at suitable sites if the time to colonisation is not more fully determined by temporal trajectories of sea warming (see Section 4), but it would appear not the likelihood of colonisation itself (Clubley et al., 2024; Wilson et al., 2024). Without a European-wide switch to triploids, action in the UK would limit the industry but not achieve limiting the spread.

4. Impacts of and Adaptation to Climate and Coastal Change

M. gigas is of subtropical origin and the future warming of waters along European and UK coastlines will likely increase the reproductive potential of this species. King et al. (2021) forecast that the majority of the NW European coastal shelf will be within the thermal niche for successful reproduction of *M. gigas* by 2100. This is further supported by modelling approaches using an ensemble of over twenty different climate models that project a substantial increase of recruitment area for *M. gigas* in UK waters (Wilson et al., 2024). Coupled with the species' already widespread distribution and extensive capacity for dispersal via planktonic larvae, it is highly likely that the wild distribution of this species will continue to expand northwards within the coming decades. Arguably, given the distribution already described, and the behaviour and dynamics of this species and its associated ecological communities across European coasts, *M. gigas* is already naturalised in UK waters.

Similar to many other native species, *O. edulis* and *M. edulis* will be challenged by factors arising from climate change including rising seawater temperatures, increased heatwave frequency and severity, and altered precipitation patterns resulting in changes in terrestrial run-off and water quality (Eymann et al., 2020; Fly et al., 2015; Oliver et al., 2019; Trenberth, 2011). The ecosystem service provision associated with the extant bivalve assemblage is therefore under threat, particularly in the intertidal. It is important to recognise that non-native species have the potential to change and reduce ecosystem service provision (Gallardo et al., 2024). However, it is important to note that it was outside the scope of Gallardo et al. (2024) to consider what, if any, positive effects on existing ecosystem service provision or new ecosystem services could be provided by the non-marine non-native species they evaluated. Coastal ecosystems in Europe may, in fact, benefit from the very similar nature of the service provisions associated with the more resilient *M. gigas,* providing a degree of redundancy in what is likely to become an increasingly stressed intertidal system (Ferreira et al., 2008; Hansen et al., 2023; King et al., 2021).

4.1. Living breakwaters

Bivalve reefs integrated into 'living breakwaters' are suggested as a strategy to mitigate against the effects of climate warming-induced sea-level rise. Living breakwaters can protect from coastal-flooding and reduce erosion of vulnerable coastal habitats such as saltmarsh while delivering additional ecological benefits (Ridge et al., 2017; Scyphers et al., 2011). Chowdhury et al. (2019) demonstrated that mudflat stability in Kutubdia Island, Bangladesh is significantly increased by the presence of the intertidal Hooded oyster *Saccostrea cuccullata*. One added benefit of a living shellfish breakwater is that shellfish reefs can grow with a rising sea level and repair themselves after damage, whereas traditional coastal defence is often limited to the costly and unsustainable installation of man-made structures, for example, groynes, seawalls or tidal barriers, that are static and have a limited lifetime (Morris et al., 2018). To be cost-effective, it is likely that future coastal defence must utilise a combination of traditional and natural engineering strategies (= hybrid engineering), and coastal defence projects would benefit from the installation of rapidly establishing, low maintenance intertidal Pacific oyster reefs as demonstrated by efforts in The Netherlands (Fivash et al., 2021). It is important to recognise that the establishment of mid- to high-intertidal living breakwaters with *M. gigas* performs a function that is not delivered in Europe from Flat oysters (*O. edulis*) and does not compete with the many other functions that Flat oysters provide.

5. Discussion and Conclusion

Hobbs et al. (2006) and Truitt et al. (2015) argue that systems in which human-induced changes have altered the natural state should be treated as ‘novel’ rather than ‘inferior’, that the changes are often impractical to reverse and that we should *’…accept them for what they are and what benefits they provide…*‘ (Hobbs et al., 2006). Particularly with contemporary climates in mind, there is a shift in the narrative on how we approach non-native species on a case-by-case basis where some certainly have the potential to deliver more benefits than costs. For example, Lundgren et al., (2024) state that the functional ecology of organisms should be considered as more important than ‘nativeness’ when assessing the impact of a species. Our review suggests that *M. gigas* is a suitable candidate for such consideration and should be regarded as legally naturalised. It has been put to us that, in effect, *M. gigas* is considered as naturalised below the 52 parallel by UK regulators, where below this line an aquaculture applicant has to give less consideration that their aquaculture activity would influence the colonisation of this species as it is already considered present. But as we have demonstrated in our review, due to substantial evidence from a range of hydrodynamic models on the high dispersive capacity, the same can be said north of the 52 parallel where – even if we were to remove all aquaculture licences or introduce a complete switch to the use of triploids only – the colonisation is predicted to be successful. During the required Habitat Regulations assessment, applicants are also asked to consider the cumulative impacts of their proposed activity elsewhere in the area on the likely significance of ecological impacts within a sensitive site or area. This provides an opportunity for regulators to consider aquaculture and naturalised populations of *M. gigas* at a larger scale than at an individual site or protected area, as applicants from anywhere in the UK can evidence that their activity is of low risk relative to the cumulative effects of an interconnected *M. gigas* biomass and reproductive capacity across Europe where the risks for colonisation are not just local.

It is important to stress that we are not advocating for a wholesale change of approach to the widely recognised impact of invasive non-native species on global biodiversity, which for the majority of invasions have not been studied, and where it has been shown that non-native species invasions are implicated as the sole or a contributing cause in many global animal extinctions (Bellard et al., 2016). While we have not seen ubiquitous expansion of *M. gigas* in the North Sea and around the UK coast, there have been sporadic successful settlement events, and we do not understand what caused these successes relative to lack of substantial wild reef expansion in most sites in most years. This points to the unpredictable nature of the expansion of invasive non-native species, and how they may respond to future climate conditions. Many small-scale and low-density establishments of *M. gigas* populations around the UK coasts could be considered as ‘sleeper populations’ that may be the source of major expansions at some point in the future (Spear et al., 2021). For these reasons there has been strong criticism of the promotion of ‘novel ecosystems’ in the context of interactions between highly abundant established non-native species and climate change (Murcia et al., 2014; Simberloff et al., 2015). But that is not to say that there are not examples where intervention for preventing or regulating introduction of non-native species, or species removal is too late, and we are at that point of making the best of a difficult ecological and policy situation. We are advocating that this is the case for *M. gigas* in the

UK, where the regulatory proposals we are experiencing may have been effective in 1960-70 but are now unlikely to address the issue.

We have reviewed the realised risks of the spread of *M. gigas*, as well as potential benefits of this new species creating novel habitat across European seascapes. We recommend regular review of the realised risks of range expansion and introduced species on habitats and this fits with the habitats regulations assessment to '…*only consider real, not hypothetical risk*…' (GB Government, 2023). Our review of the realised risks of *M. gigas* on UK habitats found that, combined with suitable mitigation, a large-scale habitat change caused by this species has not been widely observed in larger open estuaries that are dominated by mud and sand. Likewise, the reciprocal is true, where smaller and hard-substrate dominated coastal systems are likely to be more vulnerable to colonisation, which explains the concerns over *M. gigas* in the South-West of England, Wales and the chalk cliffs of Kent. It is highly likely, as the Celtic Sea and seas off western Scotland warm, we will observe widespread colonisation of these sites, as has been reported in west Sweden for example (Dolmer et al., 2014).

We have also reviewed the potential for benefits of *M. gigas* in the UK coastal seascape and research on other non-native species is also of relevance here. For example, Zhao et al. (2023) present a case study of *Spartina alterniflora* in China, a non-native cordgrass species which is marked for eradication in the country but provides a range of beneficial ecosystem services. They suggest that the carbon storage and flood prevention capacity of the species are sufficiently beneficial that it should be allowed to remain in some areas of the foreshore. *Spartina* species in the UK have had similar changes in management. *Spartina anglica*, a species resulting from hybridisation between the non-native and native cordgrass species, has in the past been subject to eradication efforts, with unknown effects on ecosystems. However, it is now understood to be a precursor to the return of saltmarsh under certain conditions, and therefore a valuable facilitator species in the restoration of this threatened habitat type (Balke et al., 2012; Lacambra et al., 2004). Likewise for *M. gigas* and from a socioeconomic perspective, the employment opportunities directly and indirectly supported by the production of oysters are essential in often deprived coastal areas (Williams and Davies, 2018). Environmentally, the potential benefits of *M. gigas* are substantial whether that be to see investment of this species as a nature-based solution to coastal defence (Fivash et al., 2021), contributions to natural capital and ecosystem services, or in increasing the role of highly sustainable, low carbon, low input-cost shellfish protein in the UK diet.

Currently during a habitats regulations assessment there is little if any scope for a regulator to consider the potential benefits of a proposal on the biodiversity or ecological status of a protected site, as the regulations asks a reviewer to assess the risk or possibility of a significant ‘adverse’ effect. Where that adverse effect is on a particular habitat type, for example ‘intertidal estuarine mud’, or on a particular species, for example ‘blue mussel’, and not on other ecological metrics such as total biodiversity or ecosystem function, it is challenging to incorporate benefits into the assessment via consideration of ‘net’ effects by balancing negative and positive effects. Likewise, risk assessments on the potential for colonisation into other European regions, or a review of possible effects has not considered the net effects or likely benefits (e.g. Dolmer et al., 2014), despite finding and presenting evidence for such benefits (e.g. higher biodiversity in oyster habitats, or evidence for net neutral effects on native shellfish). We are not the first authors to call for the net effects of species or activities to be considered in habitats regulations assessments, specifically in the context of managing the realised impacts of non-native species or in how ecosystems are changing under climate change (García-Díaz et al., 2021; Kharouba and Rivest, 2023; Sax et al., 2022; Schlaepfer, 2018). Nature is dynamic while Habitat Regulations assessments largely judge a plan or project proposal against a historical and stationary set of legal criteria.

Shellfish aquaculture is a key part of the aims set out in the aquaculture and fisheries strategies of all UK administrations to increase UK domestic production of high quality and sustainable food, and the production of *M. gigas* is recognised as an important driver to achieve this. For example, the English Aquaculture Strategy bases its forecast for the aquaculture sector in England on an assumption that the legislative approach to *M. gigas* production will become more supportive in the near future, realising that eradication is unfeasible and warming waters will encourage the natural spread of the species regardless of the activities of the UK aquaculture industry (Huntington and Cappell, 2020). This appears to be in contradiction to the rhetoric from some sectors within DEFRA and suggests a collaborative cross-department workshop would be beneficial considering our review. In a global context, the recent fifth National Climate Assessment of the US Global Change Research Program (2023) recognises that marine aquaculture may prove a vital part of securing coastal livelihoods in the face of a changing climate.

Our review suggests that the spread of *M. gigas* in UK waters will not have substantial net-negative impacts on ecosystems and in the rare cases where substantial settlement creates a conflict, the evidence for successful mitigation is strong. Further, the proposed limitations on *M. gigas* harvesting and aquaculture operations, the use of triploids, and attempts to eradicate wild populations will be ineffective in limiting the spread of a species that has become so widely naturalised and is capable of long-distance dispersal (Renton et al, in press). However, there are several substantial knowledge gaps that remain. The rate of spread following known introductions is not fully understood in the context of both the UK coast and forthcoming changes in climate. There is little in the literature about the effects of *M. gigas* on mudflat habitats. The spread of *M. gigas* into *O. edulis* restoration areas and the impact of this on transmission of pathogens merits further work – in particular, the interaction between *M. gigas* and the parasitic and often lethal *Bonamia* spp. is poorly understood (Lynch et al., 2010; Tristan et al., 1995). The potential benefits of *M. gigas* aquaculture stocks and naturalised reefs for water filtration and as living breakwaters protecting vulnerable coastlines including saltmarshes could also be substantial but are yet to be fully explored in Europe.

In conclusion, we recommend a re-consideration of the regulatory approach towards Pacific oysters and their aquaculture in UK waters. We are now past the point where effective regulatory intervention that would control the spread of this species could occur. Current proposals will create a regulatory burden on both the aquaculture sector and regulators and fail to achieve the desired outcome of limiting spread. This same regulatory approach limits any utilisation of the species in providing nature-based and hybrid-engineering solutions to contemporary coastal problems associated with climate change – such as sea-level rise and erosion, and resilience in the face of increasingly warming coastal seas. The current regulatory approach also deprives our economy of benefits of aquaculture expansion, our ecosystems of any potential benefit of water cleansing, carbon sequestration and nitrogen removal and our communities of any benefit of increased food security. With appropriate mitigation methods in place, *Magallana gigas* should be granted a legal naturalised status in the United Kingdom.

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Authors' contributions: Alex Shakspeare, Tom Cameron and Michael Steinke contributed to the study conception and design, and material preparation. Data collection and analysis for Section 3.6 were conducted by Alana Wilson and Tom Cameron. The first draft of the manuscript was written by Alex Shakspeare and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability: The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

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Figure legends

Fig. 1. Numbers of Pacific oysters harvested annually from across four aquaculture businesses in North Essex that provided an answer to this question.

Fig. 2. The relationship between employee numbers and the annual turnover of the fisheries surveyed. Linear regression fitted including the outlier (○) showing a linear regression coefficient (R^2) of 0.58 (dashed line). Linear regression fitted excluding the outlier had an R^2 of 0.73 (solid line). Each dot represents a turnover~employment relationship each year.

Online Resource 1 Shellfish business survey

Evaluating the net impacts of an established non-native species and attempts to control its spread in the UK: Addressing the oyster in the room

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Online Resource 1 Shellfish business survey

Questionnaire ID Number: XXXX

Thank you for agreeing to participate in this study. The aim of this study is to assess the economic contribution of non-native species to coastal communities. You have been contacted as you are involved in the bivalve aquaculture industry and I am specifically interested in the contribution of the Pacific Rock Oyster to Mersea Island, and in the north Essex area.

By returning this survey to us using your data to evaluate the role of pacific rock oysters and other species in coastal communities you have given consent for this anonymised data to be used by the University of Essex in research by myself.

Please return your completed survey to me (Alana Wilson) at the provided email below, similarly if you have any questions please get in touch.

You have the right to withdraw any data you provide at any point in the study, in this case please email Prof Tom Cameron with the ID number at the top of this survey.

Contact Information:

Alana Wilson, University of Essex, aw20751@essex.ac.uk

Supervisor: Prof Tom Cameron, University of Essex, tcameron@essex.ac.uk

SURVEY

Please answer these questions the best you can. You can type the answers in and then email the document back to us. Remember to not place your name, business name or contact details on the document. You can as much or little as you like and the document will extend.

What kind of business are you? E.g. Sole trader, ltd. Business

Are you the - **Business owner** **Director** **Manager** **Other**

*circle/highlight as applicable

Question 1. If policy prevented farming non-native species would native species such as mussels, oysters be a reasonable replacement for rock oyster sales? *please explain your answer.

Question 2. Compared to 10 years ago do you think that there are more / less / the same areas in your local coastal areas affected by feral free living Pacific Rock Oysters? *please add any observations or opinions.

Question 3. Have you heard or know of feral Pacific oysters causing problem for you/anyone else? And how was this resolved? *please give examples

Question 4. If authorities required the removal of rock oysters from a local area would you…..Highlight or underline your top answer *please elaborate your reasoning for your chosen answer

A. Remove them without any financial incentives
B. Remove them with financial incentive
C. Remove them and use them for your business
D. Remove them and use them for your business and take a financial incentive
E. Do nothing as it’s not your responsibility

Reason for choosing this answer:

Question 5. What is the age range of your employees, and are you concerned about future recruitment? Give as much detail as you can.

Question 6. Please complete the following table – choose up to three different years – state which years in the top row. Give your data as values

Year of Data			
Number or volume of Pacific Rock Oysters harvested annually			
Number or volume of Pacific Rock Oysters bought in from others annually			
Total Pacific Rock Oyster sales annually (in GBP £, i.e. combination of above)			
Other Non-Native shellfish sales (in GBP £) *please specify what species			
Annual native shellfish sales (in GBP £) *please specify what species			
Total Employees			
Total Business turnover			
Number of Employees supported by Pacific Rock Oysters alone			
Number of Households supported by Pacific Rock Oysters alone			