DEPARTMENT OF MARINE SCIENCES

Evaluation of invasion stages and recruitment of the Pacific oyster, *Magallana gigas,* along the Swedish west coast

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Degree project for Bachelor of Science (180 hp) with a major in Marine Sciences and Biology
MAR302 Bachelor's degree project in Marine Science: Major in Biology (15 hp)

First cycle
Semester/year: Spring 2023
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Pacific oysters observed during fieldwork, Falkenberg, Sweden: From personal gallery.

Abstract

The pacific oyster (*Magallana gigas*) is a popular aquaculture species in many countries and was introduced to Sweden for aquacultural trials during the 1970s which later were discontinued. With extensive tolerance to varying conditions, the oysters have successfully established along the Swedish west coast, bringing both positive and negative effects to the local ecosystems, and are therefore in need of management. This thesis aims to investigate a potential relationship between oyster reproduction and salinity as well as evaluating the current model by Le Gall (2022) enabling a classification of the invasion stages of the Pacific oyster along the Swedish west coast.

Oceanographic data extracted from Copernicus Marine Services and biological data collected from several sources as well as from fieldwork, were applied to a criteria-based decision tree model. This resulted in 24 municipalities classified with varying invasion stages ranging from "Future settlement possible" in Vellinge to "Established reef" in Strömstad, displaying the need of dynamic management. Salinity proved to be a significant factor impacting oyster reproduction, with higher salinity levels associated with increased recruitment proportions. The southern recruitment boarder was found to be in Båstad municipality (13.6 PSU) while the invasion front reach into Landskrona municipality (11.4 PSU). No oysters were found further south where salinities ranged between 13.9 – 8.9 PSU.

This study provided valuable insights for the development of a dynamic management model of the pacific oyster in Sweden. Further research is needed to understand the possible effects of a future invasion into the Baltic since adaptation to lower salinities is ongoing for *M.gigas*, shown in this study by observed recruitment in low salinities, and continuous monitoring is required to manage the oyster invasion as well as for preventing further expansion.

Popular Scientific Summary

Linn Martini

Distribution and management of the Pacific oyster – How far south will it go?

As a popular delicacy in many restaurants, the Pacific oyster (*Magallana gigas*) is of great commercial value. As a species living at the border between land and sea, it has extensive tolerance to various conditions and can thereby thrive in many parts of the world. The oyster is also an ecosystem engineer with the potential to drastically effect, or even transform, its surrounding when introduced to a new location and thereby becoming an invasive alien species (AIS). Managing invasive species is challenging since these effects can be both positive and negative, impacting not only the ecosystem but the society as well.

When introduced to Europe for aquaculture purposes during the 1970s, understanding of reproductive capacities were deficient, resulting in a spread of the oyster. After trials ended in Sweden in the 1970s, oysters were absent until 2006, but has today established wild populations in varying densities along the west coast. As the population density is changing in both space and time, there is a need of a dynamic type of management that takes the invasion stage into consideration.

It is yet unknown which invasion stages the oysters have reached at different parts of the Swedish west coast, making management difficult since management objectives generally are based on this. Invasion stages can be determined by evaluating certain criteria, such as e.g., oyster population structure, reproduction, and survival during early stages of life. However, this kind of data is currently lacking and prevents the previously designed decision tree model made by Le Gall (2022) to discriminate between different invasion stages and thereby also inhibits the classification of municipalities along the Swedish west coast, which are needed for implementation of the dynamic management.

The data required to make such a classification were collected from databases, previous surveys and through fieldwork whereafter it was applied to a revised version of the model, resulting in 24 municipalities successfully classified with the appropriate invasion stage. It was clear from the results that dynamic management is needed since the stage of invasion varied along the coast, ranging from no oysters present in the south, an invasion front in Landskrona, and established high density oyster reefs in the north. Results also showed that oyster recruitment, and hence their capacity to expand the population, decreased along the coastline as salinity levels decreased with the last recruitment observed in Båstad.

Although salinity may currently limit the oyster's southern establishment and further distribution into the Baltic Sea, changing conditions coming with climate change and constant oyster adaptation may lead to a more severe invasion in the future. This is only a first classification and might need revision in the future. The revised model serves as a simple and cost-effective way for stakeholders to continue the very much needed mapping of the oyster populations, providing the information required for a well-functioning dynamic management.

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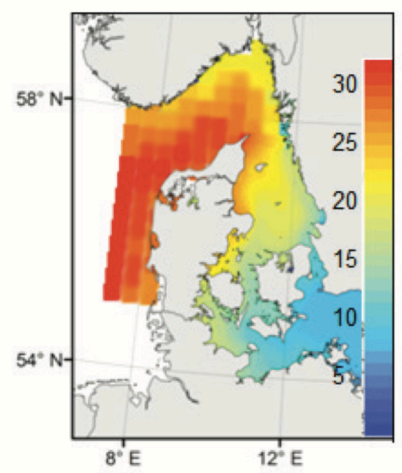
1. Introduction

Magallana gigas (hereafter: Pacific oyster, oyster, *M.gigas*) is known as an invasive alien species (IAS) originally native to the Pacific coast of Asia (Drinkwaard, 1999). It was brought and introduced to Europe for farming purposes as an alternative to the native oyster *Ostrea edulis* which had collapsed suffering from disease and overexploitation (Drinkwaard, 1999). The oysters were not believed to be reproductive in European waters due to the difference in conditions between the western Pacific and northeast Atlantic (Drinkwaard, 1999; Nehring, 2003) and after aquacultural trials in Sweden in the 1970s were discontinued, the oysters were absent for decades. However, several independent sightings between Strömstad and Hallands väderö were reported during the summer of 2007, and it was found that *M.gigas* had established wild populations along the Swedish west coast in small bays, narrow sounds, and short beaches, concentrated north of Gothenburg and decreasing in density southwards (Laugen et al., 2015).

Adapted to shallow intertidal areas, *M. gigas* has a high tolerance of varying abiotic conditions. Although, during the reproductive period, July to August (Strand et al., 2022), the optimal conditions become more restrictive. Adult oysters have a predicted surface seawater temperature (SST) range of -2 –29°C (Carrasco & Barón, 2010) and the possibility of survival in salinities of 5–55 PSU (Strand & Lindegarth, 2014). However, for reproduction to occur, the ocean temperature need to reach 16–20°C during summer (Strand & Lindegarth, 2014) while the salinity requirement for spawning is 23-28 PSU (Dolmer et al., 2014). After a successful spawning 15-41 PSU is optimal for larvae survival (Strand & Lindegarth, 2014) and winter temperatures above 3°C for juvenile survival (Child & Laing, 1998). Temperature and salinity are therefore important factors for determining the possibility of dispersal, establishment, local reproduction, and recruitment.

The abiotic conditions along the Swedish west coast vary between -1 – 24°C (SST) and the salinity increases from around 10 PSU in Öresund to around 25 PSU at the Norwegian coast (Figure 1) (Strand & Lindegarth, 2014). This falls within the tolerance range of an adult Pacific oyster, however, the salinity gradient is believed to limit recruitment in the southern region (Wrange et al., 2010). While it is still unclear exactly how far south the oysters reproduce, there are known occurrences of high densities in northern Bohuslän (Partoft, n.d.[1]), lower densities between Varberg and Malmö (Partoft, n.d.), and absence south thereof (Ahlers et al., 2020). With the warmer summers and milder winters that comes with climate change, the temperature becomes less of a limiting factor leaving the salinity as the major barrier from further expansion south and into the Baltic Sea.

Figure 1: Map over salinity gradient



Note I: Salinity (PSU) along the Swedish west coast. Modified figure taken from (Strand & Lindegarth, 2014), original by Per Jonsson based on ICES data.

Generally, IAS are recognized as one of the major threats to biodiversity and ecosystem functioning worldwide (Diversity & Centre, 2020). Although, both positive and negative effects come with the presence of *M. gigas*. The Pacific oyster can cause significant impacts on the local ecosystem and has the potential to create a shift in ecosystem structure through their reef formations, and also bring a risk of spreading parasites and/or diseases (Nehring, 2003). On the other hand, they have great commercial value and can allow for better water quality through increased filtration (Laugen et al., 2015; Ruesink et al., 2005), and as ecosystem engineers, they create opportunities for other species which could lead to increased biodiversity (Norling et al., 2015).

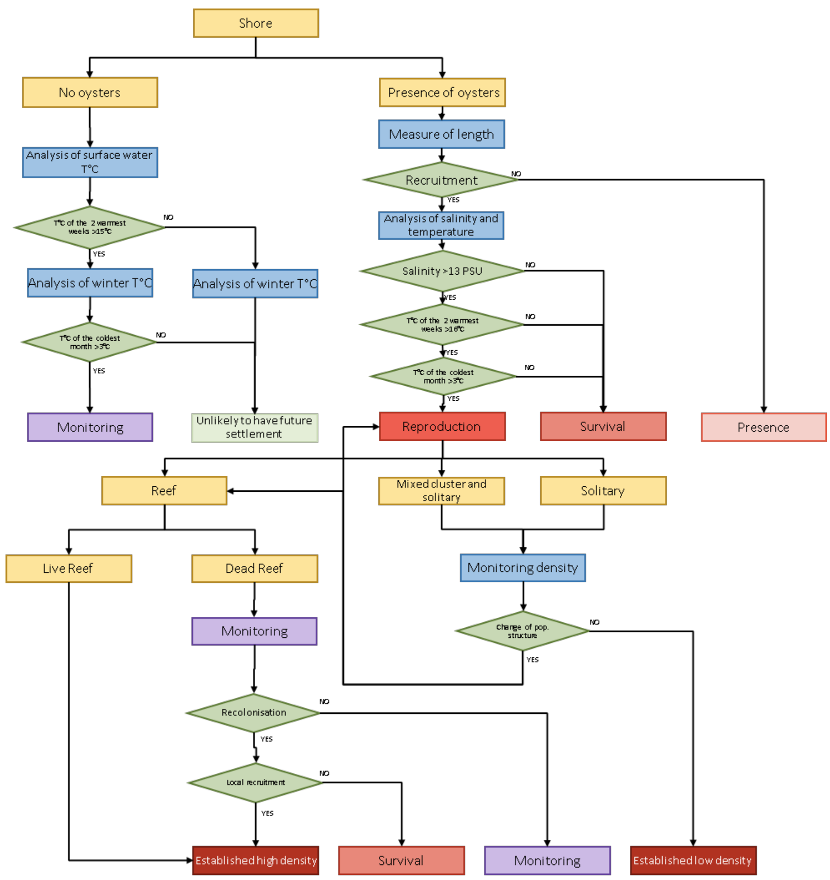
Consequently, management of the Pacific oyster is challenging, as there is a need to balance the high commercial value with the varying ecological impacts and becomes even more complex as the density of oysters differs along the coastline. Depending on the time since invasion and adaptation to its new environment, invasive species generally follow certain invasion stages that requires different forms of management (Geburzi & McCarthy, 2018; Le

[1] https://hannapartoft.shinyapps.io/shiny_oysters/?_ga=2.237831168.1686877105.1646251396-325310896.1643018757

Gall, 2022). Therefore, it is crucial to identify the invasion stages of *M.gigas* along the Swedish west coast and develop a dynamic management model. One example where this type of management has been implemented is the Norwegian approach with two management regimes for the invasive Arctic red king crab (*Paralithodes camtschaticus*). An eastern area where the crab is managed to give the best possible economical and biological output while the western management area focuses on reducing the spread south by having a free fishing policy (Jørgensen & Nilssen, 2011).

To support this work for the oyster in Sweden, a criteria-based decision tree (Figure 2) was created during 2022 (Le Gall, 2022). The model uses biotic and abiotic criteria to identify the oysters' invasion stage at a given location. The decision tree model is ready to be used, however, knowledge gaps along the west coast related to biological data, e.g. the oysters' distribution, densities, and population structure, and related to the impact of abiotic factors (primarily salinity) on biological and ecological performance, prevents application of the model.

Figure 2: The criteria-based decision tree (Le Gall, 2022)



Note II: The decision tree includes five criteria: "Recruitment", "Reproduction", "Juvenile survival", "Population structure", "Change in population structure over time". Based on biotic and abiotic conditions these criteria determine the oyster invasion stages: "Presence", "Survival", "Reproduction", and "Established high/low density".

Through addressing the above-mentioned knowledge gaps this thesis aims to further investigate a potential relationship between oyster reproduction and salinity as well as evaluating the current model by Le Gall (2022) enabling a classification of the invasion stages of the Pacific oyster along the Swedish west coast.

Hypotheses:

H_0

- Oyster recruitment is not impacted by salinity.
- The stage of invasion is homogenous along the Swedish west coast.
- The invasion stage model cannot discriminate between the invasion stages of *M.gigas* along the Swedish west coast.

H_1

- Salinity has an impact on oyster recruitment.
- Different invasion stages are found along the Swedish west coast.
- The invasion stage model (Le Gall, 2022) enables discrimination between the invasion stages of *M.gigas* along the Swedish west coast.

2. Methods

The methods include a combination of fieldwork and analysis of oceanographic and biological data. Field work allowed for assessing the applicability of the model for stakeholders and to complement the biological data. The model by Le Gall (2022) served as a framework which the data was fed into. For this study it was decided to perform the invasion stage classification on a municipality level and after a worst-case scenario.

2.1 Existing biological data

According to the model by Le Gall (2022), biological data (i.e., population structure and oyster length measurements for recruitment analysis) is needed to classify the different invasion stages. Before the start of this thesis project, existing biological data from previous surveys were explored to result in 82 selected sites along the Swedish west coast (Roesch, 2023). These were selected by the project group based on criteria such as high oyster density, water depth (0-1m), accessibility to the sites by car, and availability of information such as population structure and/or length measurements.

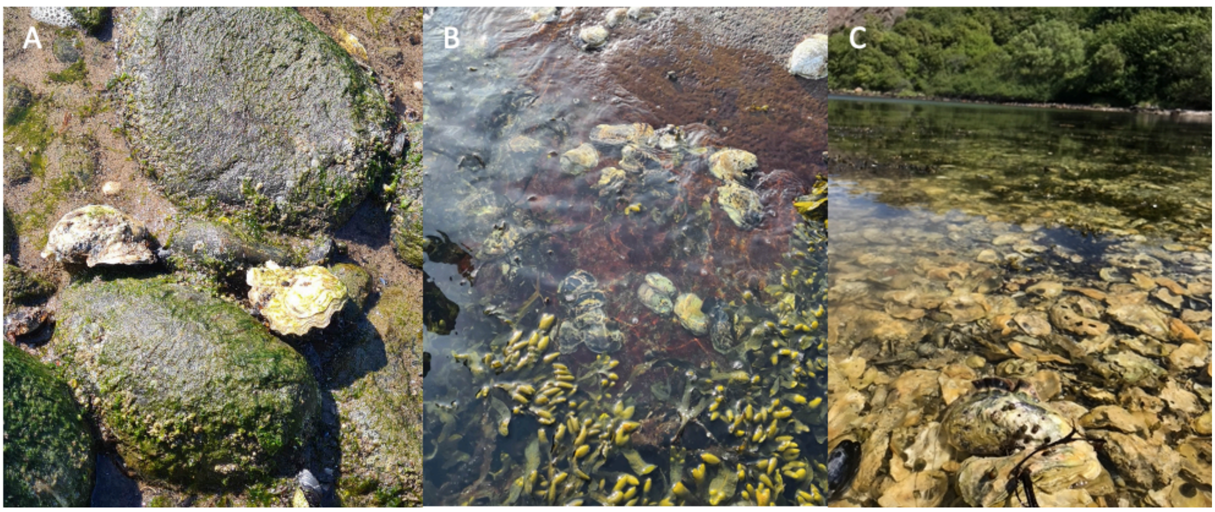
Biological data from previous surveys was available for 21 (of the 82 selected) sites from the following nine municipalities: Strömstad, Tanum, Lysekil, Uddevalla, Stenungsund, Tjörn, Kungälv, Öckerö and Göteborg. The High School of Grebbestad provided additional biological data for three sites in the municipality of Tanum during the spring of 2023. The municipalities of Munkedal and Burlöv were excluded from this study due to their minimal coastlines. Existing data was analysed for knowledge gaps related to the required parameters in the model, and 61 suitable sites for complementary field work were selected (Roesch, 2023).

2.2 Field work

Field data was obtained during a two-week period in April 2023, visiting municipalities between Vellinge and Strömstad. Field work was carried out according to the protocol (Appendix 8.1) developed by the project group based on the model produced by Le Gall (2022).

In short, arriving at a site, date and coordinates were noted as well as if there was a presence of oysters. If so, population structure at the site was determined through identifying the densest area of the oysters, estimating the percentage cover (live and/or dead). This corresponds to the population structures "reef formation" 90-100% coverage, "mix of clusters and solitary" < 90% coverage or "solitary" (Figure 3).

Figure 3: Oyster population structures

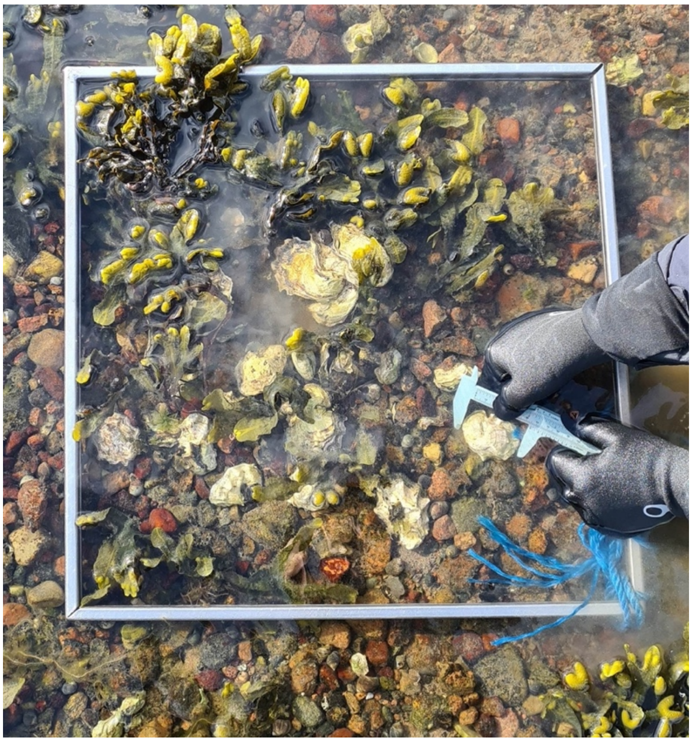


Note III: The different population structures. Solitary (A), Cluster (B), Reef (C). A and B from personal gallery, C taken by Ane Timenes Laugen.

At a high-density site, a square of 0.5 x 0.5 m was placed where signs of recruitment could be observed or if no small oysters could be seen, randomly at the site. 50-100 oysters were measured in mm from umbo (the "hinge") to the furthest side of the shell (figure 4). In case very few oysters were present, all live oysters found were measured and if only dead recruits were found, this was noted.

If oysters were present but out of reach, the area would primarily be searched for signs of recruitment and if possible, the population structure was noted and photographed. Then, the next site within the municipality was visited. Other observations of interest were also noted. If a site was found to be difficult to reach by car and/or foot, another site close by was chosen.

Figure 4: Example from square method

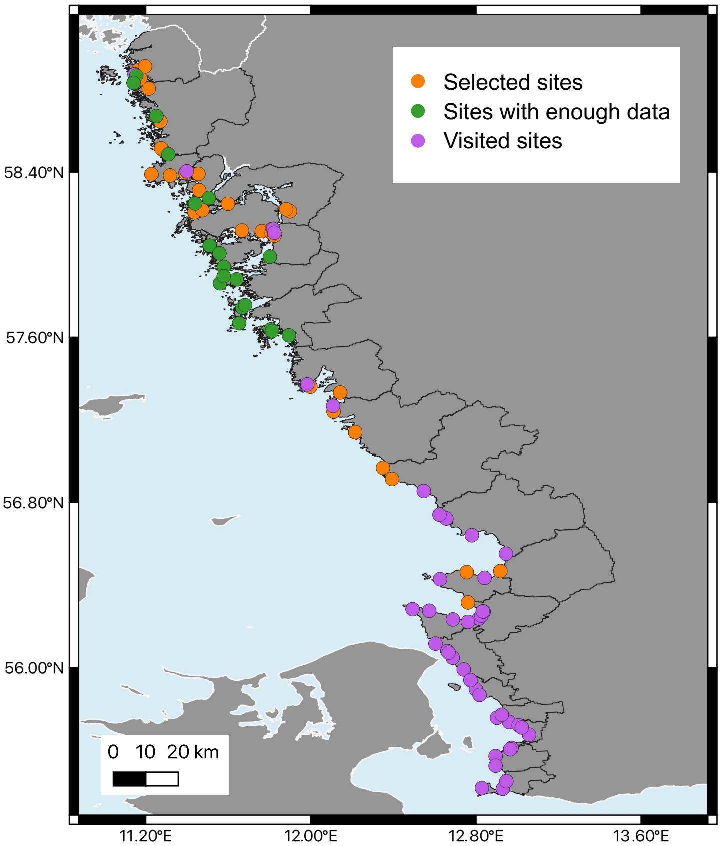


Note IV: Measurement of an oyster within the survey square (0.5x0.5m). Photo from personal gallery.

Three to five sites per municipality were visited between Vellinge and Ängelholm to ensure accuracy in determining the southern border of invasion. During field work, one site was added in in Kävlinge and Lomma, respectively, to reach the three-site minimum per municipality, and one site each in Laholm, Sotenäs, Orust and Stenungsund, respectively, due to inaccessibility of the original site. All additional sites were selected based on the oysters' preferred habitat and surrounding substrate. With the limited time in field, it was decided to identify the site with the previously recorded highest density for each municipality north of

Ängelholm and visit this site only, resulting in 39 visited and 22 unvisited sites (Figure 5). A total of 60 sites became ready for further analysis for the model (Appendix 8.3).

Figure 5 Map over the final selection of sites



Note V: Remaining sites with lacking biological data (orange, N=22), sites from previous survey with sufficient data (green, N=21), Visited sites during fieldwork (purple, N=39)). Map made in collaboration with Claire Roesch in QGIS, projection WGS84.

2.3 Oceanographic data

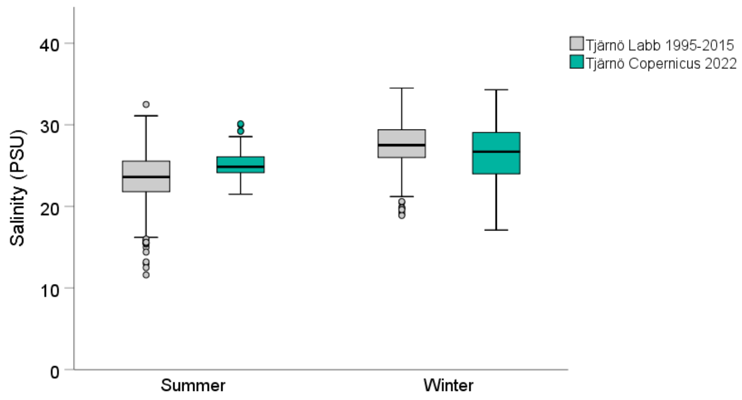
In addition to biological data, the model by Le Gall (2022) requires average summer and winter sea surface temperatures (SST) and average summer sea surface salinity (SSS) to classify a given site with the appropriate invasion stage. For summer SST and SSS, July and August were chosen since this is the spawning period for *M. gigas* (Strand et al., 2022). During winter, the seven coldest coherent weeks were chosen based on high winter juvenile survival rates (Child & Laing, 1998).

It was not a possibility to use site specific field measurements due to lack of data from previous surveys and the limited time in field. With the area in need of coverage together with the data availability at different databases, Copernicus Marine Services was selected. Winter

(Dec 2021-Mar 2022) and summer (July-August 2022) SST and SSS (daily averages) were extracted from the Copernicus database for the 60 sites using RStudio (Roesch, 2023).

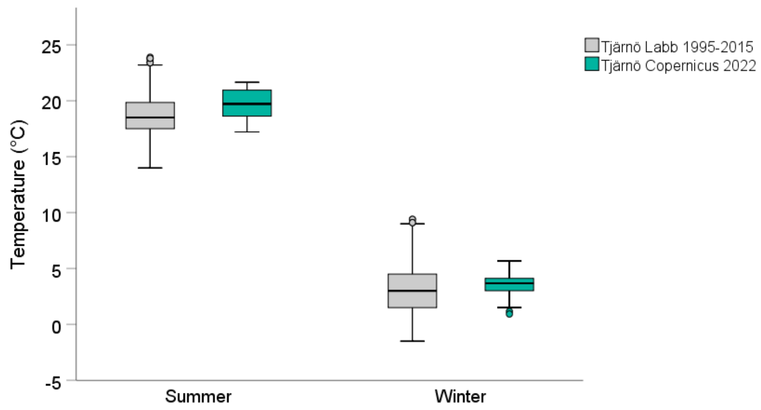
To verify that the Copernicus 2022 data represented a normal year, data extracted from a site in Tjärnö was compared in boxplots with long term (1995-2015) SST and SSS averages (Bertils brygga, lab-water) measured at Tjärnö Marine Laboratory (Figure 6-7). 1995-2015 averages were used in the comparison due to an increase in winter lab-water temperature after 2015 associated to problems with low water flow in the system, allowing the water to heat before reaching the new-installed monitoring system. The Copernicus data was then grouped by weeks, the seven coldest coherent weeks during the winter months were identified and SST averages were calculated for each site.

Figure 6: Salinity comparison



Note VI: Salinity ranges for Tjärnö data extracted from Copernicus Marine Services (2022) and Tjärnö Marine Laboratory (1995-2015, Bertils brygga) for summer and winter. The box represents the interquartile range (50% of the data) and the line within the box represents the median. The whiskers show the min. and max. values, the dots are outliers.

Figure 7: Temperature comparison



Note VII: Temperature ranges for Tjärnö data extracted from Copernicus Marine Services (2022) and Tjärnö Marine Laboratory (1995-2015) for summer and winter. The box represents the interquartile range (50% of the data) and the line within the box represents the median. The whiskers show the min. and max. values. while the dots are outliers.

2.4 Data compilation and analysis

All length data from previous surveys, the data received from other actors and the data collected during fieldwork were compiled into length-frequency histograms to evaluate recruitment (Appendix 8.2). Occurrence of recruitment for the model was evaluated on municipality level, where oysters measuring ≤ 25 mm was considered as recruits (Cardoso et al., 2007; Le Gall, 2022). Meaning, if one site within a municipality tested positive for recruitment, the whole municipality was classified accordingly. A table was created including the county and municipality for each site, and information about population structure and recruitment status (recruits found or not) for each site was added to the table.

SST and SSS for each site were then added to the table and the model (Le Gall, 2022) was used to classify each site with the appropriate invasion stage by looking at the biotic and abiotic criteria. Thereafter the municipalities were classified with the worst-case scenario of the site(s) in each municipality (Appendix 8.3). Maps over the Swedish west coast were made in QGIS where each municipality was assigned the same colour as it's classification. During this process, unclarities were observed in the model developed by Le Gall (2022) and the model was therefore revised in several steps and the results updated according to the modifications.

To assess the effects of salinity on recruitment, the analysis was done on site level using all sites with available length data (N=60, Appendix 8.4), i.e., sites visited during fieldwork as well as pre-existing length data obtained in the DynamO project during 2021 and 2022, where sites without oysters present were excluded. QQ-plots and Levene's test ($P > 0.25$) were done in SPSS to confirm compliance with parametric test assumptions. Recruitment proportions were transformed (Asin(Sqrt(x+0.01)) before analysis.

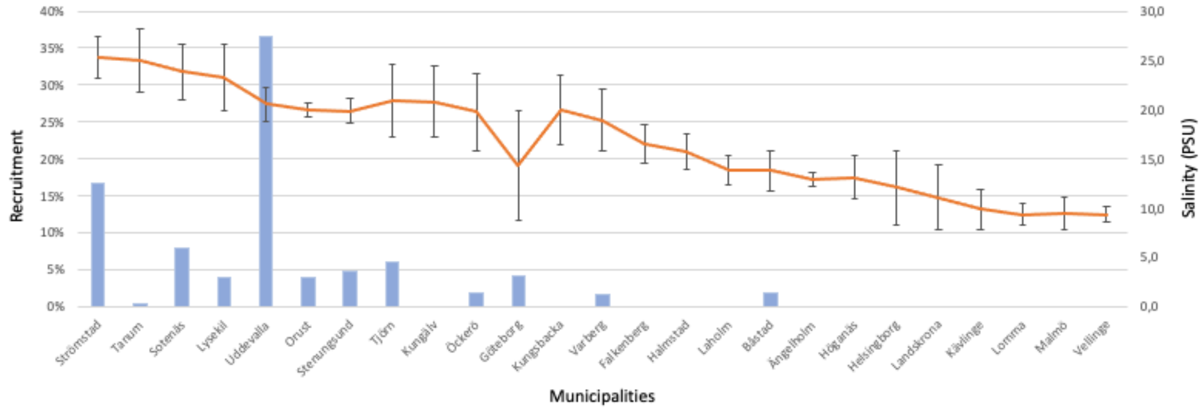
The SSS data from sites with no recruitment and sites where recruitment was observed were illustrated in boxplots and potential differences in SSS between sites with and without recruitment was analysed with an ANOVA. To further investigate the relationship between SSS and recruitment, a regression analysis was done with recruitment as the dependant-, and SSS as the independent variable. An overview visualisation of the data along the coastline including recruitment proportions and SSS mean for each municipality was also developed.

3. Result

3.1 Impact of salinity on recruitment

Based on the salinity levels (municipality averages ± STDEV) a clear declining salinity gradient was observed from north to south along the Swedish west coast. There was a drop in Göteborg municipality as a consequence of the outflow of Göta älv and Nordre älv. Recruitment ranged between 0 and 36.5% and was highest in Uddevalla municipality (Figure 8).

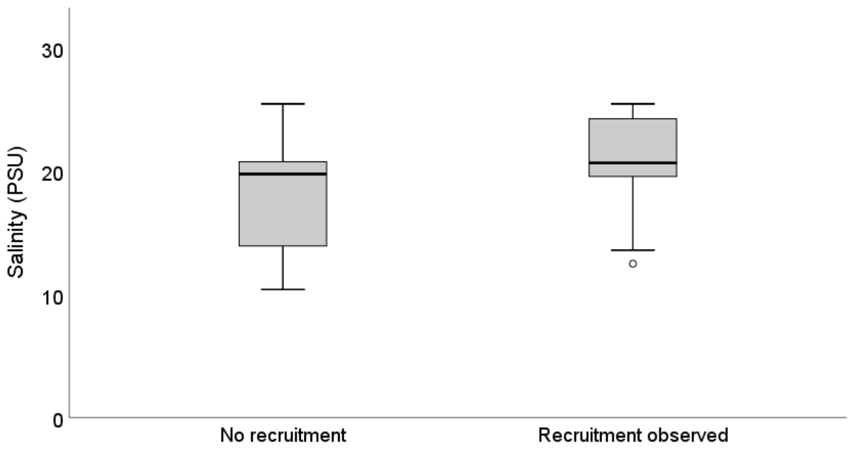
Figure 8: Overview diagram for salinity and recruitment



Note VIII: Recruitment proportion and salinity for each municipality. The primary y-axis represents the recruitment in percent (blue bars) and the secondary y-axis represents the average salinity for July and August in PSU (orange line). Whiskers show the variance in salinity for each municipality. The x-axis shows municipalities ordered from left to right, north to south.

When salinity at non-recruitment sites and sites with recruitment was analysed (Figure 9), the salinity was significantly higher at sites with recruitment (ANOVA, $F_{1, 58} = 6.23$, $P = 0.015$). Salinity for non-recruitment sites were in average (± STDEV) 18.2 ± 4.2 PSU (19.8 PSU in median) and for recruitment sites 21.0 ± 3.8 PSU (20.7 PSU in median).

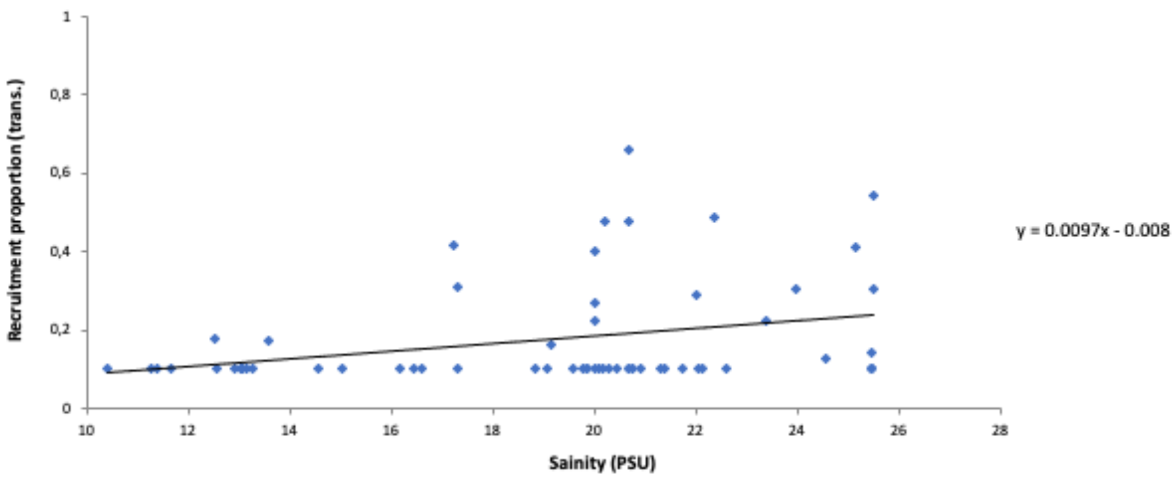
Figure 9: Salinity variations between recruitment and non-recruitment sites



Note IX: Salinity ranges in PSU for non-recruitment and recruitment sites.The box represents the interquartile range (50% of the data) and the line within the box represents the median. The whiskers show the min. and max. values. while the dots are outliers.

Sites without recruitment were observed along the whole coastline. However, no sites with recruitment were observed from Rönne in Ängelholm and southwards where the salinity ranges between 13.9 – 8.9 PSU. To further investigate the relationship between recruitment and salinity, a regression analysis (Figure 10) was carried out. Recruitment was observed to increase with increasing salinity (ANOVA, $F_{1, 18} = 11.12$, P = 0.001).

Figure 10: Regression analysis



Note X: Regression analysis on Asin(Sqrt(x+0.01) transformed recruitment proportions (y-axis) and July-August salinity averages in PSU (x-axis) for each site with oysters present. Regression line (in black) with corresponding equation.

3.2 Model adjustment

During the compilation of abiotic data and when the existing and collected field data was applied to the model (Le Gall 2022), different issues were identified and addressed. The model criteria were adjusted in accordance with recent biological findings, and modification of specific sections were carried out to further clarify the pathways (Figure 11).

In the first part of the model, the main changes were done to the abiotic criteria. For the winter SST, the criteria were changed from 4 coherent weeks to 7 coherent weeks based on Child and Laing (1998) and the temperature threshold was set to ≥ 3°C instead of >3°C. Further, the summer SST and SSS were analysed for July-August instead of the two warmest weeks since this is the full spawning period for *M.gigas* (Strand et al., 2022). The SST limit of >16 °C was kept while the salinity limit that previously was set to >13 PSU was changed to >8 PSU south of Varberg (Kinnby et al., 2023) and kept at >13 PSU for Varberg municipality and north thereof. This geographical delimitation was based on the average salinity for July-August in Varberg (19.2 PSU) which corresponded to the salinity median (19.8 PSU) for non-recruitment sites in this study, as well as a documented reduction in high density sites south of Varberg in previous studies (Partoft, n.d.[2]) indicating a potential reduction in recruitment. For the biotic recruitment criterion, no changes were made to the recruitment size of ≤ 25mm.

In the second part of the model, the main changes were done to the pathways. Going from source to established, the model calls for monitoring of the oyster density. If there is a change in population structure, the model loops back to the appropriate population structure and continues from there. During the time of monitoring, the classification will stay as "Source (reproduction)", and consequently, in this study, source populations could not be discriminated from "Established solitary" or "Established cluster" stages.

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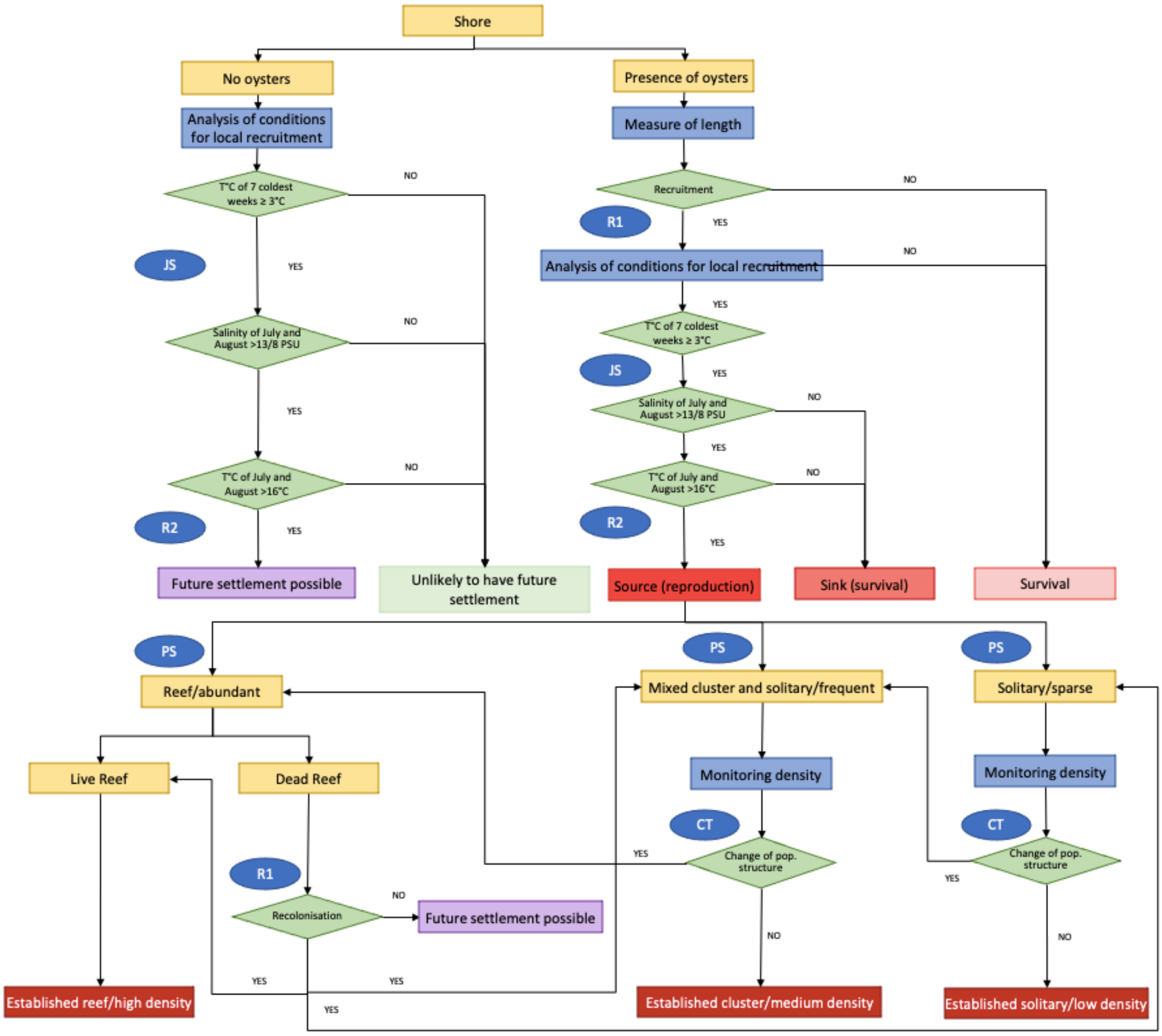
[2] https://hannapartoft.shinyapps.io/shiny_oysters/?_ga=2.237831168.1686877105.1646251396-325310896.1643018757

Figure 11: Revised model



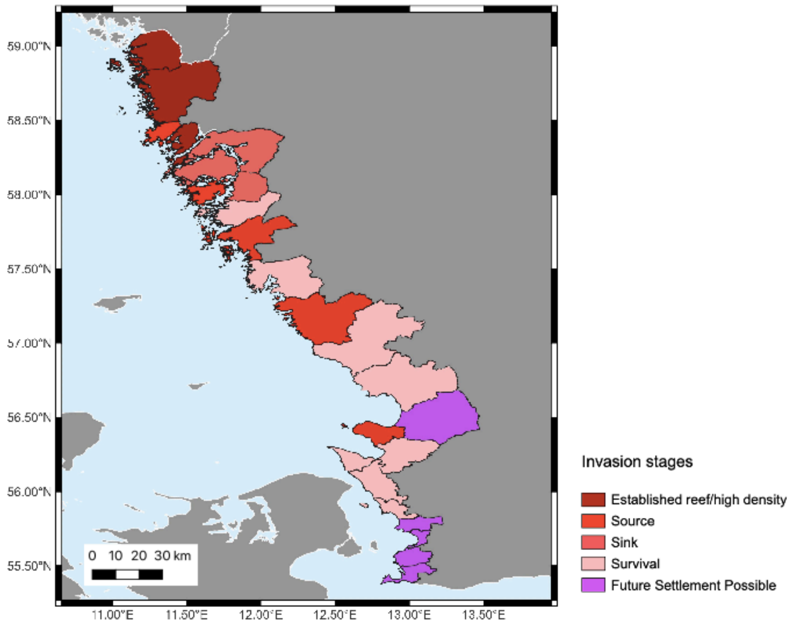
Note XI: Revised model including the five criteria: "Juvenile survival" (JS), "Recruitment" (R1), "Reproduction" (R2), "Population structure" (PS) and "Change in population structure over time" (CT). The

3.3 Classification of invasion stages

A clear trend was seen along the coastline with no oysters present in the southern regions, increasing densities northwards and reef formations in the northern regions (Figure 12). The southernmost municipality with oysters present was Landskrona. Laholm was the only municipality north of Skåne to be classified with "Future settlement possible", since no oysters were present while the SST and SSS limits passed the requirements, and Båstad was the most southern municipality with positive recruitment.

Four municipalities had an SST average below 3 °C for the 7 coldest coherent winter weeks. These were Uddevalla, Orust, Stenungsund and Laholm. Gothenburg and Halmstad respectively had one site that sank below 3 °C. This, however, did not have an impact on their classification since there were other sites in those municipalities exceeding the ≥ 3 °C limit which takes precedence according to the worst-case scenario procedure. Average SST for the July-August period didn't sink below 16 °C for any municipality along the west coast. All municipalities up to and including Falkenberg had SSS July-August averages exceeding 8 PSU, for Varberg and municipalities north thereof, all SSS July-August averages exceeded 13 PSU. Detailed information can be found in Appendix 8.3.

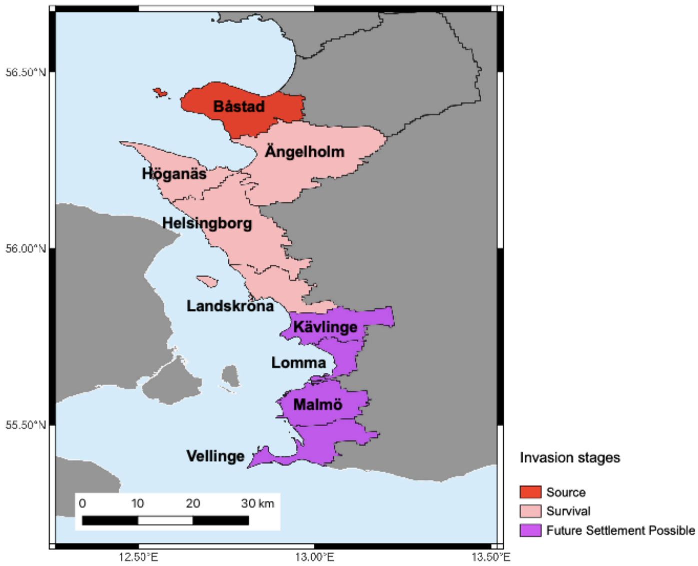
Figure 12: Overview map over classified municipalities



Note XII: Map of all classified municipalities, coloured according to their respective invasion stages. "Source" municipalities need further monitoring to reach "Established cluster/solitary", these classifications can therefore not be seen on the map. Created in collaboration with Claire Roesch in QGIS, projection WGS84.

As shown in Figure 13, in Skåne, the municipalities Vellinge, Malmö, Lomma and Kävlinge had no presence of oysters but had good abiotic conditions (i.e., winter T ≥ 3 °C, summer T > 16 °C and S > 8 psu) and were classified with "Future settlement possible". As mentioned above, Landskrona (Site: Ålabodarna) was the southernmost municipality with oysters present and hence classified with "Survival". Oysters were also found in Helsingborg, Höganäs and Ängelholm, all classified with "Survival". Båstad was the worst case in Skåne being the southernmost site with recruitment, the abiotic conditions were good, and the municipality was classified as "Source (reproduction)". Since all municipalities without oysters present had good abiotic conditions, no municipality was classified with "Unlikely to have future settlement".

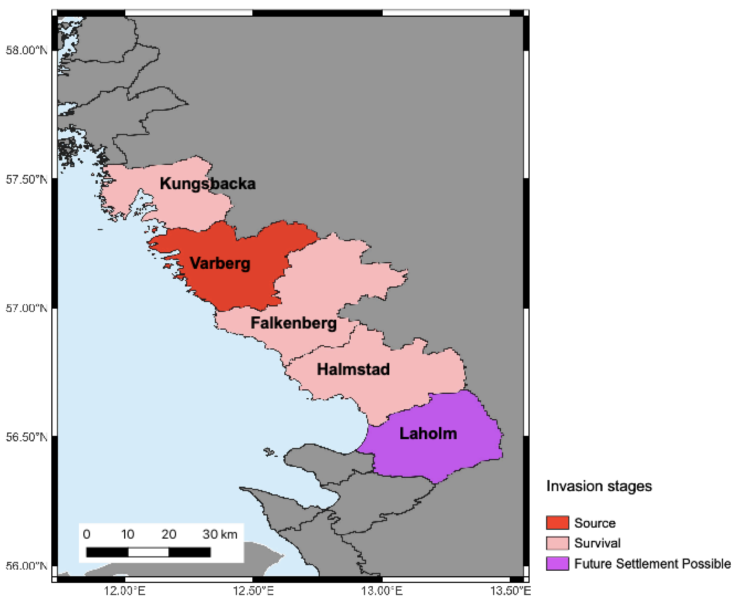
Figure 13: Classification map of municipalities in Skåne county



Note XIII: Named municipalities coloured with the three different invasion stages that can be found in Skåne. Created in collaboration with Claire Roesch in QGIS, projection WGS84.

In Halland, Laholm was the only municipality with no oysters present. The abiotic conditions in the area allowed for the classification "Future settlement possible". Varberg was the municipality with the worst case having both recruitment and good abiotic conditions. It was however a site with only solitary oysters and was therefore classified as "Source (reproduction)" until monitoring can discern the more advanced invasion stages. The remaining three municipalities tested negative for recruitment and were classified as "Survival" (Figure 14).

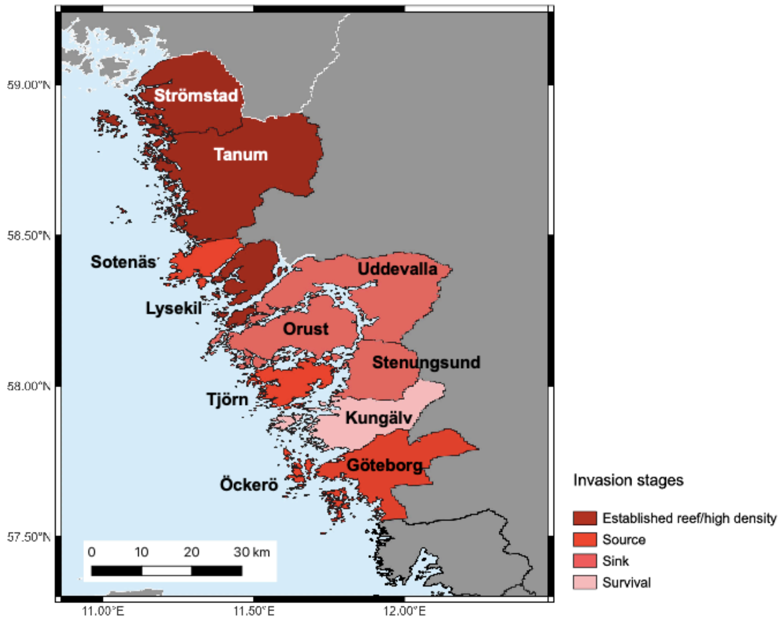
Figure 14: Classification map of municipalities in Halland county



Note XIV: Named municipalities coloured with the three different invasion stages that can be found in Halland. Created in collaboration with Claire Roesch in QGIS, projection WGS84.

In Västra Götaland all municipalities had oysters present and all tested positive for recruitment except for Kungälv where no recruits were observed and was therefore classified as “Survival”. In Uddevalla, Orust and Stenungsund recruitment was observed but winter SSTs were below 3°C and therefore they were classified as “Sink (survival)”. Göteborg and Sotenäs were classified as “Source (reproduction)” but had cluster populations as their worst-case population structure and needed monitoring to determine the actual invasion stage. Lysekil, Tanum and Strömstad all had recruitment, good abiotic conditions, and reef populations. Therefore, all were classified as the worst-case invasion stage along the west coast, “Established reef/high density” (Figure 15).

Figure 15: Classification map of municipalities in Västra Götaland county



Note XV: Named municipalities coloured with the four different invasion stages that can be found in Halland. “Source” municipalities need further monitoring to reach “Established cluster/solitary”, these classifications can therefore not be seen on the map. Created in collaboration with Claire Roesch in QGIS, projection WGS84.

4. Discussion

In this study it was confirmed that *M. gigas* had reached several different invasion stages along the Swedish west coast and therefore needs a dynamic type of management. The model developed by Le Gall (2022) provided some discrimination between different invasion stages, but some of the included criteria were, however, updated as new knowledge on the impact of abiotic conditions on the biological processes of the oysters was available. The model was further improved by adding to, and renaming the invasion stage classifications, simplifying the use for future stakeholders. Low salinity was demonstrated to have a negative impact on oyster recruitment in the southern regions, although, this might not be enough to prevent future settlement in the evaluated region.

It was clear from the overview diagram (section 3.1, Figure 8) that there was a declining salinity gradient from north to south and that the recruitment proportions were higher in the northern municipalities while there was low to no recruitment in the south. In accordance, the regression analysis showed a positive relationship with increasing recruitment in higher salinities, which is further backed up by the significantly higher salinity at sites where recruitment was observed. Also, the higher recruitment proportions in the northern regions with salinities around 25 PSU also corresponded with the optimal salinities for spawning (Dolmer et al., 2014) and larvae survival (Strand & Lindegarth, 2014). Recent studies (Kinnby et al., 2023) has, however, observed that there has been a shift in optimal fertilisation salinity for the oysters since the beginning of invasion, and that southern populations at Hallands väderö (Båstad municipality) now have a higher fertilisation percentage in lower salinities (13-18 PSU) compared to oysters from high salinity areas (28-23 PSU) and that fertilisation, although low, can occur at 8 PSU for oysters adapted to low salinities. In this study, Båstad had an average salinity of 13.6 PSU and was the southernmost municipality with observed recruitment while no sites with recruitment were observed from Ängelholm and southwards where the salinity ranges between 13.9 – 8.9 PSU. This points towards that the oysters are still adapting, and that recruitment is currently limited in the southern regions due to the low salinities. Although, it seems likely that *M. gigas* has the potential to further acclimatise to the conditions and push the invasion front further south in the future.

With regard to these findings, it was not appropriate to have the same salinity limit in the model for the entire coastline, and the limit was therefore kept at 13 PSU for the northern regions including Varberg, while the limit was lowered to 8 PSU south thereof. The geographical delimitation should however be investigated further since it was an observation rather than a focus of this study and needs to be confirmed.

This study used length measurements (≥ 25mm) as a proxy for recruitment based on Cardoso et. al. (2007). Since the Pacific oyster is in an adaptation process to lower salinities (Kinnby et al., 2023), this might also affect the growth rate for the recruits as salinity still is an environmental stressor for oysters in early stages (Sehlinger et al., 2019; Yao et al., 2015). Hence oyster lengths might not correspond to the same length in higher versus lower salinities. Due to the low recruitment proportions in the mid- to southern region it was difficult to determine the boarder of where recruitment ceased to take place. This needs to be investigated further and if it is the case that the growth rate, and hence, the size of recruits is impacted by salinity, the model would need to be further updated to account for different length criteria for different regions, similar to the criteria for the two salinity regions as discussed above.

Since recruitment can be difficult to evaluate solely by measurements, perhaps continuing the research by Kinnby et al. (2023) measuring fertilisation for populations in varying salinities or by looking into other methods to evaluate recruitment such as spat (i.e., recently settled oysters) collection (Dunér Holthuis et al., 2014) using sea based collectors could be appropriate alternatives. Using this method, timing is crucial, as generally oysters reproduce when the ocean temperature is rising during summer (Dunér Holthuis et al., 2014). In the model by Le Gall (2022) the two warmest weeks represented the start of reproduction, however, recent studies (Strand et al., 2022) have showed that reproduction most likely occurs in periods during July and August, stretching into the beginning of September which was the reason abiotic data, in this study, was analysed for the full July-August period.

In the previous model, winter temperature averages for the coldest month were used to evaluate juvenile survival. However, the high juvenile survival rates presented by Child and Laing (1998) indicate that a longer period with cold temperatures is needed for this criterion and the model was changed accordingly to the seven coldest coherent weeks. Although, considering that only two sites (one in Göteborg and Halmstad respectively) showed winter temperatures below 3 °C, the criterion for juvenile survival may need to be re-evaluated and lowered in temperature or through an extended time period. Due to the milder winters coming with climate change, the latter might be preferable. The fact that non-recruitment sites were observed along the whole coastline, and thereby also the full salinity gradient does, however, indicate that other factors (other than temperature) may also impact recruitment. One example could be virus infections such as the OsHV-1 (herpesvirus) which have been found to infect both spat and adults while it also might infect larvae (Le Deuff et al., 1994; Mortensen et al., 2016). In future research, looking at these factors together with oceanographic conditions, can be important to fully understand what might limit recruitment in different regions along the coastline.

The results presented in this study show that the southern border of invasion, the municipality of Landskrona (Site: Borstahusen), has not changed since 2020 (Partoft, n.d.). However, the oceanographic analysis show there is a possibility of future settlement in the southern municipalities as proven during 2018 with oyster findings in Malmö (Ahlers et al., 2020) which potentially could be the true southern border of invasion. The site visited 2018 was the same site visited during this survey, it was however difficult to properly assess in this study due to the depth, and hence holds some uncertainty. However, if the oysters have disappeared, this is most likely a survival site without continuous supply of larvae. The same problem was encountered at harbour sites where oysters seemed to mainly be attached to the harbour walls which, in this study, had to be investigated from land. Considering the algae growth and murky water encountered in the harbours, there is a possibility that the presence of oysters was missed. This may be less of a problem in the northern regions as the oyster densities increase and become easily detected, however, since the southern region included sites situated in city harbours, missing oyster presence and recruitment there might have caused an underestimation of the invasion front and recruitment boarder. Future studies may therefore benefit from adapting their choice of method to suit the local environment e.g., video and/or snorkelling as in previous surveys.

Further north, Laholm municipality was registered as "Absence/Future settlement possible" despite being surrounded by municipalities where recruitment was observed. Although the surveyed sites were located close to a river outlet, salinity was not a problem. The winter temperature of 3 °C was however close to the SST limit and could complicate juvenile survival. The absence of oysters could be explained by the low SST, however, an alternative cause might be the lack of substrate for larvae to settle on. M.gigas can settle on any hard substrate, anything from shell fragments and pebbles to artificial structures like harbour walls (Dolmer et al., 2014). As the municipality consisted of a long beach with no harbour or piers, nor any signs of other bivalves or rocks, lack of substrate seems likely. Furthermore, since the Pacific oyster has been found to decrease in density with increasing exposure (Bergström et al., 2021), the high exposure of the Laholm bay is also a probable cause. However, since Laholm is in close relation to the source population in Båstad, it is important to continue monitoring, especially if artificial structures are implemented in the future. Artificial structures could also become a future model criterion to take into consideration for southern municipalities since it allows for settlement although natural substrates might be absent.

5. Conclusion

The revised model provides an improved framework that enables discrimination between the invasion stages, clearly stating if a given location most likely has a population that is simply surviving, has a recurring supply of larvae and considered a sink population, or if it is a reproductive population and thereby a source. Secondly, through monitoring, it allows evaluation of whether the population in question has fulfilled its local ecological niche or if it is in the process of expanding the population (through the observations of change in population structure over time). In this study, *M. gigas* was indeed found to have several different invasion stages along the Swedish west coast, which require a dynamic type of management. Moreover, although salinity still seem to limit recruitment in the southern region there is a risk of future adaptation and expansion into the Baltic. Therefore, continued monitoring is crucial to counteract southern establishment, while future research simultaneously should be directed towards exploring the possible effects of a Pacific oyster establishment on Baltic ecosystems. Furthermore, despite the successful application of the invasion stage model using the collected field data and assessment of invasion stages along the Swedish west coast, additional data should be collected to refine the performed invasion stage classification. The information provided by this project, together with the revised decision-tree model, does, however, constitute a base that may support stakeholders in future fieldwork and classification, as well as serve as a foundation for development of a dynamic management model, which in turn may help establish an appropriate, cost-effective, management of the Pacific oyster in Sweden.

6. Acknowledgements

I would like to extend my gratitude to my supervisor Åsa Strand for her constant support during this project and to Claire Roesch for a great collaboration in field as well as during the creation of result components. Further, I would like to thank Youk Greeve for assisting in extraction of oceanographic data as well as the DynamO team for informative dialogs and discussions.

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8. Appendix

8.1 Survey protocol

Survey of Pacific oyster
DynamO Project

EQUIPMENT

- Mobile phone (to get coordinates)
- Waders
- Water binoculars
- Long gloves
- White boxes
- Caliper
- Folding rule
- Sampling square
- Clipboard, protocol, and pen

IMPLEMENTATION
Look for the densest oyster bed you can find at the site (we are interested in "worst case" scenario).

Notes:
- Date
- Coordinates (WGS84, decimal degrees)
- Are there Pacific oysters on the site? (Yes/No)
- If no, you don't have to note anything more.
- If yes:

Are the oysters alive? (Yes/No, yes may also mean a mixture of live and dead oysters). Even if all are dead the following should be done:

- Identify the densest area of oysters/oyster shells (live and/or dead), note if the oysters/oyster shells in this area are in:

1) Reef formation (= 90-100% coverage and growing on each other)
2) Clusters (<90% coverage but growing on top of each other in clumps, this includes large oysters with only small live oysters)
3) Solitary

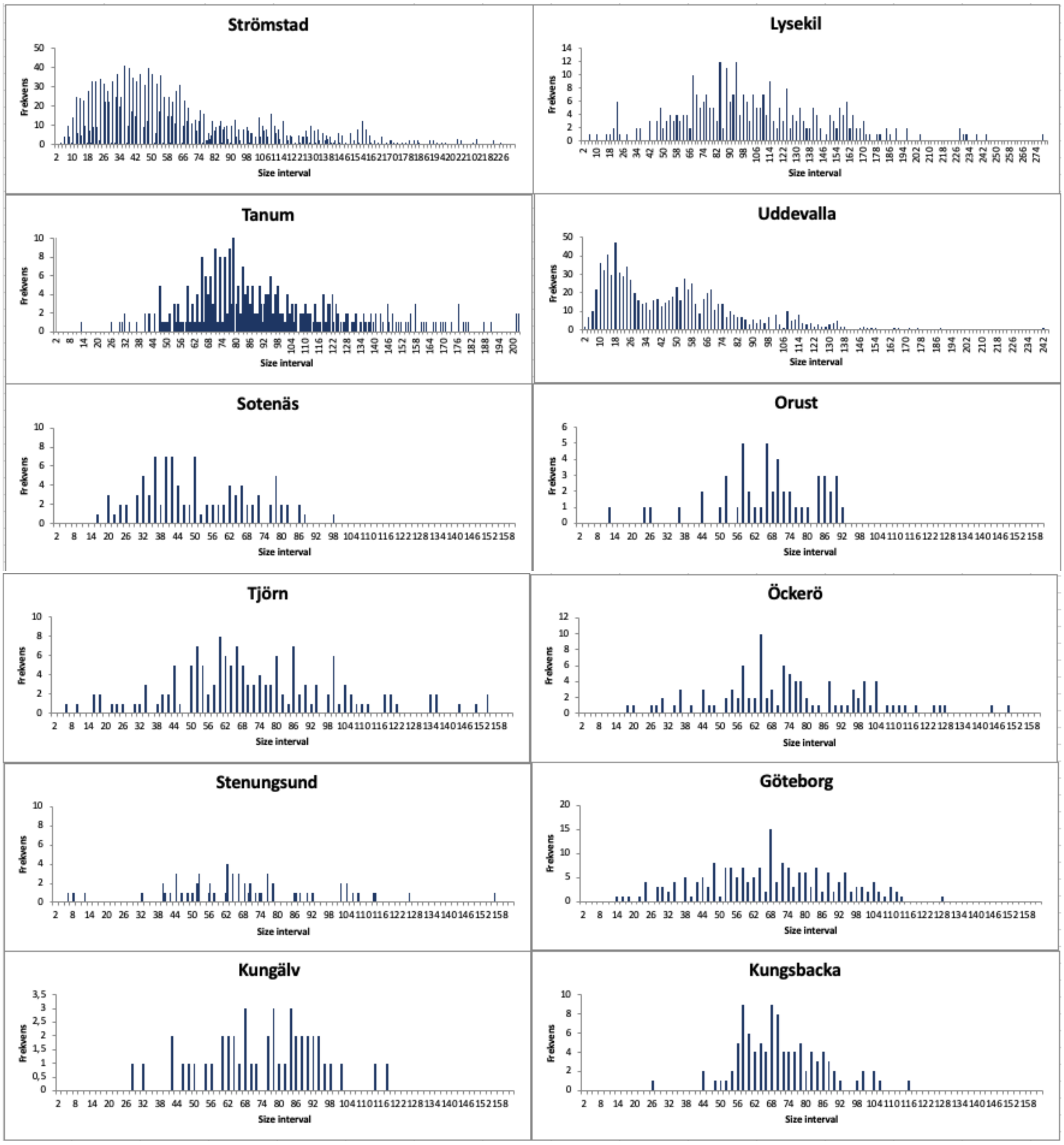
The densest type should be noted (i.e., reef > cluster > solitary), there will be several different types on some sites, but it is the densest type that determines how the site is assessed

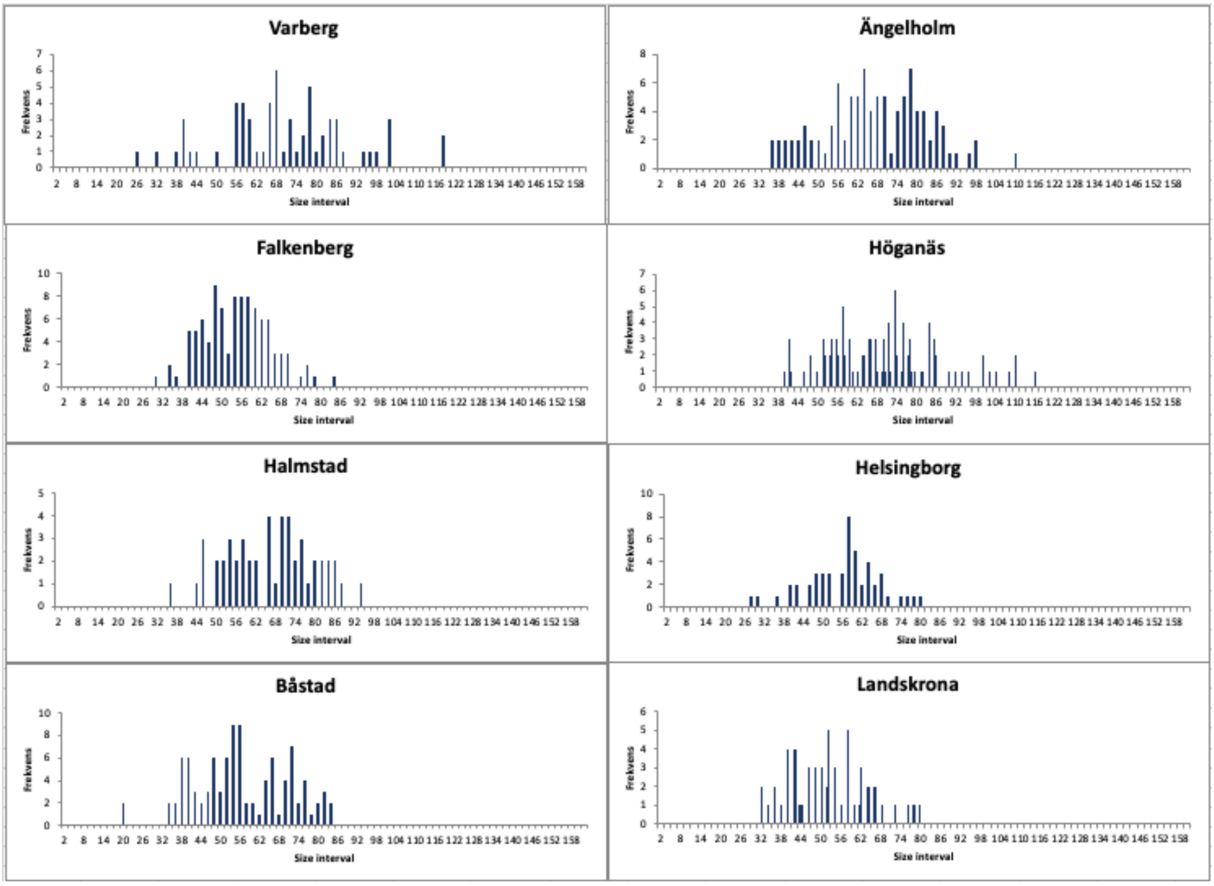
- Classify the bottom substrate as essentially: Mudflat/soft bottom, sand, gravel/shell hash, rocky bottom, boulders/stone slab.
- If live oysters are present, look for small oysters and place a sampling square (0.5 x 0.5m) where the small oysters are, if no small oysters are visible, place the square haphazardly where there are oysters and measure the length (in mm, from umbo to longest shell length) of 100 live oysters in the square. Make sure to check large oysters for attached small oysters. Write down the lengths in consecutive rows with commas in between, e.g., 102, 87, 88, 34, etc. Place the measured oysters in a box. The aim is to have a random sampling of the length so that not only large oysters are measured.

Put all measured oysters back in each square when you have finished. The measurements should be representative of the locality. If 100 individuals are not reached in a square, place a new square randomly on the locality and continue measuring. Note the number of each sampling square.

- Other observations. Please describe the area in general (e.g., depth distribution of oysters, presence of macroalgae, whether there is eelgrass adjacent to the oysters and whether you see clear signs of recruitment (i.e., oysters smaller than 20 mm).

8.2 Municipality length frequency histograms





8.3 Classification table

Table 1: Summary table for invasion stage classification

Municipality	Site	Salinity (PSU) summer	T (°C) Summer	T (°C) Winter	Recruitment	Population structure	Site classification	Municipality classification	Lat	Lon	Survey source	Visited
Strömstad	Svalhagen	25,5	18,8	4,3	Yes	Reef	Established reef/high density	Established reef/ high density	58.8683	11.1548	2022 SDM Square Survey	No
	Kockholmen	25,5	18,6	4,3	Yes	Reef/Cluster	Established reef/high density		58.8331	11.1414	2022 SDM Square Survey	No
	Tjärnö	25,2	19,7	3,1	Yes	Cluster	Source		58.8743	11.1461	Added site	Yes
Tanum	Skredsvik	25,5	18,3	4,3	No		Source	Established reef/ high density	58.4873	11.3100	2022 SDM Square Survey	No
	Grebbestad1	25,5	18,5	3,9	Yes	Cluster	Source		58.6720	11.2508	Grebbestad High school 2023	No
	Grebbestad2	25,5	18,5	3,9	No	Reef	Established reef/high density		58.6721	11.2523	Grebbestad High school 2023	No
	Grebbestad3	24,6	18,5	4,3	Yes	Reef	Established reef/high density		58.6723	11.2517	Grebbestad High school 2023	No
Sotenäs	Skepsudden	24,0	19,5	3,2	Yes	Cluster	Source	Source (reproduction)	58.4047	11.3993	Added site	Yes
Lysekil	Smalsundet	23,4	18,4	4,1	Yes	Reef	Established reef/high density	Established reef/high density	58.2484	11.4399	2022 SDM Square Survey	No
Uddevalla	Getevik	20,7	19,1	2,6	Yes	Reef	Sink	Sink (survival)	58.2754	11.5061	2022 SDM Square Survey	No
Orust	Broccoli garden	20,0	19,5	2,0	Yes	Cluster	Sink	Sink (survival)	58.1254	11.8175	Added site	Yes
Stenungsund	NG513	20,0	19,5	2,2	Yes	Cluster	Sink	Sink (survival)	57.9906	11.8018	2022 SDM Square Survey	No
	Näs	19,8	19,2	2,8	No	Cluster	Sink		58.1069	11.8238	Added site	Yes
Tjörn	NG33	22,4	18,8	3,3	Yes	Cluster	Source	Source (reproduction)	58.0446	11.5104	2022 SDM Square Survey	No
	NG90	21,3	18,8	3,7	No	Cluster	Source		57.9414	11.5793	2022 SDM Square Survey	No
	NG72	22,0	19,0	3,6	Yes	Cluster	Source		58.0072	11.5573	2022 SDM Square Survey	No

Municipality	Site	Salinity (PSU) summer	T (°C) Summer	T (°C) Winter	Recruitment	Population structure	Site classification	Municipality classification	Lat	Lon	Survey source	Visited
Kungälv	NG79	22,1	18,8	4,1	No	Cluster	Survival	Survival	57.8618	11.5599	2022 SDM Square Survey	No
	NG160	20,4	18,9	3,5	No	Cluster	Survival		57.8810	11.6409	2022 SDM Square Survey	No
	NG88	21,4	18,8	3,9	No	Cluster	Survival		57.8965	11.5784	2022 SDM Square Survey	No
Öckerö	NG223	20,7	18,9	3,8	No	Cluster	Source	Source (reproduction)	57.7444	11.6689	2022 SDM Square Survey	No
	SG179	18,8	19,0	3,7	No	Cluster	Source		57.6687	11.6530	2022 SDM Square Survey	No
	NG248	20,7	18,9	3,8	No	Cluster	Source		57.7563	11.6820	2022 SDM Square Survey	No
Göteborg	SG585	19,1	19,3	3,2	No	Cluster	Source	Source (reproduction)	57.6096	11.8942	2022 SDM Square Survey	No
	SG503	12,5	19,1	3,1	Yes	Cluster	Sink		57.6387	11.8062	2022 SDM Square Survey	No
	SG510	10,4	19,0	2,7	No	Cluster	Sink		57.6308	11.8126	2022 SDM Square Survey	No
Kungsbacka	Onsala Halvon	20,3	19,0	3,8	No	Cluster	Survival	Survival	57.3720	11.9838	l - Helsingborg Su	Yes
Varberg	Ringhals	19,2	19,3	3,8	Yes	Solitary	Source	Source (reproduction)	57.2680	12.1081	nghals Survey 20	Yes
Falkenberg	Grimsholmen	16,6	19,3	3,0	No	Cluster	Survival	Survival	56.8551	12.5476	nghals Survey 20	Yes
Halmstad	12	16,2	19,3	3,0	No	Solitary	Survival	Survival	56.6410	12.7804	nghals Survey 20	Yes
	Bengtsgård	15,3	19,5	2,9	–	Solitary	Survival		56.7406	12.6236	Artportalen	Yes
Laholm	Lagaoset	13,8	19,3	3,0	–	No oysters	Future settlement possible	Future settlement possible	56.5513	12.9457	Added site	Yes
Båstad	Bastad	13,6	19,4	3,3	Yes	Cluster	Source	Source (reproduction)	56.4348	12.8423	inez Garcia et al.	Yes
	Torekov	14,3	19,0	3,4	–	Solitary	Source		56.4283	12.6265	Ahlers et al. 2020	Yes
Ängelholm	64865852	13,1	19,2	3,4	No	Cluster	Future settlement possible	Survival	56.2382	12.8149	Artportalen	Yes
	98757030	12,7	19,2	3,5	–	No oysters	Future settlement possible		56.2517	12.8268	Artportalen	Yes
	Rönne	13,1	19,2	3,5	–	No oysters	Survival		56.2723	12.8335	nghals Survey 20	Yes
Höganäs	Arlid 2	12,9	19,2	3,8	No	Cluster	Survival	Survival	56.2751	12.5739	Ahlers et al. 2020	Yes
	Revets Badplats	13,3	18,9	3,6	No	Solitary	Survival		56.2333	12.6885	nghals Survey 20	Yes
	Molle	13,1	19,1	3,5	No	Solitary	Survival		56.2827	12.4933	nghals Survey 20	Yes
	Norra Häljaröd	13,9	18,7	3,6	–	Solitary	Survival		56.2216	12.7613	Artportalen	Yes
Helsingborg	Helsingborg	12,4	18,8	3,7	–	Solitary	Survival	Survival	56.0480	12.6877	inez Garcia et al.	Yes
	Raa	13,0	18,6	3,6	No	Cluster	Future settlement possible		55.9910	12.7409	inez Garcia et al.	Yes
	Domsten	12,7	18,7	3,7	–	No oysters	Survival		56.1162	12.6042	inez Garcia et al.	Yes
	Gravarliden/Sofiero	11,9	18,7	3,8	–	No oysters	Future settlement possible		56.0799	12.6617	Artportalen	Yes
Landskrona	Borstahusen	11,4	18,7	3,7	No	Solitary	Survival	Survival	55.8948	12.8003	inez Garcia et al.	Yes
	Alabodarna 1	11,7	18,7	3,8	No	Solitary	Survival		55.9396	12.7734	Ahlers et al. 2020	Yes
	Landskrona	11,2	18,9	3,5	–	No oysters	Future settlement possible		55.8678	12.8176	Ahlers et al. 2020	Yes
Kävlinge	Barsebackshamn	10,3	18,7	3,7	–	No oysters	Future settlement possible	Future settlement possible	55.7568	12.9023	inez Garcia et al.	Yes
	98681469	9,9	18,9	3,6	–	No oysters	Future settlement possible		55.7366	12.9606	Artportalen	Yes
	Barsebäckstrand	10,0	18,8	3,5	–	No oysters	Future settlement possible		55.7712	12.9254	Added site	Yes
Lomma	Lomma Smabatshamn	9,4	19,5	3,7	–	No oysters	Future settlement possible	Future settlement possible	55.6746	13.0579	nghals Survey 20	Yes
	Bjarred Hamn	9,5	19,4	3,6	–	No oysters	Future settlement possible		55.7206	13.0069	nghals Survey 20	Yes
	Långa bryggan	9,5	19,4	3,6	–	No oysters	Future settlement possible		55.7098	13.0222	Added site	Yes
Malmö	Malmo	9,4	19,0	3,8	–	No oysters	Future settlement possible	Future settlement possible	55.6104	12.9728	inez Garcia et al.	Yes
	Utsiktspunkt Öresund	10,1	18,7	3,8	–	No oysters	Future settlement possible		55.5710	12.8957	nghals Survey 20	Yes
	Ribersborg Kallbadhus	9,4	19,0	3,8	–	No oysters	Future settlement possible		55.6044	12.9662	nghals Survey 20	Yes
	Klagshamn Strand	10,0	18,7	3,7	–	No oysters	Future settlement possible		55.5249	12.8954	nghals Survey 20	Yes

Municipality	Site	Salinity (PSU) summer	T (°C) Summer	T (°C) Winter	Recruitment	Population structure	Site classification	Municipality classification	Lat	Lon	Survey source	Visited
Vellinge	SkaNor Hamn	8,9	18,6	3,7	–	No oysters	Future settlement possible	Future settlement possible	55.4162	12.8293	nghals Survey 20	Yes
	Höllviken Falsterbokanalen N	9,8	19,0	3,3	–	No oysters	Future settlement possible		55.4126	12.9307	nghals Survey 20	Yes
	Lilla Hammar	9,8	18,9	3,3	–	No oysters	Future settlement possible		55.4495	12.9476	nghals Survey 20	Yes

Note XVI: Sites sorted by municipality with associated abiotic and biotic data as well as source information and coordinates. Municipalities highlighted by county, where Skåne is the darkest gray, Halland in the middle and Västra Götaland as the lightest gray. Dashes in the recruitment column indicates that recruitment could not be found due to absence of oysters. Population structure is color coded by severity (low: green, high: red). Color coding for Invasion stage classification on municipality level according to the revised model.

8.4 Data for regression analysis

Table 2: Overview of regression analysis data

Sites with length measurements	Sites with recruitment	Number of recruits	Total number of live oysters measured	Recruitment proportion	Recruitment trans.
Tjärnö	yes	5	33	0,15	0,41
Svalhagen	yes	243	948	0,26	0,54
Kockholmen	yes	75	946	0,08	0,30
Grebbestad 1	no	0	52	0,00	0,10
Grebbestad 2	yes	1	103	0,01	0,14
Grebbestad 3	no	0	66	0,00	0,10
Grebbestad 4	no	0	43	0,00	0,10
Skredsvik	yes	1	158	0,01	0,13
Skeppsudden	yes	8	100	0,08	0,30
Smalsundet	yes	13	323	0,04	0,23
Getevik	yes	335	918	0,36	0,66
Broccoli garden	yes	2	50	0,04	0,23
NG408	yes	1	5	0,20	0,48
NG149	no	0	6	0,00	0,10
NG180	no	0	11	0,00	0,10
NG2	no	0	16	0,00	0,10
NG271	no	0	9	0,00	0,10
NG33	yes	5	24	0,21	0,49
NG330	no	0	13	0,00	0,10
NG37	no	0	4	0,00	0,10
NG400	yes	1	7	0,14	0,40
NG72	yes	2	28	0,07	0,29
NG90	no	0	26	0,00	0,10
NG513	no	0	13	0,00	0,10
Näs	yes	3	50	0,06	0,27

NG124	no	0	13	0,00	0,10
NG160	no	0	7	0,00	0,10
NG191	no	0	7	0,00	0,10
NG233	no	0	6	0,00	0,10
NG79	no	0	8	0,00	0,10
NG88	no	0	5	0,00	0,10
NG105	no	0	12	0,00	0,10
NG164	no	0	7	0,00	0,10
SG179	no	0	15	0,00	0,10
NG248	no	0	14	0,00	0,10
SG249	yes	1	12	0,08	0,31
NG252	no	0	15	0,00	0,10
NG223	no	0	23	0,00	0,10
NG224	yes	1	5	0,20	0,48
NG352	yes	7	46	0,15	0,41
SG434	no	0	4	0,00	0,10
SG392	no	0	7	0,00	0,10
SG472	no	0	13	0,00	0,10
SG585	no	0	48	0,00	0,10
SG445	no	0	6	0,00	0,10
SG503	yes	1	46	0,02	0,18
SG510	no	0	21	0,00	0,10
SG418	no	0	3	0,00	0,10
Onsala	no	0	101	0,00	0,10
Ringhals	yes	1	62	0,02	0,16
Grimsholmen	no	0	100	0,00	0,10
Bengtsgård	no	0	50	0,00	0,10
Båstad	yes	2	100	0,02	0,17
Rönne	no	0	100	0,00	0,10
Revet	no	0	50	0,00	0,10
N. Hjälaröd	no	0	50	0,00	0,10
Arild	no	0	3	0,00	0,10
Domsten	no	0	50	0,00	0,10
Ålabodarna	no	0	6	0,00	0,10
Borstahusen	no	0	50	0,00	0,10

Note XVII: Recruitment proportions, (Asin(Sqrt(x+0.01)) and salinity for each of the 60 sites with available length measurement data included in the regression analysis.