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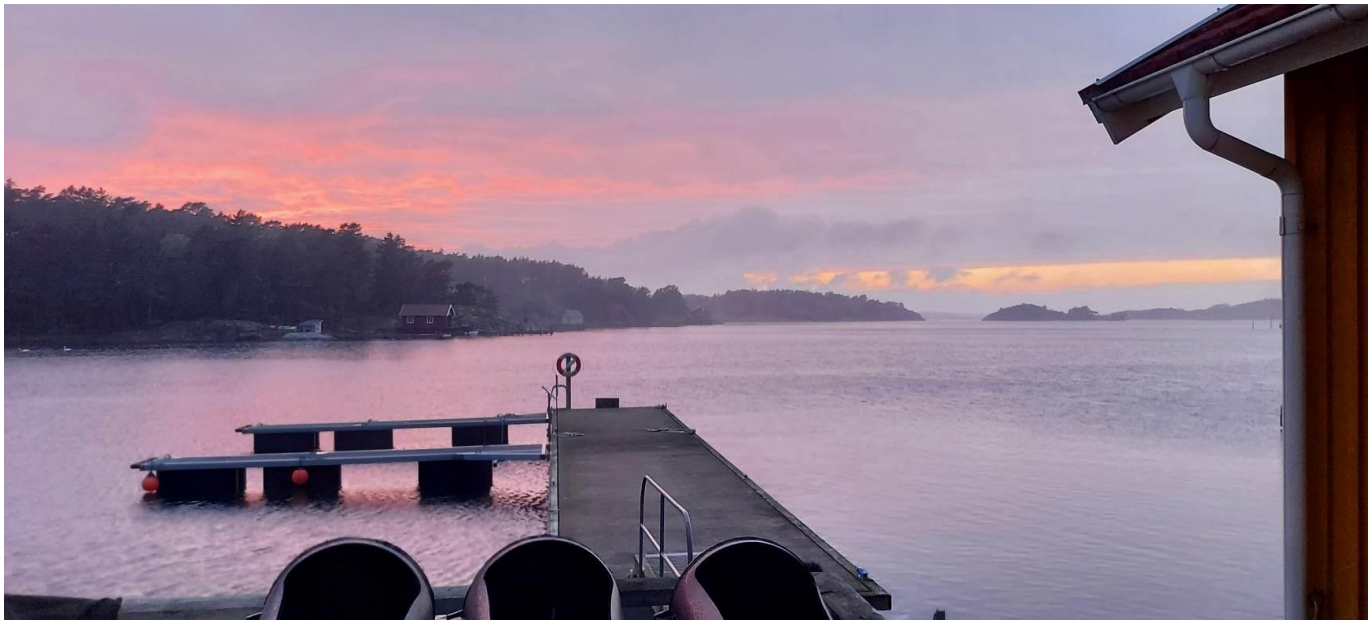
# Density dependent effects of the pacific oyster (*Magallana gigas*) on biodiversity



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Degree project for Master of Science with a major in Marine Sciences
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Photo on title page: Tor Boëthius

# Abstract

Invasive species can pose a serious threat to the biodiversity in native habitats. The invasive species can exert pressure on native species through predation or competition. The pacific oyster (*Magallana gigas)* is deemed an invasive species in Sweden, where it has been present since 2006. In Sweden, the oysters settle on hard surfaces in shallow bays and narrow straits and can quickly form reefs. The oysters act as ecosystem engineers, since they increase the flow of nutrients to the sediment and provide substrate and structure in areas otherwise dominated by soft substrate thereby increasing biodiversity. Little is, however, known about how oyster density impacts biodiversity. This study aims to explore the relationship between the pacific oyster and the species richness of infauna and macroalgae, as well was the relationship between the pacific oyster and organic content in the sediment, by taking inventory of oysters and sampling sediment, infauna and macroalgae from oyster reefs along the Swedish west coast. The hypothesis for the study was, that oyster density will influence species richness of both macroalgae and infauna, and that the oysters will influence the concentration of organic matter in the sediment. The results attained do not show a significant relationship between oyster density and infauna species richness or sediment organic content. However, an increase in oyster density significantly increased algae biomass and algae species richness. This implies that overall, the oysters had a positive impact on their surroundings and may contribute to an increase in biodiversity.

**Popular science summary**

Biodiversity is a crucial part of a healthy ecosystem, but there are many threats to biodiversity. One of the larger threats to biodiversity is the introduction of invasive species. Invasive species are non-native species that cause harm in native communities. These species are brought into new areas by humans either intentionally or unintentionally. In the new area they may impact the native ecosystem by either predating on native species, or by outcompeting native species. The invasive species can also spread parasites and diseases to native organisms.

The pacific oyster, (*Magallana gigas*), is often referred to as an invasive species. It is native to the western Pacific Ocean and has been shipped all around the world to be used in aquaculture. However, from these aquaculture sites, the oysters have dispersed and formed wild populations. Wild populations of the pacific oyster were first found in Sweden in 2006, and they have since spread to a large part of the Swedish west coast. Due to the high growth rate and faster reproduction of the pacific oyster, they can quickly colonize new areas where they settle. The oysters can form complex 3-D structures and provide hard substrate in areas dominated by soft sediments, often utilized as shelter and places to settle down by other organisms. They may also contribute with an increase in nutrients to organisms in their surroundings, but little is known about at what densities such effects start to occur.

This study aims to investigate the relationship between the pacific oysters and large seaweed as well as the relationship the oysters have with animals living in the sediment, known as infauna. The hypothesis for this study is, that the oysters will impact the number of species of both the seaweed and infauna.

To test this hypothesis, 13 locations with oysters were visited. At these locations, samples of sediment and infauna were collected at different oyster densities using plastic tubes. All of the seaweed growing on the oysters were also collected.

The results show no relationship between the number of oysters and number of species of the infauna. However, the results do indicate a positive relationship between the number of oysters, number of seaweed species and the weight of seaweed. This means that these results indicates that the oyster have an overall positive impact on their surroundings.

There is a more obvious connection between oysters and the total amount of seaweed, since the more oysters there is, the more anchoring points for seaweed there is. So, to see a larger mass of seaweed when increasing the number of oysters is not very surprising. What is perhaps more unexpected is the increase in the number of seaweed species at higher oyster densities. Increasing the total mass of seaweed and the number of unique species of algae could have positive effects for the overall biodiversity at the oyster reef since seaweed itself act as both food and shelter for other organisms.

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**Master's degree 60 credits in Marine Biology, 2023, Department of Marine Sciences, University of Gothenburg**

# Table of contents

# Introduction

An invasive species is a non-native species that is causing harm or stress in native populations, thus decreasing biodiversity, either by an increase in predation or increased competition with native species (Sieracki et al., 2014; Bradley et al., 2019). The introduction and spread of invasive species is an increasing worldwide problem (Bumann et al., 2021). In marine habitats, invasive species can spread in many ways. The introduction of invasive species is caused by human activities and the dispersal can be either intentional or unintentional. Unintentional introduction can occur when for example larva from a species travels long distances in ballast tanks of ships (Sieracki et al., 2014; Bumann et al., 2021) or if the species attaches itself to the outside of boats or on tools used in the water. The species could then later detach in an area outside of their natural range (Cole et al., 2019). Intentional introduction could occur, for example, if a species has commercial value, and is imported to be used in aquaculture. This is the case of the pacific oyster (*Magallana gigas*) (Laugen et al., 2015). The pacific oyster is native to the western Pacific Ocean and has been imported to countries all over the world with the purpose of cultivation. Wild populations have emerged from these cultivation sites and the species has spread by currents (Laugen et al., 2015; Faust et al., 2017).

The pacific oyster has been present is Swedish waters since at least 2006 when it was first found and has since spread rapidly. The exact route that the oysters came to Swedish waters by, is disputed. Based on genetic similarities between the Swedish and Danish populations, as well as based on oceanographic trajectory modelling (Laugen et al., 2015; Faust et al., 2017), it is likely that the wild populations in Swedish waters came from Danish waters. Today, the pacific oyster is a well-established species with several large reefs along the Swedish west coast (Mortensen et al., 2017). Already in 2015, 250 sites with the pacific oyster were known in Sweden, and at the time it was estimated that they had a combined biomass of between 100 000 – 500 000 tons (Strand & Lindegarth, 2014; Laugen et al., 2015). And although the pacific oyster has become well established in Scandinavian waters, the population has experienced setbacks caused by disease outbreaks (Mortensen et al., 2016) and by harsh winter conditions (Strand et al., 2012).

The pacific oyster has a high growth rate and a high reproductive output, meaning that they can rapidly colonize an area (Lenihan, 1999; Herbert et al., 2016; Guy et al., 2018; Wood et al., 2021). Furthermore, the introduction of a new species often entails the introduction of other species using the main species as a host. This is true for the pacific oyster, that can be the host of parasites non-native to their new location. The introduction of parasites and their hosts to an area often results in spillover into native species, meaning that the parasites not only infect their normal host, but also native species. When a parasite is introduced to a new area it often causes large casualties among the native populations (Goedknegt et al., 2017).

In Swedish waters the Pacific oyster prefers to settle in small, shallow bays, alternatively narrow straights and smaller beaches on substrates such as rocks, cliffsides as well as on other oysters. Oysters can also be found on soft substrates. The oysters also prefer areas with high water flow through or short residence time of the water, as they mainly feed on plankton that they filter out from the water (Laugen et al., 2015). To start colonizing an area with soft sediments, the oysters only require a small pebble or shell-fragment for their larvae to attach itself to and grow from. The oyster growing from that pebble or shell fragment becomes the most viable place for new larvae to settle in that area. This in turn leads to clusters of oysters

forming; which, in turn, often lead to the formation of a larger oyster reef (Mortensen et al., 2017). Oysters transform their surroundings, but how radical this change is, depends on where they settle. Oysters settling in areas dominated by hard substrates will have less of an effect compared to the oysters settling in areas dominated by soft substrates. This is due to the oysters contributing with hard substrate to an area lacking hard substrates, which changes the overall composition of organisms in the area (Bulleri, 2005; Laugen et al., 2015).

Oysters and other bivalves fill a very important role in marine coastal environments. Oysters are examples of organisms classified as ecosystem engineers. Being an ecosystem engineer entails contributing with structure and habitat formation to an area (Herbert et al., 2016). Oysters form reefs by growing on each other and the complex 3-D structure of a reef attract smaller animals that live in between the oysters, using the oysters as protection. The added protection also makes it a suitable place for animals to reproduce and nurse their offspring, the shelter provided by the oysters contributes to a higher juvenile survival rate (Longmire et al., 2021). An oyster reef, being a highly productive habitat, also naturally attract animals that search for food. The oysters themselves are consumed by for example birds, crabs and sea stars (Mortensen et al., 2017), and the algae growing on the oysters and the animals living between the oysters are also subject to predation (Huang et al., 2006).

By offering a hard substrate, the oysters commonly act as an anchor point for a vast array of macroalgae and sessile epifauna, such as barnacles, bryozoans and tunicates (Barnes et al., 2010; Outinen et al., 2019). The added algae will lead to an even more complex three dimensional structure, further enhancing biodiversity (Guy et al., 2018), and may provide protection from environmental stressors. The most important of these algae would be long-living, canopy forming macroalgae, that cover larger areas and are hosts to many species (Huang et al., 2006; Westerbom & Koivisto, 2022).

Another part of the oysters' ecosystem engineering is their way of consuming nutrients through the filtration of particles from the water. This transports nutrients from the water into the sediments increasing the overall nutrient concentration in the sediments around the reef. (Zwerschke et al., 2020).

The transport of nutrients mostly works through fecal matter and pseudofaeces deposition, pseudofeces being inedible material such as sand particles that is rejected by the oyster if it is ingested (Beningerll et al., 1999). Some of these deposited nutrients are consumed by infauna and the increased flow of nutrients into sediments can thereby have positive effects on the infauna in the area (Zwerschke et al., 2020).

Through the increased flow and removal of nutrients, an oyster reef could also mediate eutrophication, that might otherwise lead to a superfluous growth of for example phytoplankton or filamentous algae. When decomposed, these phytoplankton and filamentous algae could cause hypoxic conditions in the water column and sediments (Officer et al., 1982; Zwerschke et al., 2020; Buranapratheprat et al., 2021). The transport of nutrients between the water column and sediments is called the benthic-pelagic coupling and is very important for energy transfer between food-webs in aquatic systems (Griffiths et al., 2017). The presence of an oyster reef could also have positive effects for other important habitat builders in their surroundings such as eelgrass. Eelgrass is sensitive to the effects of eutrophication such as high epiphyte and phytoplankton growth, but oysters can lessen these issues by removing nutrients and phytoplankton from the water (Lapointe et al., 1994). Additionally, the oyster

reefs act to stabilize sediments, but also halt currents making waters around them calmer (Guy et al., 2018; Bergström et al., 2021).

Live oysters contribute largely to shaping their surroundings, but their effects do not stop when they die. The shells of dead oysters will remain on sediment surfaces and still be a suitable anchoring point for many plants and sessile animals and they will continue to provide animals with shelter (Norling et al., 2015).

Although previous studies have shown that oysters may increase the concentration of organic matter in the sediment, and that this may impact infauna composition and abundance, at what densities such effects appear is not well explored. Similarly, macroalgae are often observed on oyster reefs, yet the interaction between oyster density and macroalgae occurrences is largely unknown.

Therefore, this study aims to explore the effects of the pacific oyster on the Swedish coastal ecosystems by specifically study the relationship between oyster density, infauna and habitat forming macroalgae in shallow waters.

The hypothesis is that the pacific oyster will have density dependent effects on species richness of the infauna and macroalgae. The content of organic matter in the sediment is also hypothesized to change with oyster densities.

## Methods

The methods can be divided into two main parts, field sampling and lab analysis. Prior to the sampling, the sites were selected. Selection was made from two criteria. These criteria were that the mean water depth on site was between 0,5 and 0,75 m, since this depth range ensures that the oysters are always submerged and that the water is shallow enough to sample by hand, and that the oysters at a site had formed reefs or were close to forming reefs. To find these sites, a database of oyster sightings was used. The database consisted of previously collected field-data within the DynamO project, the DynamO project being a project for the management of the pacific oyster. The purpose of the data collection was to identify suitable sites for clearing trials, and hence, densities of the oysters were estimated, as was site size and population structure. These are structures such as reef formation, cluster formation or single oysters. The data was filtered based on the site criteria and the locations that fit the description and were reasonably close to Tjärnö were selected. The proximity to Tjärnö was of importance since it was the base of operations for the sample collection. In total, 13 sites were identified and later selected, and can be seen on a map in *Figure 1*. To determine how exposed these sites were, modelled wave exposure data was extracted from the SAKU data (Jan Albertsson et al., 2006) with a resolution of 25 by 25 m in Qgis. The values were plotted in a grid where every pixel is 25 by 25 meters. The values indicate how exposed a site is to environmental conditions, such as currents, waves and winds. The higher the value, the more exposed an area is.

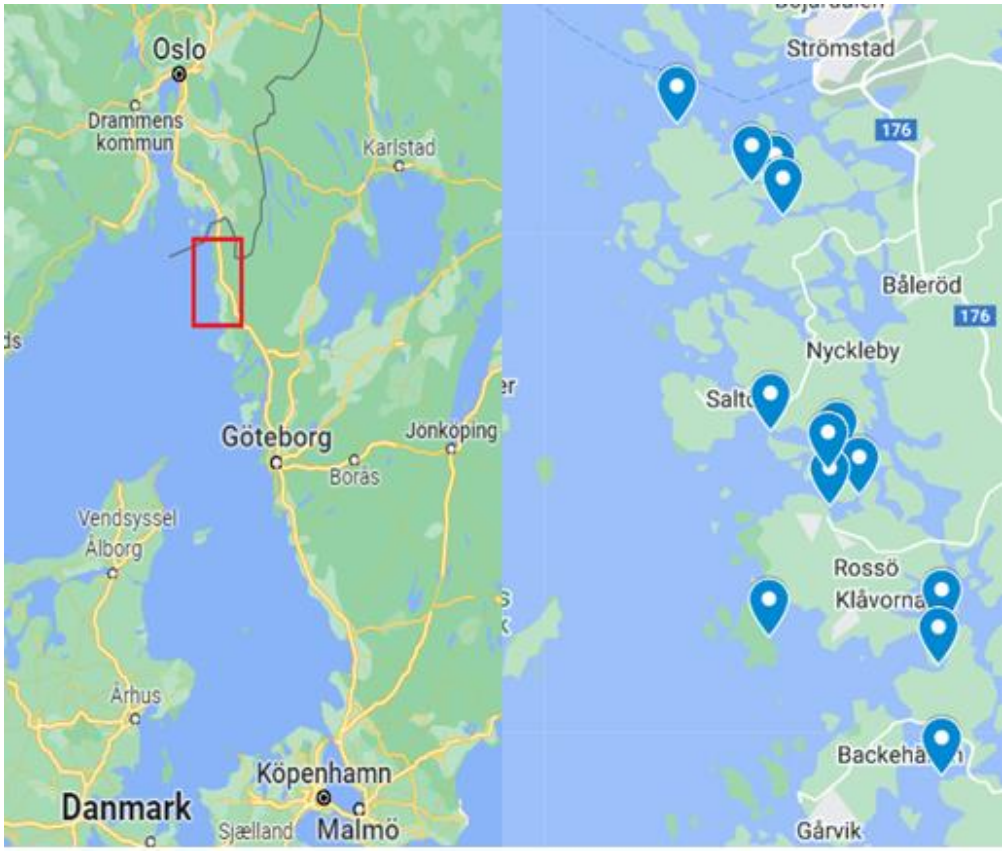


*Figure 1: Map from google maps, showing a map of southern Sweden and the selected sites on the right-hand side.*

## Field sampling

Field sampling entailed the collection of sediment samples, samples of infauna and of macroalgae. It also included estimations of oyster densities, oyster coverage as well as counting oysters for density estimation and weighing of oysters. Sample collection was mostly conducted on days with low water level to make the process easier. The water level data was collected from SMHI, from their station at Kungsvik. Thus, to estimate the depth of where samples were collected, the current water level was adjusted according to the prevailing water level to ensure that the target depth was sampled. For example, if the water level data showed the water level to be 10 cm below the average, samples were taken from between 0.4 and 0.65 cm.

### Sediment collection

The process started with the haphazardly placement of a metal square on the bottom. The square had a size of 0.25 $m^2$. Using a folding ruler, the depth was recorded to ensure sampling from an appropriate depth. The coverage of oysters on the sediment surface was estimated through ocular inspection. At this point, if possible, the samples of sediment and infauna were taken. If not possible, due to high coverage of oysters in the square, the sediment and infauna samples were collected after the removal of oysters. Sediment was sampled using a plastic tube with a diameter of 5 cm. The tube was pushed into the sediment and was then fitted with a rubber cork in the open end. The tube was then pulled out with a sediment core inside.

Approximately 5 cm of the top sediment was placed into a marked zip-lock bag, taking care to not include the water that was also in the tube, above the sediment.

### Infauna collection

The infauna was collected in a similar manner. A tube with a diameter of 10 cm was pushed into the sediment. The tube was then fitted with a plunger to enable sediment removal. After being pulled out, approximately 10 cm of top sediment was placed into two stacked sieves, one sieve was 4 mm in size and the other one was 1 mm in size. This was done to remove excessive material from the samples. The sample was then transferred from the 1 mm sieve into a marked zip-lock bag. Any larger organisms that did not pass through the 4 mm sieve were removed from the 4 mm sieve by hand and placed in the bag.

### Algae and oyster collection

Parallel to the collection of sediment and infauna samples, samples of algae were also collected. The algae sampling started with the collection of oysters from the sample square. The oysters within the square were brough ashore using a bucket. On the shore the oysters were counted and the number of oysters, both dead and alive, with algae growing on them was noted. If algae were present on the oysters, it was removed and placed in a marked zip-lock bag. The oysters were then weighed and counted before being returned to the water.

At each site, this process was repeated 12 times. Although the squares were placed haphazardly, the aim at each site was to place 4 squares at high, medium and low densities of oysters, and at least one square at each site with no oysters in it and one square where the oysters were the densest.

## Lab analysis

### Infauna

To analyze the infauna samples, they first needed to be cleaned. To clean the samples, the samples were placed into a 1mm sieve and rinsed thoroughly with deep sea water. The samples were then placed into white plastic trays with some water. With a lamp shining into the tray and using a spoon, the samples were looked through without any magnification. The contrast from the white tray helped with spotting animals in the samples. When an animal was found and the exact species could not be determined immediately, it was placed into a marked falcon tube with 95% ethanol for preservation, to ensure that the species could be determined at a later time.

### Organic content

To determine the organic content in the sediment, 10 g of wet sediment was used. The sediment was placed into metal cups that had been pre-burned in an oven. The cups were pre-burned due to them being coated in a non-stick coating. This coating may have skewed the results; hence the cups were burned once while empty to remove this coating. When 10 g of wet sediment had been placed in the cups, the sediment was placed in a drying oven of the brand Memmert, at 60$^{o}$C until completely dry, often overnight, approximately 15 to 18 h. When dry the weight was recorded to determine water content. After the weighing of the dry sediment, the sediment was placed into an oven and burned at 600$^{o}$C for approximately 5 h. The burning removes organic matter from the sediment. After 5 h the sediment was left to cool down. When cooled the sediment were weighed again. The difference in weight indicated the organic content of the sediment.

### Sediment grainsize

The first step in determining sediment grainsize was to weigh approximately 20 g of wet sediment. The sediment was then dried in a drying oven at 60°C until completely dry, similarly to the organic content it was most often left to dry overnight with time totaling to approximately 15 to 18 h. When dry, the weight was recorded to determine water content. The sediment was then placed in a solution of Sodium hexametaphosphate (6.2g $l^{-1}$) for 24 h to make the sediment easier to sieve. After 24 hours the sediment was wet sieved in a 63 µm sieve to remove some of the smallest particles. The wet sieving was done to make the next step, dry sieving, easier by removing the smallest particles that could potentially clog up the sieves during dry sieving. The sediment was then dried again until completely dry. When dry the weight of the sediment was once again recorded, and this weight indicated the weight of the particles smaller than 63 µm that had been removed in the wet sieving process. The next step was the actual grain size determination and for that purpose, a shaking table was used. On this shaking table, seven sieves in different sizes, 4 mm, 2 mm, 1 mm, 500 µm, 250 µm, 125 µm and 63 µm were stacked on top of a catch tray. The dry sediment was poured into the sieve at the top, 4mm sieve, and then left to shake for about 15 minutes. After 15 minutes, the contents of each sieve were poured into individual cups and weighed. The weight distribution was used as an estimate of the mean grainsize of the sediment.

### Algae

For the algae, the first step in the analysis was to remove them from the bag and dry them of. In this case, drying simply implies removing the water that covers the algae on the outside and not placing them in a desiccator to dry completely. This drying was done by placing the algae on paper that would soak up the water. When patted dry, the algae were placed into a container and the weight was recorded. After the weight had been recorded, the different species of algae were recorded. Focus during this species determination was on the large habitat-forming macroalgae, but common epiphytes and smaller algae were also recorded.

## Statistical analysis

The model used to estimate the relationship between the different variables was a Linear mixed model. A linear mixed model tests the relationship between a dependent variable and multiple independent variables, while also being able to take random effects into account. When executing a Linear mixed model, choosing the right independent variables is crucial. If these variables are too correlated to each other, it is called multicollinearity. Multicollinearity could lead to skewed results when trying to understand how the independent variables affect the dependent variables, since the effect on the dependent variable could come from any of the two independent variables. This could lead to misleading results and incorrect assumptions. To avoid multicollinearity, the correlation between different independent variables, Oyster density, Oyster cover, Oyster biomass and Exposure, was tested using correlation plots. Such plots display the correlations between the different variables explored. The variables that were the least correlated were selected for further analysis.

The Linear mixed model was made in R, using the lme4 package. In this model, the density of live oysters and exposure were used as fixed effects, independent variables. Site was used as a random effect. A random effect is a variable that affects the data in a random matter, a random relationship. These random effects are taken into consideration in a mixed model to more accurately interoperate data. The mixed model takes the random effects into consideration, but they are not in the model's focus. In this case, site is not the focus, but

since the data trends were observed to vary between the different sites during visual inspection of the data, a random intercept was used to more accurately estimate the impact of the target aspects, since the intercept of the y-axis varies between sites. There also seemed to be a variation in how the oyster density affected the response variable, the model therefore used a random slope in the analysis. Thus, the model was set up, as can be seen in *Equation 1*. The model was run with different dependent variables, sediment organic content, infauna species richness, algae species richness, algae biomass and the different grainsizes. In this study a 5% confidence interval was used, and thus P values at 5% or lower were regarded as significant. The P value is the likelihood of rejecting the null hypothesis even though it is correct, so if the P value is below 5% the null hypothesis can be rejected with a strong certainty of it being the right decision.

*Equation 1*: $y = \beta_0 + \beta_1 Oyster\ density + \beta_2 Exposure + \beta_3 Oyster\ density * Exposure + Oyster\ density\ u_1 + u_2 + \varepsilon$

y = Sediment organic content, Infauna species richness, Algae species richness, Algae biomass, or the different grainsizes

$\beta_0$ = intercept

$\beta_1$ = parameter for variable X, X = Oyster density

$\beta_2$ = parameter for variable Z, Z = Exposure

$\beta_3$ = parameter for interaction between oyster density and exposure

$u_1$ = random slope- for variable X, X = Oyster density

$u_2$ = random intercept-variable = random effect from Site

$\varepsilon$ = error-term

Tests were also made to determine how much of the variance in the results could be explained by random effects. When running a model, the output shows values for random effects, in this case, site, to explain the variation in intercept, and for (in this model) Oyster density, to explain variations in slope. One column of the random effect output is called variance, and to calculate the variance explained by the random effect, the variance from the random effects was divided with the total variance.

# Results

To analyze whether the variables pertaining to the sediment were correlated, a correlation plot of the sediments grainsize distribution, organic content and the exposure of the different sites was made. Significant correlations were seen between all variables, (Autocorrelation analysis, $P<0.05$, Figure 2) except between the variables “Sand part” and “Silt part”.

Negative correlations were seen between exposure and percentage of gravel in the sediment, percentage of silt in the sediment and amount of organic matter in the sediment. Negative correlation indicates that an increase in exposure will decrease the other variables. A positive correlation was seen between exposure and the percentage of sand in the sediment, meaning that increased exposure will increase the amount of sand in the sediment. There were also correlations between the sediments grainsize and sediment organic content, with positive correlations between organic content and the percentage of both silt and gravel and a negative correlation between organic content and the percentage of sand in the sediment.

Based on the correlation plot, it was decided to only use organic content as a dependent variable in the analysis, while exposure was chosen as one of the independent variables.

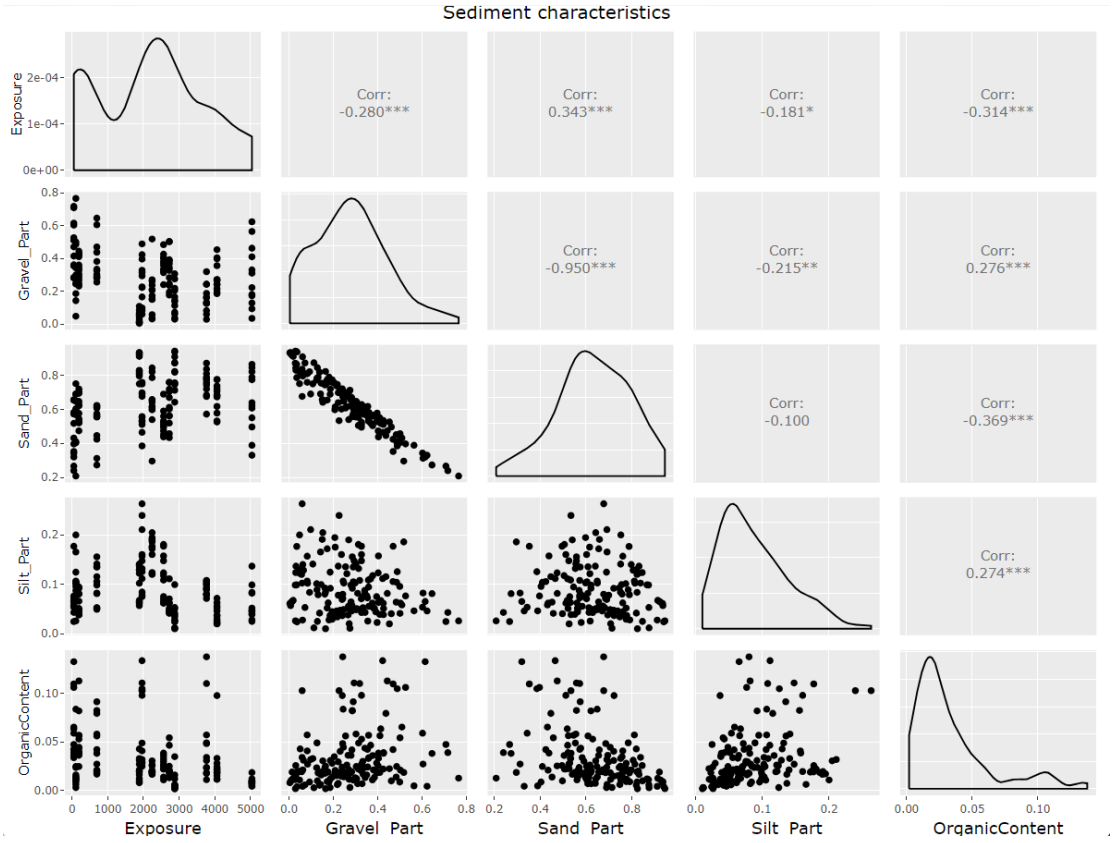


*Figure 2: Correlation plot between different variables describing the sediments characteristics.*

To select an independent variable describing oyster presence in an informative way, another correlation plot containing the different variables pertaining to oyster presence was made, i.e., oyster cover, oyster density and oyster weight, this plot also included exposure. All oyster variables were significantly correlated to each other (Autocorrelation analysis, $P<0.05$, Figure 3), thus, to avoid multicollinearity only one could be selected for further analysis. Since exposure was desired to be used as an independent variable as well, the oyster variable chosen could not be correlated with exposure. The two viable combinations of independent variables were thus Exposure and Oyster cover, or Exposure and Oyster density, since both were not significantly correlated with exposure. Ultimately, oyster density was selected to represent the oyster component in further analysis as it was deemed to best describe the presence of oysters.

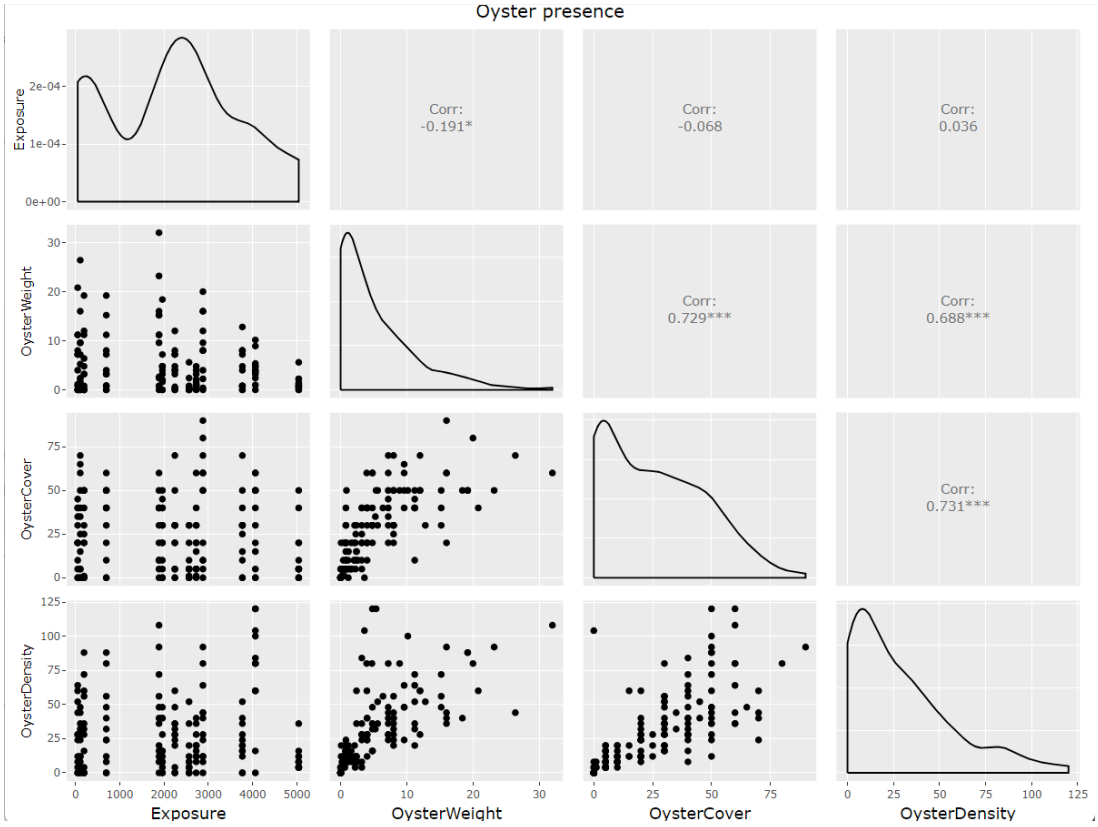


*Figure 3: Correlation plot of the different variables describing oyster presence.*

## Sediment organic content

Visualization of the effect of oyster density and exposure on sediment organic content did not reveal any general trends. However, it was observed that site had a large impact on the organic content in the sediment (*Figure 4* and *Figure 5*). The model showed the same pattern and neither oyster density nor exposure had a significant effect on the organic content in the sediment (Linear mixed model, P>0.05, *Table 1*). Random effects such as site explained 65.3% of the total variation in the data.

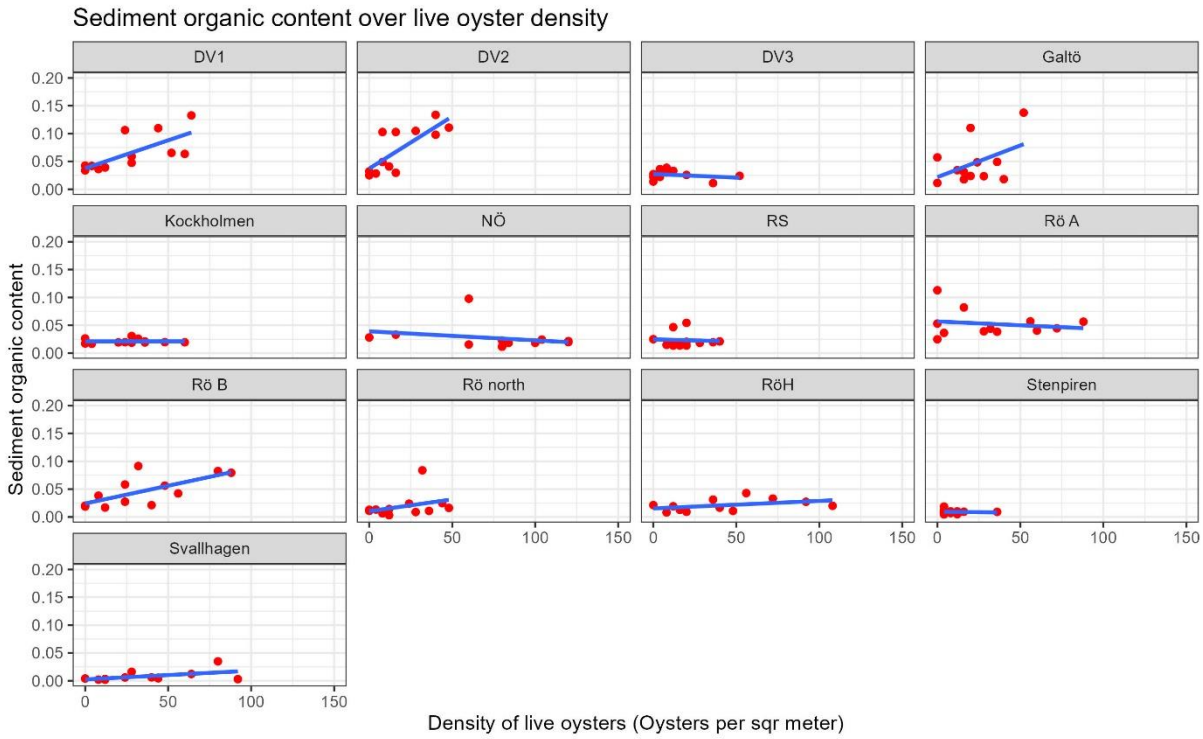


*Figure 4: Change in sediment organic content at different densities of live oysters, illustrated by site. Site name abbreviations: DV=Daftö-Valö, NÖ=North Öddö, RS=Rossö South, RÖ=Rossö, RöH=Rossö Harbor.*

All figures pertaining to the exposure data followed a similar trend to one another, and since no model pointed to any significant relationship only one is included in the results as an example.

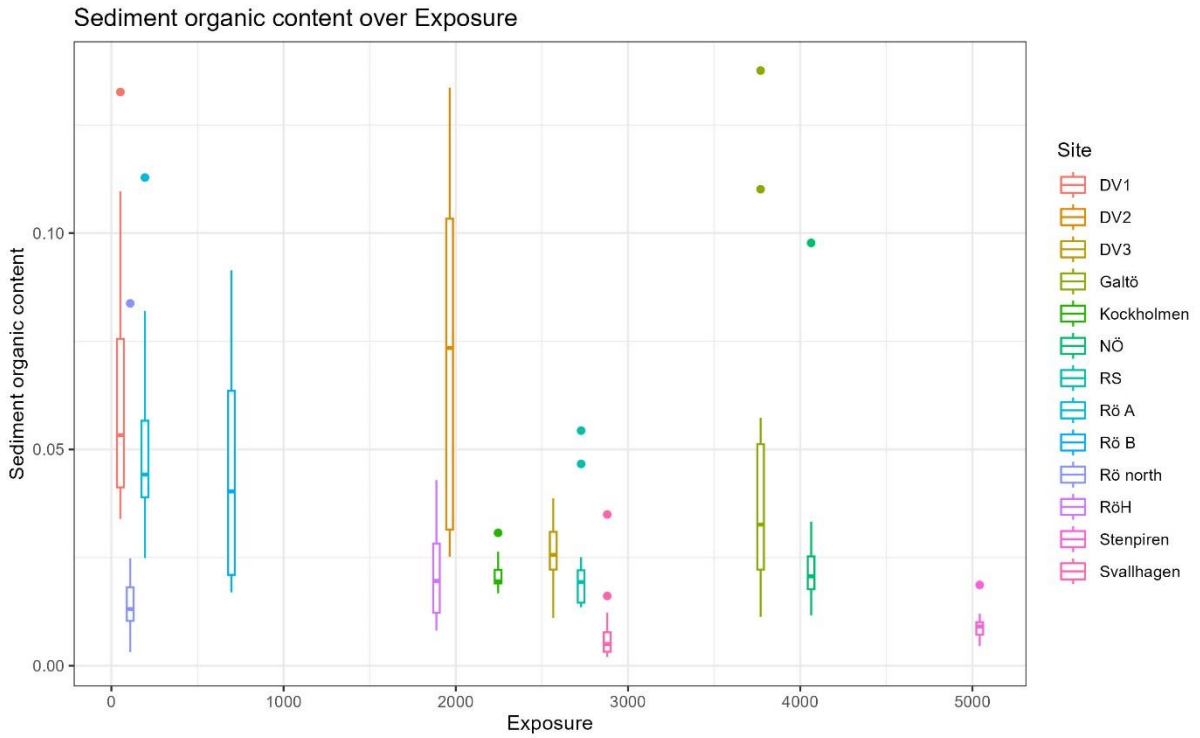


*Figure 5: A boxplot showing the change in sediment organic content at different levels of exposure. The higher exposure levels indicate more exposure, or less protection.*

*Table 1: Results from a Linear mixed model testing the relationship between sediment organic content, density of live oysters and exposure.*

| ***Fixed effects*** | ***Estimate*** | ***Std. Error*** | ***df*** | ***t value*** | ***Pr (>\|t\|)*** |
|---|---|---|---|---|---|
| *(Intercept)* | 0.04 | 0.01 | 11.01 | 5.47 | <0.001 |
| *Oyster density* | 0.0004 | 0.004 | 10.00 | 1.98 | 0.08 |
| *Exposure* | <-0.001 | 0.01 | 11.37 | -1.39 | 0.19 |
| *Oyster density * Exposure* | <-0.001 | 0.01 | 10.63 | -0.63 | 0.54 |

## Infauna species richness

Similarly, to the data for organic content, the visualizations of the infauna species richness data did not reveal ant general trends for neither oyster density nor exposure. There was, however, seemingly less variation in the data compared to the sediment organic content (*Figure 6*). The model for this data corroborates this pattern, neither oyster density nor exposure had a significant effect on the infauna species richness (Linear mixed model, P>0.05, *Table 2*). The random effects explained 25.7 % of the variation in the data.

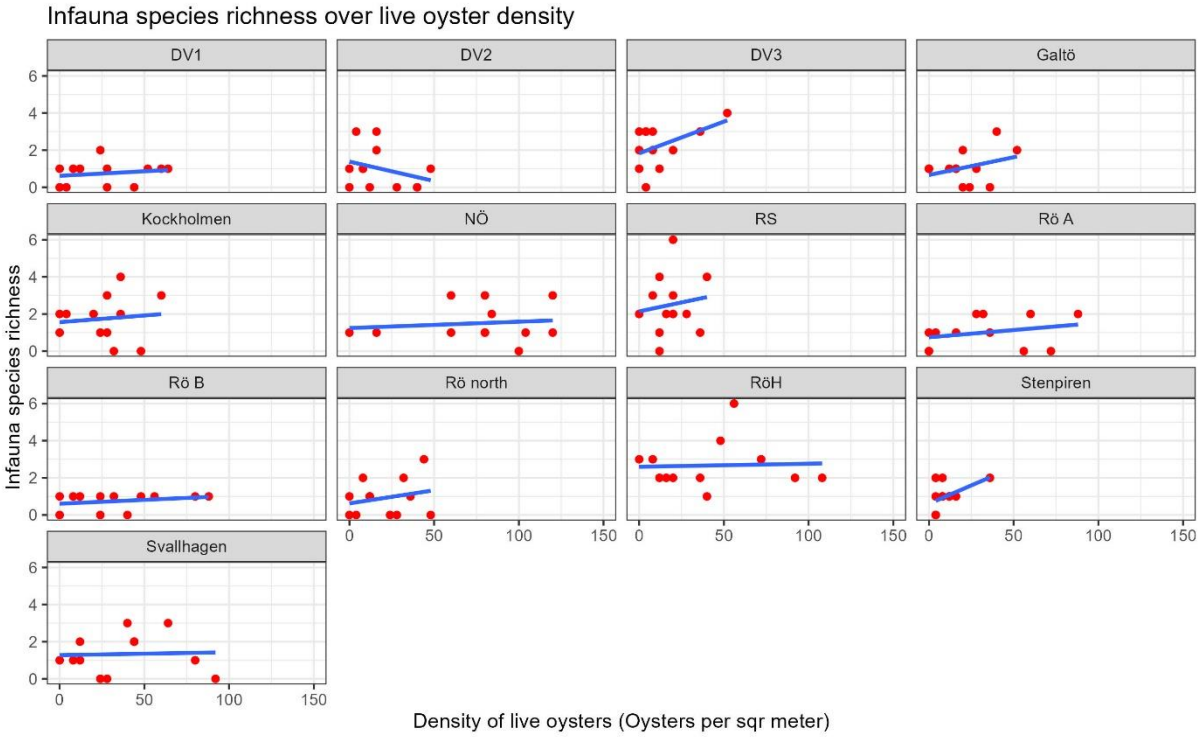


*Figure 6: Change in infauna species richness at different densities of live oysters, illustrated by site. Site name abbreviations: DV=Daftö-Valö, NÖ=North Öddö, RS=Rossö South, RÖ=Rossö, RöH=Rossö Harbor.*

*Table 2: Results from a Linear mixed model testing the relationship between infauna species richness, density of live oysters and exposure.*

| **Fixed effects** | **Estimate** | **Std. Error** | **df** | **t value** | **Pr (>\|t\|)** |
|---|---|---|---|---|---|
| *(Intercept)* | 1.42 | 0.19 | 10.89 | 7.518 | <0.001 |
| *Oyster density* | 0.01 | 0.10 | 40.61 | 1.52 | 0.14 |
| *Exposure* | 0.0001 | 0.19 | 10.90 | 0.86 | 0.41 |
| *Oyster density * Exposure* | <0.001 | 0.10 | 28.66 | 0.10 | 0.92 |

## Algae species richness

The visualization of the algae species richness showed a general positive trend with oyster density (*Figure 7*). The data generally showed either a total deficit of algae or very few algae species when the sediment was devoid of oysters. At the higher densities of oysters, 100 to 120 individuals/$m^2$, up to 8 or 9 unique species were found.

As for the other variables explored, no general trend for algae species richness and exposure was observed. This was also corroborated by the model which showed a significant positive relationship between algae species richness and oyster density (Linear mixed model, P<0.05, *Table 3*) but not between algae species richness and exposure. The random effects explained 20.8 % of the variation in the data.

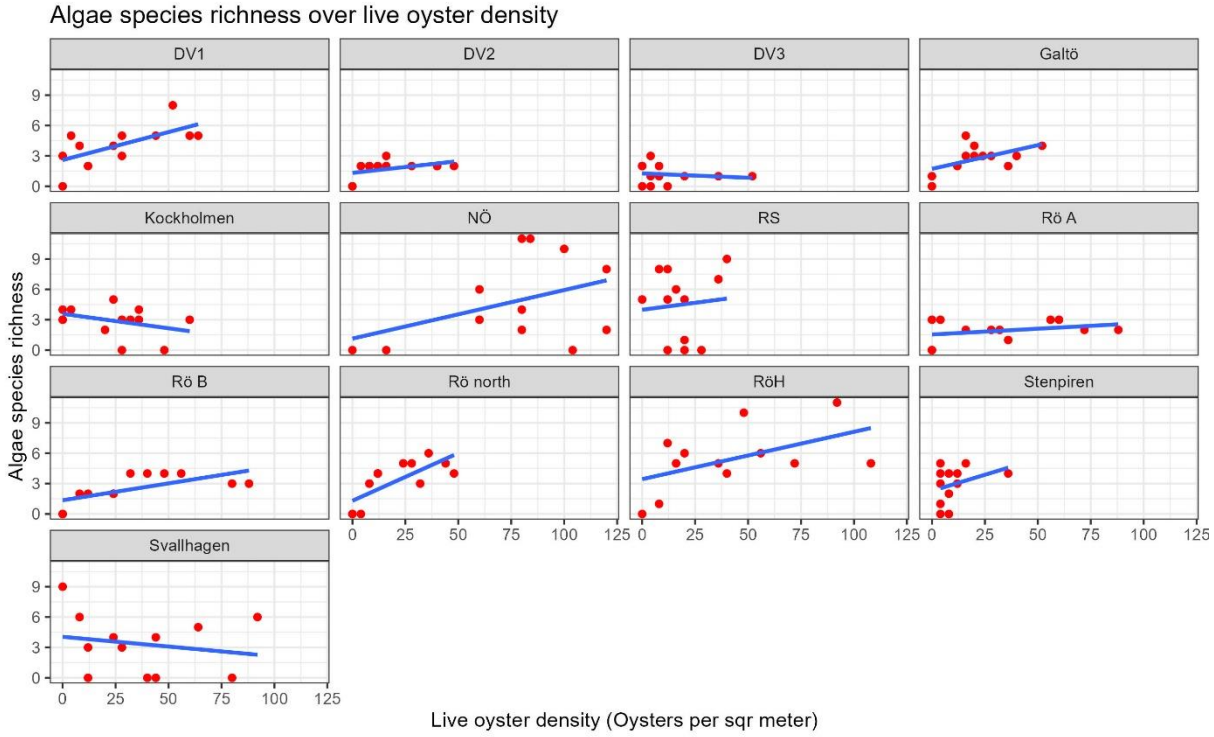


*Figure 7: Change in algae species richness at different densities of live oysters, illustrated by site. Site name abbreviations: DV=Daftö-Valö, NÖ=North Öddö, RS=Rossö South, RÖ=Rossö, RöH=Rossö Harbor*

*Table 3: Results from a Linear mixed model testing the relationship between algae species richness, density of live oysters and exposure.*

| Fixed effects | Estimate | Std. Error | df | t value | Pr (>\|t\|) |
|---|---|---|---|---|---|
| *(Intercept)* | 3.13 | 0.33 | 10.34 | 9.46 | <0.001 |
| *Oyster density* | 0.03 | 0.27 | 11.12 | 3.05 | 0.01 |
| *Exposure* | <0.001 | 0.33 | 10.50 | 0.19 | 0.85 |
| *Oyster density * Exposure* | <-0.001 | 0.28 | 10.21 | -0.43 | 0.67 |

## Algae biomass

The visualizations for the change in algae biomass over different oyster densities, showed a general positive trend is (*Figure 8*). The data generally showed either a total deficit of algae or very low mass of algae when the sediment was devoid of oysters. At higher oyster densities, 100 to 120 individuals/$m^2$, algae biomass could be up to or in excess of 1 000 g in the 0.25 $m^2$ sampling square.

As for the other variables explored no general trend for algae biomass over exposure was observed. This was also corroborated by the model, that showed a significant positive relationship between algae biomass and oyster density (Liner mixed model, P<0.05, *Table 4*), but no relationship between algae biomass and exposure. Random effects explained 34.6 % of the variation in the data.

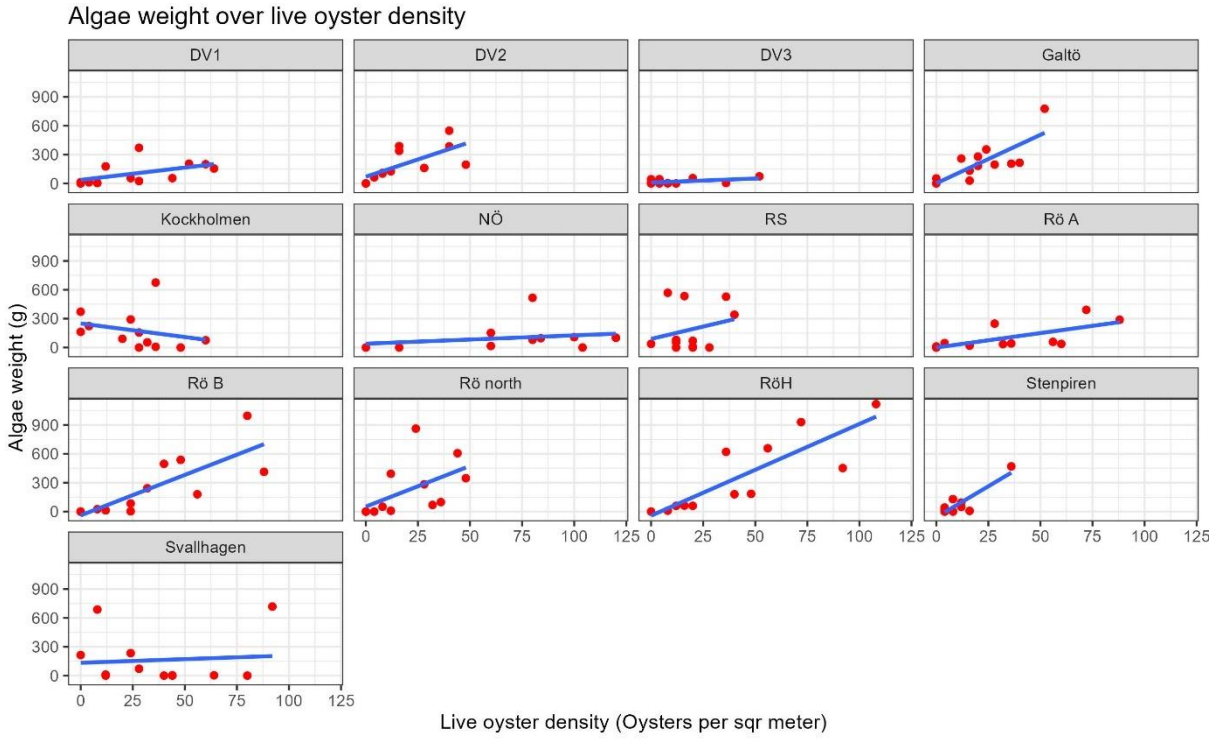


*Figure 8: Change in algae weight at different densities of live oysters, illustrated by site. Site name abbreviations: DV=Daftö-Valö, NÖ=North Öddö, RS=Rossö South, RÖ=Rossö, RöH=Rossö Harbor*

*Table 4: Results from a Linear mixed model testing the relationship between algae weight, density of live oysters and exposure.*

| **Fixed effects** | **Estimate** | **Std. Error** | **df** | **t value** | **Pr (>\|t\|)** |
|---|---|---|---|---|---|
| *(Intercept)* | 186.38 | 26.75 | 10.16 | 6.97 | <0.001 |
| *Oyster density* | 4.95 | 35.33 | 10.47 | 3.93 | 0.003 |
| *Exposure* | <-0.001 | 27.92 | 11.02 | -0.004 | 1 |
| *Oyster density * Exposure* | <-0.001 | 36.63 | 10.86 | -0.05 | 0.96 |

### Sediment grainsize

The sediment grainsize distribution was divided into three categories, Gravel, Sand and Silt. The model was run for each category, but no significant relationship was seen for any of the categories.

## Discussion

This study aimed to examine the relationship between oyster density and species richness of macroalgae and infauna. The hypothesis was that the species richness of infauna and macroalgae and the biomass of macroalgae would change with oyster density. No impacts of oyster densities between 0 and 120 individuals/$m^2$ on infauna species richness was, however, observed. In contrast, both macroalgae species richness and biomass increased with increasing oyster densities.

### The oysters' effect on the ecosystem

Even though oysters have previously been found to increase the concentration of organic matter in the sediment (Norling et al., 2015; Zwerschke et al., 2020), this study did not find a strong significant relationship between oyster density and sediment organic content. The model in this study merely showed a moderately significant relationship, meaning that it was larger than the decided significance of 5 %, but not larger than 10 %, so still not strong enough to discard the null hypothesis, but strong enough to perhaps warrant further studies.

From their experiments, Norling et al. (2015), found that the mean concentration of organic content in the sediment when there were no oysters present was between 1 and 2% and that organic content in sediment covered by oysters was significantly higher, at around 3%. Studies have also previously found that oysters impacted the grainsize of the sediment. This study saw an overall higher concentration of organic matter in the samples taken from sediment devoid of oysters. The mean concentration of organic matter in these samples was 3%±2% (N=21). The sediment samples taken from sediment with the highest oyster densities, densities over 80 individuals/$m^2$, had a mean concentration of organic matter just slightly higher, at 3.02%±2% (N=15). The mean concentration for all of the samples was 3.4 %±3% (N=156). The sediment organic content seen in this study overall do not differ largely from what has been seen in other studies (Nohrén et al., 2009; Norling et al., 2015). Moreover, Castel et al. (1989) saw an increase in the sedimentation of small particles in areas occupied by oysters, meaning that they saw that the oysters affected the sediments grainsize (Castel et al., 1989). Although this study only briefly investigated the relationship between sediment grainsize and oyster density, no significant relationships between oyster density and grainsize were observed. It was, however, observed that the sediment in and around the oyster reefs often was softer and finer than the surrounding sediment. This would indicate that the oysters do influence the sediments grainsize, but the model did not corroborate this.

For future studies, samples for organic content could also be collected from sites completely devoid of oysters. The samples collected with zero cover in this study were still near oysters, that might have affected the organic content of these samples as well.

At the beginning of this study, it was expected that an increase in organic content could have a positive impact on infauna as a consequence of the increased amount of nutrients that would be available for the infauna (Norling et al., 2015). Consequently, as no effects of oysters on sediment organic content was observed, it is not surprising that no effects of oysters on

infauna was observed. Additionally, it has previously been seen that a high load of bivalves, such as mussels and oysters can have a negative effect on infauna. This is mainly due to the high nutrient loading from the bivalves that, in areas with lower circulation, could lead to hypoxia in the sediment. Overall, this indicates that bivalves could be beneficial for infauna at low or medium densities, but if they get too dense, they might become more detrimental (Castel et al., 1989; Dittmann, 1990; Commito et al., 2008; Markert et al., 2010).

In accordance with the results from this study, Norling et al. (2015), did not see any significant effects of oyster presence on infauna. A trend towards reduced abundance was, however, observed. This is also corroborated by other studies that found that oysters had a positive effect on infauna of a smaller size, but simultaneously hindered infauna of larger sizes, ultimately reducing diversity (Castel et al., 1989). Yet, other studies have found a distinct increase in infauna abundance in and around oyster reefs when compared to bare sediment (Kochmann et al., 2008; Markert et al., 2010). Both Kochmann et al., (2008) and Markert et al., (2009) sampled at oyster densities far greater than what was found in this study, around 2 000 individuals/$m^2$. Kochmann et al. (2008) mentioned that most of the oysters they observed were 30 mm or smaller, while many of the oysters observed in this study were larger, hence this difference in oyster size could explain the observed discrepancies in outcome. Nevertheless, the relationship between oyster density and infauna is unclear. Moreover, as the infauna data in this study showed a large amount of variation, further investigation might be needed to fully understand the interaction between oyster density and infauna.

Reefs of bivalves are known to benefit epifauna and other organisms, and macroalgae are no exception. In accordance, this study found a positive significant effect of pacific oysters on both species richness and biomass of macroalgae, and other studies have shown similar patterns for both oysters and other bivalves (Westerbom & Koivisto, 2022). As stated in Mortensen et al. (2017), areas where oysters settle will, if the oysters are left to form reef structures, start functioning as a hard bottom area, which is more suitable for macroalgal growth than soft bottom areas. Consequently, the relationship between oyster density and algae species richness and the relationship between oyster density and algae biomass observed in this study are both expected and confirm the posed hypothesis.

This study focused on species richness and there was not enough time to evaluate the effects of oyster density also on species composition. This, and analyzing species abundance, might be interesting prospects for future studies. This could be analyzed using a multivariate analysis, to explore how the combined effects of both oyster presence and exposure might affect the species composition and abundance of both infauna and macroalgae, as illustrated by Norling et al. (2015).

### The effects of exposure and site

When looking at the correlation plot of sediment characteristic, a relationship between the exposure at the site, sediment grainsize, and organic content was observed. The amount of very small sediment particles was highest at low exposure and with increasing exposure the percentage of small particles decreased. This is expected since larger particles require more energy to be moved, thus increased exposure hinders the settlement of finer particles (Westerbom, 2006; Le Minor et al., 2022). The organic content in the sediment was observed

to follow the same pattern with increasing exposure lowering the concentration of organic matter. This might be due to higher retention of organic matter in finer sediments, and finer sediments being more prevalent at sites with lower exposure (Martinez-Garcia et al., 2015).

Looking at the other correlation plot, *Figure 3*, regarding oyster presence, there is no clear relationship between exposure and oyster presence. The only significant relationship seen in this figure, is that between oyster biomass and exposure. This relationship indicates a negative relationship, meaning increased exposure leads to lower oyster biomass. This has been seen in other studies as well, such as (Bergström et al., 2021), where a decrease in oyster abundance was observed at increasing levels of exposure.

Macroalgae can also be sensitive to exposure. Larger canopy-forming macroalgae, such as *Fucoids*, tend to be less prevalent in areas with high exposure. This is partly due to the risk of dislodgement but also due to higher prevalence of grazers feeding on them in these high exposure areas (Jonsson et al., 2006). This is, however, not a trend seen in this study, where no relationship between exposure and algae biomass was seen. The general low exposure of the sites visited in this study may explain the lack of impact of exposure on macroalgae.

Overall, trends in the figures are not necessarily clear, since values and trends vary to different extents between the sites. This variation between the different sites is not as prevalent for all the variables, but they occur for all the variables. This is the reason for including site as a random factor in the statistical model. Variation between sites have previously been seen in other similar studies, and may be an important factor to consider in future studies as well (Hollander et al., 2015; Laugen et al., 2023).

## Conclusions

Considering that the pacific oyster had a positive effect on algae biomass and species richness, and no effect on infauna, increasing densities of oysters seemingly had an overall positive effect on biodiversity where they grow. As macroalgae could also increase biodiversity by providing shelter and food for many animals, and since the presence of oysters increase the abundance of algae in an area, it can be assumed that oysters both directly and indirectly can contribute positively to biodiversity at large. How oysters and macroalgae together influence biodiversity both within the sediment and above it is not apparently clear. The interaction between these variables and how they together influence biodiversity was not looked at in this study, however it is an interesting prospect to investigate in the future.

Moreover, the impacts of the oysters documented in this study (no effect on infauna, positive effects on macroalgae) may be of relevance for management of the invasive species. On one hand it is an invasive species that might change the natural environment in an area. Areas that would naturally be soft bottoms quickly change to act as hard bottom areas. But on the other hand, the oysters might also have positive effects on their surroundings, possibly contributing to an increase in biodiversity and mitigation of eutrophication (Officer et al., 1982; Kochmann et al., 2008; Markert et al., 2010; Zwerschke et al., 2020). Whether or not the pacific oysters changing the natural environment should be considered an issue is up for debate, but since they do have some positive effects, they might still be beneficial for biodiversity to some extent. Perhaps management of the species should be dictated by weather or not negative effects are observed. From the data retrieved in this study, the pacific oysters do not seem to

be a very large issue, at least at the densities sampled in this study. Removing the pacific oyster completely from Swedish waters would likely be difficult, time consuming and expensive, given how well established they are. Management of the pacific oyster might most effectively be, to limit the spread and keeping populations down as best as possible. The management efforts could be focused on areas most sensitive to the pacific oysters, such as biogenic reefs (Mortensen et al., 2017).

## Methodological considerations

When it comes to the shortcomings of this study, many of them arose due to a limitation of time. Generally, when infauna samples are collected there is a compromise between sample volume and sample number. Large samples take longer to process, reducing the number of replicates that can be collected, while small samples infer a risk to not collect a representative sample since some animals might not be caught in the smaller volume. The tube used in this study had a diameter of 10 cm, which could be considered a normal size for infauna sampling, but larger tubes could also be used. This sample volume was preferred in this study since the samples were sieved through a 1 mm sieve, which retained some of the sediment in the collected samples. This tube size was also used since a large variation between sites, as seen in Hollander et al. (2015) and Laugen et al. (2023), was expected, and thus it was prioritized to get a larger number of samples to try and compensate for this variation. Had a larger sampling tube been used, the collected samples would have been of a volume too large to analyze. When a larger tube is used, it is more common to only use a 4 mm sieve, but since this study also took smaller infauna species into account, a smaller sieve had to be used. Collecting smaller samples also allowed for collection more samples at each site, which increased the spread of the samples at each site, hence more accurately represent reality. For future studies, if time allows it, it could be beneficial to try and combine the two methods for collecting infauna. Collecting larger samples with a larger tube while also not compromising with fewer samples. This would combine the benefits of both methods, although it would be more time consuming, and may result in less sites being explored.

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