DEPARTMENT OF MARINE SCIENCES

Habitat preferences of the Pacific oyster (*Magallana gigas*) in the early invasion stages

Alice Hedensjö

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Supervisors:	Ane T Laugen (Department of Natural Sciences, University of Agder) and Åsa Strand (Department of Marine Sciences, University of Gothenburg; Department of Environmental Intelligence, IVL Swedish Environmental Institute)
Examiner:	Ann Larsson (Department of Marine Sciences)

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Alice Hedensjö – POPULAR SCIENTIFIC SUMMARY

Pacific oysters like rocks and love marinas when they spread along southern Swedish coasts

Invasive species have harmed ecosystems and economies worldwide. Many invaders, however, can have both negative and positive impacts. One example of such species is the widespread Pacific oyster (*Magallana gigas*). While Pacific oysters can change coastal environments and disturb recreational areas, they can also create habitat for many native species and become a new food resource.

To assess Pacific oysters' overall impact and to detect them early when they arrive in new areas, we need to predict where they are most likely to invade. Several environmental factors likely influence where the oyster can thrive, including wave exposure, water depth, the availability of hard surfaces to settle on, and salinity (how salty the water is). Yet, few studies have investigated which habitats Pacific oysters prefer to invade first when they spread to new areas.

To address this research gap, I aimed to identify habitat preferences of the Pacific oyster on the Swedish southwest coast (Gothenburg-Malmö). Using field surveys and complex modeling, I predicted where and in what numbers the oysters occur along the coast based on their habitat preferences. Furthermore, I estimated the total population size and weight of oysters across different habitat types.

I found that Pacific oysters prefer to inhabit rocks, boulders, cliffs, or human-made structures. These consolidated surfaces may act like steppingstones, helping the oysters to spread. In particular, Pacific oysters thrived in


Pacific oysters in Vejby strands marina, Ängelholm

marinas, with 4-6 times more oysters and 11-15 times more oyster weight per unit area compared to natural rocky habitats.

I also found that salinity didn’t affect where the oysters were found. This was unexpected based on prior beliefs but could be because the oysters are adapting to their new environment, as recent genetic evidence suggests.

Overall, my findings suggest that Pacific oysters can have specific preferences for where they live when they invade new areas. This information is important for guiding strategies of how to limit Pacific oysters’ spread and for assessing their impacts on the Swedish southwest coast.

Supervisors: **Ane T Laugen and Åsa Strand**

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ABSTRACT

Predicting the spread of invasive species is crucial for early detection and assessment of ecological and economic impact. One emerging tool that can assist such predictions habitat suitability modeling (HSM, also known as species distribution modeling). While only species in the latest invasion stage meet the environmental equilibrium assumption underlying HSM, models calibrated in the early invasion stages can reveal initial habitat preferences and potential niche shifts, thus playing a crucial role in assessing factors promoting dispersal and impact. Hitherto, early-stage models are scarce for the Pacific oyster (*Magallana gigas*), a widespread non-native species. The Pacific oyster has spread along Scandinavian coastlines over the past two decades, but its habitat preferences on the Swedish southwest coast have never been quantified. Using region-specific surveys and two-stage HSM, I quantified habitat preferences, predicted occurrences (presence-absence) and abundances, and estimated population sizes and biomasses of the Pacific oyster in the early invasion stages on the Swedish southwest coast. The availability of consolidated substrate (rock, boulder, cliff, or artificial substrates) emerged as a key predictor of occurrence and thus abundance, suggesting that rocky shores and artificial structures may act as ‘stepping-stones’ facilitating range expansion. Particularly, marinas were identified as ‘hotspot’ habitats at the invasion front, predicted to favor 4-6 times more abundance and 11-15 times more biomass of Pacific oysters per unit area than natural rocky habitats. Surprisingly, salinity had neglectable influence on oyster occurrences, potentially reflecting local adaptation as suggested by recent genetic insights. Based on these findings, I suggest that Pacific oysters can have both specific and distinct habitat associations in regions where they are in the early invasion stages. My study forms a critical basis for management priorities and further studies quantifying overall impact of the Pacific oyster on the Swedish southwest coast.

KEYWORDS Habitat suitability modeling • Occurrence-abundance distributions • Early invasion stages • *Magallana gigas* • Habitat preferences • Population size and biomass

1 INTRODUCTION

Invasive species are considered one of the most severe human-induced threats to global biodiversity (e.g., Essl et al., 2020), including to that of marine ecosystems (e.g., Anton et al., 2019; Bax et al., 2003). Alongside adversely affecting communities of native species, invasive species can have extensive impact on ecosystem function (Anton et al., 2019) and associated services, including those supporting fisheries (Haubrock et al., 2020), human health (Mazza et al., 2014), and social well-being (Jones, 2016). Marine species introductions are mostly mediated through shipping and aquaculture pathways (Tricarico et al., 2016). Once introduced in the wild, unaided dispersal within and between non-native regions can also occur via natural means (Hulme, 2009; Wood et al., 2021). Early interventions of invasive species are believed to be the most effective in the long-term (Geburzi & McCarthy, 2018). Yet, management of invasive species tends to lag their proliferation due to delayed detection and challenges involved in assessing, often context-dependent, impacts of the invader (Ahmed et al., 2022; Essl et al., 2017; Katsanevakis et al., 2014).

To enable early detection and objective impact assessments, it is crucial to identify and predict habitats exposed to invasion. Habitat suitability modeling (HSM), also known as species distribution modeling, has become a popular tool to spatiotemporally predict species invasions (e.g., Goldsmith et al., 2020; Sarà et al., 2018). The goal of HSM is to statistically link field observations of the species to environmental conditions and thereby approximate its realized niche (Guisan et al., 2017). Applying HSM to biological invasions, however, is challenging because the spatiotemporal distribution of the species changes over the course of invasion (e.g., Hattab et al., 2017). Following the introduction to a non-native area, the species typically begin by exhibiting localized presences of overall low abundances (i.e., lag stage) before rapidly expanding spatially and in population size (i.e., expansion stage, Geburzi & McCarthy, 2018). During these early stages of invasion, the species is not in equilibrium with its environment. Only in the latest invasion stage (i.e., established stage, Geburzi & McCarthy, 2018), the species meet the environmental equilibrium assumption underlying HSM (Gallien et al.,

2012) and accordingly, most HSMs appear to have been calibrated in global or established species ranges (e.g., Beaumont et al., 2009; Bergström et al., 2021; Gallien et al., 2012).

While HSMs calibrated in late stages of invasions may prevent the underestimation of the species' habitat suitability (Václavík & Meentemeyer, 2011, but see Barbet-Massin et al., 2018), they may also overlook important information about advancing populations (Gallien et al., 2012). For example, populations at invasion fronts may differ from established ones in their environmental requirements due to ecological or evolutionary reasons (i.e., niche shifts, e.g., Battini et al., 2019; Pack et al., 2022). It is also possible that species in the early invasion stages prefer to invade certain suitable habitat types before others (e.g., due to habitat selection, Morris, 2003; Núñez-Tobajas et al., 2024; Pinochet et al., 2020; Rosenzweig, 1981). Hence, the deficiency of HSMs calibrated in early invasion stages, particularly those considering abundance distributions, limits the ability to identify key factors driving dispersal and impact, thereby hindering the development region-specific management strategies and early-detection monitoring programs. Importantly, early-stage models can reveal conditions and areas that initially favor high prevalences and abundances of the invader, thus playing a crucial role for assessing ecological impact linked to exposure-time (Green & Crowe, 2013; Mortensen et al., 2018). This is especially relevant for invasive species with the ability to alter and/or create habitats as the magnitude and nature of impact by these ‘ecosystem engineers’ (Jones et al., 1994) over time depends on both the types of habitats they invade and their abundances (Green & Crowe, 2013; Green & Crowe, 2014; Sousa et al., 2009).

One example of an invasive ecosystem engineer with highly context-dependent effects is the Pacific oyster (*Magallana gigas*, e.g., Hansen et al., 2023; Herbert et al., 2016; Padilla, 2010). Originating from southeast Asia and introduced mainly for aquaculture, feral Pacific oysters have spread intensively along European coastlines in recent years (e.g., Laugen et al., 2015; Reise et al., 2017a; Wrange et al., 2010). The oysters have become a problem in recreational areas, where their sharp shells have injured visitors

(Herbert et al., 2016). Furthermore, observations of Pacific oysters cooccurring with the declining blue mussel (*Mytillus edulis*) and flat oyster (*Ostrea edulis*) have raised ecological concern (e.g., Andriana et al., 2020; Baden et al., 2021; Guy et al., 2018; Kochmann et al., 2008; Zwerschke et al., 2018), although there is no evidence of competitive exclusion. Many studies rather suggest that the oyster can replace lost ecosystem functions and services of these native bivalves and potentially even facilitate their comeback (e.g., Christianen et al., 2018; Markert et al., 2010; McAfee & Connell, 2021; Mortensen et al., 2019; Reise et al., 2017b; Zwerschke et al., 2020). Furthermore, while Pacific oysters have been shown to enhance local species richness, notably in sedimentary habitats due to structurally complex assemblages providing novel habitat for native species, they have also been linked to changed community structures and the spread of secondary invaders (Dolmer et al., 2014; Green & Crowe, 2013; Lang & Buschbaum, 2010; Markert et al., 2010; Mortenssen et al., 2022; Norling et al., 2015).

Despite extensive research on its context-dependent effects, studies quantifying habitat preferences of the Pacific oyster in its early invasion stages are surprisingly scarce, with existing HSMs relying on presence-absence data (Kochmann et al., 2013; Reamon et al., 2021). Wave exposure is one factor that can affect the abundance of introduced bivalves (e.g., Branch et al., 2008) and Pacific oysters tend to generally be more abundant in sheltered than in wave-exposed sites, such as in marinas (Teschke et al., 2020) or on sheltered sedimentary shores (e.g., Reise et al., 2017). However, findings on the predictive influence of wave exposure on occurrence (presence-absence) distributions of the oyster has varied (Bergström et al., 2021; Kochmann et al., 2013; Reamon et al., 2021; Reamon et al., 2022). For example, Pacific oysters have been observed to successfully colonize offshore windfarms in the north sea (De Mesel et al. 2015). An apparent trend in wave-exposed areas is that the oysters firmly cement to surfaces of consolidated substrates, such as large rocks or artificial structures (pers. observation). Adhesion to these stable substrates seems to be common also in areas where the Pacific oysters are in the early invasion stages (Kochmann et al., 2013; Teschke et al., 2020). This suggests that, if consolidated substrates are preferred in the early invasion stages, wave exposure might have limited influence on where Pacific oysters are found.

Traditionally, shallow depths (<3 m), temperatures above 20°C and salinities above 20 psu are believed to be important factors for the establishment of the Pacific oyster in new temperate areas (e.g., Diederich et al., 2005; Dolmer et al., 2014; Fabioux et al., 2005; Muranaka & Lannan, 1984). Recent insights, however, suggest that niche shifts in temperature and salinity may enable invasion of colder and less saline habitats compared to native or established ranges (deWit et al., in prep.; Pack et al., 2021). Yet, salinity has been hypothesized to influence the distribution of Pacific oysters in the southern edge of their Swedish range (e.g., Durkin 2021; Wrange et al., 2010). In this region, however, the oyster's habitat preferences have never been quantified.

The aim with this study was therefore to quantify habitat preferences and predict the distribution of the Pacific oyster on the Swedish southwest coast. More specifically, I employed a two-stage HSM approach with the objectives of (1) quantifying habitat preferences, (2) spatially predicting occurrences and abundances, and (3) with abundance predictions estimating regional population sizes and biomasses of the Pacific oyster. I hypothesized that the coverage of consolidated substrates is a stronger predictor of Pacific oyster occurrences than wave exposure, but that wave exposure influences the abundance of the oysters. Furthermore, I addressed the hypothesis that salinity influence occurrences and abundances of Pacific oysters at the invasion front.

2 METHODS

The Swedish southwest coast shows a southward decline in surface salinity from about 25 psu in northern Kattegat to about 10 psu in Öresund (E.U. Copernicus Marine Service Information, 2019) and a tidal range often less than 0.2 m (Fonselius, 1987). In the northern part of the coast, between Gothenburg and Varberg, the coast is fragmented and encompasses a diversity of habitat types that vary in bottom substrate composition and wave conditions. In this region, the Pacific oyster was first observed in 2007 (Wrange et al., 2010) and although field observations have been reported from a growing number of localities, the oyster is presumably still in the early invasion stages (Le Gall, 2022). South of Varberg, the coastline shows a more homogenous morphology characterized by extensive stretches of sandy beaches exposed to wave action. Here, the Pacific oysters seemingly arrived around 2013 and have in the last six years primarily been observed inhabiting marinas and piers, with an apparent overall southward decline in abundance (Laugen & Strand, pers. communication). The Pacific oyster's current Swedish range seemingly does not extend south of Malmö (Durkin, 2021; Laugen., pers. observation; Roesch, 2023).

To account for both transitions in the coastal environment and potentially two, yet early, invasion stages, I applied separate survey designs in the two regions (section 2.1) for subsequent modeling and parameter estimations (section 2.3). While I aimed to delineate the current distribution of Pacific oysters between Gothenburg and Varberg, I aimed to predict invasion-susceptible habitats southwards between Varberg and Malmö, that is, preferred conditions and areas likely to be, but not necessarily yet have been, invaded.

2.1 Site selection and field surveys

I conducted (assisted by a team) field surveys of Pacific oysters and associated habitats along the Swedish southwest coast between June and September 2023 (see section 3.1 for information about study area and site locations).

In the northern region, from Gothenburg (57.7 N°, 11.9 E°) to Varberg (57.1 N°, 12.2 E°), I surveyed 89 sites using a stratified random survey design over three depth categories: 0.0-0.5, 0.5-3.0 and 3.0-6.0 m. I decided not to survey deeper than 6 m as the prevalence of the oyster has been predicted to be almost zero deeper than 4 m in its core distributional range in northern Sweden (Bergström et al., 2021). I adopted a field protocol used in previous surveys for distribution models of the Pacific oyster in Scandinavia (Bergström et al., 2021; Reamon et al., 2021; Reamon et al., 2022). To avoid spatial autocorrelation issues in subsequent modeling, study sites were separated by at least 100 m.

I surveyed the shallowest depth category (0.0-0.5 m) using a 40 m manual line transect and five 0.5x0.5 m replicate squares. In each square, I counted live and dead Pacific oysters and measured live shell sizes (length, height, and width to nearest mm). Furthermore, I classified and quantified a variety of habitat variables (Table A1), including minimum and maximum water depth adjusted for the current water level (RH2000 system) and the percent coverage of various substrate types. If I observed the Pacific oyster in any of the five squares or within 1.5 m on each side of the line transect in the correct depth interval, I noted the oyster as present at a study site.

I surveyed the two deeper depth categories (0.5-3.0 and 3.0-6.0 m) using a 0.8 x 40 m video transect (Thorngren et al., 2017). To film each transect, I towed a sledge mounted with a GoPro hero 8 camera along the seafloor with a motorboat. To ensure visual quality of the videos, I limited the tow speed to ≤0.4 kts. I measured the maximum and minimum water depth of each transect using boat sonar or a measuring stick. I adjusted measured depths for the current water level and, if obtained from the sonar, for its attachment depth. After field work, I analyzed filmed transects using the CyberLink software (CyberLink Corp, 2022). In two approximately 0.8 x 20 m video replicates of each transect, I assessed live and dead Pacific oyster counts and, in 10 images, the substrate composition. If types of bottom substrates were not possible to distinguish under canopies of macroalgae or eelgrass, I made assumptions based on knowledge of the biology of the vegetative genera (e.g., Køie & Kristiansen, 2022) or on visible sections of the image or replicate transect.

In the southern region, from Varberg (57.2 N°, 12.2 E°) to Malmö (55.5 N°, 12.9 E°), where I aimed to predict invasion-susceptible habitats, I developed a targeted survey design to optimize the probability of finding the oyster while avoiding bias in subsequent modeling. To account for previous field observations of Pacific oysters in this region while representing environmental variability, I surveyed 45 sites to 1.0 m depth over three habitat categories: marinas, piers, and natural rocky habitats, that is, sites having rock, boulders, or cliff present (as defined in Table A1). To avoid bias in the site selection, I randomized 4-6 sites in total (1-2 per habitat category, separated by at least 100 m) in each municipality along the coast.

If the Pacific oyster was present at a study site at inspection, I conducted the survey in the highest abundance area (assessed upon visual inspection) using five 0.5x0.5 m squares placed within a larger rectangle. This larger rectangle varied in size (10x0.5, 10x1.0 and 10x10 m) based on a visual assessment of the overall surface inclination of the survey area (>50%, 20-50% and 0-20% inclination, respectively). In each of the five replicate squares, I recorded live and dead Pacific oyster counts and habitat variables, including adjusted minimum and maximum depth and the percent coverage of various substrate types (Table A1). I measured sizes of all live Pacific oysters in the larger rectangle if they were less than 100 individuals. If they exceeded 100 individuals, I measured sizes only in the five replicate squares. To ensure capture of small-scale habitat conditions representing oyster presences while avoiding bias in count estimates, I consistently placed the first replicate square to cover as many oysters as possible but randomized the placement of remaining four within the larger rectangle. If the Pacific oyster was absent at a study site, I randomized placement of all five squares in the inspected study area to record the habitat structure of the site.

2.2 Quantifying observed abundance variations between habitat- or depth categories

To investigate whether observed Pacific oyster abundances (sum of counts across replicate squares/video transects standardized by the sampled area) differed between depth- or habitat categories, I fitted zero inflated negative binomial models (ZINB, pscl package, Zeileis et al., 2008) for each region. I chose ZINB based on comparisons of chi-squared tests of dispersion and alike information criteria (AIC) with standard Poisson, zero-inflated Poisson, and standard negative binomial models (Blasco-Moreno et al., 2019). I selected the best-fit ZINB model based on the lowest AIC of models under either constant or different levels of zero-inflation across categories (Blasco-Moreno et al., 2019).

2.3 Modelling of Pacific oyster occurrences and abundances

To quantify the habitat preferences and spatially predict occurrences and abundances of the Pacific oyster, I implemented a two-stage modeling approach (Hill et al., 2017, Fig. 1). In the first stage, I modelled occurrences using ensembles of multiple models fitted with a variety of model algorithms (section 2.3.1). In the second stage, I modelled oyster abundances using random forest regressions (section 2.3.2). These abundance models included continuous predicted probabilities of occurrence as a predictor variable in addition to a set of habitat variables (Fig. 1).

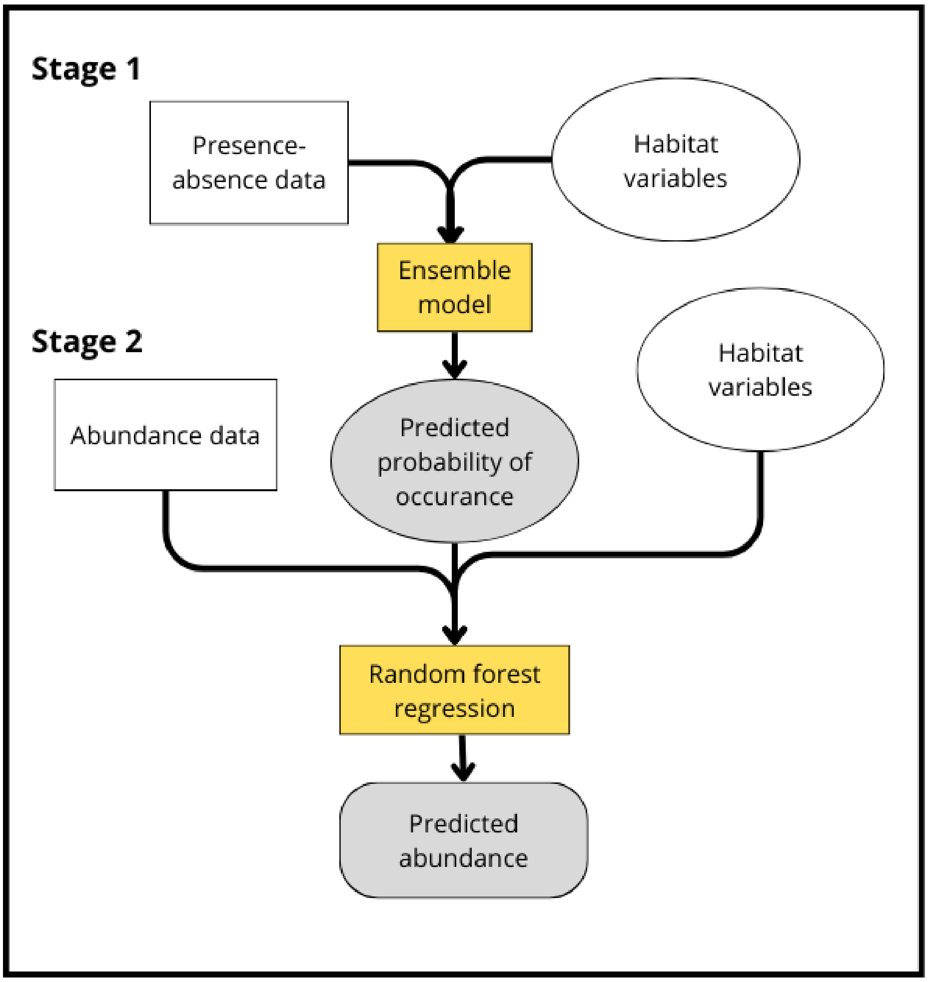

Fig. 1. The general process of modelling of occurrence and abundance of a species in two stages (adapted from Hill et al., 2017). The circles represent predictor variables, and the rectangles (white) represent observed response variables used to fit the models (yellow). Continuous probabilities of occurrence predicted by ensemble models constructed in stage one serves as an additional predictor variable during abundance-modelling in stage two. Model outputs are in grey.

The habitat variables I used in occurrence and abundance models included different combinations of water depth, wave exposure, salinity, and percent consolidated substrate (Table 1). These variables have previously been used, although not specifically consolidated substrate, in distribution models of the Pacific oyster in Scandinavia (Bergström et al., 2021; Reamon et al., 2021; Reamon et al. 2022). I defined consolidated substrate as the sum coverage of rock, boulder, cliff, and artificial substrates (as defined in Table A1). I obtained data of water depth (average of adjusted minimum and maximum depths) and percent consolidated substrate from field measurements and filmed transect (as described in section 2.1). I extracted the wave exposure from a simple wave model at a spatial resolution of 25 m (Wennberg et al., 2006) and subsequently depth attenuated it according to Bekkby et al. (2008). To account for the enclosure of marinas by wave-protecting walls, seemingly not accounted for by the exposure model in certain marinas, I substituted marina exposures exceeding 100 000 m^{-2} s^{-1} (i.e., classified as above sheltered, Wennberg et al., 2006) with the average exposure of those below this threshold. I extracted the average minimum monthly salinity for 2021/2022 from a model with a spatial resolution of about one nautical mile (E.U. Copernicus Marine Service Information, 2019). If a surveyed site was not covered by a salinity pixel, I assigned it with the salinity of the spatially nearest pixel.

I constructed two pairs of occurrence and abundance models for the Pacific oyster in each study region, each featuring a set of two to four habitat variables (Table 1). I used the fitted models jointly to assess the importance and predictive power of all four habitat variables. I decided, however, to exclude salinity in both Gothenburg-Varberg model pairs due to its low spatial resolution and invisible latitudinal gradient in the region. Furthermore, while I included depth (0-1 m) in both occurrence models for Varberg-Malmö to explore its potential predictive influence, I excluded this variable in the pair of best-fit abundance models. One purpose of the pairwise modeling within regions with and without specific variables was to compare the models' predictive performances and parameter estimates for population size. Another purpose was to enable full-covering spatial predictions. Except the -Cs models, I projected the models only partially in space (section 2.3.3) due to the current lack of full-covering quantitative data of consolidated substrate along the Swedish southwest coast. I performed all modeling in R version 4.3.0 (R core team, 2023).

Table 1. Occurrence and abundance models constructed for *Magallana gigas* in a northern (Gothenburg to Varberg, red) and southern region (Varberg to Malmö, blue) on the Swedish southwest coast. Continuous predictor variables used to fit the models include water depth (m), wave exposure (m^2 s^{-1}), consolidated substrate cover (%), salinity (psu) and predicted probabilities of *M. gigas* occurrences. Positive and negative signs in model names represent the inclusion and exclusion, respectively, of either consolidated substrate (Cs) or salinity (Sal).

Region	**Occurrence model name**	**Predictor variables included in occurrence models**	**Abundance model name**	**Predictor variables included in abundance models**
Gothenburg to Varberg	-Cs	Depth Wave exposure	-Cs	Depth Wave exposure Probability of occurrence
	+Cs	Depth Wave exposure Consolidated substrate	+Cs	Depth Wave exposure Consolidated substrate Probability of occurrence
Varberg to Malmö	-Sal	Depth Wave exposure Consolidated substrate	-Sal	Wave exposure Consolidated substrate Probability of occurrence
	+Sal	Depth Wave exposure Consolidated substrate Salinity	+Sal	Wave exposure Consolidated substrate Salinity Probability of occurrence

2.3.1 Stage 1: Occurrence modeling

I modelled Pacific oyster presence-absence with an ensemble modelling approach using the BIOMOD2 packages (Thuiller et al., 2009; Thuiller et al., 2023). I fitted candidate models for the ensemble models using four algorithms with default parameters: General Linear Models, General Additive Models, General Boosting Models and Random Forest.

For the Gothenburg-Varberg models, where I aimed to predict the current distribution of Pacific oysters based on their habitat preference, I used averaged habitat variables from all five replicate squares. For Varberg-Malmö models, where I aimed to identify invasion-susceptible habitats, I used observed habitat variables only from the first sampling square across surveyed sites. This enabled capturing of small-scale habitat associations and thus separation between preferred and unpreferred conditions, as the first sampling square always represented the oyster's presence if presence occurred at a site. To explore habitat structures and select uncorrelated habitat variables to include in the models (Guisan et al., 2017), I conducted principal component analyses (PCA, vegan package, Oksanen et al., 2017), visual inspections of correlation plots (ecospat package, Di Cola et al., 2017) and variance inflation factor (VIF) tests (usdm package, Naimi et al., 2014) of the variables. As thresholds for variable inclusion, I used the recommended Pearson R=0.70 (Green, 1979) and VIF=5 (Guisan et al., 2017).

I used repeated split samples to train and validate candidate models (Guisan et al., 2017). During model fitting, the data set randomly split into 80% training data and 20% validation data. The function of the training data is to calibrate the model while the function of the validation data is to evaluate the predictive performance of the trained models on "unseen" (semi-independent) data (Guisan et al., 2017). I repeated the process of cross-validation 100 times, allowing for stable internal evaluations of the models.

I evaluated candidate models using both the area under the curve (AUC) and the true skill statistic (TSS). While AUC is a measure of sensitivity (i.e., proportion of presences correctly predicted) versus false positive rate (i.e., proportion of absences incorrectly predicted) at all binary cutoff values between 0 to 1 (Guisan et al., 2017), TSS is a measure of the balance between sensitivity and specificity (i.e., proportion of absences correctly predicted) at a set binary cutoff, such as the one that maximizes both measures (Guisan et al., 2017). After inspection of the evaluation metrics, I included "good" to "excellent" models in the final Gothenburg-Varberg ensembles, with validation AUC and TSS above 0.80 and 0.70, respectively (Araújo et al., 2005; Duan et al., 2014; Nuchel et al., 2018). Due to overall lower cross-validation scores, I included models that were considered at least "fair", with validation AUC and TSS above 0.70 and 0.50, respectively, in the Varberg-Malmö ensembles (Araújo et al., 2005; Duan et al., 2014; Nuchel et al., 2018).

I constructed the final ensemble models using the mean algorithm. The mean algorithm generates the ensemble model by averaging probabilities of occurrence predicted by included models. I confirmed metric correspondence by also implementing the weighted model mean and committee average algorithms (Guisan et al., 2017). Using BIOMOD2 functions, I obtained the importance of each habitat variable based on a three-fold permutation of 1-Pearson R between randomly 'shuffled' and reference predictions (Thuiller et al., 2023). Furthermore, I generated response plots of each habitat variable based on 100 ensemble model predictions of varying values within their observed range (Elith et al., 2005), while the remaining (N-1) habitat variables remained constant at their median (Thuiller et al., 2023). I evaluated the final ensemble models based on the mean calibration AUC of included models.

2.3.2 Stage 2: Abundance modeling

I modelled Pacific oyster abundances with a random forest regression approach using the caret (Kuhn et al., 2008) and randomForest (Liaw & Wiener, 2002) packages. Random forest is a machine-learning technique that builds multiple decision trees during training and then uses the consensus among trees to make predictions (Guisan et al., 2017). Random forest can cope with many zero observation and is robust to overfitting and potentially colinear variables (Guisan et al., 2017; Hill et al., 2017; Prasad et al., 2006; Segal, 2004), making it particularly useful for abundance predictions of the Pacific oyster at an early invasion stage, where both zero-inflation and complex environmental relationships may occur.

I fitted abundance models with site-averages of observed Pacific oyster abundances (individuals · m^{-2}, hereafter ind. m^{-2}) and different sets of predictor variables, which included both habitat variables and ensemble model predicted probabilities of occurrence (Table 1, Fig. 1). To prevent overestimating observed abundances for the Gothenburg-Varberg 0.0-0.5 m sites, I set the abundance to 0.001 ind. m^{-2} for each oyster presence observed between replicate squares within a site. To get representative Varberg-Malmö site-estimates of max abundance, I used, in contrast to the occurrence models, averages of abundances and field observed habitat variables across all five replicate squares for each site.

I used a k-fold cross-validation approach to train and validate the models (Guisan et al., 2017). I selected the k integer to yield approximately five non-zero density points per validation set (i.e., 1/k of the full data set, Hill et al., 2017). I specified the maximum number of trees to be 500, and subsequently visually confirmed a decline and stabilization in the models' error rate before this threshold was reached. I evaluated the models using Root Mean Square Error (RMSE) and Mean Absolute Error (MAE). I selected the optimal model based on the smallest validation RMSE. After letting the selected model predict on the full data set of predictor variables, I calculated the MAE as the mean absolute difference between observed and predicted abundances. Using caret functions with default parameters, I obtained the importance of each predictor variable scaled from 0-100 (Kuhn et al., 2008).

2.3.3 Projecting models

To predict occurrences and abundances of the Pacific oyster in unsampled areas, I projected the models onto geospatial data representing current environmental conditions. Due to availability of high-resolution (25 x25 m) raster layers of depth and depth-attenuated exposure, I was able to make full-covering spatial predictions with the -Cs models between Gothenburg and Varberg. However, due to the current lack of quantitative substrate data of the Swedish southwest coast, I instead let the +Cs models predict on a set of 100 randomly selected 0.0-0.5 m depth pixels distributed in the region. In each of these pixels, I estimated the percent consolidated substrate in satellite images.

This approach allowed me also to project models over marinas and natural habitats between Varberg and Malmö. I did not predict occurrences nor abundances over unsampled piers as I considered their depth and percent cover of consolidated substrate infeasible to representatively estimate or assume. Additionally, I estimated piers to constitute order of magnitudes less total habitable area than marinas and natural habitats. I predicted occurrences in all 54 marinas in the region and in 108 depth pixels (0-1 m) of natural habitats. I did not restrict “natural” occurrence predictions to rocky shores, as these models were trained to predict also in the absence of consolidated substrate (because of site-estimates being from the first replicate square). In contrast, I restricted predictions by abundance models only to “rocky pixels” having more than 0% consolidated substrate, as these models were only trained in the presence of consolidated substrate (because of site-estimates being an average of the five replicate squares). In marinas, I assumed a constant average depth of 0.25 m and a consolidated substrate coverage of 100% to represent floating docks, which upon visual assessments constitute more than 60% of the habitat overall. As when building the models, I substituted exposures in marinas exceeding 100 000 m^{-2} s^{-1} with the average exposure of marinas below this threshold.

In each projection of occurrence models, I used the ensemble model’s default cutoff value (calculated to maximize sensitivity and specificity) to separate presence from absence predictions.

2.4 Estimating regional population sizes and biomasses

Through spatial model predictions of Pacific oyster abundances, shell length measurements and information about the areal extent of different depth- and habitat categories, I made regional predictions of population size and biomass. Between Gothenburg and Varberg, I obtained the areal extent of the three depth categories using raster data. Between Varberg and Malmö, I obtained the areal extent of marinas (0.0-0.5 m depth) through visual satellite measurements and that of rocky habitats by multiplying the prevalence of “rocky pixels” by the total area of 0.0-1.0 m depths.

I estimated total (Gothenburg-Varberg) and maximum total (Varberg-Malmö) population size predicted by each abundance model and depth- or habitat category as:

$$Population\ size_{model,\ category} = Mean\ predicted\ abundance_{model} * Areal\ extent_{category}$$

To estimate the wet weight of individual Pacific oysters observed in the field, I used a length-weight regression equation based on over 6 000 individual oyster samples from the Swedish west coast (Strand et al., unpublished data, Fig. A1):

$$Wet\ weight\ (g) = 0.0023\ x\ Length\ (mm)^{\ 2.3547}$$

In addition to predicting total regional biomasses, I predicted the contribution of distinct size groups to these predictions. I grouped individual oysters sampled in each region into 5 mm length classes and estimated the total number of oysters in each class based on the predicted total population sizes for each region. I then used the mean observed wet weight per length class ($\bar{x}\ weight_{\ length\ class}$) to obtain biomass contributions. By summing the biomass contributions of length classes, I obtained estimates of the total biomass for each region per model and habitat- or depth category as:

$$Biomass_{model,\ category} = \sum_{length\ class\ =1}^{n} \bar{x}\ weight_{\ length\ class} * \ p_{length\ class} * Population\ size_{model,\ category}$$

where n is the number of length classes and $p_{length\ class}$ is the proportion of sampled individuals in each length class.

3 RESULTS

3.1 Observed Pacific oyster occurrences and abundances

Between Gothenburg and Varberg, I observed live Pacific oysters in 32 out of 89 sites (36.0%, Fig. 2), although mostly in the shallowest (0-0.5 m) depth category (24 out of 37 sites, 64.8%). In half of these presence sites, oysters occurred exclusively outside of replicate squares, contributing to a wide range of estimated abundances, ranging from 0.001-9.6 ind. m^{-2} across presence sites (Fig. 3). Across these sites, 11 had abundances exceeding 1 ind. m^{-2} (Fig. 3). At 0.5-3.0 m and 3.0-6.0 m depths, I identified live Pacific oysters in seven out of 29 (24.1%), and in one out of 23 (4.3%), sites, respectively. At these depths, estimated abundances did not exceed 0.41 ind. m^{-2} (Fig. 3). The single Pacific oyster presence observed in the deepest depth category occurred on the bottom of Varbergs marina. As indicated by the ZINB model, the 0.0-0.5 m category had a higher mean abundance (1.23 ind. m^{-2}) than the 0.5-3.0 and 3.0-6.0 m depth categories (0.03 and 0.007 ind. m^{-2}, respectively, P<0.001, Fig. 3, Table A2).

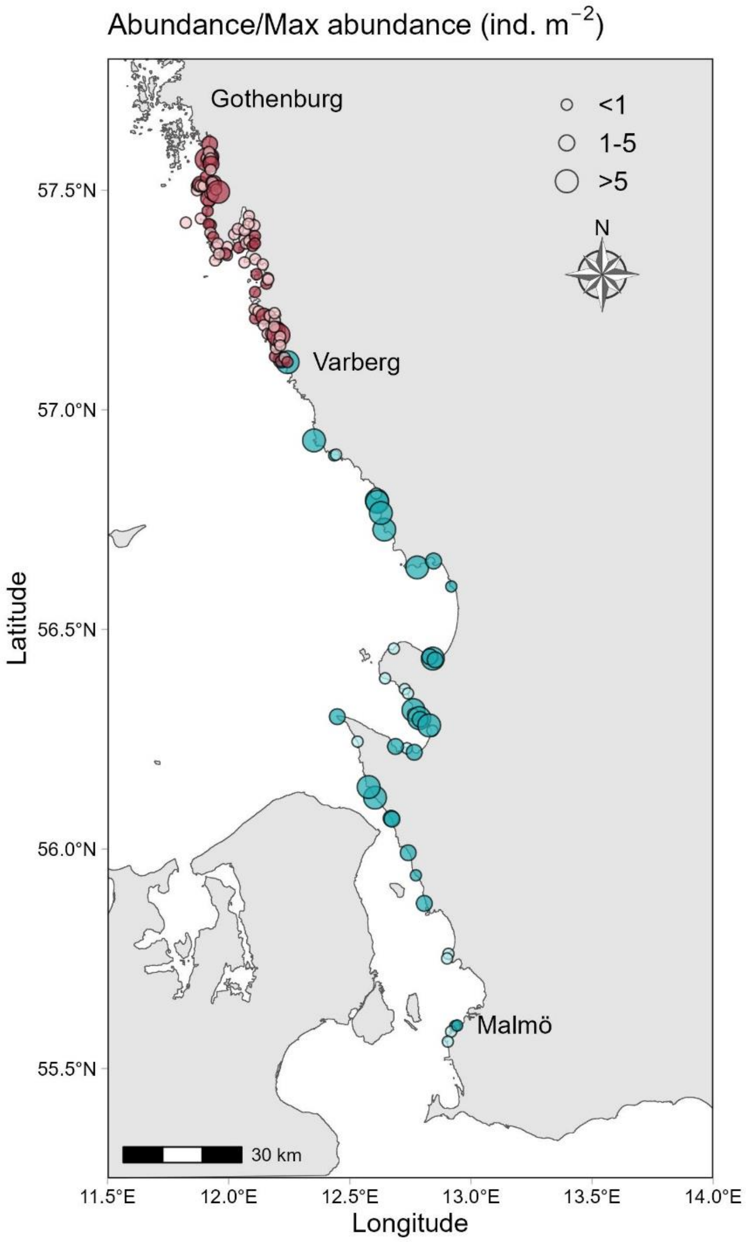

Fig 2. Map of the study area and observed *Magallana gigas* abundances between Gothenburg and Varberg (red, 89 study sites) and max abundances between Varberg and Malmö (blue, 45 study sites) on the Swedish southwest coast. The lighter version of each color represents absences (0 ind. m^{-2}) of the oyster.

From Varberg to Malmö, I found live Pacific oysters in 30 out of the total 45 surveyed sites (66.7%) and presences were distributed across the entire range of the surveyed region (Fig. 2). The three habitat categories had identical prevalence of oysters (10 presences in each, 66.7%) but marinas had a higher mean max abundance (6.9 ind. m^{-2})

than piers (2.2 ind. m^{-2}) and natural rocky habitats (1.9 ind. m^{-2}), as indicated by the ZINB model (P<0.001, Table A3). This despite all habitat categories, but notably marinas, showing great variability in max abundance among presence sites, ranging from 0.8 to 6.4 (natural rocky), 9.6 (pier) and 23.2 (marina) ind. m^{-2} (Fig. 3).

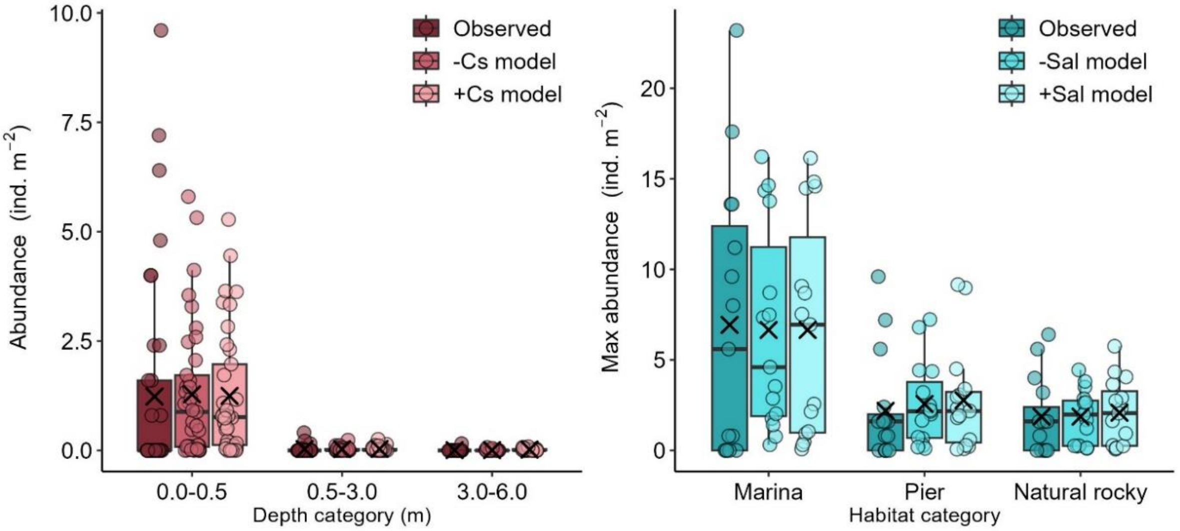

Fig 3. Observed and predicted *Magallana gigas* abundances between Gothenburg and Varberg (left graph in red) over three depth categories (n=37, 29 and 23 from left to right) and max abundances between Varberg and Malmö (right graph in blue) over three habitat categories (n=15 each). Boxes cover the interquartile range (IQR, 25th to 75th percentile), and the whiskers extend 1.5 IQR above or below the box edges. The x marks represent means and the transverse lines medians. Note that the median for the observed abundance in the 0.0-0.5 m depth category is at the 25th percentile. The plus and minus signs represent the inclusion or exclusion of consolidated substrate (Cs) and salinity (Sal) in the abundance models, respectively.

3.2 Occurrence models of the Pacific oyster

Ensemble models of Pacific oyster presences-absences performed excellently (Araújo et al., 2005) for both regions, with mean calibration AUC scores above 0.90 (Table 2). By including consolidated substrate as a variable (+Cs) in the Gothenburg-Varberg ensemble models, the mean calibration AUC increased from 0.92 to 0.96, indicating an increase in predictive power (Table 2). However, the two ensemble models showed opposite trends in sensitivity and specificity. The -Cs model, with a higher specificity (0.93) and cutoff (0.71) than the +Cs model, correctly predicted observed absences about 8% more often (Table 2). In contrast, the +Cs model, with higher sensitivity (0.92) but lower cutoff (0.46) than the –Cs model, correctly identified observed presences about 15% more often (Table 2).

The Varberg-Malmö ensemble models showed excellent calibration (AUC>0.95, Table 2), but were built by fewer models selected by lower internal validation thresholds (AUC: 0.70, TSS: 0.50) compared to the Gothenburg-Varberg ensembles (Table 2). Furthermore, adding an additional variable, in this case salinity, did not yield more candidate models exceeding validation thresholds, but slightly improved the AUC (Table 2). Indeed, the calibrated +Sal model showed the highest AUC (0.97), sensitivity (0.93) and specificity (0.97) across all models and regions (Table 2). The -Sal and +Sal models showed a 6% and 3% higher specificity than sensitivity, respectively, indicating that they were slightly better in predicting absences than presences of the Pacific oyster (Table 2).

Table 2. Comprehensive summary of ensemble models constructed to predict *Magallana gigas* occurrences between Gothenburg and Varberg (red) and Varberg and Malmö (blue). The +Cs model includes consolidated substrate as a predictor in addition to depth and wave exposure. The +Sal model includes salinity as a predictor in addition to depth, wave exposure and percent consolidated substrate. Model algorithms include General Linear Models (GLM), General Additive Models (GAM), General Boosting Models (GBM) and Random Forest (RF). The number of individual models included in an ensemble are those that exceeded the validation thresholds during cross-validation. The binary cutoff is calculated to maximize sensitivity and specificity. The AUC represents the mean calibration Area Under the Curve (AUC) of included models selected by AUC and the True Skill Statistic (TSS).

Ensemble model	**Validation thresholds AUC**	**TSS**	**Model algorithms included**	**Number of models included**	**Binary cutoff**	**Sensitivity**	**Specificity**	**AUC**
-Cs	0.80	0.70	GLM, GAM, RF, GBM	206	0.71	0.78	0.93	0.92
+Cs	0.80	0.70	GLM, GAM, RF, GBM	233	0.46	0.92	0.85	0.96
-Sal	0.70	0.50	GLM, GAM, RF, GBM	104	0.59	0.87	0.93	0.95
+Sal	0.70	0.50	GLM, RF, GBM	68	0.59	0.93	0.97	0.97

Analyses of variable importance showed consistent trends across Gothenburg-Varberg ensemble models (Fig. 4, Table 3). Depth was the most important predictive factor (0.77), followed by the availability of consolidated substrate (0.16), and lastly wave exposure (0.03, Fig. 4, Table 3). Excluding consolidated substrate as a predictor preserved the relative importance between depth and wave exposure but increased the absolute importance of depth (0.92) and decreased that of wave exposure (0.01, Table 3). The highest predicted probability of oyster occurrences was when the depth was less than 1 m, when the availability of consolidated substrate was more than 30%, and when the wave exposure was below 100 000 $m^2 s^{-1}$ (Fig. 4).

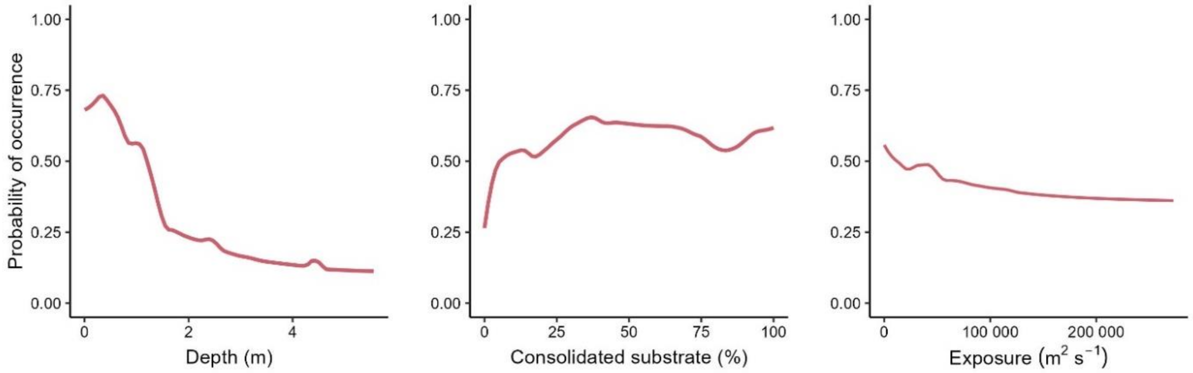

Fig 4. Response plots showing predicted occurrence probabilities of *Magallana gigas* between Gothenburg and Varberg in response to changes in water depth, percent cover of consolidated substrate and wave exposure. Each curve is based on 100 ensemble model predictions on varying values within the range of the observed habitat variable, while remaining (N-1) habitat variables are kept constant at their median.

Depth (sampled to 1 m) showed neglectable influence in the Varberg-Malmö ensemble models (0.06-0.07, Fig 5, Table 3). Instead, the most important factor in this region was the availability of consolidated substrate (0.70-0.74, Table 3). Further emphasizing the importance of this predictor, I could only successfully fit ensemble models (i.e., generating candidate models above validation thresholds) when they included consolidated substrate as a variable. Neither salinity, nor exposure, were found to contribute significantly to the ensemble models (Table 3). Albeit having little influence in the models (<0.07, Table 3), response curves tended to peak at wave exposures between 50 000-100 000 $m^2 s^{-1}$, at depths between 0.2-0.6 m and at salinities above 12 psu (Fig. 5). For consolidated substrate, the highest predicted probability of Pacific oyster occurrences was observed when the cover was >50% (Fig. 5).

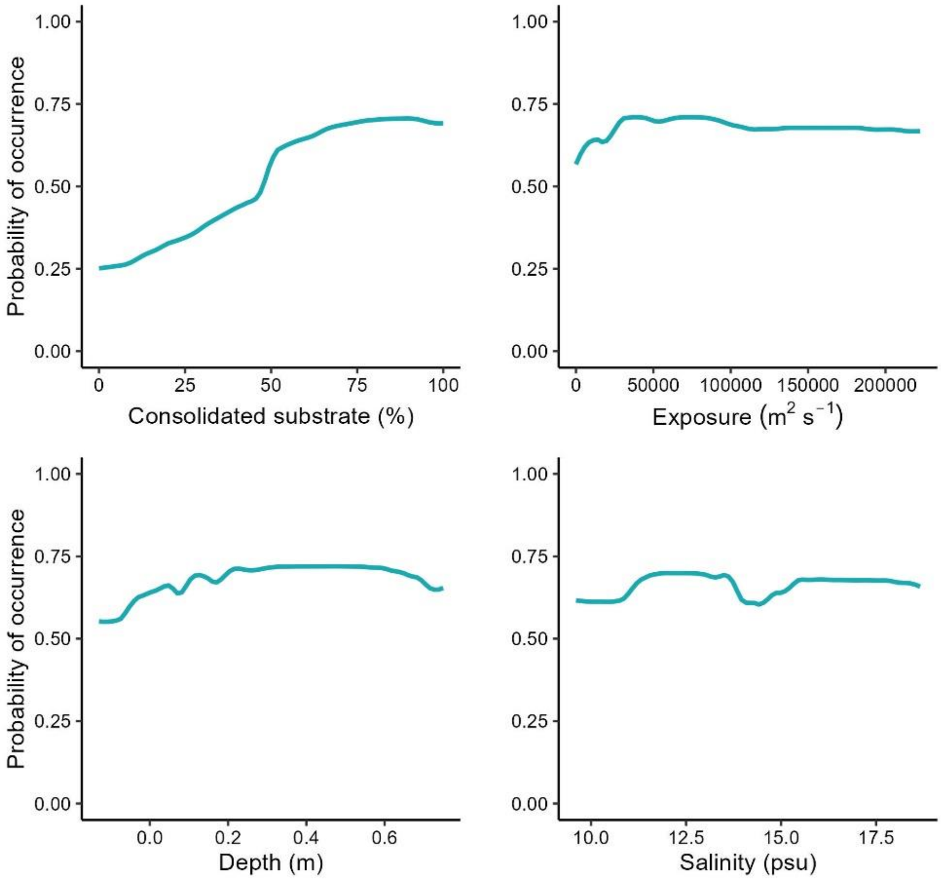

Fig. 5. Response plots showing predicted occurrence probabilities of *Magallana gigas* between Varberg and Malmö in response to changes in percent consolidated substrate, wave exposure, water depth and salinity. Each curve is based on 100 ensemble model predictions on varying values within the observed range of the habitat variable, while remaining (N-1) habitat variables are kept constant at their median.

Table 3. Importance of predictors in ensemble models of occurrence constructed for *Magallana gigas* between Gothenburg and Varberg (red) and Varberg to Malmö (blue). Models are fitted both with consolidated substrate (+Cs) or salinity (+Sal) as predictors and without (-Cs and -Sal, respectively).

Ensemble model	Depth	Wave Exposure	Consolidated substrate	Salinity
-Cs	0.92	0.01	-	-
+Cs	0.77	0.03	0.16	-
-Sal	0.07	0.01	0.67	-
+Sal	0.06	0.07	0.74	0.05

3.3 Abundance models of the Pacific oyster

Abundance models were in general successful in predicting observed Pacific oyster abundances (Figs. 6 & 7). The root-mean-square error (RMSE) after a 6-fold cross-validation was <2 for both the Gothenburg-Varberg models, and ≤4 for both Varberg-Malmö models (Table 4). When the models predicted over full data sets, the mean absolute error (MAE) between observed and predicted abundances was <0.35 ind. m^{-2} for Gothenburg-Varberg models and <1.20 ind. m^{-2} for Varberg-Malmö models (Table 4). Across all models and regions, the predicted probability of the oyster's occurrence was the most important abundance predictor (Table 4).

Table 4. Summary of random forest models constructed to predict *Magallana gigas* abundances between Gothenburg and Varberg (red) and Varberg and Malmö (blue). The plus and minus signs represent the inclusion and exclusion, respectively, of consolidated substrate (Cs) or salinity (Sal) as predictors in the models. RMSE represents the root mean square error of predicted and observed abundances during a 6-fold cross-validation. MAE represents the mean absolute error between predicted and observed abundances after the model predicted on the full data set of predictor variables. A predictor is included as top three only if it exceeded an importance score of zero.

Random forest model	RMSE	MAE	Top three predictor contribution	Predictor importance
-Cs	1.47	0.35	1. Occurrence probability 2. Depth 3. –	100.0 12.4 –
+Cs	1.43	0.33	1. Occurrence probability 2. Depth 3. Consolidated substrate	100.0 44.9 10.8
-Sal	4.03	1.19	1. Occurrence probability 2. Exposure 3. –	100.0 91.2 –
+Sal	3.18	1.09	1. Occurrence probability 2. Exposure 3. Salinity	100.0 81.9 4.0

Between Gothenburg and Varberg, predicted oyster abundances tended to be higher at high occurrence probabilities (>0.60), at shallow water depths (<0.5 m) and at high coverages of consolidated substrate (>60%, Table 4). Despite these models showing high predictive accuracies overall (Table 4), they tended to overpredict zero and low (<0.001 ind. m^{-2}) abundances (Fig. 6). This trend was driven by the 0.0-0.5 m depth category having overall high occurrence probabilities (0.69-0.74 on average) but a wide observed abundance range (0.0-9.6 ind. m^{-2}). Conversely and yielding both convergences toward the observed 0.0-0.5 m abundance mean (Fig. 3) and overall low MAEs (Table 4), both models generally underpredicted high observed abundances (>3 ind. m^{-2}, Fig. 6).

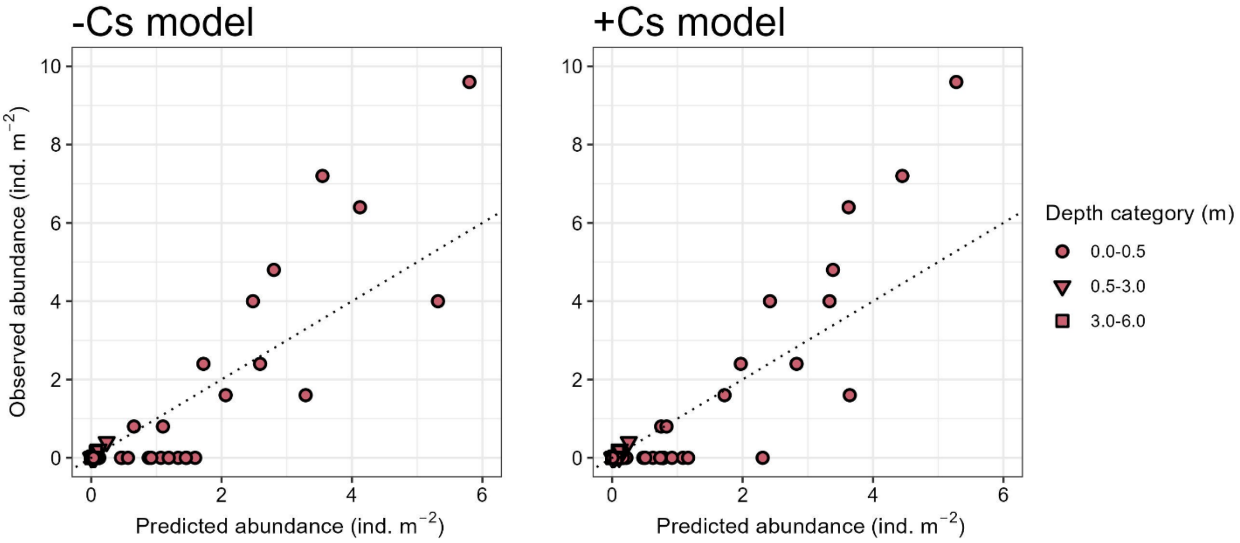

Fig 6. Observed versus predicted *Magallana gigas* abundances between Gothenburg and Varberg. Predicted abundances are from the abundance model with consolidated substrate as a predictor (+Cs) and the one without (-Cs). Shapes represent depth intervals in which observed and predicted abundances occurred.

Between Varberg and Malmö, predicted max abundances of the Pacific oyster tended to be higher at high probabilities of occurrence (>0.55), at low wave exposures (<50 000 m^2 s^{-1}) and at salinities >12 psu (Table 4). While the observed and predicted max abundances for this region corresponded well (Fig. 7), the -Sal model showed a trend of underpredicting observed abundances above five ind. m^{-2} and those in marinas (Figs. 3 & 7).

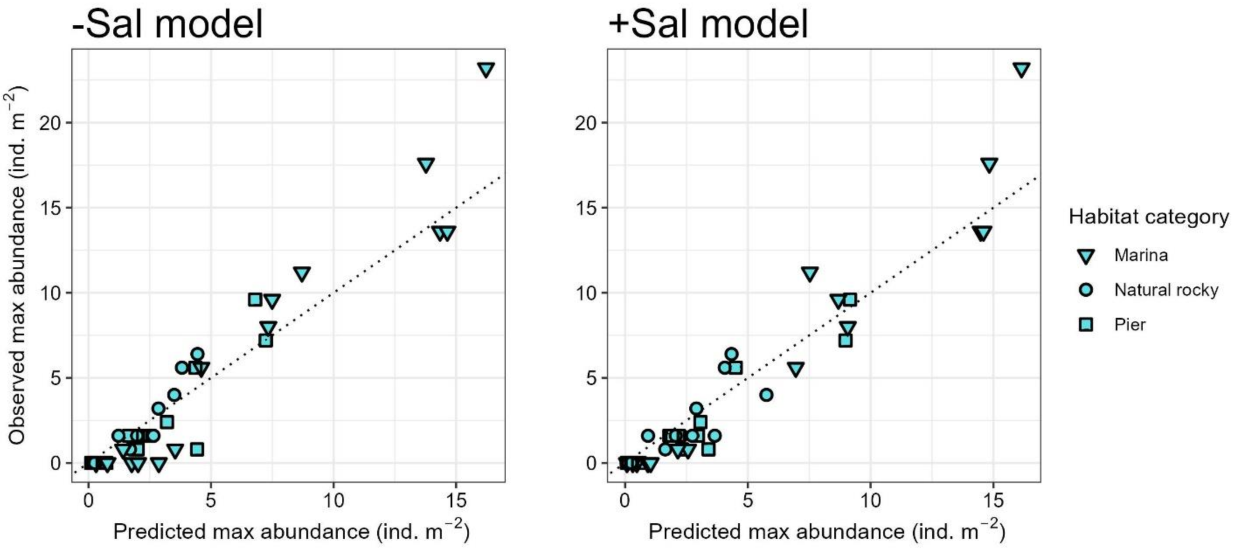

Fig 7. Observed versus predicted max abundances of *Magallana gigas* between Varberg and Malmö. Max abundances are predicted by the abundance model with salinity as a predictor (+Sal) and the one without (-Sal). Shapes represent habitat categories in which observed and predicted max abundances occurred.

3.4 Regional predictions of occurrences, abundances, and biomasses

Between Gothenburg and Varberg, the full-covering -Cs model predicted the Pacific oyster to be present in 10% of the entire area of 0.0-6.0 m depths (Fig. 8A). These presences (i.e., 25x25 m pixels having a probability of occurrence >0.71, Table 2) occurred exclusively at depths shallower than 0.6 m. Between 0.0-0.5 m depths, this model predicted the oyster to be present in 83% of the area. In the same depth range, the +Cs model forecasted, despite having a lower binary cutoff (0.46, Table 2), an 81% prevalence of the oyster (Fig. 8C). Furthermore, this model predicted a 42% and 100% prevalence at 0% and >20% consolidated substrate cover, respectively.

Abundances predicted by the +Cs model ranged from 0.0-3.7 individuals m^{-2} while those predicted by the –Cs model ranged from 0.0-5.8 individuals m^{-2} in the 0.0-0.5 m depth range (Fig. 8B & 8D). Individual +Cs predictions did not exceed 1 ind. m^{-2} in areas where consolidated substrate was absent. As indicated by non-overlapping 95% confidence intervals, the -Cs model predicted a higher mean abundance (1.4 ind. m^{-2}) at 0.0-0.5 m than the +Cs model (1.1 ind. m^{-2}, Table 5). Consequently, at these shallow depths, the

-Cs model estimated about 6.5 million and 370 tons more oysters between Gothenburg and Varberg than the +Cs model (Table 5).

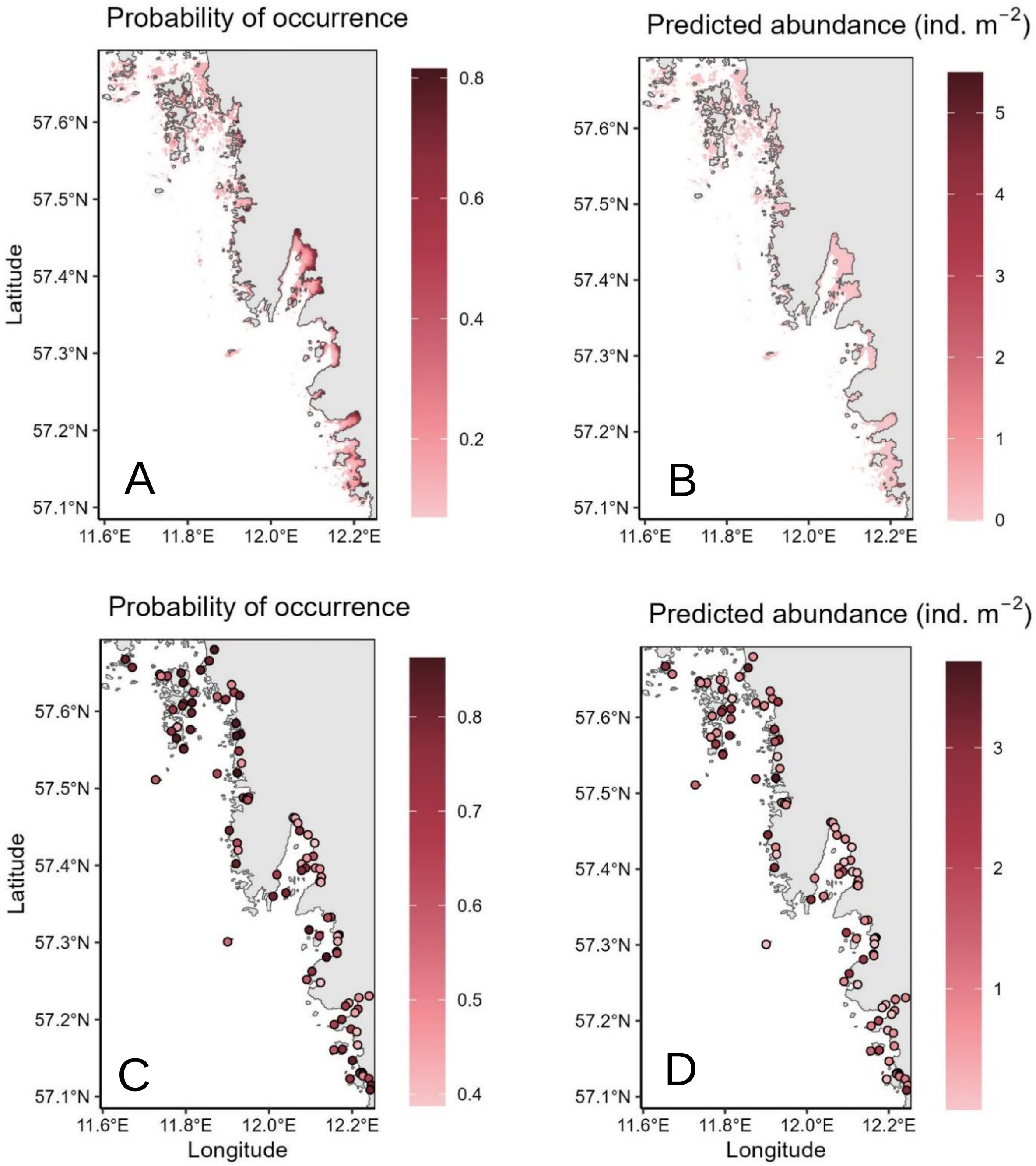

Fig. 8. Predicted distributions of *Magallana gigas* between Gothenburg and Varberg. Models with depth and wave exposure as predictors predict occurrence probabilities (A) and abundances (B) in the entire area of 0.0-6.0 m depths. Models including consolidated substrate predict occurrence probabilities (C) and abundance (D) on a set of 100 pixels (25 x 25 m) in the depth interval 0.0-0.5 m. Note the varying ranges of occurrences and abundances between regions.

Table 5. Predicted population parameters of *Magallana gigas* between Gothenburg and Varberg. Mean abundances, total populations size and biomass are predicted by abundance models which either included or excluded consolidated substrate as a predictor (+Cs, and -Cs, respectively). While -Cs estimates are based on a spatially full-covering model projection, +Cs estimates are based on a set of 100 spatial pixel predictions. 95% confidence intervals for mean predicted abundances are obtained through bootstrapping (100 x resampling).

Depth category (m)	Predicted mean abundance (ind. m^{-2}, 95% CI)		Areal extent (km^2)	Predicted total abundance (ind.[6])		Predicted total biomass (tons)	
	-Cs model	+Cs model		-Cs model	+Cs model	-Cs model	+Cs model
0.0-0.5	1.39 (1.38-1.40)	1.09 (0.89-1.28)	21.74	30.17	23.79	1744.8	1376.1
0.5-3.0	0.03 (0.03-0.03)	-	62.42	1.72	-	-	-
3.0-6.0	<0.01 (0.00-0.00)	-	87.73	0.26	-	-	-

Between Varberg and Malmö, the +Sal and -Sal models predicted the Pacific oyster to be present (i.e., having an occurrence probability >0.59, Table 2) in 68.5% and 81.5% of marinas, in 20.8% and 18.8% of natural rocky habitats in 9.2% and 8.3% of all natural habitats, respectively (Fig. 9A & 9C). The oyster was predicted to be absent in areas where consolidated substrate was absent.

Both models predicted marinas to have a higher mean abundance than natural rocky habitats (Fig. 9B & 9D), as indicated by non-overlapping 95% confidence intervals (Table 6). Hence, while the total predicted maximum population size and biomass were order of magnitudes greater in natural habitats, simply due to the larger habitable area (Table 6), marinas were predicted to have, per unit area, 4-6 times more abundance and strikingly 11-15 times more biomass of the Pacific oyster.

The large biomass in marinas per unit area was due to Pacific oysters in marinas being overall large relative to natural rocky habitats (Fig. 10). Oysters 105-110 mm (about 140 g, Fig. A1) were as a size class important contributors to the total biomass in marinas, while oysters about 60-65 mm (about 40 g, Fig. A1) were key contributors in natural rocky habitats (Fig. 10). Size trends observed between Gothenburg and Varberg fell between these habitat categories, where oysters about 80-85 mm (about 75 g, Fig. A1) were important contributors to the total biomass between 0.0-0.5 m depth (Fig. 10).

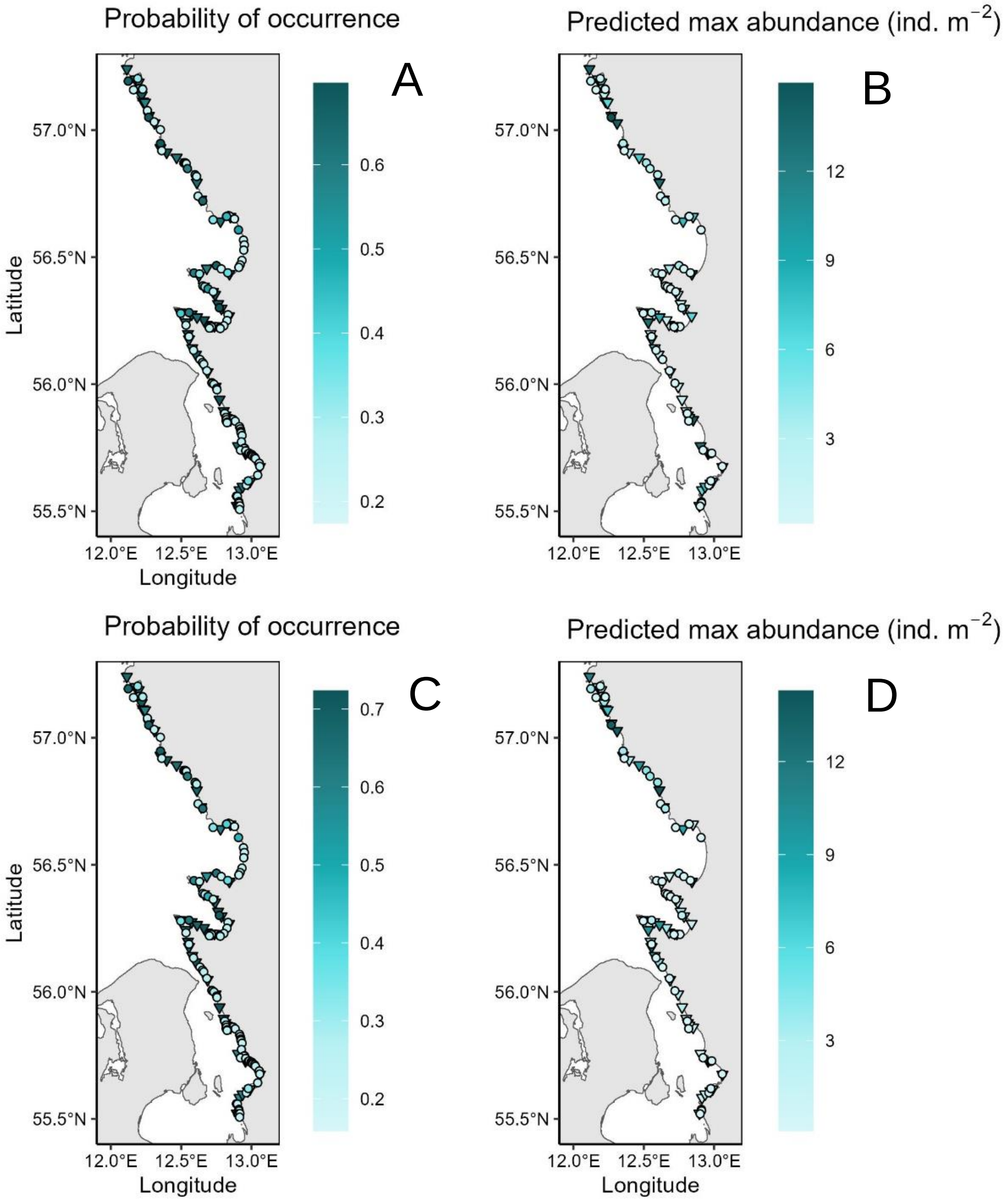

Fig. 9. Predicted invasion-susceptibility of *Magallana gigas* between Varberg and Malmö. Predictions of occurrence probabilities without salinity (A) and with salinity (C) as a predictor are for marinas (N=54) and natural habitats (n=108) as represented by triangle and circles, respectively. Max abundance predictions without salinity (B) and with salinity (D) as a predictor are for marinas and natural rocky habitats (>0% consolidated substrate cover, n=48).

Table 6. Predicted maximum population parameters of *Magallana gigas* between Varberg and Malmö. Mean maximum abundances and total maximum population size and biomass are predicted by abundance models which either included or excluded salinity as a predictor (+Sal, and -Sal, respectively). Mean abundance predictions, and subsequently parameter estimates, in marinas (N=54) are for the assumed 0.0-0.5 depth interval while those in natural rocky habitats (n=48) are for the 0.0-1.0 m interval. 95% confidence intervals for mean predicted abundances are obtained through bootstrapping (100 x resampling).

Habitat category	Predicted mean abundance (95% CI, ind. m^{-2})		Areal extent (km^2)	Predicted total max abundance (ind.^{6})		Predicted total max biomass (tons)	
	-Sal model	+Sal model		-Sal model	+Sal model	-Sal model	+Sal model
Marina	6.46 (5.21-7.77)	4.74 (3.14-6.09)	0.02	0.15	0.11	16.5	12.1
Natural rocky	1.15 (0.29-1.71)	1.14 (0.37-1.72)	31.68	36.51	36.22	1485.6	1473.9

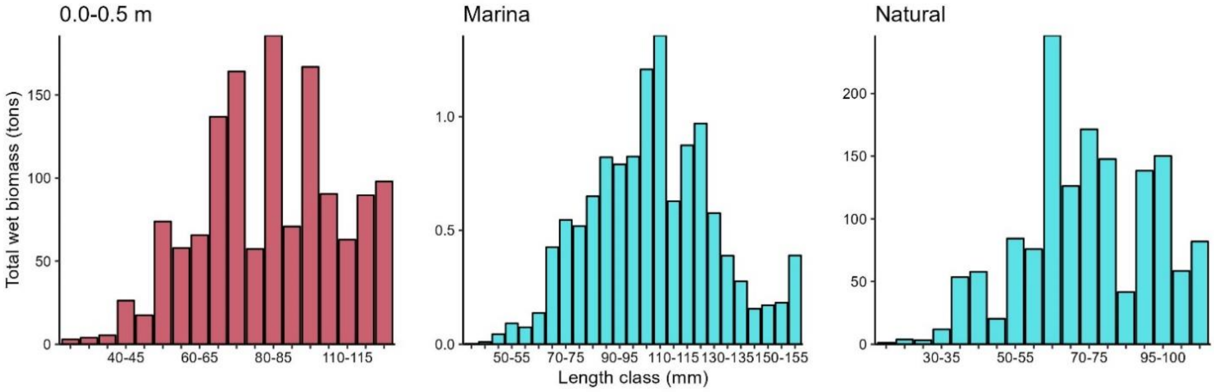

Fig. 10. Contribution of *Magallana gigas* length classes to the total biomass in the 0.0-0.5 m depth category between Gothenburg and Varberg (red) and in marinas and natural rocky habitats between Varberg to Malmö (blue). The total biomass constituted by the length classes are based on frequencies of observed live shell lengths, their mean wet weight, and the population size predicted by the best-fit abundance models (see Table 4). Note varying value ranges on the x and y axes.

4 DISCUSSION

In this study, I demonstrate the successful development of occurrence and abundance models of the Pacific oyster on the Swedish southwest coast, providing novel and important insights into the dynamics of a species invasion in its early stages. Despite inherent limitations in these models (section 4.2), they revealed biologically plausible and specific habitat preferences of the Pacific oyster towards consolidated substrates (rock, boulder, cliff, or artificial substrate) and, particularly, marinas (section 4.1). These findings have important implications for both further research and region-specific management (section 4.3).

4.1 Habitat preferences of the Pacific oyster

My finding of consolidated substrate being an important predictor of Pacific oyster occurrences, and thus also of their abundances, aligns well with my observations of live individuals predominantly being cemented to rock, boulder, cliff, or artificial substrates. Correspondingly, a similar study in intertidal areas in Ireland indicated a positive association between the coverage of 'hard reef' (constituted by bedrock, pebbles, cobbles, or biogenic reefs) and Pacific oyster occurrences at comparable low abundances (0.009-8.5 ind. m^{-2}, Kochman et al., 2013). This is, however, to my knowledge the only distribution model calibrated in the oyster's early invasion stages considering similar substrate types. Indeed, field observations from elsewhere have rarely reported the oyster to mainly invade rocky shores on regional scales (but see Ruesink, 2007), although exploitation of artificial structures, as reflected in my results from the southern area, and blue mussel beds are common (e.g., Diederich, 2005; Dolmer et al., 2014; Reise et al., 2017a; Teschke et al., 2020). The Pacific oyster has also, in contrast to my predictions, extensively colonized and formed reefs in sedimentary habitats (e.g., Herbert, 2016; Troost, 2010), such as in its established Swedish range (pers. observation; Roesch, 2023).

While Pacific oysters are considered generalists, an early-stage preference for stable substrate types (e.g., consolidated substrates) may arise if the hydrodynamic conditions are seldom, in space or time, sufficiently calm for the oysters to establish on sedimentary shores. The initial colonization of soft bottoms (e.g., mud or sand) starts with the oyster settling on unstable hard substrates such as shell debris or gravel (e.g., Troost, 2010), but this can be unfavorable due to dislodgment or turnover by hydrodynamic forces (Fivash et al., 2021; Sousa, 1979). Thus, the invasion of soft bottom requires not only the presence of hard fragments but also repeated long periods of calm hydrodynamic conditions, allowing Pacific oysters to establish and stabilize the substrate by their own mass. These periods of suitable conditions likely occur rarely, especially along homogenous coastlines such as the one between Varberg and Malmö, leaving already stable substrate as the inhabitable option for Pacific oysters in the early invasion stages. Interestingly, a series of field experiments recently demonstrated that the addition of stable artificial structures allowed Pacific oysters to expand their range in an intertidal marsh (Fivash et al., 2021). This 'stepping-stone' function of artificial structures has also been suggested on regional scales (De Mesel et al. 2015; Wood et al., 2021). Furthermore, while Kochman et al. (2013) found influence of 'hard reef' in their logistic model of early-stage Pacific oyster presence-absence in Ireland, they found neglectable influence of wave exposure. This aligns with my hypothesis and findings, suggesting that both artificial and natural consolidated substrates at shallow depths have the potential to facilitate the spatial expansion of Pacific oysters in the early invasion stages.

However, while wave exposure may have little influence on the presence of Pacific oysters across consolidated habitats, it likely plays a complex role in their abundance distribution on natural rocky shores by affecting various pre- and post-recruitment processes (Ruesink, 2007). Although Pacific oysters generally tend to be more abundant in sheltered sites (e.g., Bergström et al., 2021; Greeve et al., 2023; Ruesink, 2007; Teschke et al. 2022), reduced wave-induced stress may not translate into population proliferation on sheltered rocky shores, due to strong biotic pressures like interspecific competition and predation (e.g., Menge & Sutherland, 1987). Similarly, while wave-exposed rocky shores can facilitate the recruitment of opportunistic species by providing bare space for settlement, they are also expected to have a high population turnover due to frequent disturbance (e.g., Dayton, 1971; Sousa, 1979). These population trade-offs associated with levels of wave exposure may be reflected in the Wadden sea, where Pacific oysters in established ranges are present on rocky shores but in seemingly low abundances (<100 ind. m^{-2}, Reise et al., 2017a). They might potentially also explain the unexpected zero influence of wave exposure in my abundance model for the northern region, where the surveyed consolidated substrates were almost exclusively natural. Alternatively, there was an abundance trade-off in the preference for consolidated substrate itself because rocky habitats in this region tend, albeit nonlinearly, also to be wave-exposed (pers. observation).

Potentially by providing both extensive bare space for settlement and shelter from waves, marinas may become early ‘hotspots’ habitats for non-native species (e.g., Airoldi et al. 2015; Connell, 2001; Dafforn et al., 2012; Firth et al., 2021; Teschke et al., 2020). In concurrence, a full coverage of consolidated substrate coupled with wave-shelter drove my southern models to predict marinas to be highly susceptible both to the presence and abundance of Pacific oysters. Corresponding to my occurrence predictions, Pacific oysters have been reported to be twice as prevalent in marinas than in natural bedrock habitats in the southwest UK (Firth et al., 2021). Furthermore, Teschke et al. (2022) showed that marinas promoted a five times higher abundance of Pacific oysters than wave-exposed artificial habitats, reflecting my abundance findings in marinas versus piers. Strikingly, we observed abundances in marinas comparable to those in later invasion stages of the oyster in Scandinavia (20.8-52.5 ind. m^{-2}, Bergström et al., 2021; Reamon et al., 2022). This suggests that marinas may promote the establishment of pioneering populations at the Swedish invasion front.

Another important mechanism by which invasive species can expand their spatial range is local adaptation (e.g., Allendorf et al., 2022). Invasive species generally exhibit high fecundity which may, coupled with multiple source introductions, maintain standing genetic variation allowing for rapid (10-20 generations) adaptation (Allendorf et al., 2022; Lee, 2002; Prentis et al, 2008). With striking correspondence to recent genetic insights (deWit et al., in prep.), I found neglectable influence of salinity in the occurrence model of the Pacific oyster. This finding contradicts not only my hypothesis, but also the previous belief that salinity limits the southward range of the oyster in Sweden (Wrange et al., 2010). For example, in 2007 the southernmost presence of the oyster was observed in Falkenberg (Wrange et al., 2010), approximately 150 km linear distance from its current invasion front. Moreover, preliminary experimental and genetic findings now suggest that southern Pacific oyster populations in Sweden have adapted to an optimal salinity for reproduction of 18 psu and have the potential to further adapt to salinities at 13 psu (deWit et al., in prep.). In interesting correspondence, while I found neglectable influence of salinity on occurrences, the abundances of the oyster were suppressed below approximately 12 psu. In established ranges of northwest Sweden, the optimal salinity for reproduction currently is about 28 psu (deWit et al., in prep.), importantly suggesting that southern Pacific oyster populations have undergone a niche shift. The selective pressure of salinity may reflect even on a global scale, where the Pacific oyster has shown a wider salinity niche in its invaded range compared to its native range (Pack et al., 2021).

Recently, the Pacific oyster was first recorded in the German Baltic sea with a minimum yearly salinity of about 12 psu (Ewers-Saucedo et al., 2020). In interesting correspondence to my findings and suggestions, these oysters attached to cement walls in a marina or to a metal pipe (Ewers-Saucedo et al., 2020). Along the Swedish coast south, the oyster seems to currently be absent south of Malmö (Laugen pers. observation). This is possibly due to both low salinities (about 10 psu) and the scarcity of consolidated substrates on the Swedish southernmost cape. Yet, an ongoing adaptation to lower salinities, coupled with other factors such as temporal variations in the prevailing northward currents, suggest that further spread of the Pacific oyster into the Swedish Baltic Sea may be possible (deWit et al., in prep).

4.2 Model limitations

My occurrence and abundance models were successfully applied based on internal evaluation. Ideally, however, robust generalizations require external evaluation on independent data (Araújo et al., 2005; Guisan et al., 2017). Yet, externally validated HSMs are scarce, leaving it questionable to what extent they can accurately predict species invasions (but see e.g., Barbet-Massin et al., 2018). I did not have enough data points to set aside fully independent test sets, so my models were, like most existing HSMs, only evaluated based on their cross-validation and calibration performance (e.g., Bergström et al., 2021; Reamon et al., 2021). Notably, my occurrence and abundance data came from the same sites, so the ‘probability of occurrence’ found to be the most influential predictor in the abundance models were inherently linked to the rest of the data. While this predictor being important for abundance was not surprising, a more reliable and unbiased approach is to construct the occurrence model on separate data, and then extract independent occurrence probabilities for the abundance model from the spatial projections (Hill et al., 2017). Furthermore, random forest predictions, as reflected in my findings, tend to converge towards the mean (Greeve, pers. communication), which could make the method less accurate in individual site predictions than in estimates of population parameters on regional scales.

Furthermore, my models did not account for methodological absences, that is, the species is present but not detected by the observer (Lobo et al., 2010). I cannot exclude that some oysters in filmed transect of deeper depths (>0.5 m) were missed, especially as dense vegetation often tended to impair the bottom visibility. Hence, it is possible my Gothenburg-Varberg models, and other Scandinavian HSMs using the video methodology, bias the Pacific oyster distribution towards shallow depths (<0.5-3.0, Bergström et al., 2021; Reamon et al., 2021; Reamon et al., 2022). Recent insights suggest that the video method underestimates the Pacific oyster abundance by 23% (Reamon, in prep). This raises a strong need to develop the method of surveying deeper depths, particularly for established ranges, where the Pacific oyster in some areas might have extended its depth range (Reamon et al., in prep). Conversely, however, the spatial depth data in Sweden may potentially underestimate the prevalence and abundance of the oysters at shallow (0-0.5 m) depth, as these 2D pixels do not include vertical cliff walls along the coast.

4.3 Scientific and management implications and outlook

If an invasive species prefers to inhabit consolidated habitats, as illustrated by my findings for the Pacific oyster, its ecological effects will likely be especially pronounced in rocky shores and artificial habitats. While Pacific oysters on consolidated substrate likely induce less direct modification of the underlying substrate compared to those on soft bottoms, their potential impacts on native species communities should not be overlooked. Limited research suggest that the oysters interact with other species in consolidated habitats (Ruesink, 2007), with facilitation and inhibition effects varying depending on their abundances and whether the substrate is natural or artificial (Firth et al., 2020; Green & Crowe, 2013). This context-dependence underlines the need for knowledge building on the ecological and economic impacts of Pacific oysters along the Swedish southwest coast, focusing on artificial structures and natural rocky shores.

My findings suggest that controlling and monitoring consolidated habitats, but notably marinas, at and beyond the invasion front may be crucial for early detection and mitigation, and thereby in preventing the Pacific oyster's range expansion and further establishment in Sweden. Marinas have been shown to source nearby natural rocky habitats with an invasive kelp species (Epstein & Smale, 2018), pointing to the possibility that this may also be the case for the Pacific oyster at the Swedish invasion front. This larval 'spillover' may be especially likely considering the large abundances and individual oyster sizes I observed in marinas. Both population abundance and individual fecundity determines larval production (e.g., Plumbi & Pinsky, 2014), and hermaphroditic oysters generally become more frequently females and produce more eggs with increasing size (e.g., Marshall et al., 2020; Moore et al., 2016). Despite this potential of inducing strong propagule pressure, it is also possible that the marinas host mainly self-sustaining populations. Many marinas can likely experience water residence times exceeding the 3-4 weeks Pacific oyster larvae spend in the water column before settling (Quayle, 1988), thus promoting local retention. Interestingly, I only observed Pacific oysters in the 3-6 depth range in Varbergs marina, suggesting that sink populations fueled from those at shallower depths (<1 m) may occur within the marina itself. This aligns with field observations reported by stakeholders in the region. Regardless of the dispersal dynamics, marinas and floating docks therein have been suggested by multiple studies to host early source populations non-native invertebrates and has been recommended to be prioritized in management (e.g., Arenas et al., 2006; Bishop et al., 2015; Connell, 2001; Foster et al., 2016; Glasby et al., 2007).

My study highlights the need for quantitative spatial substrate data. Due its current lack in Sweden, my best-fit models predicted the distribution and estimated population parameters of the oyster at shallow natural depths, based on less than 1% of total available habitat. I suggest that not accounting for the availability of consolidated substrate may misinform management on the Swedish southwest coast by potentially overestimating population parameters on shallow depths. In addition, overlooking substrate preferences may lead to inaccurate assessments of which habitat types are exposed or susceptible to invasion. The Swedish Agency for Marine and Water Management in Sweden is working on producing full-covering maps of bottom substrate, which will be crucial to enhance the accuracy in my spatial predictions and to quantify ecological impact of the Pacific oyster on the Swedish southwest coast.

I demonstrate the utility of HSM calibrated in the early invasion stages to identify specific and distinct habitat association. I suggest that relying only on models calibrated on established populations may lead to limited accuracy when projected onto early invasion stages due to excessive false-presence error (i.e., predicting the species to be present when it is currently absent), which in turn may misguide early management efforts. In addition, species at invasion fronts, as partly suggested by my results, may have undergone niche shifts (e.g., Pack et al., 2021), limiting the precision of niche estimations from other regions. On the other hand, my models do not delineate the potential range of suitable habitats for Pacific oysters on the Swedish southwest coast. This raises a scientific inquiry of how the Pacific oyster realized niche changes temporally over the course of invasion. A comprehensive approach to investigate changes in niche breadth over time could be to make a time-series of models in an invaded region (Reamon et al., in prep.). For present-day monitoring purposes, however, projecting models from core distributional areas onto the Swedish southwest coast could in some respects be informative, for example, to map depth intervals or sedimentary shores potentially suitable for future establishment of Pacific oysters.

5 CONCLUSION

Occurrence and abundance models for invasive species need to be constructed for different regions and stages of invasion to inform about dynamic habitat associations and prevent misleading impact assessments and management prioritizations. Models calibrated in the early invasion stages can reveal habitats initially favored by the species, thus playing a critical role in identifying factors promoting spread and impact and enabling early detection. Moreover, rapid adaptability among invasive species suggests that niche shifts are likely to emerge at invasion fronts, limiting the spatial transferability of models constructed in other regions. Based on my findings, I suggest that consolidated habitats, in particular marinas by favoring high abundances, can act as steppingstones, facilitating dispersal of Pacific oysters in the early invasion stages. Furthermore, my results contradict prior believes that salinity influence Pacific oyster occurrences in southern Sweden. This suggests, in line with recent genetic insights, that these southern populations may have undergone a niche shift due to local adaptation. My study highlights the need for studies quantifying ecological and economic impact of Pacific oysters in rocky shore ecosystems and in artificial habitats. Furthermore, I recommend that controlling and monitoring marinas at and beyond the invasion front may be critical to limit the range expansion of Pacific oysters in Sweden.

6 REFERENCES

Ahmed, D. A., Hudgins, E. J., Cuthbert, R. N., Kourantidou, M., Diagne, C., Haubrock, P. J., … & Courchamp, F. (2022). Managing biological invasions: the cost of inaction. *Biological Invasions*, *24*(7), 1927-1946.

Airoldi, L., Turon, X., Perkol-Finkel, S., & Rius, M. (2015). Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. *Diversity and Distributions*, *21*(7), 755-768.

Allendorf, F., Funk, W., Aitken, S., Byrne, M., Luikart, G., & Antunes, A. (2022). *Conservation and the genomics of populations* (3d ed., pp. 298-319). Oxford university press.

Andriana, R., van der Ouderaa, I., & Eriksson, B. K. (2020). A Pacific oyster invasion transforms shellfish reef structure by changing the development of associated seaweeds. *Estuarine, Coastal and Shelf Science*, *235*, 106564.

Anton, A., Geraldi, N. R., Lovelock, C. E., Apostolaki, E. T., Bennett, S., Cebrian, J., ... & Duarte, C. M. (2019). Global ecological impacts of marine exotic species. *Nature ecology & evolution*, *3*(5), 787-800.

Araújo, M. B., Pearson, R. G., Thuiller, W., & Erhard, M. (2005). Validation of species–climate impact models under climate change. *Global change biology*, *11*(9), 1504-1513.

Arenas, F., Bishop, J. D. D., Carlton, J. T., Dyrynda, P. J., Farnham, W. F., Gonzalez, D. J., ... & Wood, C. A. (2006). Alien species and other notable records from a rapid assessment survey of marinas on the south coast of England. *Journal of the marine biological association of the United Kingdom*, *86*(6), 1329-1337.

Baden, S., Hernroth, B., & Lindahl, O. (2021). Declining populations of Mytilus spp. in North Atlantic coastal waters—a Swedish perspective. *Journal of Shellfish Research*, *40*(2), 269-296.

Barbet-Massin, M., Rome, Q., Villemant, C., & Courchamp, F. (2018). Can species distribution models really predict the expansion of invasive species?. *PloS one*, *13*(3), e0193085.

Battini, N., Farías, N., Giachetti, C. B., Schwindt, E., & Bortolus, A. (2019). Staying ahead of invaders: using species distribution modeling to predict alien species' potential niche shifts. *Marine Ecology Progress Series*, *612*, 127-140.

Bax, N., Williamson, A., Aguero, M., Gonzalez, E., & Geeves, W. (2003). Marine invasive alien species: a threat to global biodiversity. *Marine policy, 27*(4), 313-323.

Beaumont, L. J., Gallagher, R. V., Thuiller, W., Downey, P. O., Leishman, M. R., & Hughes, L. (2009). Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions*, *15*(3), 409-420.

Bekkby, T., Isachsen, P. E., Isæus, M., & Bakkestuen, V. (2008). GIS modeling of wave exposure at the seabed: a depth-attenuated wave exposure model. *Marine Geodesy*, *31*(2), 117-127.

Bergström, P., Thorngren, L., Strand, Å., & Lindegarth, M. (2021). Identifying high-density areas of oysters using species distribution modeling: lessons for conservation of the native Ostrea edulis and management of the invasive Magallana (Crassostrea) gigas in Sweden. *Ecology and Evolution*, *11*(10), 5522-5532.

Bishop, J. D., Wood, C. A., Yunnie, A. L., & Griffiths, C. A. (2015). Unheralded arrivals: non-native sessile invertebrates in marinas on the English coast. *Aquatic Invasions*, *10*(3).

Blasco-Moreno, A., Pérez-Casany, M., Puig, P., Morante, M., & Castells, E. (2019). What does a zero mean? Understanding false, random and structural zeros in ecology. *Methods in Ecology and Evolution*, *10*(7), 949-959.

Branch, G. M., Odendaal, F., & Robinson, T. B. (2008). Long-term monitoring of the arrival, expansion and effects of the alien mussel Mytilus galloprovincialis relative to wave action. *Marine Ecology Progress Series*, *370*, 171-183.

Christianen, M. J. A., Lengkeek, W., Bergsma, J. H., Coolen, J. W. P., Didderen, K., Dorenbosch, M., ... & Van Der Have, T. M. (2018). Return of the native facilitated by the invasive? Population composition, substrate preferences and epibenthic species richness of a recently discovered shellfish reef with native European flat oysters (Ostrea edulis) in the North Sea. *Marine Biology Research*, *14*(6), 590-597.

Connell, S. D. (2001). Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. *Marine Environmental Research*, *52*(2), 115-125.

CyberLink Corporation. (2022). CyberLink PowerDirector 365. PowerDirector version 21.1.2401.0.

Dafforn, K. A., Glasby, T. M., & Johnston, E. L. (2012). Comparing the invasibility of experimental “reefs” with field observations of natural reefs and artificial structures. *PLoS One*, *7*(5), e38124.

Dayton, P. K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, *41*(4), 351-389.

De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., & Degraer, S. (2015). Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. *Hydrobiologia*, *756*, 37-50.

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., d'Amen, M., Randin, C., ... & Guisan, A. (2017). ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, *40*(6), 774-787.

Diederich, S. (2005). Differential recruitment of introduced Pacific oysters and native mussels at the North Sea coast: coexistence possible?. *Journal of sea research*, *53*(4), 269-281.

Diederich, S., Nehls, G. J. E. E., Van Beusekom, J. E., & Reise, K. (2005). Introduced Pacific oysters (Crassostrea gigas) in the northern Wadden Sea: invasion accelerated by warm summers?. *Helgoland Marine Research*, *59*, 97-106.

Dolmer, P., Holm, M. W., Strand, Å., Lindegarth, S., Bodvin, T., Norling, P., & Mortensen, S. (2014). *The invasive Pacific oyster, Crassostrea gigas, in Scandinavia coastal* *waters: A risk assessment on the impact in different habitats and climate conditions*. Institute of Marine Research. Fisken og Havet Vol. 2.

Duan, R. Y., Kong, X. Q., Huang, M. Y., Fan, W. Y., & Wang, Z. G. (2014). The predictive performance and stability of six species distribution models. *PloS one*, *9*(11), e112764.

Durkin, A., (2021). *Mapping the invasion: spatiotemporal distribution of the Pacific oyster in Scandinavia* [MSc thesis Coastal Ecology]. University of Agder.

Elith, J., Ferrier, S., Huettmann, F., & Leathwick, J. (2005). The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. *Ecological modelling*, *186*(3), 280-289.

Epstein, G., & Smale, D. A. (2018). Environmental and ecological factors influencing the spillover of the non-native kelp, Undaria pinnatifida, from marinas into natural rocky reef communities. *Biological Invasions*, *20*(4), 1049-1072.

Essl, F., Hulme, P. E., Jeschke, J. M., Keller, R., Pyšek, P., Richardson, D. M., ... Rabitsch, W. (2017). Scientific and normative foundations for the valuation of alien-species impacts: Thirteen core principles. BioScience, 67, 166–178.

Essl, F., Lenzner, B., Bacher, S., Bailey, S., Capinha, C., Daehler, C., ... & Roura-Pascual, N. (2020). Drivers of future alien species impacts: An expert-based assessment. *Global Change Biology*, *26*(9), 4880-4893.

E.U. Copernicus Marine Service Information. (2019). Baltic Sea Biogeochemistry Analysis and Forecast (publication no. https://doi.org/10.48670/moi-00009).

Ewers-Saucedo, C., Heuer, N., Moesges, Z., Ovenbeck, K., Schröter, N., & Brandis, D. (2020). First record of the Pacific oyster Magallana gigas (Thunberg, 1793) in the Baltic Sea proper. *Marine Biodiversity Records*, *13*, 1-5.

Fabioux, C., Huvet, A., Le Souchu, P., Le Pennec, M., & Pouvreau, S. (2005). Temperature and photoperiod drive Crassostrea gigas reproductive internal clock. *Aquaculture*, *250*(1-2), 458-470.

Firth, L. B., Duff, L., Gribben, P. E., & Knights, A. M. (2021). Do positive interactions between marine invaders increase likelihood of invasion into natural and artificial habitats?. *Oikos*, *130*(3), 453-463.

Fivash, G. S., Stüben, D., Bachmann, M., Walles, B., van Belzen, J., Didderen, K., ... & Bouma, T. J. (2021). Can we enhance ecosystem-based coastal defense by connecting oysters to marsh edges? Analyzing the limits of oyster reef establishment. *Ecological Engineering*, *165*, 106221.

Fonselius, S. (1987). *Kattegatt-havet i väster*. SMHI Oceanografi No. 18.

Foster, V., Giesler, R. J., Wilson, A. M. W., Nall, C. R., & Cook, E. J. (2016). Identifying the physical features of marina infrastructure associated with the presence of non-native species in the UK. *Marine Biology*, *163*, 1-14.

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N. E., & Thuiller, W. (2012). Invasive species distribution models–how violating the equilibrium assumption can create new insights. *Global Ecology and Biogeography*, *21*(11), 1126-1136.

Geburzi, J. C., and McCarthy, M. L. 2018. How do they do it?–Understanding the success of marine invasive species. In S. Jungblut, V. Liebich & M. Bode (Eds.), *YOUMARES 8–oceans across boundaries: learning from each other* (pp. 109-124). Springer, Cham.

Glasby, T. M., Connell, S. D., Holloway, M. G., & Hewitt, C. L. (2007). Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions?. *Marine biology*, *151*(3), 887-895.

Goldsmit, J., McKindsey, C. W., Schlegel, R. W., Stewart, D. B., Archambault, P., & Howland, K. L. (2020). What and where? Predicting invasion hotspots in the Arctic marine realm. *Global change biology*, *26*(9), 4752-4771.

Green, R. H. (1979). *Sampling design and statistical methods for environmental biologists*. John Wiley & Sons.

Green, D. S., & Crowe, T. P. (2013). Physical and biological effects of introduced oysters on biodiversity in an intertidal boulder field. *Marine Ecology Progress Series*, *482*, 119-132.

Green, D. S., & Crowe, T. P. (2014). Context-and density-dependent effects of introduced oysters on biodiversity. *Biological Invasions*, *16*, 1145-1163.

Greeve, Y., Bergström, P., Strand, Å., & Lindegarth, M. (2023). Estimating and scaling-up biomass and abundance of epi-and infaunal bivalves in a Swedish archipelago region: Implications for ecological functions and ecosystem services. *Frontiers in Marine Science*, *10*, 1105999.

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: with applications in R*. Cambridge University Press.

Guy, C., Blight, A., Smyth, D., & Roberts, D. (2018). The world is their oyster: Differences in epibiota on sympatric populations of native Ostrea edulis and non-native Crassostrea gigas (Magallana gigas) oysters. *Journal of Sea Research*, *140*, 52-58.

Hansen, B. W., Dolmer, P., & Vismann, B. (2023). Too late for regulatory management on Pacific oysters in European coastal waters?. *Journal of Sea Research*, *191*, 102331.

Hattab, T., Garzón-López, C. X., Ewald, M., Skowronek, S., Aerts, R., Horen, H., ... & Lenoir, J. (2017). A unified framework to model the potential and realized distributions of invasive species within the invaded range. *Diversity and Distributions*, *23*(7), 806-819.

Haubrock, P. J., Bernery, C., Cuthbert, R. N., Liu, C., Kourantidou, M., Leroy, B., ... & Gozlan, R. E. (2022). Knowledge gaps in economic costs of invasive alien fish worldwide. *Science of the Total Environment*, *803*, 149875.

Herbert, R. J., Humphreys, J., Davies, C. J., Roberts, C., Fletcher, S., & Crowe, T. P. (2016). Ecological impacts of non-native Pacific oysters (Crassostrea gigas) and management measures for protected areas in Europe. *Biodiversity and Conservation*, *25*, 2835-2865.

Hill, L., Hector, A., Hemery, G., Smart, S., Tanadini, M., & Brown, N. (2017). Abundance distributions for tree species in Great Britain: A two-stage approach to modeling abundance using species distribution modeling and random forest. *Ecology and Evolution*, *7*(4), 1043-1056.

Hulme, P. E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of applied ecology*, *46*(1), 10-18.

Jones, B. A. (2017). Invasive species impacts on human well-being using the life satisfaction index. *Ecological Economics*, *134*, 250-257.

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as Ecosystem Engineers. *Oikos*, *69*(3), 373–386.

Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Ertan Çinar, M., Oztürk, B., Grabowski, M., Golani, D., & Cristina Cardoso, A. (2014). Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions*, *9*(4), 391–423.

Kochmann, J., Buschbaum, C., Volkenborn, N., & Reise, K. (2008). Shift from native mussels to alien oysters: differential effects of ecosystem engineers. *Journal of Experimental Marine Biology and Ecology*, *364*(1), 1-10.

Kochmann, J., O'Beirn, F., Yearsley, J., & Crowe, T. P. (2013). Environmental factors associated with invasion: modelling occurrence data from a coordinated sampling programme for Pacific oysters. *Biological Invasions*, *15*, 2265-2279.

Køie, M., & Kristiansen, A. (2022). *Havets djur och växter* (Second ed.). Mareld Media.

Kuhn, M. (2008). Building Predictive Models in R Using the caret Package. *Journal of Statistical Software*, *28*(5), 1–26.

Lang, A. C., & Buschbaum, C. (2010). Facilitative effects of introduced Pacific oysters on native macroalgae are limited by a secondary invader, the seaweed Sargassum muticum. *Journal of sea research*, *63*(2), 119-128.

Laugen, A. T., Hollander, J., Obst, M., & Strand, Å. (2015). The Pacific oyster (Crassostrea gigas) invasion in Scandinavian coastal waters: impact on local ecosystem services. In: Canning-Clode J (ed). *Biological invasions in changing ecosystems: vectors, ecological impacts, management and prediction.* De Gruyter Open, 230-252.

Lee, C. E. (2002). Evolutionary genetics of invasive species. *Trends in ecology & evolution*, *17*(8), 386-391.

Le Gall, L. (2022). *Development of a model to categorize the invasion phases of Magallana gigas on the Swedish west coast*. [MSc thesis Marine Science in Sea and Society], University of Gothenburg.

Liaw, A., & Wiener, M. (2002). Classification and Regression by randomForest. *R News*, 2(3), 18-22.

Lobo, J. M., Jiménez-Valverde, A., & Hortal, J. (2010). The uncertain nature of absences and their importance in species distribution modelling. *Ecography*, *33*(1), 103-114.

Markert, A., Wehrmann, A., & Kröncke, I. (2010). Recently established Crassostrea-reefs versus native Mytilus-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological invasions*, *12*, 15-32.

Marshall, D. A., Moore, S. C., Sutor, M., La Peyre, J. F., & La Peyre, M. K. (2020). Using reproductive potential to assess oyster population sustainability. *Restoration Ecology*, *28*(6), 1621-1632.

Mazza, G., Tricarico, E., Genovesi, P., & Gherardi, F. (2014). Biological invaders are threats to human health: an overview. *Ethology Ecology & Evolution*, *26*(2-3), 112-129.

McAfee, D., & Connell, S. D. (2021). The global fall and rise of oyster reefs. *Frontiers in Ecology and the Environment*, *19*(2), 118-125.

Menge, B. A., & Sutherland, J. P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*, *130*(5), 730-757.

Moore, J. L., Lipcius, R. N., Puckett, B., & Schreiber, S. J. (2016). The demographic consequences of growing older and bigger in oyster populations. *Ecological applications*, *26*(7), 2206-2217.

Morris, D. W. (2003). Toward an ecological synthesis: a case for habitat selection. *Oecologia*, *136*, 1-13.

Mortensen, S., Bodvin, T., Strand, Å., Holm, M. W., & Dolmer, P. (2018). Effects of a bio-invasion of the Pacific oyster, Crassostrea gigas (Thunberg, 1793) in five shallow water habitats in Scandinavia. *Management of Biological Invasions*, *8*(4), 543-552.

Mortensen, S., Dolmer, P., Strand, Å., Naustvoll, L. J., & Laugen, A. T. (2019). *Policy brief: the Pacific oyster–a new Nordic food resource and a basis for tourism*. Nordic Council of Ministers.

Mortensen, S., Timenes Laugen, A., Strand, Å., Dolmer, P., Naustvoll, L. J., Jelmert, A., ... & Bøgwald, M. (2022). *Stillehavsøsters i Norden: Datainnsamling og bestandsvurderinger som grunnlag for forvaltning og høsting av nordiske bestander av stillehavsøsters, Crassostrea gigas*. Nordic Council of Ministers.

Muranaka, M. S., & Lannan, J. E. (1984). Broodstock management of *Crassostrea gigas*: environmental influences on broodstock conditioning. *Aquaculture*, *39*(1-4), 217-228.

Naimi, B., Hamm, Na., Groen, TA., Skidmore, AK., & Toxopeus, AG. (2014). Where is positional uncertainty a problem for species distribution modelling. *Ecography*, 37, 191-203.

Norling, P., Lindegarth, M., Lindegarth, S., & Strand, Å. (2015). Effects of live and post-mortem shell structures of invasive Pacific oysters and native blue mussels on macrofauna and fish. Marine Ecology Progress Series, 518, 123-138.

Nüchel, J., Bøcher, P. K., Xiao, W., Zhu, A. X., & Svenning, J. C. (2018). Snub-nosed monkeys (Rhinopithecus): potential distribution and its implication for conservation. *Biodiversity and Conservation*, *27*, 1517-1538.

Núñez-Tobajas, Z., Senar, J. C., Rodríguez-Pastor, R., Carrillo-Ortiz, J. G., & Cardador, L. (2024). Niche shifts over spread of a biological invasion: Unveiling the role of changing habitat preference and density-dependence. *Diversity and Distributions*, *30*(1), 4-12.

Oksanen, F.J., et al. (2017). *Vegan: Community Ecology Package*. R package version 2.6-4.

Pack, K. E., Mieszkowska, N., & Rius, M. (2022). Rapid niche shifts as drivers for the spread of a non-indigenous species under novel environmental conditions. *Diversity and Distributions*, *28*(4), 596-610.

Padilla, D. K. (2010). Context-dependent impacts of a non-native ecosystem engineer, the Pacific oyster Crassostrea gigas. *Integrative and Comparative Biology*, *50*(2), 213-225.

Palumbi, S., & Pinsky, M. (2014). Marine dispersal, ecology, and conservation. In M. Bertness, J. Bruno, B. Silliman, & J. Stachowicz (Eds.), *Marine community ecology and conservation* (1st ed., pp. 57–84). Sinauer Associates.

Pinochet, J., Urbina, M. A., & Lagos, M. E. (2020). Marine invertebrate larvae love plastics: Habitat selection and settlement on artificial substrates. *Environmental Pollution*, *257*, 113571.

Prasad, A. M., Iverson, L. R., & Liaw, A. (2006). Newer classification and regression tree techniques: bagging and random forests for ecological prediction. *Ecosystems, 9*, 181-199.

Prentis, P. J., Wilson, J. R., Dormontt, E. E., Richardson, D. M., & Lowe, A. J. (2008). Adaptive evolution in invasive species. *Trends in plant science*, *13*(6), 288-294.

Quayle, DB. (1988). Pacific oyster culture in British Columbia. *Canadian Bulletin of Fisheries and Aquatic Sciences*, *218*, 241.

R Core Team. (2023). R: A Language and Environment for Statistical Computing. R version 4.3.0. Vienna, Austria: R Foundation for Statistical Computing. URL https://www.R-project.org/.

Reamon, M., Marcussen, J. B., Korslund, L., & Laugen, A. T. (2021). *Species distribution modelling as a tool for dynamic management of the invasive Pacific oyster*. Report for the Norwegian Directorate of the Environment; Unpublished.

Reamon, M., Marcussen, J. B., & Laugen, A. T. (2022). *Habitatskartlegging av stillehavsøsters. [Habitat mapping of Pacific oysters]*. Report for the County Governor in Agder; Unpublished.

Reise, K., Buschbaum, C., Büttger, H., Rick, J., & Wegner, K. M. (2017a). Invasion trajectory of Pacific oysters in the northern Wadden Sea. *Marine biology, 164*, 1-14.

Reise, K., Buschbaum, C., Büttger, H., & Wegner, K. M. (2017b). Invading oysters and native mussels: from hostile takeover to compatible bedfellows. *Ecosphere*, *8*(9), e01949.

Roesch, C., *Classification of invasion boundaries of Magallana gigas on the Swedish west coast and involvement of stakeholders in the dynamic management plan* [MSc thesis Marine Science in Sea and Society]. University of Gothenburg.

Rosenzweig, M. L. (1981). A theory of habitat selection. *Ecology*, *62*(2), 327-335.

Ruesink, J. L. (2007). Biotic resistance and facilitation of a non-native oyster on rocky shores. *Marine Ecology Progress Series*, *331*, 1-9.

Sarà, G., Porporato, E. M., Mangano, M. C., & Mieszkowska, N. (2018). Multiple stressors facilitate the spread of a non-indigenous bivalve in the Mediterranean Sea. *Journal of Biogeography*, *45*(5), 1090-1103.

Segal, M. R. (2004). Machine learning benchmarks and random forest regression. *UCSF: Center for Bioinformatics and Molecular Biostatistics*.

Sousa, W. P. (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, *60*(6), 1225-1239.

Sousa, R., Gutiérrez, J. L., & Aldridge, D. C. (2009). Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions*, *11*, 2367-2385.

Teschke, K., Karez, R., Schubert, P. R., & Beermann, J. (2020). Colonisation success of introduced oysters is driven by wave-related exposure. *Biological Invasions*, *22*(7), 2121-2127.

Thorngren, L., Dunér Holthuis, T., Lindegarth, S., & Lindegarth, M. (2017). Developing methods for assessing abundance and distribution of European oysters (Ostrea edulis) using towed video. *PloS one*, *12*(11), e0187870.

Thuiller, W., Georges, D., Gueguen, M., Engler, R., Breiner, F., Lafourcade, B., & Patin, R. (2023**).** *biomod2: Ensemble Platform for Species Distribution Modeling***.** R package version 4.2-5.

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography*, *32*(3), 369-373.

Tricarico, E., Junqueira, A. O., & Dudgeon, D. (2016). Alien species in aquatic environments: a selective comparison of coastal and inland waters in tropical and temperate latitudes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(5), 872-891.

Troost, K. (2010). Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster Crassostrea gigas in continental NW European estuaries. *Journal of Sea Research*, *64*(3), 145-165.

Václavík, T., & Meentemeyer, R. K. (2012). Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. *Diversity and Distributions*, *18*(1), 73-83.

Wennberg, S., Lindblad, C., Albertsson, J., Bergström, U., Isæus, M., Kilnäs, M., ...Sandman, A. (2006). *Sammanställning och analys av kustnära undervattensmiljö (SAKU).* Naturvårdsverket.

Wood, L. E., Silva, T. A., Heal, R., Kennerley, A., Stebbing, P., Fernand, L., & Tidbury, H. J. (2021). Unaided dispersal risk of Magallana gigas into and around the UK: combining particle tracking modelling and environmental suitability scoring. *Biological Invasions*, *23*(6), 1719-1738.

Wrange, A. L., Valero, J., Harkestad, L. S., Strand, Ø., Lindegarth, S., Christensen, H. T., ... & Mortensen, S. (2010). Massive settlements of the Pacific oyster, Crassostrea gigas, in Scandinavia. *Biological Invasions*, *12*, 1145-1152.

Zeileis, A., Kleiber, C., Jackman, S. (2008). Regression Models for Count Data in R**.** *Journal of Statistical Software*, *27*(8).

Zwerschke, N., Kochmann, J., Ashton, E. C., Crowe, T. P., Roberts, D., & O'connor, N. E. (2018). Co-occurrence of native Ostrea edulis and non-native Crassostrea gigas revealed by monitoring of intertidal oyster populations. *Journal of the Marine Biological Association of the United Kingdom*, *98*(8), 2029-2038.

Zwerschke, N., Eagling, L., Roberts, D., & O'Connor, N. (2020). Can an invasive species compensate for the loss of a declining native species? Functional similarity of native and introduced oysters. *Marine Environmental Research*, *153*, 104793.

7 APPENDIX

Table A1 Full list of variables recorded in the field of both study regions in addition to live and dead Pacific oyster (*Magallana gigas*) counts and, if sampled from land, sizes.

Variable name	**Specification**
Site geographical coordinates	WGS 84. Recorded in sampling squares or in the start and end of video transects.
Depth (m)	Maximum and minimum in each square or video transect. Record the measured and adjusted depth.
Blue mussel (*Mytilus edulis*) cover and counts	Separate between live and dead.
Flat oyster (*Ostrea edulis*) counts.	Separate between live and dead.
Substrate composition (%):	Measured in each sampling square or video image, should equal 100%.
• Rock	Rocks >5 cm loosely aggregated, can be lifted.
• Boulder	Larger rocks (but still loose from the bottom) that cannot be lifted by hand.
• Cliff	Mass of bedrock. Cannot be moved/part of mainland.
• Artificial	Stable human-made substrate >30 cm of cement, metal or plastic.
• Soft	Mud-like substrate, usually more humid than sand.
• Sand	Granular material composed of finely divided rocks and minerals, finer than gravel and coarser than silt.
• Shell/Shell hash	Loose shell accumulations with a median particle size of 2mm to <64mm. Shells may be broken or whole.
• Gravel	Loose aggregation of rock fragments ranging from 2mm to 5cm.
Percent vertical surface (%)	If cliff, boulder or artificial substrate are present in the square or video image, estimate the percent vertical surface (>60°) of these substrates (e.g., if 40% cliff in square but all of it is vertical, then the percent vertical surface is 100%).
Vegetational cover (%):	Measured in each sampling square or video image. Not included in the cover of bottom substrate (i.e., can sum up to <100%).
• Macroalgae	Multicellular algae of robust structure. Specify the proportion of the macroalgae that is *Fucus* spp.
• Filamentous algae	Thread-like, stringy algae, less structurally robust than macroalgae.
• *Zostera* sp.	Eelgrass.

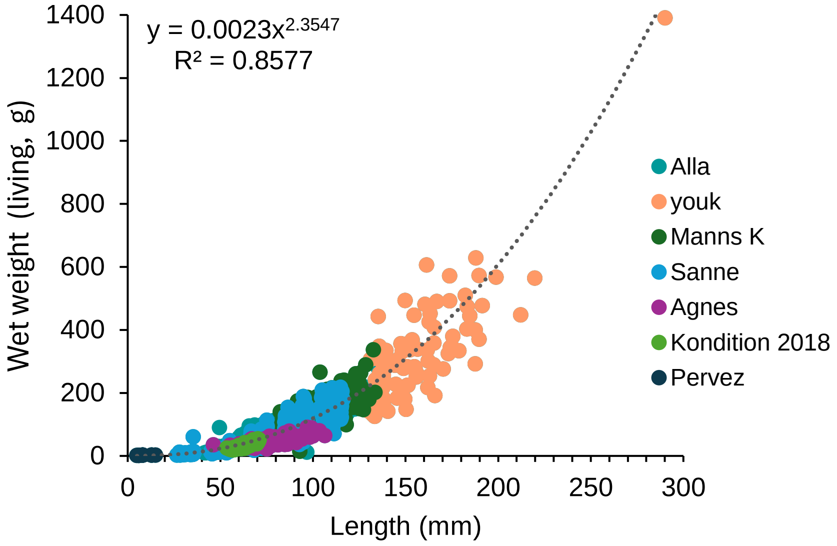

Fig. A1. Power relationship between Pacific oyster length and living wet weight (Strand et al., unpublished data). R^2 is the coefficient of determination. The different colors represent the study/survey in which oysters were sampled.

Table A2. Summary of coefficients in a zero-inflated negative binomial model (AIC=269.5) predicting Pacific oyster (*Magallana gigas*) abundance (counts standardized per surveyed area) in relation to depth categories between Gothenburg and Varberg. The count component (negative binomial with log link) models the relationship between depth category and oyster abundance in areas where oysters are present, accounting for overdispersion in the count data. The zero-inflated component (binomial with logit link) models the probability of oyster absence (excess zeros) as a function of depth category. The model assumes varying probabilities of the oyster being absent across depth categories.

Count component				
Coefficient	**Estimate**	**SE**	**z**	**p>z**
Intercept (0.0-0.5 m)	4.776	0.216	22.136	0.000***
0.5-3.0 m	-3.318	0.433	-7.672	0.000***
3.0-6.0 m	-2.278	0.930	-3.525	0.000***
Zero inflation component				
Intercept (0.0-0.5 m)	0.733	0.304	3.603	0.000***
0.5-3.0 m	0.461	0.351	2.087	0.441
3.0-6-0 m	2.242	0.598	2.044	0.037*

Table A3. Summary of coefficients in a zero-inflated negative binomial model (AIC=225.6) predicting Pacific oyster (*Magallana gigas*) abundance (counts across 5 x 0.25 m^2 squares for each site) in relation to habitat categories between Varberg and Malmö. The count component (negative binomial with log link) models the relationship between habitat category and oyster abundance in areas where oysters are present, accounting for overdispersion in the count data. The zero-inflated component (binomial with logit link) models the probability of oyster absence (excess zeros) in the abundance data. The model assumes constant probabilities of the oyster being absent across habitat categories.

Count component				
Coefficient	**Estimate**	**SE**	**z**	**p>z**
Intercept (Marina)	2.519	0.278	9.063	0.000***
Natural rocky	-1.437	0.410	-3.510	0.000***
Pier	-1.261	0.406	-3.111	0.002**
Zero inflated component				
Intercept	-1.129	0.497	-2.272	0.023*