

Research Article

Invasive non-native species management under climatic and anthropogenic pressure: application of a modelling framework

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Citation: Teixeira Alves M, Tidbury HJ (2022) Invasive non-native species management under climatic and anthropogenic pressure: application of a modelling framework. *Management of Biological Invasions* 13(2): 259–273, <https://doi.org/10.3391/mbi.2022.13.2.01>

Received: 25 August 2021

Accepted: 9 February 2022

Published: 11 April 2022

Handling editor: Thomas Therriault

Thematic editor: Joana Dias

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Abstract

Mitigation of impacts from already established invasive non-native species (INNS) relies on reducing species abundance and onward spread. However, there is limited understanding regarding the effectiveness of INNS management approaches in the short and long term, in particular in the marine environment. Further, the interplay between management and key population drivers is not well explored. The Pacific oyster *Crassostrea gigas* Thunberg, 1793, also known as *Magallana gigas* Thunberg, 1793, is native to the north-eastern Pacific coast of Asia and has been introduced in the UK for aquaculture purposes, with wild populations now widely established along the South coast. Concern over the potential impact of this species has led to trial of its management, yet clear evidence to support management decisions around this species is still lacking. This study applied a modelling framework, based on differential equations representing *C. gigas* life stages, to explore the effect of adult oyster population management on population persistence and density, under changing temperatures and external larval recruitment. The outputs highlight that population control may be possible and intuitively population density is negatively correlated with management frequency and effort. However, the exact relationship between population density and management is influenced by spawning and external recruitment. Specifically, outputs indicate that while the effects of climate change could be counterbalanced by an increase in management effort, the impact of external recruitment can only be reduced through management, rather than reversed. The wider application of this framework to inform INNS management decisions is discussed.

Key words: population model, marine species control, differential equations, Pacific oyster, intertidal species, non-indigenous species

Introduction

With their high and increasing ecological (Havel et al. 2015; Mollot et al. 2017; Spatz et al. 2017; Shabani et al. 2020) and economic impact (Diagne et al. 2021), the need for effective and informed management of invasive non-native species (INNS) is particularly acute. Prevention of introduction is deemed the most cost-effective approach to reducing and managing impacts associated with INNS (Convention on Biological Diversity 2013; Manchester and Bullock 2000). However, for already established INNS, mitigation of impacts may rely on reducing species abundance and onward

spread (Sundet and Hoel 2016). While there is tendency to focus on eradication as an INNS management endpoint (e.g. Booy et al. 2017, 2020), eradication is rarely feasible, especially in open systems such as the marine environment (Thresher and Kuris 2004; Simberloff 2020). Still, since impacts associated with INNS may increase with their density (Sofaer et al. 2018), the condition status of priority sites under key legislation may be driven by the impact of an INNS on site integrity, rather than their presence alone (e.g. under The Conservation of Habitats and Species Regulations 2017 (UK 2017)). Therefore, INNS management to reduce population density (termed “maintenance management” (Simberloff 2020) or “suppression” (Robertson et al. 2020)) needs consideration alongside eradication.

INNS management strategies generally fall into three categories: physical, chemical and biological (Herbert et al. 2016; Giakoumi et al. 2019; Simberloff 2020). Such approaches have been successfully implemented to manage aquatic INNS. For example, in Great Britain freshwater species such as fathead minnow (*Pimephales promelas* Rafinesque, 1820), black bullhead catfish (*Ameiurus melas* Rafinesque, 1820) and topmouth gudgeon (*Pseudorasbora parva* Temminck and Schlegel, 1846) have been successfully eradicated using chemical control (GBNNS 2015). However, there have been very few eradication successes in the marine environment, mainly limited to intertidal species, such as the Caribbean black-striped mussel (*Mytilopsis sallei* Recluz, 1849) in Cullen Bay, Australia (Bax et al. 2002; Simberloff 2020). In general, there is limited understanding regarding the effectiveness of management in the marine environment in the short and long term (Kopf et al. 2017). In particular, the interplay between INNS management and key population drivers remains unclear, largely due to the absence of data and baseline understanding. This is a concern given that tools used to prioritise management often rely on an understanding of its likely success (Booy et al. 2017, 2020). Mathematical modelling provides a promising tool to enhance understanding and contribute to the evidence base which informs INNS management decisions (Vander Zanden and Olden 2008). In particular, population modelling based on ordinal differential equations can be used to test the impact of different management strategies, under varied management effort and temporal frequency, on the density and persistence of INNS populations.

The Pacific oyster, *Crassostrea gigas* Thunberg, 1793 (also known as *Magallana gigas* Thunberg, 1793), is native to the north-eastern coast of Asia but has been introduced into the UK for aquaculture purposes (Mann 1979). While in the early 1990s only sporadic settlements were reported in the UK waters, persistent wild *C. gigas* populations are now widely reported throughout the UK coastline, especially in Southern England and Wales (Herbert et al. 2012; Humphreys et al. 2014). Given the temperature dependence of maturation and reproduction, the increase in oyster

prevalence is likely the consequence of increased ocean temperatures associated with climate change (Rinde et al. 2017; King et al. 2021). Recent work has also shown that population persistence and density are linked to external recruitment, for example via natural dispersal of pelagic life stages via ocean currents (Wood et al. 2021) or via anthropogenic transport of pelagic life stages (e.g. in ship's ballast) (Anglès d'Auriac et al. 2017), and to resource availability (Teixeira Alves et al. 2021). In the UK, *C. gigas* may be associated with ecological impacts such as potential displacement of native species and habitat (Diederich et al. 2005; Ruesink et al. 2005; Smaal et al. 2005; Cognie et al. 2006), and socio-economic impacts such as injuries caused by shells on leisure beaches (Herbert et al. 2016; Reise et al. 2017). Further, if associated with alteration of the ecological integrity of a site, this species may impact the condition classification of protected sites under the UK Conservation of Habitats and Species Regulations 2017 (UK 2017). Given its potential impacts, in combination with its commercial value and potential natural dispersal over large distances, the “what”, “how” and “where” with respect to management of this species is the subject of some debate.

Management options for wild *C. gigas* populations are limited, with focus on manual removal of adults (Herbert et al. 2016). Though localised short-term manual removal of adults has been trialled, conclusive evidence around the effectiveness of such management on population persistence and density is not available (McKnight and Chudleigh 2015; Morgan et al. 2021). In this study we aim to address this evidence gap in order to facilitate more informed decisions around *C. gigas* management into the future. Specifically, we applied a modelling framework, based on differential equations representing *C. gigas* life stages, to explore the effect of removing adults on population persistence and density. Simulations over a range of management frequencies (number of management events over 20 years) and management effort (proportion of population removed) per event were run. The effect of different spawning frequencies (simulating the effects of climate change) and levels of external larval recruitment were also explored. The outputs highlight that, intuitively, population density is negatively correlated with management frequency and effort but that the exact relationship is influenced by spawning and external recruitment. More specifically, outputs indicate that while the effects of climate change could be counterbalanced by an increase in management effort, the impact of external recruitment can only be reduced through management, rather than reversed.

Materials and methods

Crassostrea gigas life history

Pacific oysters can live 20 to 40 years and form reefs in coastal and estuarine waters (Strand et al. 2011). *Crassostrea gigas* has a very high

fecundity with r-type life history and a strong temperature dependence (Hedge and Johnston 2014). Gametogenesis occurs at the end of the winter at a water temperature above 8 °C to 10 °C (Fabioux et al. 2005). Spawning usually occurs when water temperatures exceed 18 °C to 20 °C (Mann 1979; Diederich et al. 2005; Mills 2016), though partial or complete spawning below 18°C has been documented (Li and Hedgecock 1998; Chávez-Villalba et al. 2002; Rico-Villa et al. 2009; Dutertre et al. 2010). The spawning temperature for *C. gigas* in Poole, UK, has been estimated at 19.7 °C (Pastor et al. 2010). *Crassostrea gigas* fertilization occurs in the water column, which if successful, results in development of planktonic larvae which then metamorphose into juvenile spat (Li and Hedgecock 1998; Rico-Villa et al. 2009; Kheder et al. 2010). Larval development and settlement can take from 2 to 4 weeks at 25 °C and 17 °C, respectively, with a longer duration increasing risk of mortality via predation (Kennedy and Breisch 1981). Juvenile spat, once settled, are sensitive to low temperatures and cannot survive in waters below 3 °C (Child and Laing 1998). Juvenile development to adult oysters can take 1 to 3 years (Helm 2006).

Model framework

Differential equation-based models have been developed to represent stage-structured oyster populations (Jordan-Cooley et al. 2011; Lipcius et al. 2019). This modelling approach was subsequently adapted to incorporate different spawning frequencies and levels of external recruitment and implemented to examine the drivers of wild oyster population dynamics (Supplementary material Table S1, Teixeira Alves et al. 2021). Specifically, Teixeira Alves et al. (2021) represented spawning frequency as the frequency of temperature-dependent adult oyster annual reproduction events, and external recruitment level as a discrete annual influx of larvae from farmed oyster populations in close proximity or from long-distant wild oyster populations spatially distinct from the modelled population (expressed as R , the number of recruited larvae per m^2), both occurring under the assumption of optimal pH, salinity, turbidity and oxygen levels. In the present study, this modelling framework was extended to incorporate management strategies.

Management

The modelling framework by Teixeira Alves et al. (2021) was adapted to include the discrete removal of adult oysters during a management event at time $t = \tau_m$, according to:

$$t = \tau_m \begin{cases} L = L, \\ J = J, \\ A = A(1 - m), \end{cases} \quad (1)$$

where L is the number of larvae per m^2 , J is the number of juveniles per m^2 and A is the volume of adults per m^2 (Table S1). The proportion of the adult population manually removed was defined as the management effort, m , *i.e.* the proportion of the population that can be physically removed given accessibility to population and resources available, and ranged from 0 (no removal) to 1 (total adult population removed). The time of the removal event was such that it occurred prior to spawning.

Scenarios

To assess the impact of climate change and external larval recruitment on the success of *C. gigas* management, simulations representing a range of management efforts and frequencies, in combination with different levels of external recruitment and climate change scenarios (reflected by different spawning frequencies), were run.

Low, moderate and high management effort was associated with the removal of 0.25, 0.5 and 0.75 of the adult population, respectively, during each management event. Management events were simulated over 20 years under 5 scenarios: 1) no event, 2) events every 10 years, 3) events every 5 years, 4) biannual events, and 5) annual events. Spawning frequency was simulated under 3 scenarios: 1) no spawning, 2) spawning every 5 years, and 3) annual spawning. External larval recruitment levels were none ($R = 0$), low ($R = 20$ larvae. m^{-2}), medium ($R = 200$ larvae. m^{-2}), and high ($R = 2,000$ larvae. m^{-2}).

The initial density of established oyster populations was considered low ($A_0 = 0.01$ $m^3.m^{-2}$), medium ($A_0 = 0.05$ $m^3.m^{-2}$) or high ($A_0 = 0.1$ $m^3.m^{-2}$). Simulations were conducted over a period of 20 years and outputs were summarised as average adult densities at year 20 and number of years before reaching the management objective defined as a 90% reduction in density.

All parameters were based on the literature as detailed in Teixeira Alves et al. (2021) (Table S1). In particular, the level of external larval recruitment was based on oyster larvae monitoring data (Pouvreau et al. 2016). In Teixeira Alves et al. (2021), parameter uncertainty due to environmental variability (*i.e.* temperature) was explored using an elasticity analysis, highlighting that model outputs were highly sensitive to spawning threshold temperature, number of larvae produced by adult volume and conversion of juvenile into adult volume. In the present study, simulations covered a wide range of environmental and parameter values, representative of relevant real-world scenarios. All simulations were performed using the statistical software R (R Core Team 2020) and the package deSolve (Soetaert et al. 2010).

Results

Management under low spawning frequency and low external recruitment level

The management of populations which spawn irregularly with no or low-level external recruitment accelerates population density decline (Figures 1, S1).

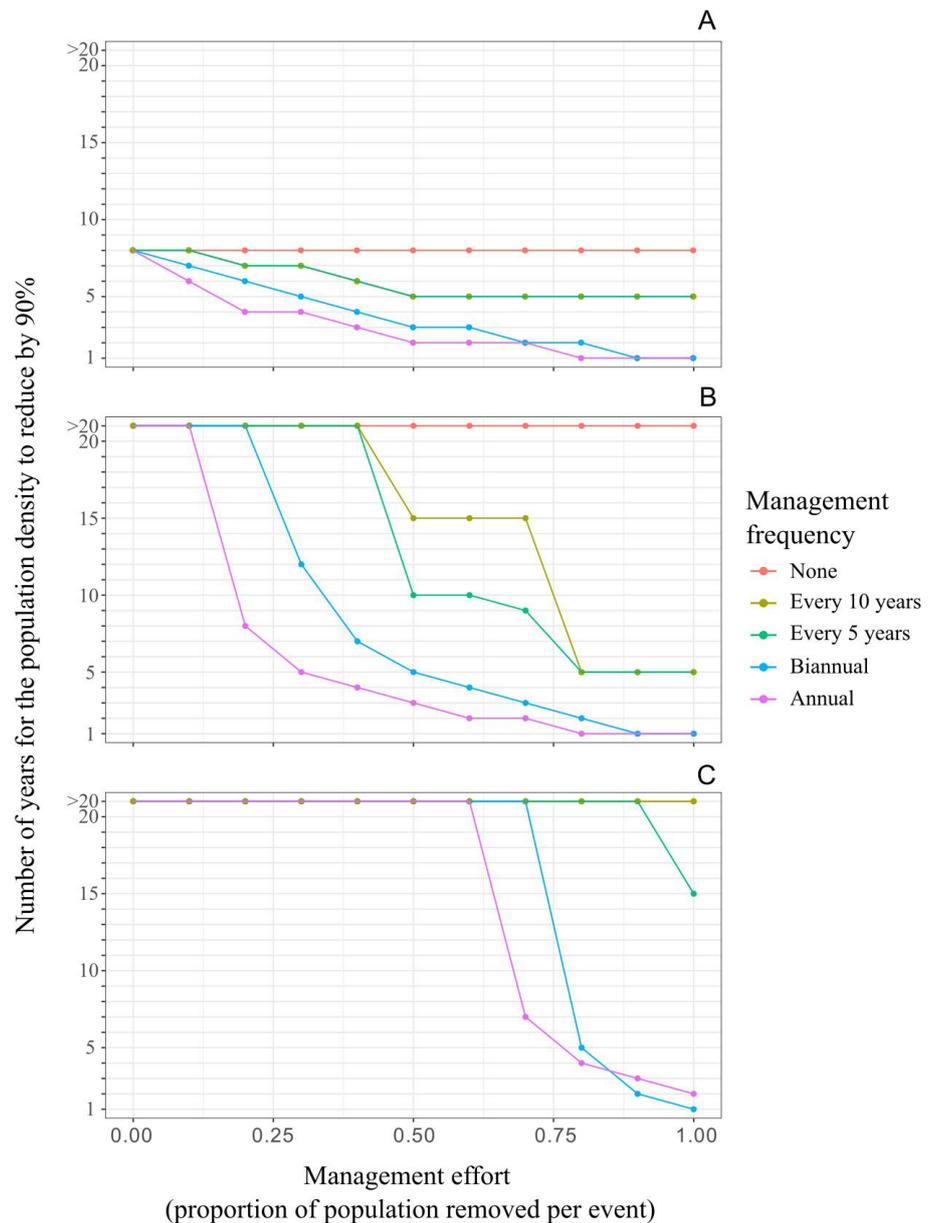


Figure 1. The number of years taken for the population density to reduce by 90% over the management effort (proportion of population removed per event) for 5 scenarios of management frequency (orange: none; olive: every 10 years; green: every 5 years; blue: biannual; pink: annual) with $A_0 = 0.1 \text{ m}^3 \cdot \text{m}^{-2}$ and (A) $R = 20$ and no spawning, (B) $R = 200$ and no spawning, and (C) $R = 200$ and annual spawning.

In particular, under high initial density, with no spawning and low external recruitment, the number of larvae is too small to support persistence of the adult population, which naturally declines by 90% of its initial density after 8 years, despite no management (Figure 1A). This time reduces to 2, 3 and 5 years when moderate removal effort is employed annually, biannually and every 5 or 10 years, respectively. However, little difference is seen in population density in the long term between scenarios, as populations tend to extinction across all management and no management scenarios due to such a low recruitment.

Impact of more frequent spawning

Environmental changes, *i.e.* increased ocean temperature, that permit more frequent spawning, reduce the impact of management under all scenarios (Figures 1, S1). For example, under high initial density, with no spawning and medium external recruitment, management effort greater than or equal to 0.60 reduces population density by greater than 90% (Figure 1B). The time taken for population density to reduce by 90% is however dependent on the frequency of management events, taking 2 years when employed annually, up to 15 years when employed every 10 years. Under annual spawning, a 90% reduction in density occurs only if management effort is greater than or equal 0.60 or 0.70, and management is employed annually or biannually, respectively (Figure 1C). Moreover, the time taken for the density to reduce by 90% increases from 2 years (no spawning) to 7 years (annual spawning) with management effort of 0.60 employed annually.

Management under high spawning frequency and external recruitment level

The density of populations that spawn regularly and/or have high levels of external recruitment is markedly impacted by management in the short and long term, irrespective of initial population density (Figures 2, S2). For example, under medium initial density, with annual spawning and low external recruitment, the adult population density is reduced by greater than 93% under annual and biannual removal frequency and moderate removal effort (Figure 2A). A reduction in population density by 90% is achieved through multiple management effort and frequency combinations, including an annual management effort of at least 0.25, a biannual management effort of at least 0.45 and a management effort of at least 0.85 employed every 5 years. In addition, the density of the adult population is reduced by 30% under moderate removal effort employed every 10 years. However, if management frequency is increased to every 5 years, biannual or annual, management effort can be reduced to 0.40, 0.20 and 0.10, respectively, to achieve a 50% reduction in population density.

Impact of high external recruitment level

While the density of populations subject to high levels of external larval recruitment can be reduced markedly through management, a reduction of 90% of the initial density can never be achieved (*i.e.* high levels of external recruitment prevent achievement of the theoretical management objective), irrespective of the initial density, spawning frequency and management effort/frequency combination (Figures 2, S2). External larval recruitment contributes animals to the population acting to prevent extinction even under the most extreme management scenario (complete removal undertaken

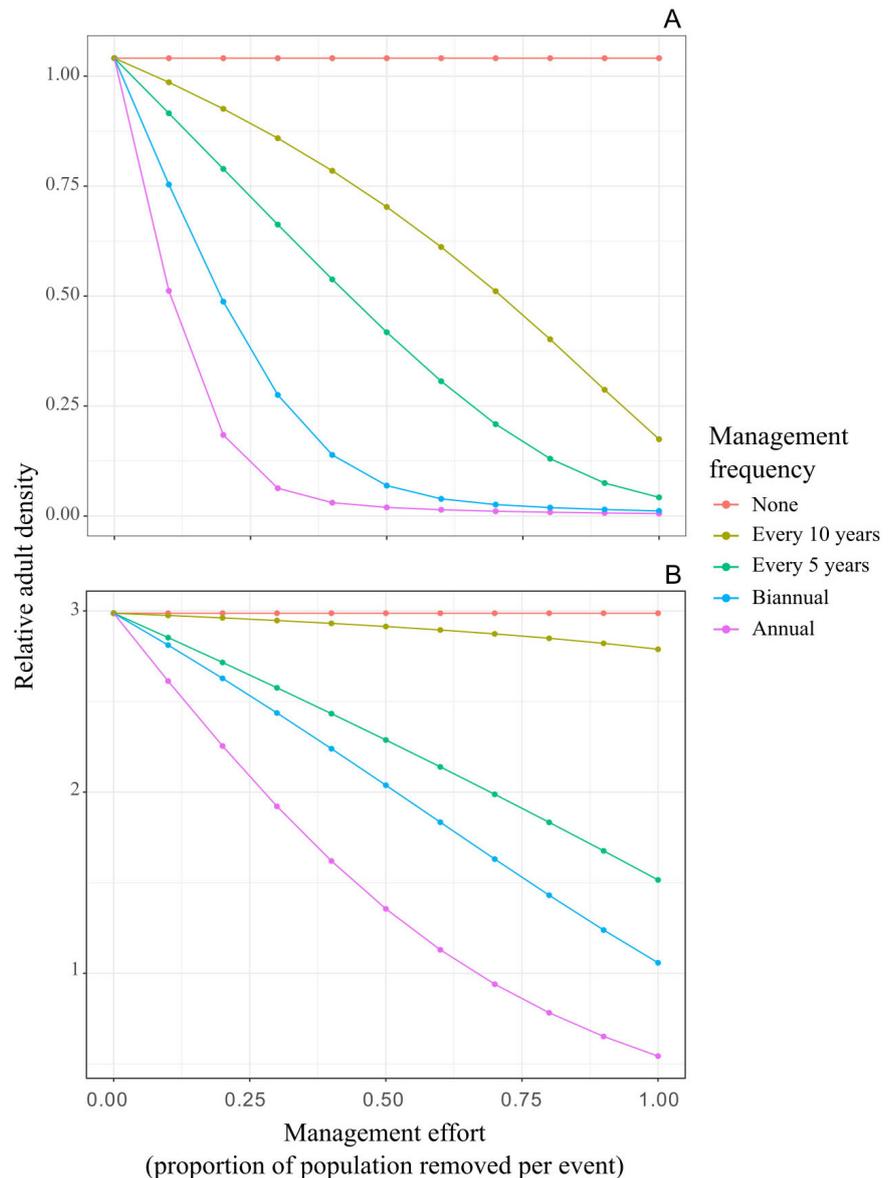


Figure 2. The relative density of the adult population after 20 years, relative to its starting density, over the management effort (proportion of population removed per event) for 5 scenarios of management frequency (orange: none; olive: every 10 years; green: every 5 years; blue: biannual; pink: annual) with $A_0 = 0.05 \text{ m}^3 \cdot \text{m}^{-2}$, annual spawning, and (A) $R = 20$, and (B) $R = 2,000$.

annually). Still, the density of managed populations is lower than unmanaged populations, despite high levels of external recruitment. Under medium initial density, with annual spawning and high external recruitment, the relative increase in population density is thus less than half (1.5 times the initial density) under moderate management effort employed annually compared to no management (3 times the initial density) (Figure 2B).

Comparison of impact from spawning frequency and external recruitment level

External recruitment level affects the impact of management to a greater extent than the spawning frequency (Figures S1, S2). For example, the density of a population which experiences high external recruitment but at most

spawns every 5 years, is greater than that of a population which spawns annually, for the same management and initial density. However, the population density predicted under a management effort of 0.90 employed biannually is similar to that of populations which spawn annually or do not spawn but experience low external recruitment.

Discussion

There is mounting pressure globally to mitigate the increasing ecological, social and economic impacts of INNS (Lovell et al. 2006; Williams et al. 2010; Diagne et al. 2021). For already established INNS, mitigation of impacts largely relies on management to reduce species abundance and onward spread (Herbert et al. 2016; Sundet and Hoel 2016; Robertson et al. 2020; Simberloff 2020). The short- and long-term impact of management approaches is complex and difficult to predict in the context of changing climate and human mediated drivers of population dynamics. This study applied a modelling framework to examine the effect of population management strategies based on manual removal of adults on the persistence and prevalence of *C. gigas*, under different spawning and external larval recruitment scenarios.

The key findings of this study are: 1) a reduction in population density can be achieved through the manual removal of adult oysters, with population density negatively correlated with management frequency and effort, 2) population density increases which result from more frequent spawning, reflecting increased temperatures associated with climate change, reduce the effect of management, implying that management effort and frequency may need to be upregulated in the future to counteract the impacts of climate change, and 3) the increased population density resulting from external larval recruitment can be reduced with management but not reversed, so that under high external larval recruitment the relative density is always high, irrespective of the management effort and frequency combination, though the absolute density reduces as management effort and frequency increase.

Climate change may alter the effectiveness and outcome of management. There is a large consensus that mechanical control of INNS is less efficient under climate change pressure (Hellmann et al. 2008; Pyke et al. 2008; Kernan 2015). Temperature dictates the lifecycle of many INNS and, in the case of *C. gigas*, is an important driver of maturation, reproduction and establishment (Reise et al. 2017; Teixeira Alves et al. 2021). Since the reproductive success of *C. gigas* substantially improves in warmer waters, climate change may increase the spawning frequency. In addition, climate change may increase external larval recruitment from aquaculture sites and wild populations through larval dispersion on ocean currents and anthropogenic vectors (Anglès d'Auriac et al. 2017; King et al. 2021; Wood et al. 2021). Management of a population into which external recruitment

does not occur acts to reduce adult density in the short term but also reduces the source of subsequent recruitment. For populations subject to external recruitment, similar management has less impact as the source of future external recruitment is not affected, so that the influx of larvae remains the same. In terms of management, the approach used for a small, isolated population in cold waters is likely to be more feasible, less costly and less intensive than the approach required to manage a substantial population experiencing frequent spawning and high levels of external larval recruitment. Such variability highlights the complexity of predicting management outcomes and that management decisions may need to be tailored to the specific spatial and temporal context, accounting for environmental variability including changes to the frequency, duration and intensity of extreme climate events.

A dynamic approach to management is required to optimise management of INNS populations. The accuracy with which the effect of management can be inferred depends on temporal and spatial understanding of the population size, the local environment, and external environmental and anthropogenic influences (Escapa et al. 2004; Hily et al. 2009). This presents a number of challenges. Firstly, intertidal species, such as *C. gigas*, may settle underwater and only be detected at low tide, reducing the ability to estimate population density accurately (McKnight and Chudleigh 2015). It also means that remaining individuals in less accessible marine spaces may be harder and more time consuming to find and remove, with implications for the successful management of populations which may require higher, though still feasible, effort to achieve desired outcomes, as demonstrated in trials conducted in the North East Kent Marine Protected Areas (McKnight and Chudleigh 2015; Morgan et al. 2021). In addition, the potential for temporal and spatial changes in spawning frequency via climate change and external larval recruitment via natural and anthropogenic pathways highlights the need for continuous review and likely refinement of the management strategy. The ecological and economic balance between the INNS, its impact and its management, also requires consideration (McAfee and Connell 2021). In particular, while negative impacts of *C. gigas* are documented, such as potential displacement of native species and habitat (Diederich et al. 2005; Ruesink et al. 2005; Smaal et al. 2005; Cogne et al. 2006), positive impacts of *C. gigas* reefs have also been presented, including their role in native species restoration (Christianen et al. 2018). Further, the influence of external recruitment on management highlights the need for its mitigation, for example, via use of triploid *C. gigas* in aquaculture (Suquet et al. 2016) or ballast water management (Patil et al. 2005), but also in the wider context of the status of neighbouring waters, with emphasis on the value of transboundary cooperation and collaboration (Wood et al. 2021). Finally, while the disparity between economic investment in management and the costs resulting from INNS needs to be addressed

(Cuthbert et al. 2021), investment in management of a particular INNS should be proportionate to the impacts caused.

Management of INNS predominantly focusses on eradication, which is rarely achievable for well-established species and in open systems such as the marine environment where organisms are not easy to detect, access or contain (Thresher and Kuris 2004; Simberloff 2020). Consequently, the perception is that marine INNS management failure is high. While examples of long-term success of maintenance management of marine INNS are not well known (Simberloff 2020) there is merit to examining the effect of maintenance management, especially for circumstances where successful achievement of management goals depends on targeted reduction in species density in a specific location, rather than its complete eradication. While indicating that management may be possible in certain circumstances, this study demonstrates opportunity beyond eradication. In particular, management and its success are focussed on the population density. It is important however that these outputs are considered more holistically, for example, in the context of potential non-target or indirect effects and with broader and more fundamental social, economic and ecological goals in mind (Prior et al. 2018). This study sheds light on factors which may impact the success of INNS management, specifically with respect to environmental and anthropogenic pressures. While focussing on *C. gigas* management, the modelling framework is broadly applicable and can be adapted to determine the feasibility of maintenance management and likely effort required for INNS in aquatic and terrestrial environments while providing much needed evidence to inform decisions around management of INNS in light of current and future pressures. However, there is urgent need for future research into INNS management in order to improve capability and capacity to tackle this ever increasing global biodiversity threat. This is particularly true for marine INNS which are consistently understudied relative to their freshwater and terrestrial counterparts (Crystal-Ornelas and Lockwood 2020) with clear biases in research towards specific phyla, topics, habitats, locations, and species (Watkins et al. 2021), limiting the accuracy with which species can be assessed and prioritised for management.

Acknowledgements

The authors thank Nicola McPherson and Paul Stebbing for their input into the initial project proposal, and the project steering group for their support throughout the project. We would like to thank the two anonymous reviewers for their constructive comments.

Funding declaration

This work was funded by DEFRA under project C7838: Pacific Oyster Population Modelling to Evidence Management.

Authors' contribution

MTA and HJT contributed to the research conceptualization and methodology. MTA simulated the model. MTA and HJT investigated and interpreted the results. HJT ensured funding provision. MTA and HJT wrote the manuscript.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. The number of years taken for the population density to decline by 90% over the management effort for 5 scenarios of management, 5 spawning frequency and 4 external recruitment levels.

Figure S2. The relative density of the adult population after 20 years, relative to its starting density, over the management effort for 5 scenarios of management frequency, 5 spawning frequency and 4 external recruitment levels.

Table S1. The Pacific oyster population model, parameters and associated assumptions extracted and adapted from Teixeira Alves et al. (2021).

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http://www.reabic.net/journals/mbi/2022/Supplements/MBI_2022_Teixeira_Tidbury_SupplementaryTable.xlsx

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