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Development of a model to categorise the invasion phases of *Magallana gigas* on the Swedish west coast

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Popular Scientific summary

The invasive Pacific oyster was introduced in the second half of the 20th century in Sweden for farming intent. When the farming projects stopped the oyster wasn’t spotted before 2007. Since, it has been spreading along the west coast. However, this invasive species has notable positive and negative ecological and commercial impact at certain densities. It is in this context of invasion that a need for a management of the population emerged. Invasive species invasion patterns have already been identified in previous literature and split into invasion phases depending on how long since the establishment and how well established the invasive species were. Those stages will be coupled to different management actions, hence the importance of knowing in which stage the invasion is locally. Moreover, the oyster invasion is irregular in Sweden, with high density in the north, to almost non-existent in the south of the west coast. This leads for a need to adapt the management to the region and to the oysters.

The scale of existing invasion models were too broad and in the case of this study, it needed to be focused on more local populations. The boundaries of the invasion phases were changed based on existing knowledge regarding the oyster’s needed conditions for survival. This led to the selection of criteria that, depending on their measured value, allowed to determine the invasion phase of a site. Put together, those criteria were organised into a decision tree which can be used rapidly and with low costs in order to get a conclusion regarding the invasion.

However, this model is still a prototype and some improvement might be needed. First there are knowledge gaps regarding oysters’ responses to different abiotic conditions. Secondly, stakeholder feedback could provide valuable insight to improve it. Thirdly, additional criteria such as level of human disturbance of the site or the substrate type might be decisive in a context of colonisation of new areas.

Abstract

Magallana gigas is a non-indigenous species in Sweden. Since 2007, it has been spreading along the west coast and can now be found in high density. However, this alien species has notable positive and negative ecological and commercial impact at certain densities. It is in this context of invasion that a need for a dynamic management of the population emerged.

The scale of existing non-indigenous species invasion models was applied to the whole range of the population habitat and in the case of this study, we decided to modify it to be applied to a local municipality level. The phases in the standard invasion models were changed into: “SURVIVAL”, “REPRODUCTION” and “ESTABLISHED HIGH/LOW DENSITY”. The boundaries of the phases were changed based on existing knowledge regarding the oyster’s needed conditions for development, reproduction and survival. This led to the selection of five criteria that, depending on their measured value, allowed to determine the invasion phase of a site. Those criteria were determined to be: “recruitment”, “reproduction”, “juvenile survival”, “population structure” and “change of population structure over time”. Put together, those criteria could be organised into a decision tree which can be used rapidly and with low costs. When tested in the field, the model proved its capacity to discriminate sites between different invasion stages, as well as its efficiency.

However, this model is still a prototype and some improvement will certainly be needed. First, there are knowledge gaps regarding salinity impacts on oyster development and on local adaptation patterns to the abiotic conditions. Second, stakeholder feedback could provide valuable insight to improve it and make it more directly useful in management. Thirdly, some other criteria might be decisive in a context of colonisation of new areas, so care should be taken if applying this model in other areas than the Kattegat-Skagerrak area.

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Introduction

Magallana gigas (hereafter: oyster, Pacific oyster, *M.gigas*) is an invasive species introduced in Europe through shellfish aquaculture in the middle of the 20th century (Miossec et al, 2009). The first introduction of this bivalve in Sweden goes back to 1973 for farming attempt purposes in the vicinity of Tjärnö (Eklund et al, 1977). During those attempts, the oyster survived and grew but they did not reproduce, and there were no reports of spread after the farming attempts were discontinued. However, in 2007, the public reported observations of Pacific oysters in the same area (Laugen et al., 2015). Today, the species is well established in the Skagerrak and some have been found in Kattegat (Laugen et al., 2015). With densities of more than 50 (up to 144) oysters per square meter at some locations near Koster Havet National park and 0.2 oyster per square meter around Copenhagen (Mortensen et al, 2022).

Once introduced and passed the abiotic filter (surviving the environment condition of the new habitat), the invasion pattern of a non-indigenous species (NIS) can be divided into three different stages, depending on the impact and ecological effects (Figure 1): Lag time, expansion and persistence (Geburzi & McCarthy, 2018). The lag time, right after the introduction of the invasive species by different vectors, is the slow settling phase. The low number of individuals makes the growth of the population slow. The expansion correspond to a sharp rise in area colonized as well as invader abundance. Those number rise up until the persistence phase, where the full extent of the ecological niche is colonized and only seasonal variation in individual number can be observed.

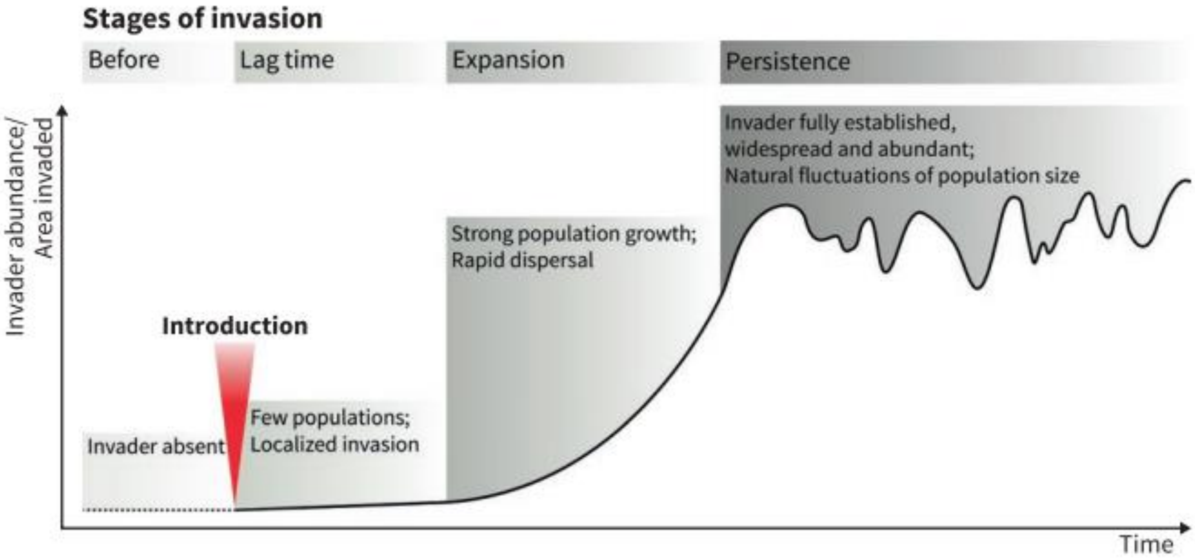

Figure 1 Stages of invasion of a NIS. Credit: Geburzi & McCarthy, 2018.

Being an intertidal invasive species, *M. gigas* is versatile and can adapt to a wide range of conditions. Adults can survive sub-zero temperatures for more than a day and up to 30 degrees for 4 weeks (Le Gall et al. 1988; Strand et al. 2011). The pacific oyster is likely to have multiple impacts, both negative and positive, on local ecosystems. For example, introduction of oyster are linked to increases of local native species populations, which could also include disease inducing organisms. Moreover, the reefs create habitats for other species but have an impact in local hydrodynamic which changes sediment deposition (Ruesink et al. 2005). *M. gigas* is currently limited in the south by the steep salinity gradient in the Öresund area and is predicted to not be able to colonize the Baltic by the year 2100 (Laugen et al. 2015). However, current models of the invasion do not take into account potential adaptation to low salinity along the invasion front (Laugen et al, 2015). These evolutionary probabilities are yet to be measured and studied.

In Sweden, the species is used in a wide array of situations (Mortensen et al. 2019). The oyster is harvested on private stretches of coasts, some also use it as a tourist attraction (oyster safaris). The Swedish oyster production with 2 tons in 2020 (FAO fisheries and aquaculture statistics) is still far from the biggest European producers such as France, which produced 79 500 tons or Ireland with 9 242 tons in 2020 (FAO fisheries and aquaculture statistics). This is mainly due to the fact that farming *M. gigas* is not authorized due to the species status as invasive in Sweden. It is, however, still a source of employment and income through wild harvesting, sales and gastronomic tourism. The latest aspect illustrating the potential for innovation in business models (Mortensen et al. 2019). Moreover, this species falls into the "oyster" (in Swedish "ostron") category in the Swedish fishery law with no differentiation made between invasive and native species (Fiskelag (1993:787)). This makes *M. gigas* a private commodity and thus the property of the land owner, limiting its exploitation by the general public. Furthermore, professionals aiming at exploiting oysters for commercial interest need a permit and the authorization of the land owner if the oysters are collected less than 200 m away from the coast (Fiskelag (1993:787)), which is most often the case.

While it is important to fight the invasion, the species constitute a resource of commercial and ecological value (Mortensen et al. 2019). This leads to the need to develop management models where commercial interests can be combined with management activities. In order to manage the species efficiently, an exhaustive survey of the current phases of the invasion along the Swedish coast, needs to be done. Each invasion phases calls for different types of management. Which can be adapted to different areas, to balance the negative ecological impacts against the use of this new resource.

Basing the management of the invasive species on real time data in order to steer the commercial and ecological interests has been described as "Dynamic management" (Lewison et al. 2015). The use of the invasion stages as a framework for future decisions can allow for individual adaptation of management plans based on the evolution of local conditions. Today, the different invasion phases are known, however, the boundaries and criteria that differentiate one phase from the other are not precisely drawn. It is apparent that in Sweden, populations of oyster are at different development stages, but those phases are not properly defined which leads to an inefficient management effort. This is what this thesis aims for, to develop a model that would define precisely the invasion stages of *M. gigas* and their boundaries. This is a needed preliminary step that will potentially guide future dynamic management efforts. By doing this, knowledge gaps and future needs for research can be identified.

Aim

The aim of this thesis is to define criteria to assess the stage of the invasion of *M. gigas* based on ecological data, and to structure the criteria into a model. This model will be a way to classify invasion phases along the coastline, which then can be linked to specific management objectives. Development of management strategies is, however, outside of the scope of this thesis.

Method

Method Literature review

The first part of this study was conducted as a literature review. In order to develop a model and to select criteria, papers were gathered online, using the web site “Web of science”, accessed as a student of the University of Gothenburg, and Google Scholar. Some papers were also found using the references in the papers found with the method described above and some were already cited in the official presentation of the DynamO project. Some papers were also included after personal conversations with the supervisory team. Public Swedish law texts were also used. The papers were selected or rejected based on their abstract and figures.

Only peer-reviewed papers were selected for inclusion in the study. This is the reason why Web of Science was preferred over the other mentioned browsers, since it is possible to filter the search hits to show only peer-reviewed ones. However, Google Scholar was also used using the library of Gothenburg University and Lane Community College, allowing to identify peer-reviewed article among the other papers.

The online databases was searched using key words such as: “pacific oyster” “growth rate” “temperature” “juveniles” “Magallana gigas” “Crassotrea gigas” “alien species” “invasive species” “invasion phases”, “Sweden”, “Kattegat”, “age”, “size”, “shell”. Combinations of those key words were used using the function “AND”.

The literature was searched in both French and in English, therefore, the key words were used in both languages: “Huitre du Pacific”, “espèces invasives”, “Suède”, “gestion”, “juvénile”, “température”, “taille”, “coquille”.

In total 29 documents were used for this study.

Then, for the models development, existing literature (Blackburn et al, 2011; Geburzi & McCarthy, 2018), was used. The base model is the one from Geburzi & McCarthy (2018) then, inspired by the Blackburn et al (2011) model, which was taking a more local approach, the different invasion phases of the model were renamed. They also had to be precisely split, with no overlap, and Blackburn’s work allowed to emphasize important criteria. Those criteria were then organized by order of relevance regarding the phases and regarding their cost to measure. Once the relevant criteria were identified, a decision model had to be created. If first, a point system was developed, but it was arbitrary, in the end it is the organisation tree that was selected.

Method fieldwork

In order to improve the model and identify potential issues, a part of the thesis goal was to test it using field data. Here, the goal was not to survey objectively the whole west coast but to test the model for a future extensive survey. In order to do so, six sites were selected. The aim when selecting sites was to overlook the different local situations representing the invasion stages that might be encountered along the Swedish west coast. The sites were therefore spread along the invasion gradient. There were between 67 and 116 km of coast between each of the main sites (4), and 2 additional sites were chosen a few hundred meters away from the main sites. This was done to test the scope of the model. The sites had known presence of oysters from a previous surveying campaign.

Even though each site was different, a common protocol was followed regarding data collection. Once a site had been reached, the stretch of shore was selected by visually assessing the presence of oyster. Then, depending on the density of the population, either a quadrat survey or an exhaustive survey was conducted. In high density populations, quadrats were used until the number of oysters measured reached approximately one hundred. At sites with a lower oyster density, all oysters were measured up to a hundred individuals. In the case where fewer oysters where found, all oysters found were measured. All surveys, except at site 6, were done at a depth of 0 to 30 cm from the water level at the survey date, which was accessible by wading. The survey at site 6 was part of the sampling campaign of another project, and was thus done with a boat and snorkelling equipment. All visible oysters were collected, with an objective of approximately a hundred total. They were then measured in the context of this study. There was no size requirement for oyster collection so it is here assumed that the size distribution of the collected oysters were representative of the population.

The oyster length (mm) was measured from the umbo to the furthest side using a calliper. The measurements were then compiled in a histogram comparing the size distributions of the studied populations. If the population included individuals measuring up to 25 mm, which can be considered individuals that are less than a year old (Cardoso et al, 2007), then the “recruitment” criterion is considered positive for that population.

Moreover, the site coordinates, the type of substrate, the level of human disturbance as well as the population structure were noted.

According to the model, depending on the result of the fieldwork more data were collected. If the “recruitment” criterion was positive (see below), then temperature data from the past year’s 2 warmest week and salinity during this period, as well as the coldest month were gathered from the marine station databases.

The northernmost site (Site 1) (Figure 2) is in a sound between the islands of Tjärnö and Saltö in the municipality of Strömstad. It stretches from 58°52'27.1"N 11°08'46.4"E to 58°52'26.6"N 11°08'47.0"E with a parking and an artificial shore to the east side and a salt marsh to the west. The length of 102 oysters were measured in a succession of 4 randomly placed quadrats of one square meter each.

The second, from 58°16'53.6"N 11°25'50.3"E to 58°16'53.6"N 11°25'49.7"E, and third sites, from 58°16'57.2"N 11°25'49.4"E to 58°16'57.5"N 11°25'49.0"E, are located on the North West coast of the municipality of Lysekil.
The second site **(Site 2)** (Figure 2), is composed of rocks and boulders near an artificial concrete slab. The site is near a beach and a walkable path (Ålevik). The length of 96 oysters were measured in a succession of 5 randomly picked quadrats of a square meter.
On the third site **(Site 3)** (Figure 2) the oysters were attached on the exposed bedrock. Because the number of individuals was low, the length of all the oysters were measured.

The fourth and fifth sites were situated in Västra Hagen, which is part of the Kungsbacka municipality.
The fourth site **(Site 4)** (figure 2) is on the eastern side of a peninsula going from 57°25'44.6"N 11°55'09.9"E to 57°25'44.4"N 11°55'08.4"E. The site is mostly composed of

loose rocks and bedrock and show a lot of macroalgae growth. The presence of piers and cinder blocks in the water make for a slightly anthropogenically modified site. It is near a walkable path and a bathing location (Smarholmens Badplats). Because of the low number of individuals, all visible oysters (47) of the site were measured

The fifth site **(Site 5)** (figure 2) is in a bay, from 57°25'22.2"N 11°55'31.8"E to 57°25'20.1"N 11°55'32.8"E, surrounded by a residential neighbourhood. It is composed of sand and loose rock and presence of a large amount of macroalgae. The oysters were only growing on the rocks and because of their small density, all visible individuals (23) were measured.

The sixth site **(Site 6)** (Figure 2) is in a bay of the island of Hallands Väderö from 56°26'36.8"N 12°34'08.1"E to 56°26'39.8"N 12°34'11.0"E. The site is part of a natural reserve and show a sandy bottom with patches of gravel. Here, the oysters were collected regardless of their sizes during a sampling campaign and then measured in the lab. In total, 117 oysters were measured.

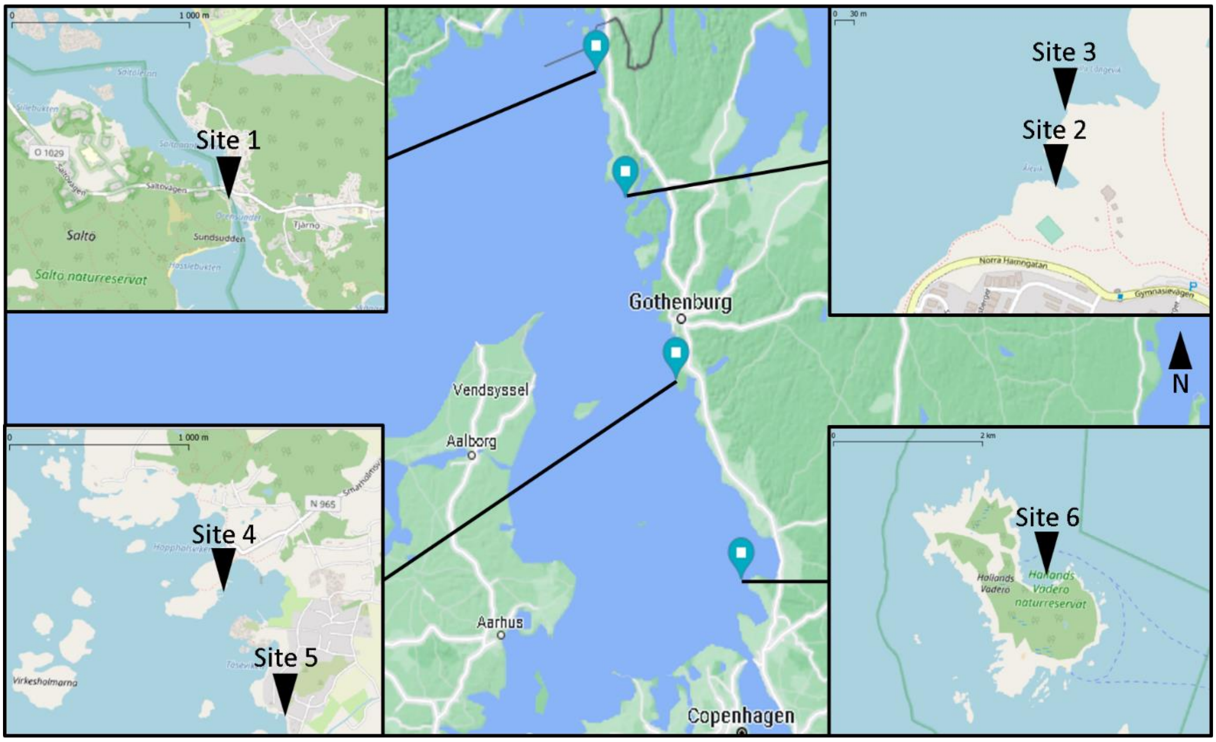

Figure 2 Map of the sites. Map credit: OSM and Google map

Result

Oysters criteria and creation of the model

For this study, two figures representing the invasion process were used. The first one (Figure 1) from Geburzi & McCarthy, 2018, describes the invasion of a species on a large scale, taking account the whole invasion range. The second one (Appendix 1) from Blackburn et al, 2011, is more focus on one population among the whole invasion range. This model is also completed with the steps that the population has to go through in order to get to the next invasion phase. In the context of this study, the first model was adapted to a specific population of the invasion range using the tools of the second one (Figure 3). The name of the invasion phases and as well as their specificities were modified in order to fit a population specific scale.

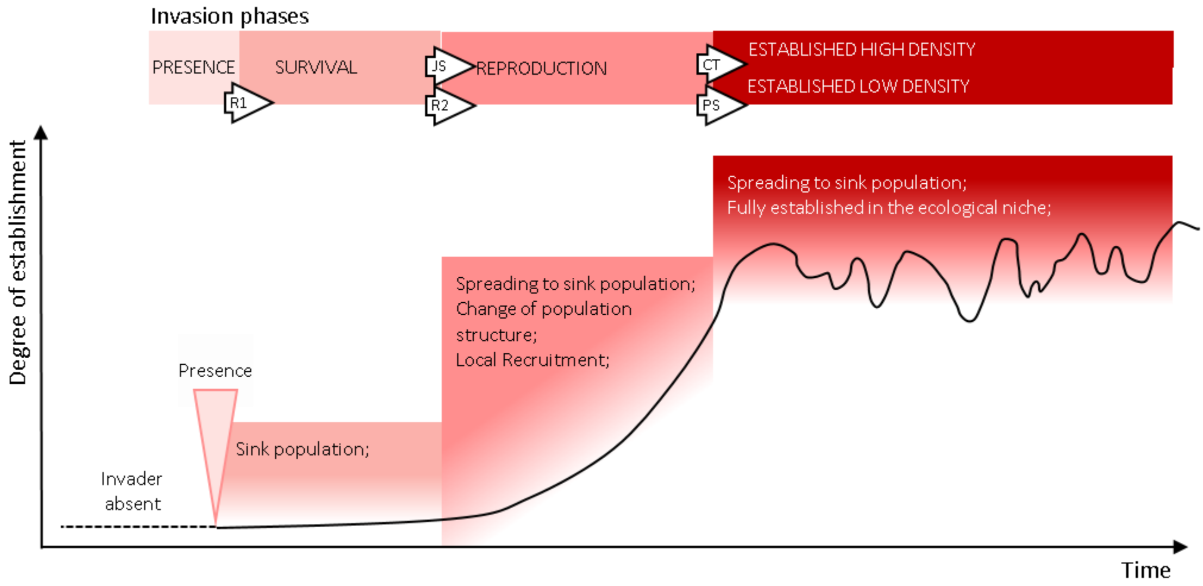

Figure 3 Invasion phases curve. R1: Recruitment (foreign and local recruitment); JS: Juvenile Survival; R2: Reproduction (local recruitment); PS: Population structure; CT: Change of population structure over Time. Personal adaptation inspired by figure 3 of Geburzi & McCarthy, 2018.

The invasion was split into five phases: "Presence", "Survival", "Reproduction", "Established high density" and "Established Low density". Each of those phases represent a set of specific population patterns that can be found along the Swedish west coast.

In order to identify the transition from one invasion phase to the other, precise population and abiotic criteria have to be assessed. The objective of those criteria is to represent key life stages and/or impact on population structure. Based on the literature study, information regarding *M. gigas* that had a link with quantifying the different invasion pattern was gathered. In the beginning eleven criteria were selected based on Blackburn et al, 2011 model. The goal was to be able to assess the health of the population locally, where the recruit were coming from, the reproduction and fertilisation conditions, the density of the population, the spreading capacity of the population, the sediment composition, the percentage of time with surface ice, the conditions for the larvae as well as the local abiotic conditions.

However, in an objective of making this model as widely applicable as possible, those criteria had to be assessed rapidly and with as low costs as possible. In order to reduce costs, reducing field work time and complexity, relying as little as possible on laboratory work such as genetic or virology or using data that was widely measured and available was essential.

In total, five criteria were selected (Figure 3). Out of those, three of them were based on field data. The other two can be assessed from already modelled abiotic data broadly available in databases. The first field-measured criterion, “Recruitment” (R1), make the separation between the “PRESENCE” and the “SURVIVAL” invasion phase. Then the two abiotic criteria, “Reproduction” (R2) and “Juvenile survival” (JS) are between the “SURVIVAL” and “REPRODUCTION” invasion phase. Lastly “Population structure” (PS) and “Change of population structure over time” (CT) make the link between the “REPRODUCTION” and the “ESTABLISHED HIGH/LOW DENSITY” invasion phases. The selected criteria are described in more detail below:

-**Recruitment**: This is the ability of the local population to be replenished by new individuals. For *Magallana gigas*, being a sessile organism, the only way to recruit juveniles in a local population is through local reproduction and/or larval drift from other locations during the planktonic phase. This criterion is decisive in the model since it assesses if there is a source for new individuals. It can also indicate the habitat suitability of a population locally. If no recruitment is observed for an entire generation, physio-chemical criteria can be the cause of it. In the case of this study, recruitment was measured through the distribution of different shell lengths in the population.

-**Reproduction**: This is the ability of the population to be self-sufficient regarding recruitment. Absence of reproduction at the same time as a positive recruitment criterion is also a sign that the studied population is the sink of another source population. The ability to reproduce locally is dependent on physio-chemical parameters. Below 16 °C during the mating season, the reproduction does not occur (Ruiz et al, 1992). Salinity also has an impact on reproduction, with no known reproduction occurring below 13 PSU (Kinnby & Havenhand personal communication). If the conditions for local reproduction exist, it is more likely that the population may expand and spread. The measurement of the average surface water temperature and salinity during the two warmest weeks were here used as a proxy to define the possibility of reproduction.

-**Juvenile survival**: This is the ability for the spat to survive the first winter settled on benthic substrates. If the spat cannot survive or attach themselves to the substrate, then recruitment will be negative even if the population is in the range of a source and/or is able to reproduce locally. Below 3°C during the coldest month, the spat a very low chance of survival and will most likely not replenish the local stock (Child and Laing, 2008). Therefore, this temperature threshold was used here to define the possibility of juvenile survival.

-**Population structure**: This criterion was based on how the population is distributed in the wild. 3 types of oyster density have been identified for this study. The densest of them is the “Reef”. In a reef structure, the oysters are growing on top of each other in a dense carpet, often sheltering other species (Ruesink et al, 2005). The least dense structure is “solitary”, where oysters grow in isolated parts of the substrate and they do not touch each other. The intermediate is a “mix of cluster and solitary”, where some oysters are isolated but they also use each other as a substrate, forming clusters of two or more.

-Change of population structure over time: The abovementioned population structures could represent the full occupation of the local niche but they can also change in density over time, or because of events such as viral infections (Mortensen et al, 2016) or sea ice (Strand et al, 2012). Monitoring in time is then necessary to assess this change. Different structures call for different management and a changing population density might make management outdated by the time it can be implemented.

For the creation of the model, directions and decisions were taken by the author and discussed with the supervisor team. It was developed in an iterative way. The previous versions will not be described but can be mentioned in the text to justify changes of direction.

The model is a decision tree based on the different criteria and phases described previously. Each tests (in yellow) and binary tests (in green) calls for new measurements (in blue) and allow for a more precise conclusion (in shades of red). The model can be split into two parts. The first can be used to achieve a quick evaluation of a zone without reproduction. The second one delves more in detail and demands longer monitoring.

The full model can be found in Appendix 2, only parts of it will be discussed here.

The first test of the model is the “presence” or the “absence” of live oysters on the shore. The idea is to be able to monitor stretches of coast without requiring a previous survey of the zone. In the case of an absence of oysters (Figure 4), temperature and salinity of the place have to be assessed. In the case of favourable physio-chemical conditions for reproduction and juvenile survival, the model calls for monitoring of the zone to manage potential future settlement. When those conditions are, however, not suitable, then it is unlikely to have future settlement.

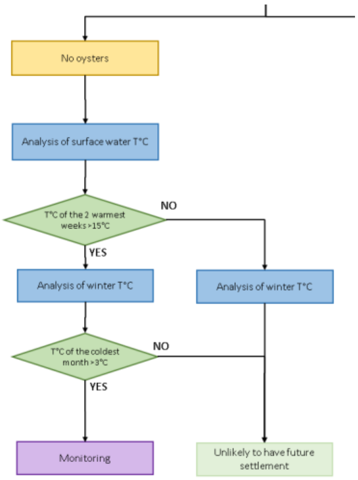

Figure 4 No oyster pathway

If there are live oysters at a site then the model becomes more precise (Figure 5). The objective of the next test is to assess the possibilities of recruitment. In order to do so, the length of the oysters have to be measured and is used as a proxy for recruitment (Cardoso et al, 2007). In the case of a negative answer to the recruitment test, the zone is categorized as a “PRESENCE”. A lack of recruitment means the population will grow slowly and regenerate slowly when severely impacted by local variation of conditions.

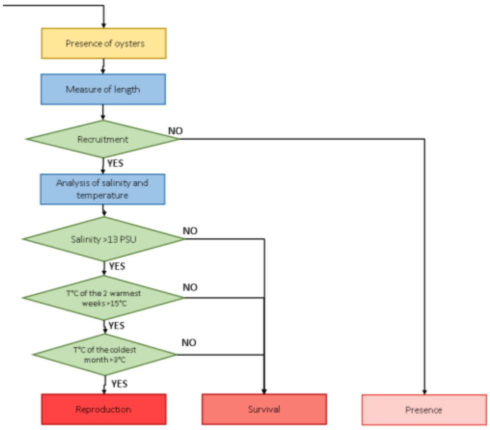

Figure 5 Presence of oyster pathway

In the case of a positive recruitment, tests to assess reproduction and juvenile survival have to be conducted (Figure 5). As described previously, those tests use temperature and salinity as a proxy. This part of the model is a succession of three test that have to all be positive in order to get to the next phase. If one of them are negative, the zone gets categorized as “SURVIVAL”. This is most likely a sink site and the recruitment is obtained from a source population. Those three test are performed subsequently because they are considered interconnected. The salinity and temperature during the warmest weeks correspond to the reproduction period and are thus necessary for recruitment. Moreover, the temperature of the coldest month reflects the juvenile survival in their early stages of life. In the case where all of those test are positive, the zone gets categorized as “REPRODUCTION”.

This marks the transition between the first part of the model and the second part. Past that step, the conclusion is that the oysters spawn new larvae that will contribute to local recruitment and sustain the current population at that specific site. Moreover, at this point, the population is most likely a source population and is spreading offspring to other populations.

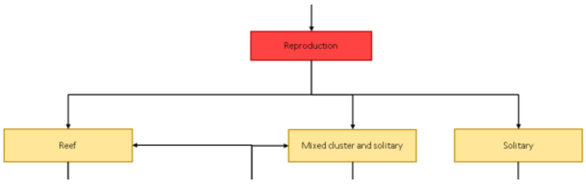

Figure 6 Population structure’s test

In the initial stage of the second part of the model, the structure of the population is in focus (Figure 6). The goal with this test is to make sure that the surveyed population is filling its local ecological niche. In the case of this study, “Solitary” (Figure 7) refers to single oysters with no traces of growth on top of each other. “Mixed cluster and solitary” (Figure 7) refers to oyster growing on top of each other and sharing substrate. “Reef” is a dense carpet of oysters with patches where it is not possible to see the substrate beneath them.

Figure 7 Population structure. From left to right: Solitary, Mixed cluster and solitary and Reef. Personal gallery.

In a high density/reef formation situation, the conclusion is straight forward, with the model concluding that the population is in “ESTABLISHED HIGH DENSITY” (Figure 8). This shortcut is made to facilitate the conclusion in extreme cases. There is, however, a possibility that a thriving reef can collapse because of sea ice or pathogens. In that case, the reef is categorized as a “dead reef” (Figure 8). Monitoring the population changes is necessary, in the model, this is represented by “recolonization” which is similar to “recruitment” and “local recruitment” which is similar to the physio-chemical test discussed above.

In the case of a lower density population structure such as “solitary” and “mixed cluster and solitary”, monitoring in time is necessary (Figure 8). This has to be done to assess if the surveyed population is currently occupying the integrity of the ecological niche or not. This is done to optimise the management effort and tailor it as precisely as possible for the site. If there is a change of the population structure, then the model loops back until it doesn't change anymore. However, if the population structure don't change over time then it is assumed that the population is fully occupying its ecological niche and is categorised as "ESTABLISHED LOW DENSITY" (Figure 8).

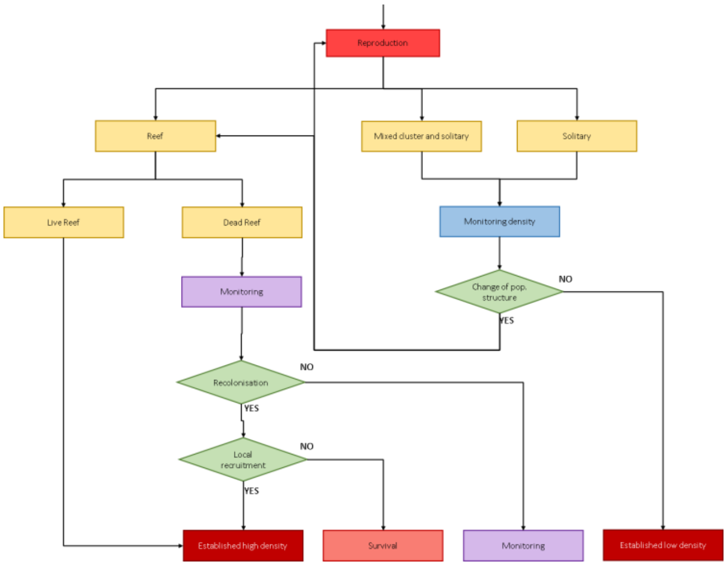

Figure 8 Reproduction and population structure loop pathway

Results of the model on the field

The model was applied to six different sites along the west coast of Sweden (Figure 2). Criteria for phase selection for the different sites are summarised in Table 1.

Table 1 Summary table of the field test

	Oyster	Min size (mm)	Max size (mm)	Average size (mm)	Recruitment	Salinity	T°C Win.	T°C Sum.	Pop.Structure	Result
Site 1	102	7	144	57	Yes	24	6.2	19	Reef	EST. HIGH DENS.
Site 2	96	20	130	60	Yes	26	6.4	19	Mixed	REPRODUCTION
Site 3	19	37	106	66	No					PRESENCE
Site 4	47	37	89	62.5	No					PRESENCE
Site 5	23	28	81	58.7	No					PRESENCE
Site 6	117	42	107	68.2	No					PRESENCE

Site 1 holds a high density of oysters that grow on a reef like structure on sandy sediment (sand and gravel). The measured lengths ranged from 7 to 144 mm. The lengths were then compiled in a histogram (Figure 9). For this site, the average temperature in °C of the two warmest weeks of the past year is 19 (Tjärnö Labbvatten). The average salinity of the warmest weeks is 24 PSU (Tjärnö Labbvatten). The average temperature in °C of the coldest month is 6.2 (Tjärnö Labbvatten).

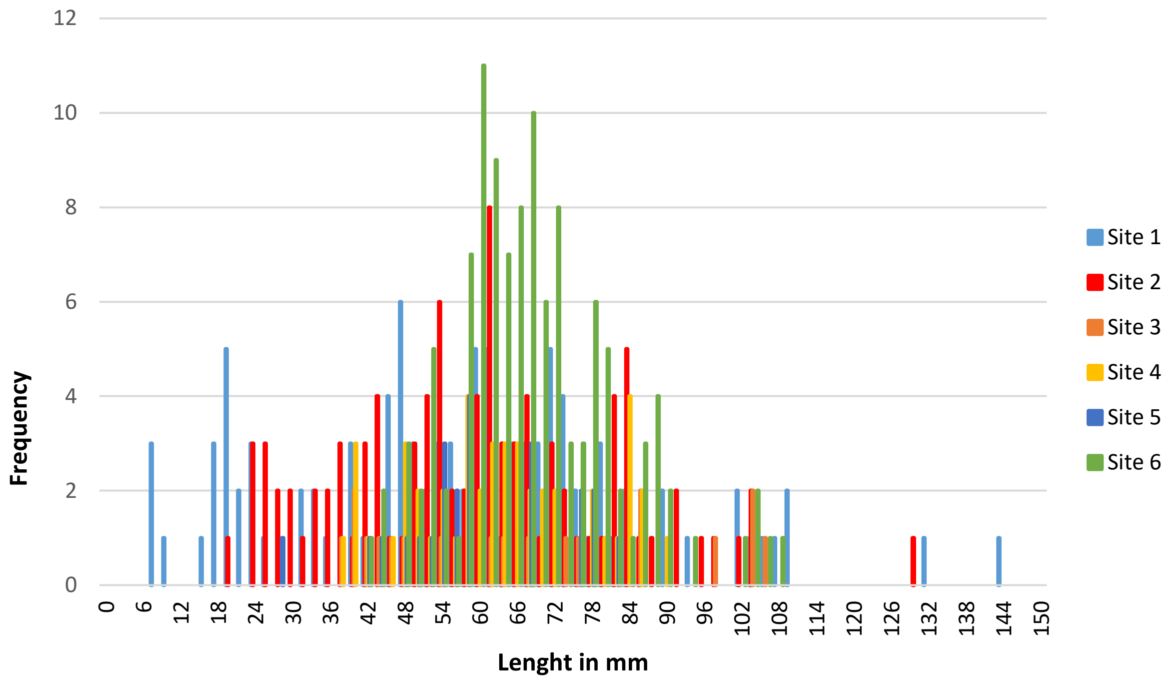

Figure 9: Size distribution of all six sites.

Based on the different criteria, this site can be classified according to the model. The recruitment histogram (Figure 9) shows a distribution of sizes that can be interpreted as a positive recruitment, thus, the answer to the “recruitment” test is positive. The physio-chemical criteria (temperature and salinity) of the past year are favourable for both reproduction and juvenile survival. According to the model, the oyster population in this place is then at least in the reproduction phase. Furthermore, the population structure is a reef, which means that according to the model, this site is in the "ESTABLISHED HIGH DENSITY" phase.

Site 2 oyster's lengths ranged from 20 to 130 mm. The lengths were then compiled in a histogram (Figure 9). For this site, the average temperature in °C of the two warmest weeks of the past year is 19 (Kristineberg marina). The average salinity of the warmest weeks is 26 PSU (Kristineberg marina). The average temperature in °C of the coldest month is 6.4(Kristineberg marina). The oyster population structure is a mix of cluster and solitary individuals.

On site 3, 19 oysters were measured with lengths going from 37 to 106 mm. Those length were then compiled in a histogram (Figure 9).

Based on the different criteria, the sites can be classified according to the model. The recruitment histogram of site 2 (figure 9) shows a size distribution that can be interpreted as a positive recruitment. Thus, the first test of the model is passed. However, the histogram of site 3 (figure 9) shows a distribution of sizes that cannot be interpreted as a positive recruitment, with a lack of smaller sized oysters. The abiotic criteria of the past year are favourable for reproduction and for larval survival. According to the model, the oyster population on site 2 is in the "REPRODUCTION" phase, while site 3 is in the "PRESENCE" phase. As mentioned previously, the area surveyed is characterised by the most advanced phase, hereby in this case "REPRODUCTION". And the model call for a monitoring of the zone to be able to assess any change in the population structure.

On Site 4, the oyster's length ranged from 37 to 89 mm. Those lengths were then compiled in a histogram (Figure 9).
Site 5 oyster's length ranged from 28 to 81 mm. Those length were then compiled in a histogram (Figure 9).

The recruitment histogram of site 4 and 5 (figure 9) shows a distribution of sizes that cannot be interpreted as a positive recruitment, with an absence of lower than 25mm oysters. Thus, it didn't pass the recruitment test. The physio-chemical criteria (temperature and salinity) are as a consequence unnecessary to measure, since it is already possible to draft a conclusion because of the absence of recruitment. According to the model, the oyster population on site 4 and 5 are in the "PRESENCE" phase.

On site 6, oyster's length ranged from 42 to 107 mm. Those lengths were then compiled in a histogram (figure 9).

The recruitment histogram of site 6 (figure 9) shows a distribution of sizes that cannot be interpreted as a positive recruitment, with a lack of smaller sized oysters. Thus, it didn't pass the first test of the model. According to the model, the oyster population on site 6 is in the "PRESENCE" phase.

Discussion

This paper positions itself as a joined management and ecology study of an NIS that represent an economic interest. A similar case, the management of the red king crab (*Paralithodes camtschaticus)* in northern Norway delved on the same problematics decades prior (Sundet et al, 2016). One of those problematics is the lack of control on the source from where the invasion spreads. Russian management of a sustainable fishery rather than eradication negates all potential Norwegian effort towards eradication, with recruitment coming from the east (Sundet et al, 2016). In comparison, the Pacific oyster larvae in Sweden are likely to come from the settled populations in Denmark (Laugen et al, 2015; Faust et al, 2017), and it has been concluded that the species will not be exterminated as a consequence of natural events (i.e. winter mortality or pathogen outbreaks (Mortensen et al, 2016; Strand et al, 2012)The way the red king crab invasion was dealt with in Norway, was by monitoring the stocks extensively, which led to the development of a fishery which fitted in the international agreement of control of the NIS (Sundet et al, 2016). West of 26 °E, yearly surveys are conducted which lead to quotas being implemented. This allows for a dynamic management of the resource and an "on-and-off fishery" (Sundet et al, 2016). The pacific oyster in Sweden is still in the early stages of management. A call for a monitoring plan and the development of research with the objective to create a management project was made in 2015 (Laugen et al, 2015). In order to get an overview on the invasion of the pacific oyster, with the objective to determine suitable management targets, the species invasion phases and their boundaries need to be identified. In this paper, criteria for easy assessment and a model for classification of the invasion stages were developed.

The first task was to define the scale of the study and define whether the model would be relevant to the whole country, regions, municipalities or individual sites. With the model being aimed at the people taking decisions regarding conservations, such as NGO and County administration boards, the municipality scale was chosen. County administration boards are expected to be local enough to understand the importance of managing the invasive species locally while having enough assets to actually act. This is a difference with the Norwegian red king crab, whose management was a national effort (Sundet et al, 2016).

As part of the development of the model, using field data allowed an evaluation of it. Its main strength is the speed of the assessment. In under an hour, a team of two students, familiar with the species, could survey enough oyster to answer the tests. In order to accelerate data collection for criteria evaluation, the model was paired with data from previous survey campaigns. However, this was done with the objective of testing the model. In its intended use, even oyster-less sites could be potentially surveyed, with no previous mention of invasion. Nonetheless, this permitted to draw a conclusion on the phases of the invasion rapidly, allowing for multiple surveys during a day and in the end, reducing the costs. The choice of using the worst invasion phase to make a conclusion for a bigger area (here, a municipality) allows the surveyor to omit less dense sites, which would reduce the time spent in the field. It is important when selecting site boundaries to select the highest density area and locate patches with recruitment (if present). The conclusion from the model evaluation is that sampling does not need to be randomised, as the most developed invasion phase will determine the invasion stage of the whole area.

There are ways the models could be improved. The choice of sites is important especially in sites with an early invasion stages. In this study, five of the six sites selected as test sites were easily accessible with a nearby road. They were also shallow, allowing access by foot for the sake of convenience and time. Site 6 illustrates that at less accessible sites, a larger effort and budget might be needed. The site was known for the presence of oysters, but they were found as deep as 3 m under water, which called for previous monitoring efforts and would never have been observed from the shore. This shows that the surveying could be done in two steps. First, survey the easy-to-access sites. If any of them show signs of a late invasion stage there is no need to progress to more sites. Secondly, if easily accessible sites do not show signs of late invasion stages, put more effort into the identified “PRESENCE” sites.

Moreover, even though the sampling team was composed of experienced snorkelers, the depth might have made spotting smaller oyster difficult, potentially biasing the distribution toward larger oysters. In a 1990 study, by K. Y. Arakawa, spat collectors made out of scallop shells treated with extract of oyster meat were deployed and allowed to assess recruitment. In the case of this study, plastic coupelles used in oyster aquaculture can work. This type of collector could provide a solution if deployed in deeper or less accessible sites in key places from mid-July to the 30th of august, which covers the main settlement period (personal communication, Å. Strand; Diederich, 2005), followed by an assessment of colonisation. This solution renders the model less efficient in time, but allows for spending less time on the field in offshore sites.

The level of human disturbance and urbanisation can also be a problem, since it is not being taken into account in the model as it is currently constructed. A highly urbanised environment advantage colonising species (Cadotte et al, 2017). Moreover, artificial substrate such as piers, jetties and dykes are all substrates that allow NIS to colonize habitats (Dafforn et al, 2012; Lam et al, 2009). In the case of *M. gigas*, artificial substrates tend to support more and bigger oysters (Stagličić et al, 2020). And thus, by identifying those substrate, a different path of management could be adopted. The model could benefit of an “identification of substrate” step, which play a role in oyster settlement and thus could drive the management effort accordingly.

As it is currently built, the model’s criteria are based on proxies in order to draw conclusions on various invasion stages and development of the oyster populations. It has been shown that temperature alone is not responsible for the survival of juveniles. In fact, the abundance of food might also be decisive (Cardoso et al, 2007). However, the Kattegat and Skagerrak areas are eutrophicated and have been quantified as “high opportunity location for shellfish […] aquaculture” (Theuerkauf et al, 2019), proving the possibility of aquaculture and by extension, showing that a lack of food is unlikely to limit oyster growth.

With the aim of keeping the cost associated to the assessment of invasion phases low, some more expensive data might be skipped over. The identification of source population and their genetic correlation with the sink population could be a more precise way of assessing the recruitment (Faust et al, 2018). Consequently, this would allow for a more efficient management by focusing on the most active sources. However, Swedish pacific oysters appear to have few genetic differences from the Danish ones in sample sites north of Gothenburg (Faust et al, 2017). More precise genetic identification methods must be developed with samples from colonised areas south of Gothenburg. One potential identification method could focus on genetic adaptations of local individuals to lower salinity conditions, on the most southern part of the west coast of Sweden. It has been demonstrated that by their euryhaline nature, some Pacific oysters have genetic adaptations to low salinity (She et al, 2018). This adaptation could lead to the selection of certain individuals over others (She et al, 2018) and the identification of a more hyposalinity-resistant population.

This model was also submitted to the expertise of a group of actors, NGO's and county administration board's member in order to get their input on the project and how it could fit in their management plan of the invasive species. Unfortunately, although the model could have benefited from those input, it was not possible to get a precise answer. However, the process will continue after this thesis and the model will be tested and evaluated more thoroughly in forthcoming studies.

The model, as it is designed right now is specifically tailored for the Pacific oyster in Sweden. However, there are situations where it could be modified to fit other species characteristics. For example, the invasive *Ensis directus*, is another introduced bivalve in Sweden (IS compendium, CABI). With a change in the abiotic criterion to pass the reproduction tests, as well as the population structure to fit with *E. directus* characteristics then it could possibly be used. The adaptation to another type of invasion could also raise issues that were unnoticed before and it could be a way to improve the existing model.

This model can only be used to classify a stretch of shore depending on the local state of the invasion. Management and future decisions fall outside the scope of the thesis, as this is a preliminary step. However, this is the groundwork for defining management targets linked with each phases whether it is the eradication of the NIS, the mitigation of the invasion or its controlled exploitation (Larson et al, 2011). An exhaustive survey like this could, for example, steer decision makers to invest in a fishery like in the Norway's red king crab case (Sundet et al, 2016) on "ESTABLISHED HIGH DENSITY" sites. "ESTABLISHED LOW DENSITY" sites could be dealt with by allowing the public to pick the oysters, after a modification of the law mentioned earlier. "REPRODUCTION" and "SURVIVAL" sites could undergo early eradication program, which would slow down settlement by taking away existing shells and thus, settlement substrate for larvae (K. Y. Arakawa, 1990). "PRESENCE", could be managed with yearly monitoring, to assess evolution of the density.

Conclusion

This study was sparked from a need to categorise the invasion phases of the Pacific oyster on the Swedish west coast in order to manage this resource. Existing invasion models were on a different scale of study and they had to be adjusted to fit the local conditions. This led to the development of an exclusive invasion model built on the existing knowledge available on *M. gigas*. With the creation of phases and criteria, this study allowed to categorise the different densities and population structures found in Sweden.

When taken out on the field, the model (and by extension the decision tree that allow to place sites on the model), fulfilled its objectives of being cheap and fast. However, it showed some flaws, such as knowledge gaps, which could hopefully be resolved in the future. Moreover, the model being a preliminary work that would, ultimately, fit in a bigger management process, future connected projects could shine a light on ways to improve it. For instance, the models could become more specific, with more phases, as ecological knowledge increases. This would then make the management answer more effective.

Overall, this study showed that existing invasion models can be adapted and be used together to fit specifically to a species and a region. As a result, the decision tree and invasion model of this thesis are functional in their current state, but could use some testing and feedback from future actors.

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ANNEX 1: Blackburn et al, 2012 model

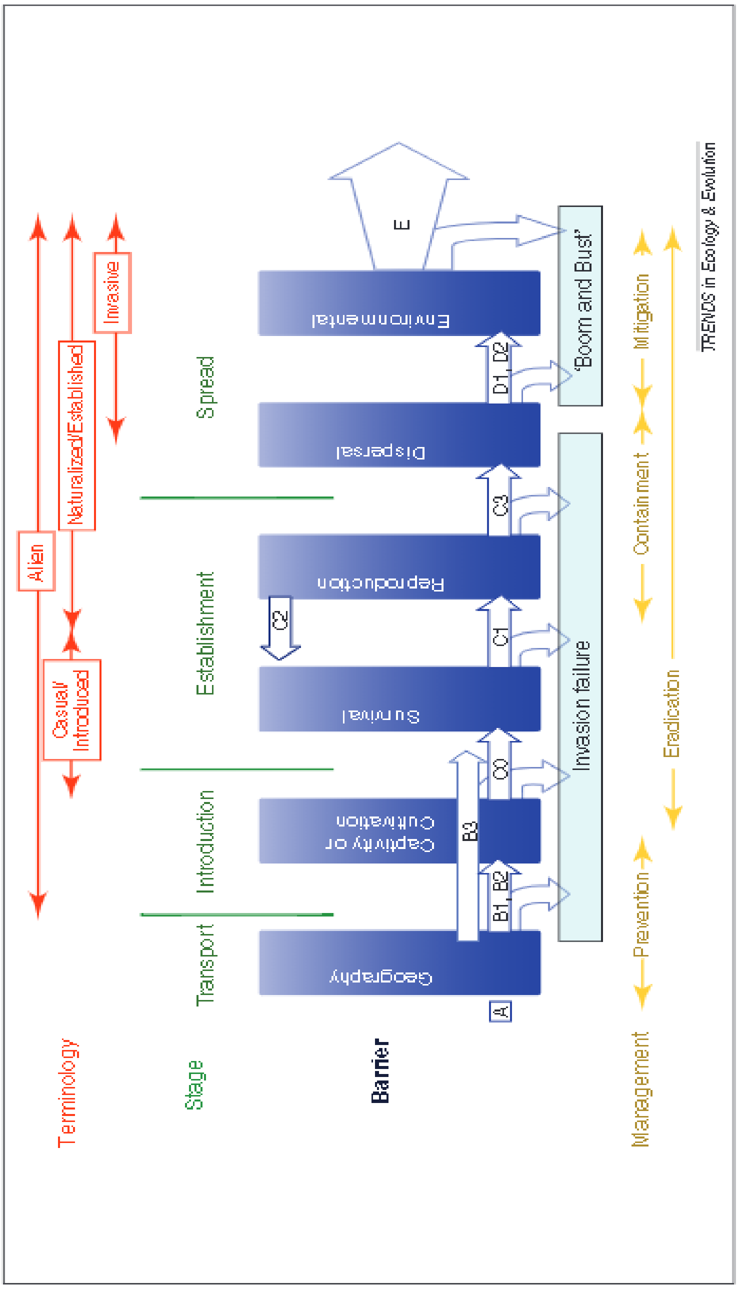

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Figure 1. The proposed unified framework for biological invasions. The proposed framework recognises that the invasion process can be divided into a series of stages, that in each stage there are barriers that need to be overcome for a species or population to pass on to the next stage, that species are referred to by different terms in the terminology depending on where in the invasion process they have reached, and that different management interventions apply at different stages. Different parts of this framework emphasise views of invasions that focus on individual, population, process, or species. The unfilled block arrows describe the movement of species along the invasion framework with respect to the barriers, and the alphanumeric codes associated with the arrows relate to the categorisation of species with respect to the invasion pathway given in Table 1 (main text).

Table 1. A categorisation scheme for populations in the unified framework[a]

Category	Definition
A	Not transported beyond limits of native range
B1	Individuals transported beyond limits of native range, and in captivity or quarantine (i.e. individuals provided with conditions suitable for them, but explicit measures of containment are in place)
B2	Individuals transported beyond limits of native range, and in cultivation (i.e. individuals provided with conditions suitable for them but explicit measures to prevent dispersal are limited at best)
B3	Individuals transported beyond limits of native range, and directly released into novel environment
C0	Individuals released into the wild (i.e. outside of captivity or cultivation) in location where introduced, but incapable of surviving for a significant period
C1	Individuals surviving in the wild (i.e. outside of captivity or cultivation) in location where introduced, no reproduction
C2	Individuals surviving in the wild in location where introduced, reproduction occurring, but population not self-sustaining
C3	Individuals surviving in the wild in location where introduced, reproduction occurring, and population self-sustaining
D1	Self-sustaining population in the wild, with individuals surviving a significant distance from the original point of introduction
D2	Self-sustaining population in the wild, with individuals surviving and reproducing a significant distance from the original point of introduction
E	Fully invasive species, with individuals dispersing, surviving and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence

[a] Human-mediated dispersal has created several novel categories of dispersal pathway (i.e. B1 and B2) [38], and human intervention has also significantly increased the frequency and duration that populations can persist in other categories (C0, C1 and C2).

ANNEX 2: Decision tree