UiA University of Agder

Master

Mapping the invasion: spatiotemporal distribution of the Pacific oyster in Scandinavia

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Abstract

The Pacific oyster (*Magallana/Crassostrea gigas*) is an invasive species to Scandinavia, originating on the Pacific coasts of Asia. Introduction to Europe of these oysters was a result of farming initiatives, put in place following declines of the native oyster species (*Ostrea edulis*). The oysters were introduced to Denmark, Sweden, and Norway in farming trials during the 1970s, however Norwegian and Swedish populations have also been a consequence of larval drift. They are not currently commercially farmed in any of the three countries due to the effects that wild populations have on the areas they invade. To map historical and present distribution and identify trends this study assembles all available datasets in each of the three countries from 2005-2020. Temperature and salinity both limit reproductive effort in the oysters, which is why an analysis of those readings has been included in this study. Nine surveys are included; two surveys from Denmark, three from Sweden, and four from Norway. One of the Norwegian surveys was conducted by our team in the Laugen lab in July 2020. Mapping the datasets suggested that the number of oyster populations were increasing in Denmark and showing both increase and decrease in Sweden and Norway, depending on the survey. An increase in temperature and salinity against latitude was found in Denmark, a decrease in average temperature and increase in average salinity in Sweden, and both positive and negative short trends in Norway. Periods with low temperature and/or low salinity can lead to increased adult oyster mortality, as well as limiting reproduction. Overall, the findings suggest that populations are fluctuating in Sweden and Norway but that these fluctuations are unlikely to result in widespread extinction; the connectivity between the three countries will enable larval drift to re-establish populations. Future recommendations are that a standardized protocol for Scandinavian oyster surveying be created, as well as establishing large-scale annual surveys.

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Preface

I would like to thank my supervisor, Ane Timenes Laugen, for her endless help and feedback while I worked through this project and for always checking in with me. Also, this study would not have been possible without the cooperation of various researchers and institutions. Data on Swedish oyster populations was obtained from Per Carlsson and his students at Lund University in 2018 and 2020, Åsa Strand at IVL Swedish Environmental Research Institute, and Hanna Partoft, Jack Räisänen, Kari Løe, Elin Lygård in the Ringhals survey. Data on Norwegian oyster populations was obtained from the Institute for Marine Research, Jan Erik Tangen and the Fylkesmannen of Telemark, Håkon Aamodt with Nord University, Hans Olav Sømme with the Fylkesmannen of Rogaland, and finally Haakon Braathu Haaverstad with the Norwegian Environmental Protection Agency. Data on Danish oyster populations was obtained from Bent Vismann at the University of Copenhagen and verified citizen science observations by Thomas Eske Holm (Aarhus University). I am very grateful to all of those who happily agreed to contribute data to this study, as well as Per Dolmer who took the time to discuss the Danish situation with me.

A massive thank you to my colleagues Sevan Esagholian and Molly Reamon, Stein Mortensen from IMR, Pontus Eriksson, Meghedi Orbelians, and Samantha Page for being the best fieldwork partners I could have asked for. It was a real joy to work alongside you all.

And of course, thank you to my ever-supportive family who accepted me moving halfway across the world and have continued to cheer me on ever since.

Kristiansand 03.06.21

Alice Durkin

1. Introduction

1.1 Background

The introduction of invasive species to coastal communities can have serious impacts on the ecosystems in which they come to inhabit; disrupting food chains by replacing key species, bringing disease, altering the physical landscape, and disturbing nutrient flow (Molnar et al., 2008). Once a species is introduced it can be very difficult to remove them, especially if their introduction was a result of larval dispersion from a nearby area; the other population could be under different jurisdiction and management and could possibly continue to act as a source population.

The Pacific oyster, *Magallana*/*Crassostrea gigas,* is one such invasive species that has come to inhabit shorelines across the globe and is now considered endemic in many places. This oyster originates on the Pacific coasts of Japan, China, and Russia, and has been introduced in many places including British Columbia and the Netherlands as a suitable oyster species for farming (Troost, 2010). Pacific oysters were first introduced to Europe in the 1960s following declines in populations of the native European flat oyster (*Ostrea edulis*), and imports continued well into the 1990s (Troost, 2010). Both oyster seed and adults were introduced to French coastlines in the 1970s in an attempt to restore their ailing oyster industry, and the species was so successful that the industry recovered within only a few years (Goulletquer, 1997). As far back as the 1860s there were introductions of *Crassostrea angulata*, or the 'Portuguese oyster', which was previously considered to be a separate species from *C. gigas,* but which subsequent genetic studies have shown to be the same (Humphreys et al., 2014). In terms of the ecological and societal impacts of Pacific oysters, there are both positives and negatives. They can change the physical habitats they take over, block waterways, and be a source of injury for swimmers. But they can also reduce eutrophication through their role as a filter feeder, increase biodiversity, and are in many places harvested and can be of great commercial value (Smaal et al., 2019). These conflicting effects can make deciding what to do with the oysters more difficult for authorities.

1.2 Pacific oysters in Scandinavia

Previously it was believed that the waters in northern Europe were too cold for the oysters to reproduce and subsequently spread, however by the 1970s this was proven to be incorrect as wild populations were spawning (Humphries et al., 2014). Danish populations are a result of introduction for farming (1970s-1990s), Swedish populations are a result of a combination of farming trials in the 1970s and larval dispersion (Laugen et al., 2015), and in Norway there were some farming attempts in the 1970s, but the first wild sighting is believed to have been in 2003 (Jelmert et al., 2020). The types of coastlines in Norway, Sweden, and Denmark that Pacific oysters have established themselves in are quite different, with large and exposed tidal areas common in Denmark versus more sheltered bays and inlets in both Sweden and Norway (Mortensen et al., 2017). This can make predicting where they will establish themselves difficult. A risk assessment was conducted in 2014 by Dolmer et al. for the Institute of Marine Research (IMR) that evaluated both habitat types and climate conditions and predicted the effects of bio-invasion by Pacific oysters in the short and long-term future. This has not been followed up, therefore a study like this one that collects all available surveys to identify populations trends could be an important step towards validating those predictions.

A genetic analysis by Faust et al. (2017) of individuals from sites in France, the Netherlands, Ireland, Denmark, Sweden, and Norway indicated that Swedish populations likely originated from Danish spat and that both Norwegian and Danish populations had a mixed pattern of origin. The interconnectivity of these populations is important to understand when approaching management strategies as an extinction of Pacific oysters from Swedish or Norwegian waters would likely be followed by recolonization from Danish populations (Faust et al., 2017). The relative closeness of Denmark, Sweden, and Norway informs the way that Pacific oyster larval distribution will occur, and the impact it will have if different management strategies are taken.

A potential issue when it comes to managing Pacific oysters is their status as an invasive species. Commercial farming of these oysters, though practiced in other countries, is currently banned in Denmark. In Norway there have been no approvals given for projects that involve their commercial farming, and in Sweden there has been a recent change in that they will now allow farming of triploid Pacific oysters, which are genetically modified to be sterile. With an invasive species that takes over and transforms habitats, a risk is that allowing commercial farming could lead to oyster larvae leaking from the farm out to the wild and making the management problem even worse, though wild populations would still contribute more larvae.

In terms of large-scale surveys to track population changes, there has been no such survey in Denmark, instead there are individual research groups doing small surveys as well as citizen science contributions which have been verified. In Sweden the largest scale survey is the Strömstad-Helsingborg survey, which is not state run and includes a lot of volunteer work. In Norway the largest survey was conducted by the Institute of Marine Research (Havforskningsinstituttet/IMR), with sites ranging from the Swedish border to north of Bergen. However, this did not run longer than 2017-2018. Monitoring of Pacific oysters in all three countries is relatively small scale and patchy, and in order to manage a trans-boundary invasive species we need to have some kind of wide-reaching and systematic Scandinavian monitoring protocol.

1.3 Biological and Physical Factors

Pacific oysters are filter feeders that attach themselves to hard substrates such as rocks or other oysters, eventually forming reefs when the population gets large enough. This can significantly alter the habitat structure in an area, as well as changing water and nutrient flow (Ruesink et al., 2005). The oysters are oviparous and release their eggs when the water temperatures are warm, with the range of temperatures that they can tolerate and reproduce in expanding as the oysters have adapted to new areas, in connection with warming water temperatures over the years (Fleury et al., 2010, Laugen et al., 2015). After their pelagic stage the larvae settle on any hard substrate they can find and can reach maturity as soon as a year after becoming sedentary. Adults have extremely sharp edges and can become a hazard when reefs are established in popular swimming areas.

Salinity and temperature are two variables that may have an influence on a Pacific oyster's reproduction and mortality; oysters release their eggs when the temperatures are warm, and they cannot function properly at low salinity levels (Fabioux et al., 2005). They are important factors in the oysters' ability to spread, with temperatures and salinity needing to be above 20°C and 30 ppt respectively (Fabioux et al., 2005). While it can be difficult to obtain an accurate picture of temperature and salinity in all areas of a coastline (other factors such as water currents, outflow, and tidal patterns can have an impact), these could be two explanatory variables in the spread of the Pacific oyster in Scandinavia.

Another factor in the spread and success of oyster spat are the currents between Denmark, Sweden, and Norway. Fresh water from the Baltic Sea moves around the southern tip of Sweden and up along its eastern coast and through the Kattegat, where it then is pushed up and along the

Norwegian coast and through the Skagerrak. The Skagerrak feeds into the Norwegian Coastal Current, which flows along the coast of Norway and into the Barents Sea. Because of this system of movement, larvae from Swedish coastlines could disperse to Norwegian coasts, and be taken as far up in northern Norway as the oysters can survive. In the other direction, water from the North Sea flows down Denmark’s east coast, through the Danish straits and down towards Germany. We know from the aforementioned genetic analysis that has been done that Swedish populations were likely established as a result (at least in part) of Danish oyster dispersal. This physical connectivity further highlights the need for international agreement on management.

1.4 Study objectives

To get an overview of the current distribution of Pacific oysters in Scandinavia I collected data on individuals from a wide range of surveys and plotted their distribution. To gain a historical picture on how populations have changed, I framed the study with a timespan of fifteen years (2005-2020). Because salinity and temperature are potential factors that could influence the establishment and success of the oysters, I chose to include an analysis of any changes that may have occurred in the same time frame as is being studied with the oyster populations. It is expected that populations of oysters in all three countries will show long-term growth, though there may be years with higher apparent mortality. Populations in Norway are expected to be smaller than those in Denmark and Sweden due to their more recent establishment.

2. Materials and Methods

2.1 Study area

The area being investigated in this study (*Figure 1*) includes the west coast of Sweden from the Norwegian border down to the southern coast at Malmö, the Norwegian coastline from the Swedish border along to the area in and around Bergen, and the Danish east coast, including around Zealand. Locations were chosen based on historical survey data available in each country within the allotted time frame, including both repeated and one-time studies.

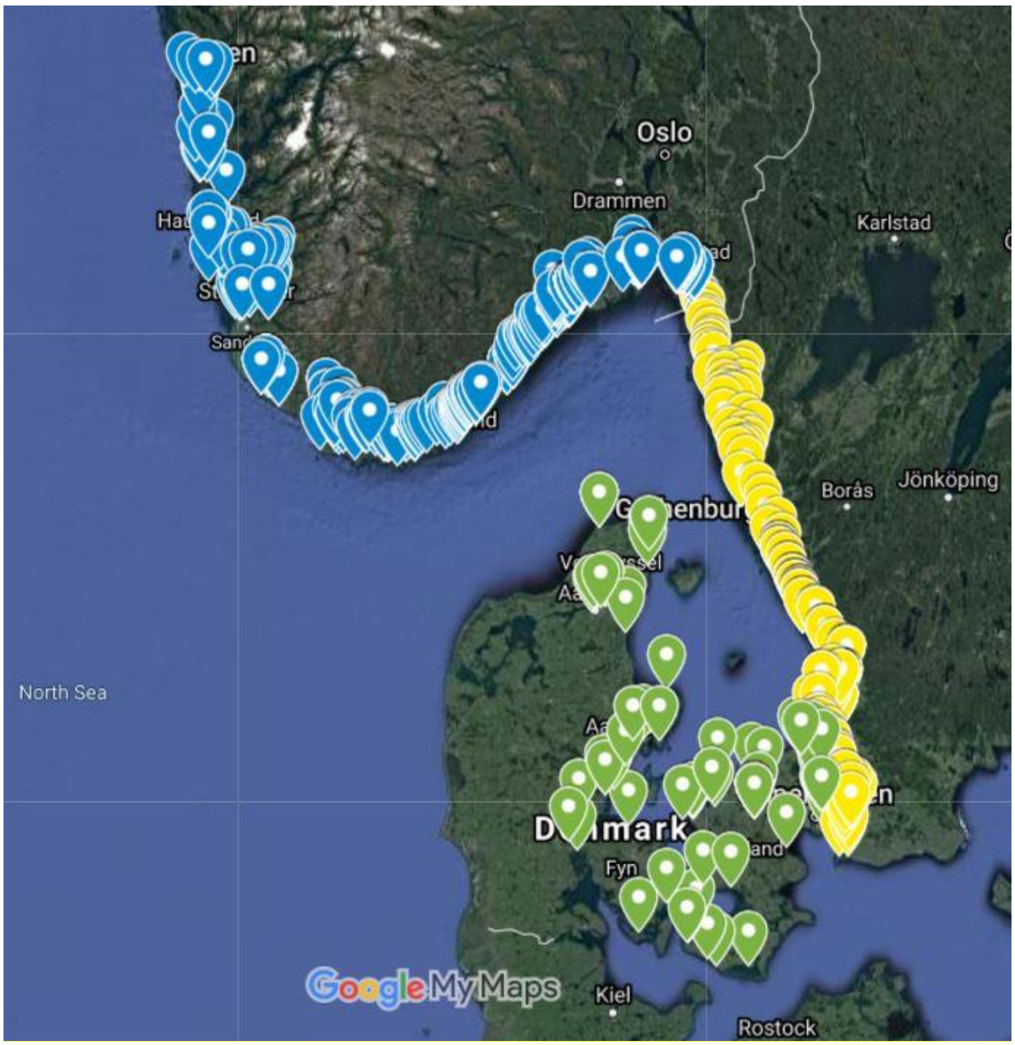

Figure 1: Overview of survey locations included in this study. Norwegian locations are depicted in blue, Swedish in yellow, and Danish in green. Photo: Google MyMaps.

2.2 Data collection

This study focuses on a fifteen-year period (2005-2020) and therefore only surveys within this period were included. All surveys included were retrieved through supervisor collaboration. Multiple datasets were available for some sites as recurring surveys used the same locations. Other datasets were one-off location checks. Historical data on Swedish oyster populations was obtained from the Strömstad-Helsingborg, Ringhals-Falsterbo, and Båstad-Malmö surveys. Data on Norwegian oyster populations was obtained from an IMR survey and the Telemark, Haaverstad, and Laugen lab surveys. Historical data on Danish oyster populations was obtained from a bachelor's thesis at the University of Copenhagen and from Naturbasen – Danmarks Nationale Artsportal.

To evaluate the possible impacts of temperature and salinity on oyster settlement and success, relevant data for the study period was downloaded from Denmark's Overfladevandatabasen, Sweden's meteorological and hydrological institute (SMHI), and from the Norwegian Marine Data Center (NMD) at the Institute for Marine Research . In all three countries the data came in the form of CTD readings; CTD stands for conductivity, temperature, and depth and is an instrument used to measures these variables in the water. Data was obtained primarily from the areas of relevance to this study, i.e. the areas surveyed, focusing on the relevant coastlines. Criteria for download included salinity measurement, temperature measurement, depth reading, year, and relevant municipality or research station. Environmental data collected was to be as close in area as possible to the sites surveyed for oysters to obtain the most accurate picture of local conditions.

2.3 Surveying

Due to the nature of this study not all data could be collected within one season, thus many datasets were obtained via collaboration with other researchers and institutions (see *Table 1* for a breakdown of surveys). Survey variables and methods occasionally differed between datasets but those recorded when available were individual counts, presence/absence data, mortality, individual sizes, and density estimates. Survey techniques included transects, snorkeling, and underwater drones.

Table 1: Surveys included in this study including years covered and data collected.

Country	**Study**	**Year**	**Data Collected**
Denmark	University of Copenhagen thesis	2019	Presence/absence, individual count, density
	Citizen science data	2005-2020	Presence/absence, individual count
Sweden	Strömstad-Helsingborg	2007, 2013, 2019	Presence/absence, individual count, individual size, density
	Ringhals-Falsterbo	2017	Presence/absence, individual count, individual size
	Båstad-Malmö	2018, 2020	Presence/absence, individual count, individual size
Norway	Haaverstad	2015-2016	Presence/absence, individual count, mortality
	Telemark	2017-2020	Presence/absence, individual count, mortality
	IMR coastal survey	2017	Presence/absence, mortality
	Laugen lab survey	2020	Presence/absence, population estimates, mortality

A portion of the 2020 Norwegian data was collected by our team in July of that year along the west coast, in collaboration with Stein Mortenson from IMR. Forty-six locations (see *Figure 2*) ranging from Bergen to Lyngdal were checked for Pacific oysters, with some of these points being chosen based on reports from artskart – a species databank for professional observations – and modelled points from a model created by DHI Water & Environment AS in connection with the Norwegian Environment Agency. The model had different stages of invasion predictions depending on climate scenarios, both predicted current and future locations.

Notes were taken at each location including flat oyster (*Ostrea edulis*) and blue mussel (*Mytilus edulis*) presence, Pacific oyster presence, environmental conditions, and a single temperature and salinity reading at around 30cm depth. The salinity and temperature readings were later chosen to be excluded from this study, due to a lack of data points and possible tidal and location biases. At some sites size data on the Pacific oysters found was collected. Methods for surveying included snorkeling, the DTG3 ROV from Deep Trekker, and wading; the methods used at each site were dependent on the physical environment.

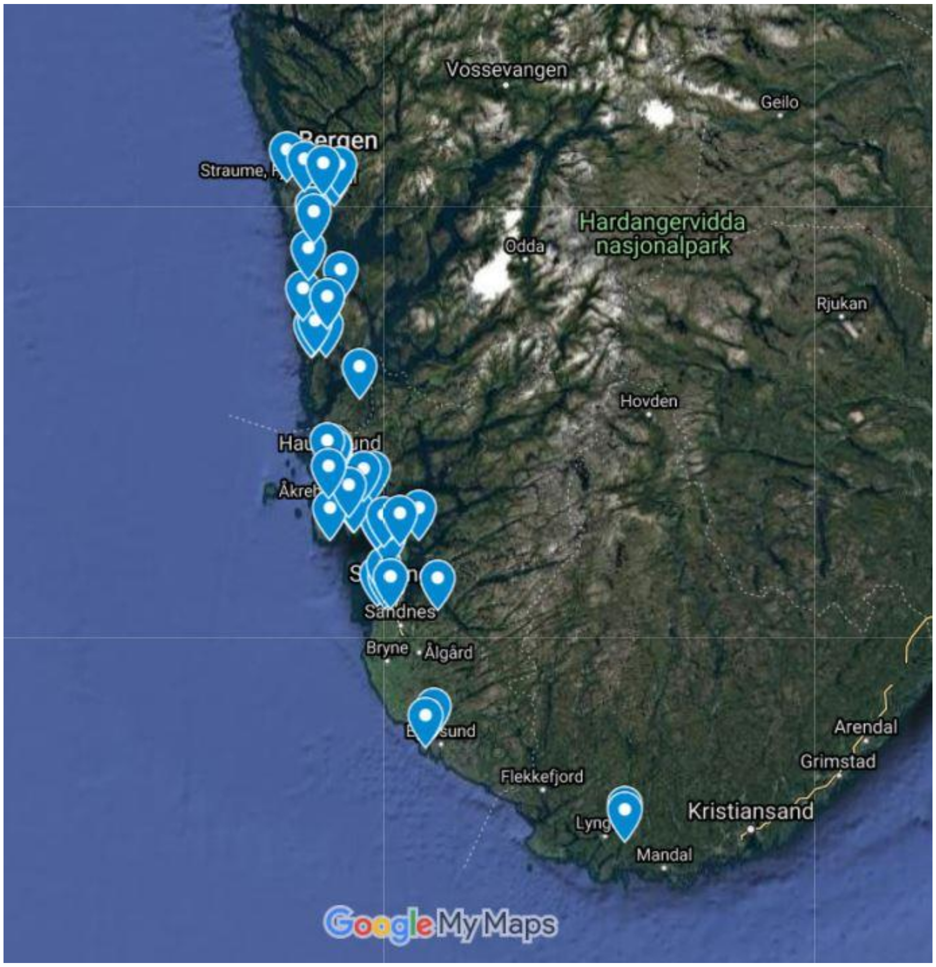

Figure 2: Locations surveyed by our team from the Laugen lab in July 2020. Photo: Google MyMaps.

2.3 Data analysis

All data analysis was done using R (version 4.0.3; R Core Team (2021)). Oyster data from Denmark came in the form of a bachelor thesis from 2019 and a set of verified citizen science data spanning multiple years. Maps of individual counts over time were created to display trends, as well as showing areas with absences. From Sweden there were multiple surveys with several spanning more than one year, allowing for comparisons over time to be made with maps. Norwegian data contained multiple surveys (several with multi-year data), as well as data from IMR and our own field work. In surveys that recorded only presence absence data, that data was mapped in a similar manner to individual counts.

Salinity and temperature data was used from depths of 0-2m to better identify trends in the areas with higher oyster density. Data was averaged monthly to identify seasonal trends, as well as annual maximum and minimum values. Regression analyses were done with regards to yearly values against latitude and maximum and minimum values against latitude, for both temperature and salinity, which were then plotted. Visualizing potential trends was the aim of these analyses, in an attempt to provide an explanatory variable for any oyster trends that might be identified.

3. Results

3.1 Oyster data

3.1.1 Denmark

In Denmark there was both a survey from a 2019 bachelor thesis (University of Copenhagen) and a verified citizen science dataset from Naturbasen – Danmarks Nationale Artsportal available for studying Pacific oyster presence. The 2019 bachelor thesis data was mapped to visualize oyster densities (*Figure 3*), which were calculated in the original paper as the number of individuals divided by the length of transect in metres. Densities are highest on the east coast of Zealand, with less areas with oyster presence on the western and southern coasts. There are also dense populations around areas of Lolland and Falster.

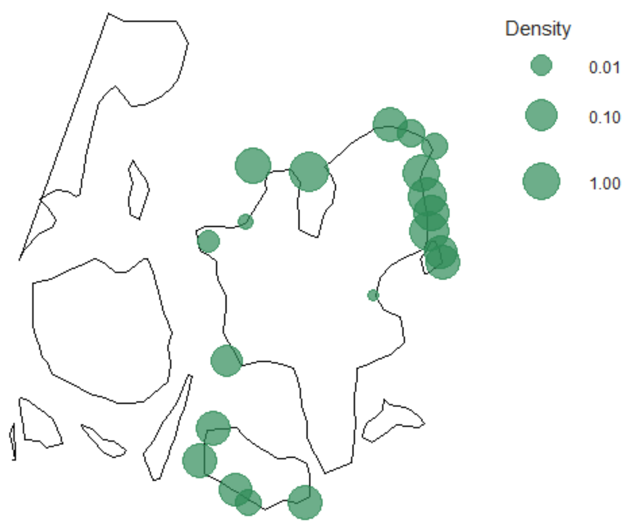

Figure 3: Bachelor thesis from the University of Copenhagen (by Julie Elmegaard Andersen, Mille Bolander, Peter Kristian Petersen, and Søren Baadegaard) depicting oyster density around Zealand. Density is measured in oysters per metre.

Citizen science data submitted to Naturbasen and verified by Thomas Eske Holm (Aarhus University) was available for a range of years, and the data was split into three periods for further clarity: 2005-2010, 2011-2015, and 2016-2020. Numbers of individual oysters were plotted instead of density due to the type of data available (*Figure 4*). Observations from the west coast of Denmark were excluded due to the focus of this study being on the east coast and its connectivity to the Swedish west coast (and in turn to the Norwegian coastline). A clear increase in the number of observations submitted can be seen over the three periods, with the largest jump between the 2011-2015 and the 2016-2020 periods. The beginnings of small populations can be observed in *Figure 4b*, with those areas increasing in the number of individuals in *Figure 4c*.

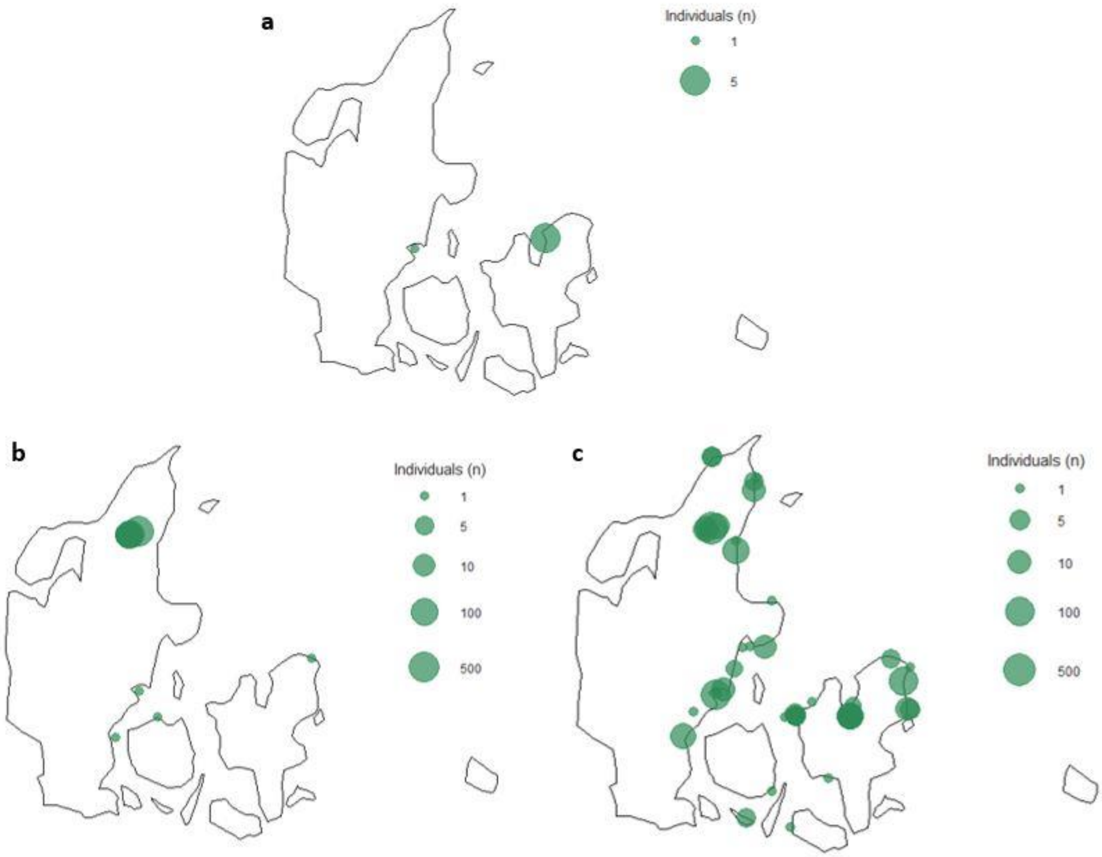

Figure 4: Verified citizen science observations from Naturbasen – Danmarks Nationale Artsportal , Denmark plotted in three periods: a) 2005-2010, b) 2011-2015, and c) 2016-2020.

3.1.2 Sweden

The Strömstad-Helsingborg survey (*Figure 5*) was the largest dataset included from Sweden and provided three years of oyster data along the west coast of Sweden (2007, 2013, 2019), from the Norwegian border to the Helsingborg area. Population size in this survey was classified into four levels: 1 = 0 individuals, 2 = less than 30, 3 = between 30 and 150, and 4 = more than 150 individuals. The number of sites in level 1 increased overall, from 30 sites in 2007 to 42 sites in 2019. The number of sites in levels 2, 3, and 4 all decreased over time, from 17 to 13, 12 to 4, and 9 to 4 respectively. The change in density can be noticed particularly between 2007 and 2013, followed by another smaller reduction five years later.

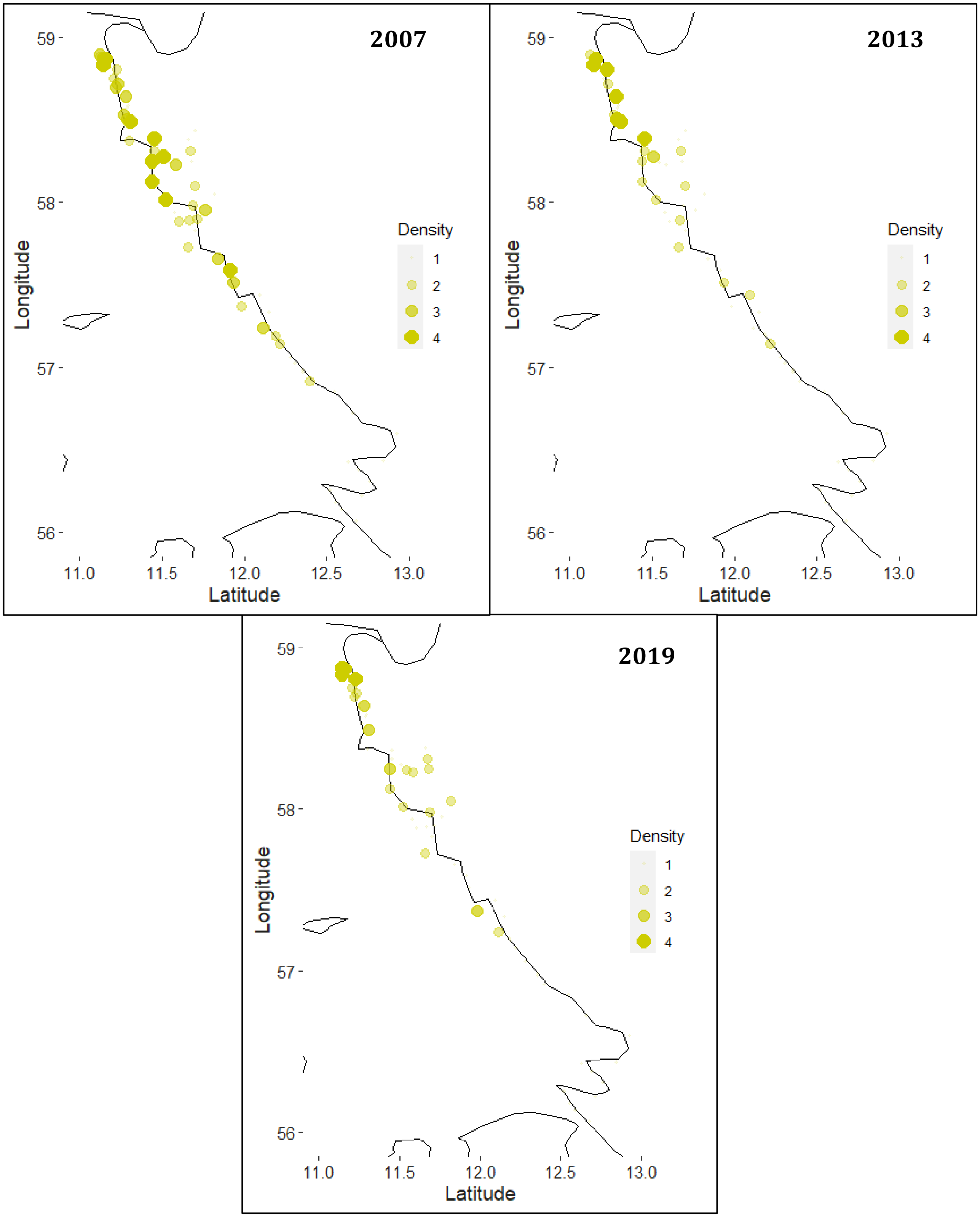

Figure 5: Data from the Strömstad-Helsingborg survey in western Sweden in 2007, 2013, and 2019. Density follows a scale of 1-4 (1 = 0, 2 = <30, 3 = 30-150, 4 = >150).

The Ringhals-Falsterbo survey from 2017 included a range of locations along Sweden's west coast, from just south of Gothenburg to the southern point of Sweden. *Figure 6* shows a side-by-side of the plotted oysters found on the left, and a total of all the locations surveyed on the right; out of the 56 locations, 34 did not have any oyster presence. The areas without oysters were the more northern sites as well as the more southern sites towards the Baltic Sea.

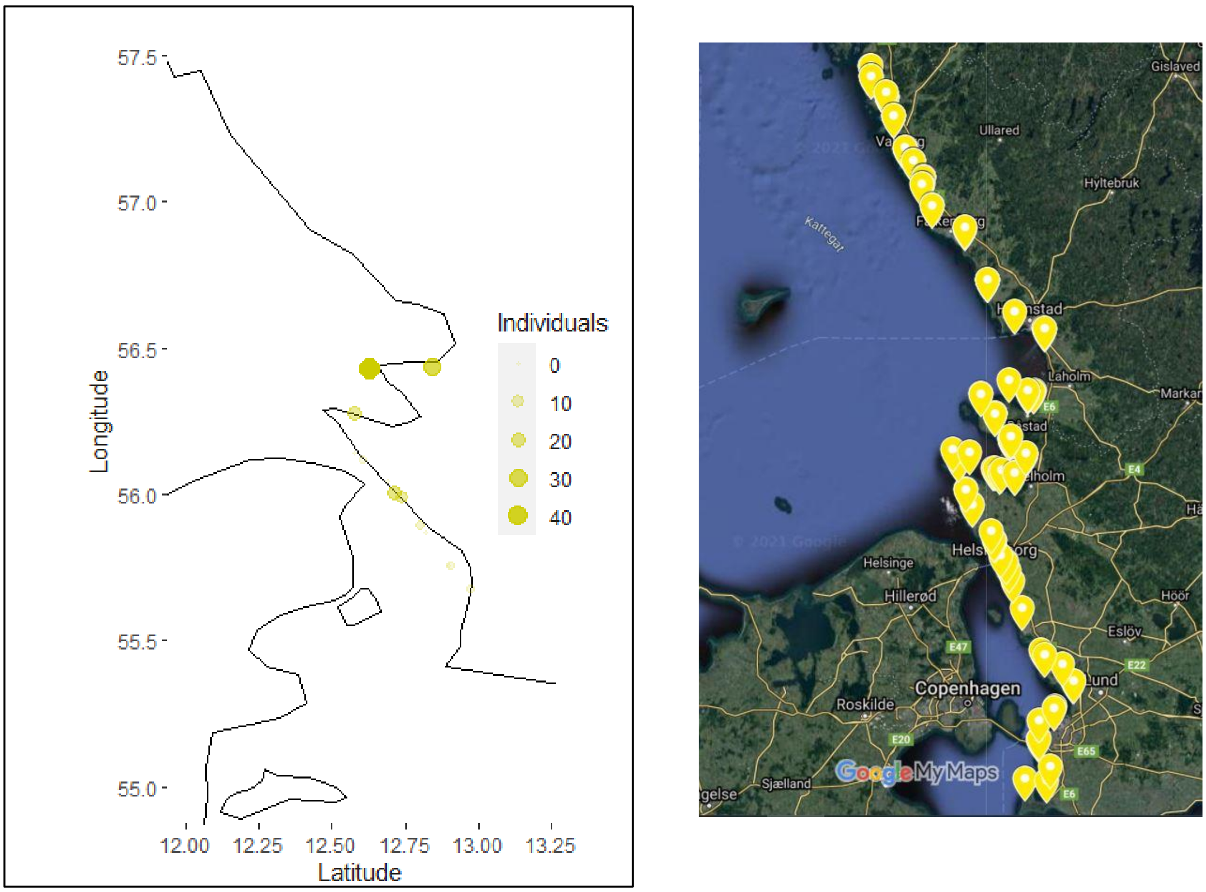

Figure 6: Number of oysters at each site (left) and all locations surveyed (right) in the 2017 Ringhals-Fasterbo survey. Right photo: Google MyMaps.

There were two years of data available from the Båstad-Malmö survey in repeated locations (plotted in *Figure 7*). In 2018 4 out of 14 locations had zero oysters, and in 2020 there were also 4 locations (out of 15) with zero oysters, but only two of the locations were the same in each year. Only 5 out of the 15 locations showed an increase in the number of oysters, with 6 locations showing a decrease and 3 no change. The number of oysters increased between the two years, but the more northern sites reported less oysters.

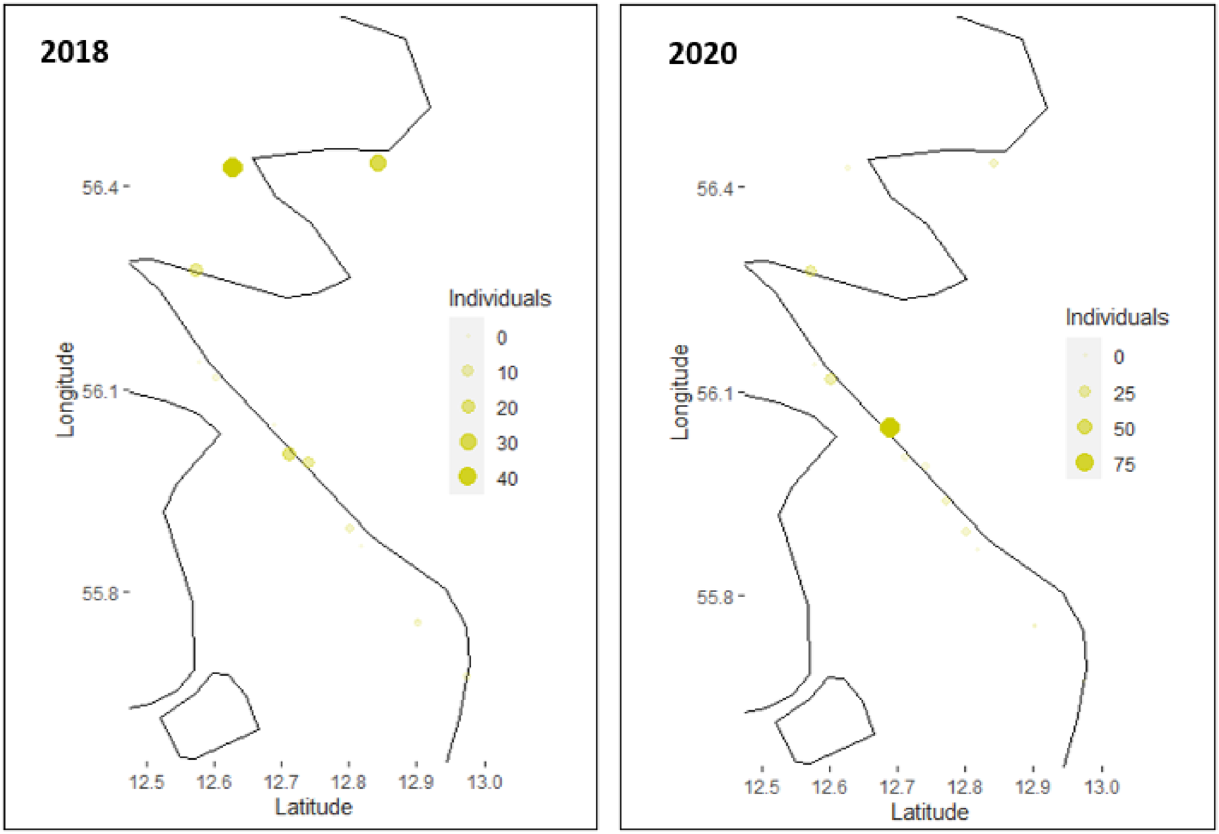

Figure 7: Individuals counted in the same locations in the Båstad-Malmö survey in 2018 and 2020.

3.1.3 Norway

The Institute of Marine Research collected data on Pacific oysters in several locations around the Norwegian coastline in 2017. The number of individuals at each site can be seen in *Figure 8*. Populations are the most dense in the east, decreasing as you go west along the coastline. Small, possibly more recently established populations can be seen in the area around Stavanger and larger populations seen around Kristiansand, Porsgrunn, and the Oslofjord. Many of the locations surveyed did not have oysters, with the most absences occurring between Kristiansand and Stavanger.

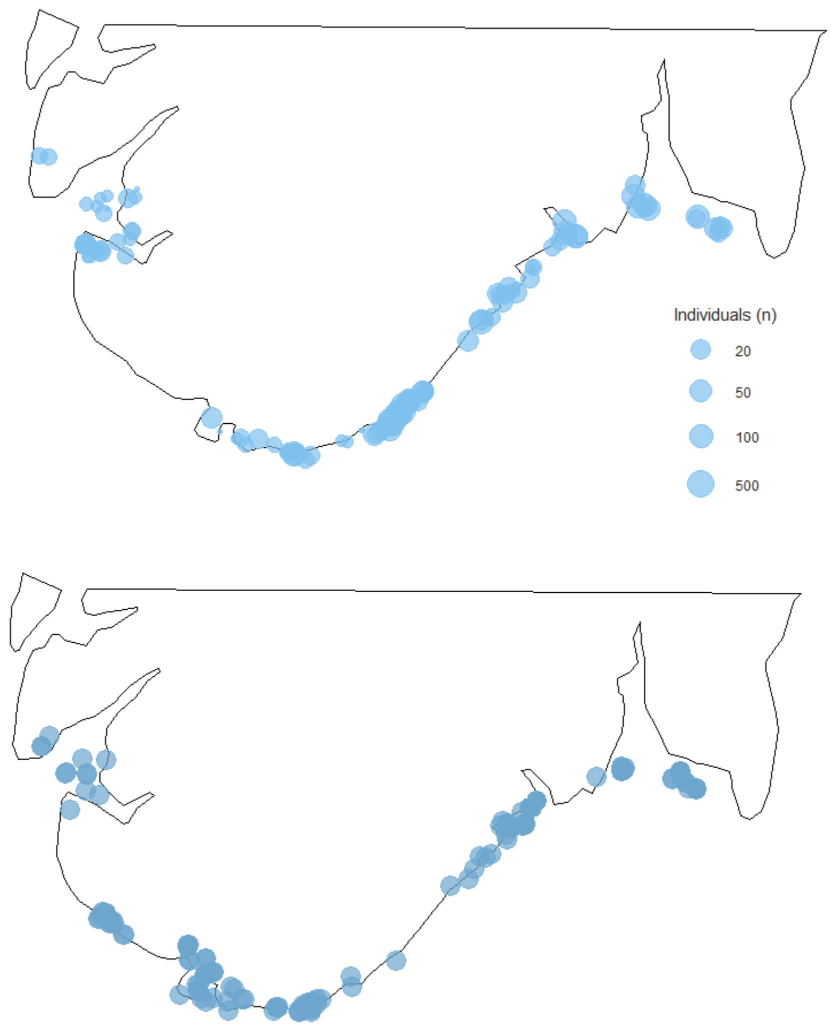

Figure 8: Survey data from the Institute of Marine Research on Pacific oysters in 2017. Locations without land mass visible are islands. Live individuals are mapped in the top map and locations where oysters were absent are mapped in the bottom map.

Our 2020 survey from the west coast of Norway was predominately a presence/absence survey, with some measurements and oyster counts taken depending on the location. The results of the presence/absence information can be seen in *Figure 9*. Out of the 46 locations surveyed, 26 were chosen based on them being DHI model points, i.e. predicted areas of oyster settlement. A further 19 of the locations were taken from artskart, a place to submit professional observations, and 1 point was a location that IMR had surveyed before. Out of those 46 locations, 26 had oysters, and 20 did not. Many of the locations had as little as one or two Pacific oysters, and the majority were clearly in the beginning stages of invasion. Many of the predicted sites from the DHI model did not have oysters, with some of the points being on land and some in areas likely too exposed for oysters to successfully settle. At one location the locals had been picking many of the oysters because they did not want them there.

Figure 9: Presence/absence data collected from the Laugen 2020 survey on the west coast of Norway. Presence is shown on the left and absence shown on the right.

From the Telemark region there was a multi-year survey spanning four years (2017-2020). Number of individuals counted each year can be seen plotted in *Figure 10*. In 2017 and 2019 there are many areas with a small number of oysters, and four larger sites in 2017 and 2018, followed by only two larger sites in 2019 and 2020. The larger oyster populations appear to occur in the southwest range of this survey compared to the northeast range where it could be expected due to proximity to the Swedish border.

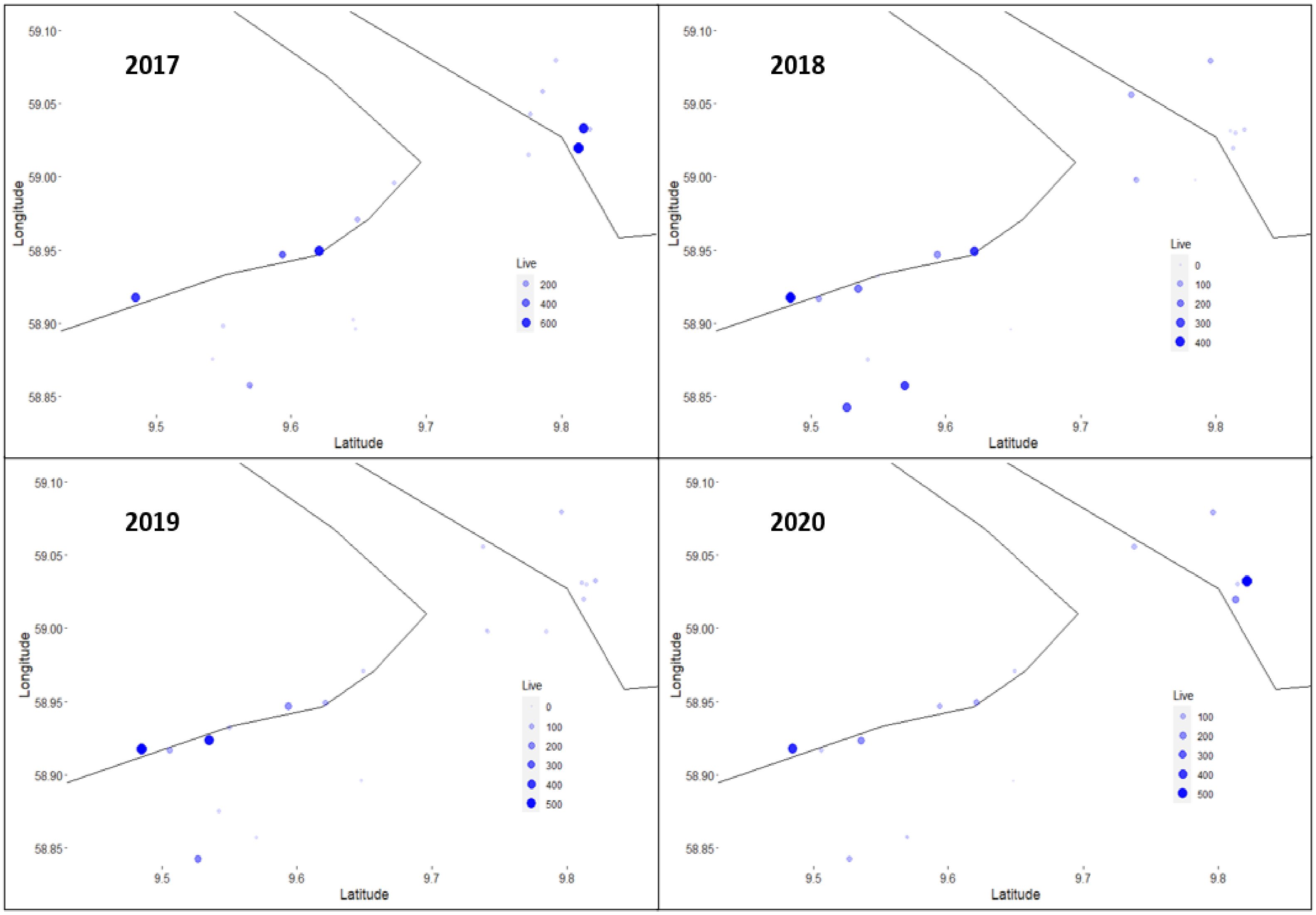

Figure 10: Data from the Telemark survey: 2017, 2018, 2019, and 2020.

Two years of surveys (2015 and 2016) were available for Agder and Vestfold in the Haaverstad survey. Number of individuals is plotted in *Figure 11*. The number of oysters increases between the two years with existing populations growing larger (with the exception of the southernmost site which saw a decrease). The larger populations are found at the sites at a higher latitude, but there were fluctuations within these populations. For instance, one of the three more northern sites grew smaller while another grew larger.

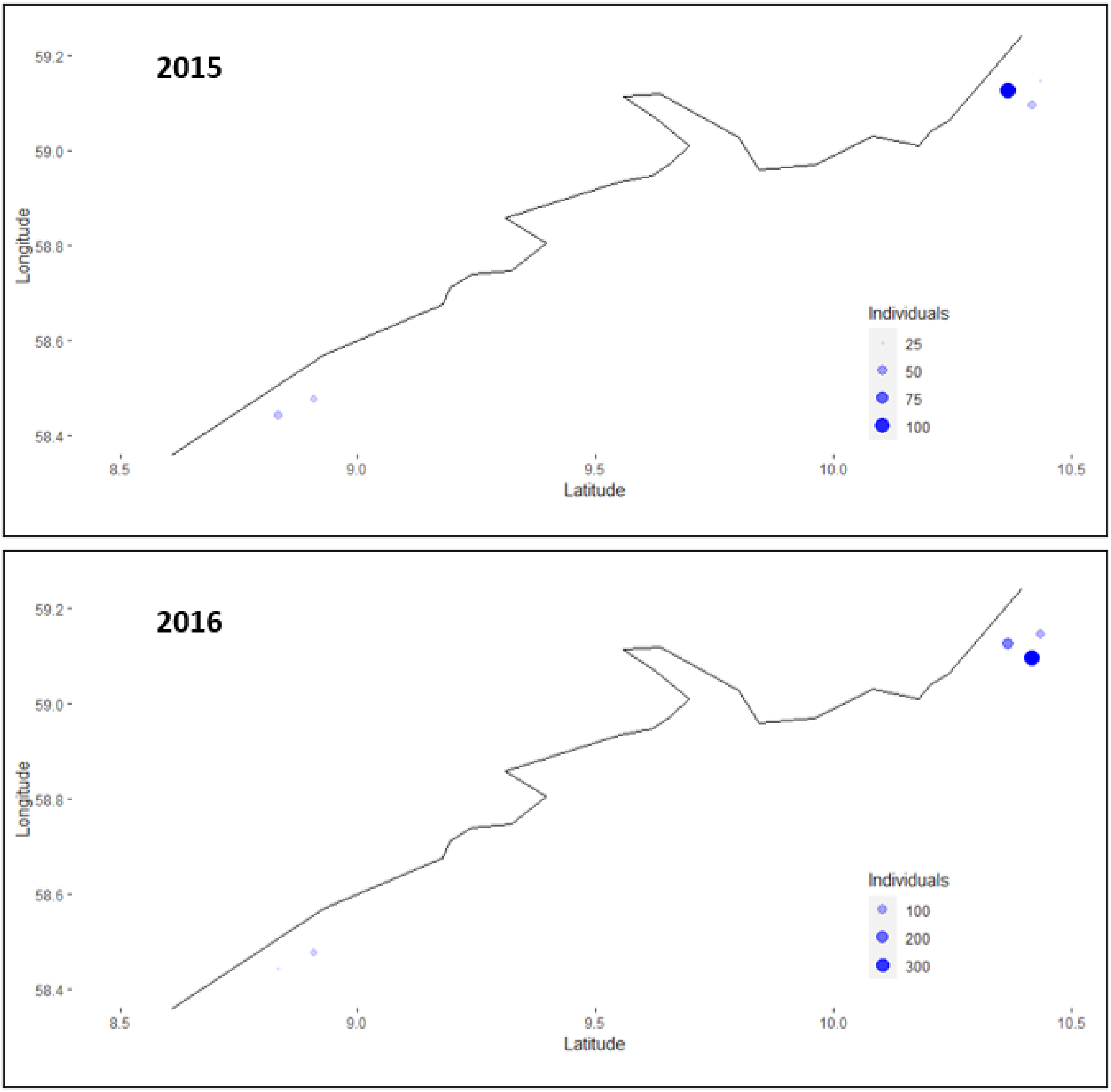

Figure 11: Data from the Haaverstad survey in 2015 and 2016.

3.2 Temperature and salinity

3.2.1 Denmark

The data on temperature and salinity in Denmark was collected from CTD data at field stations located in and around the east coast. Shown in *Figure 12* are the results of the average monthly temperatures (°C) in each year, plotted against latitude and smoothed using linear regression analysis. There is quite a mix of increase and decrease over the fifteen years, however there is a slight trend of increasing average temperatures over time. From this data 2014 appears to be the warmest year, followed by 2020. A marked difference can be seen between the range seen in 2005 versus that seen in 2020.

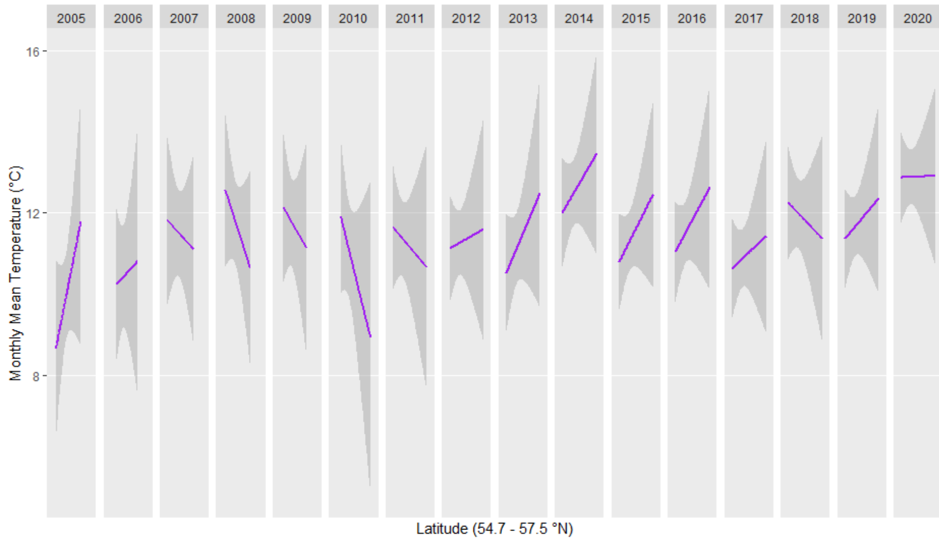

Figure 12: Temperature data from field stations on the east coast of Denmark. Average monthly values plotted against latitude, smoothed by linear regression and faceted by year.

The same analysis was carried out on average salinity readings (*Figure 13*) with salinity values recorded in PSU. There appeared to be much less variation with salinity averages than with temperature averages, but a trend of increasing readings can still be seen over the fifteen years. The last three years appear to have been quite similar, and the changes between other years quite gradual.

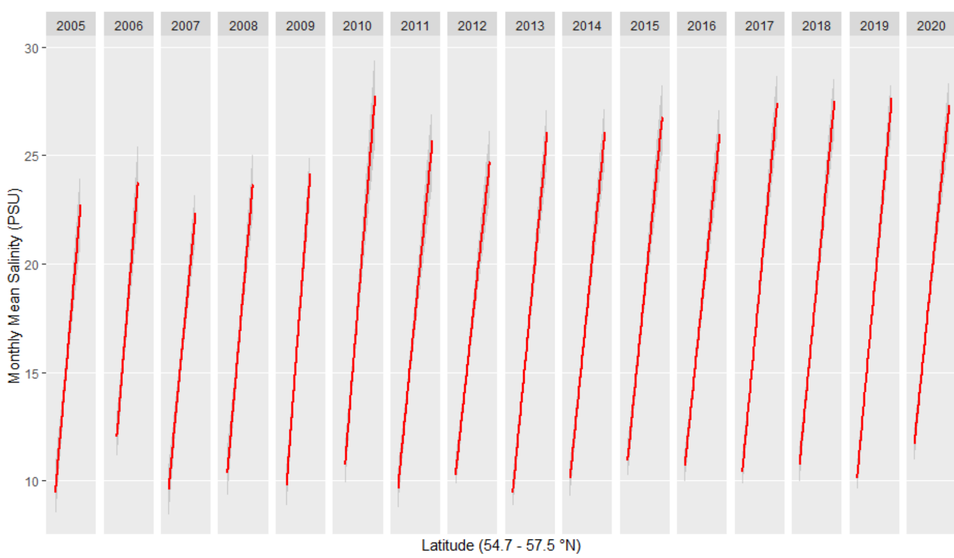

Figure 13: Salinity data from field stations on the east coast of Denmark. Average monthly values plotted against latitude, smoothed by linear regression and faceted by year.

In addition, annual maximum and minimum temperatures and maximum and minimum salinity readings were plotted against latitude (*Figure 14*). There is much more variation present in the temperature minimums than in the maximums, and there does not appear to have been a large increase or decrease in either. Salinity maximums only show a slight increase over the fifteen years, and minimums show an increase in the difference between readings at lower and higher latitudes.

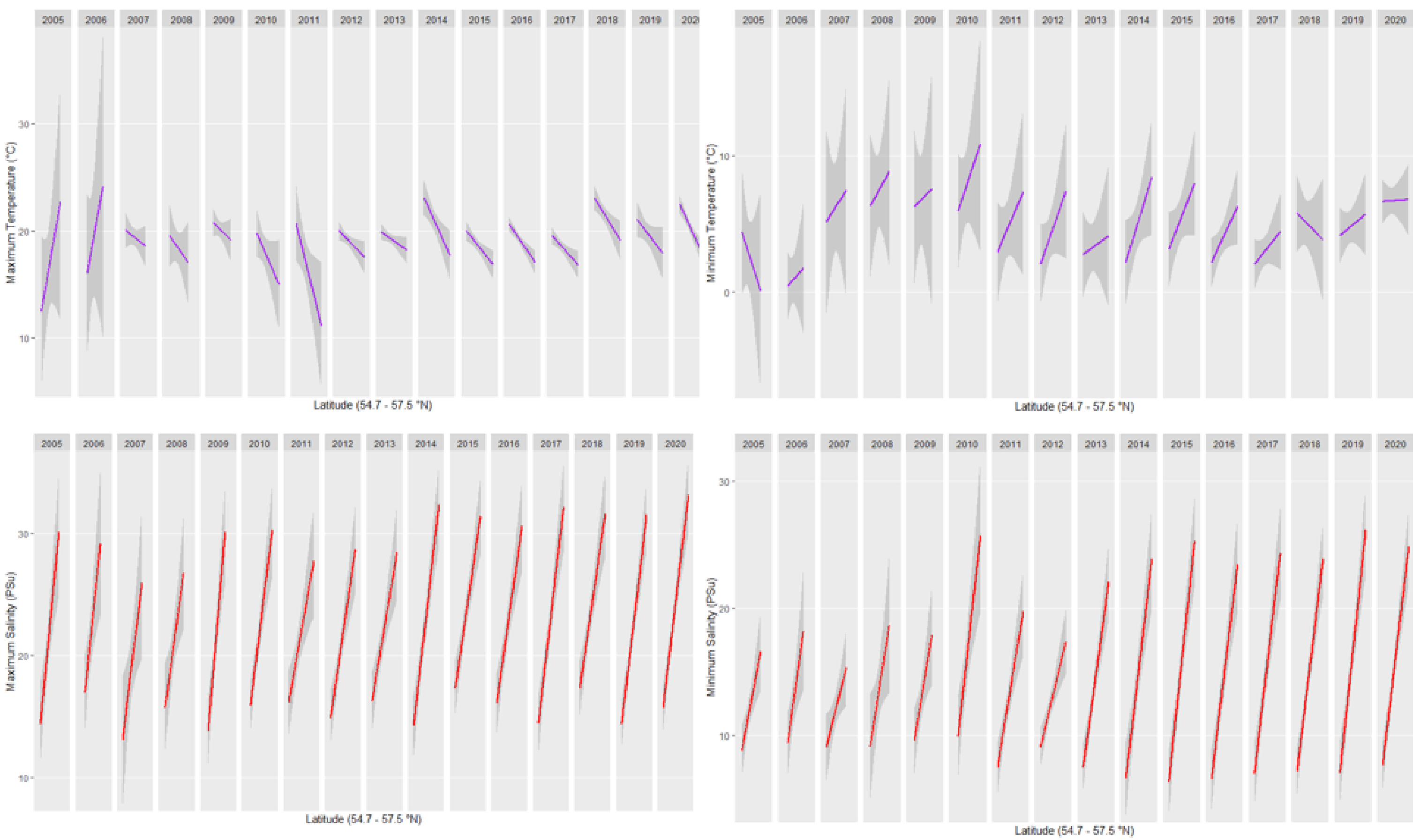

Figure 14: Maximum and minimum yearly temperatures and salinity readings plotted against latitude, smoothed using a linear regression and faceted by year.

3.2.2 Sweden

The data on temperature and salinity in Sweden was collected from CTD data at stations located in and around the west coast, but not every station was taking the same number of measurements each year – for example in 2005 only one station recorded data and so this year is missing in the analysis. Shown in *Figure 15* are the results of the average monthly temperatures in each year, plotted against latitude and smoothed using linear regression analysis. Because of how patchy the data is it is difficult to draw conclusions about any potential trends related to latitude, but there at least appears to be a large amount of variation in the years where we have data.

Figure 15: Temperature data from field stations on the west coast of Sweden. Average monthly values plotted against latitude, smoothed by linear regression and faceted by year.

The same analysis was carried out on average salinity readings (*Figure 16*), and here we can see a little bit more. There is an increase in the average readings, at least from 2008 onwards.

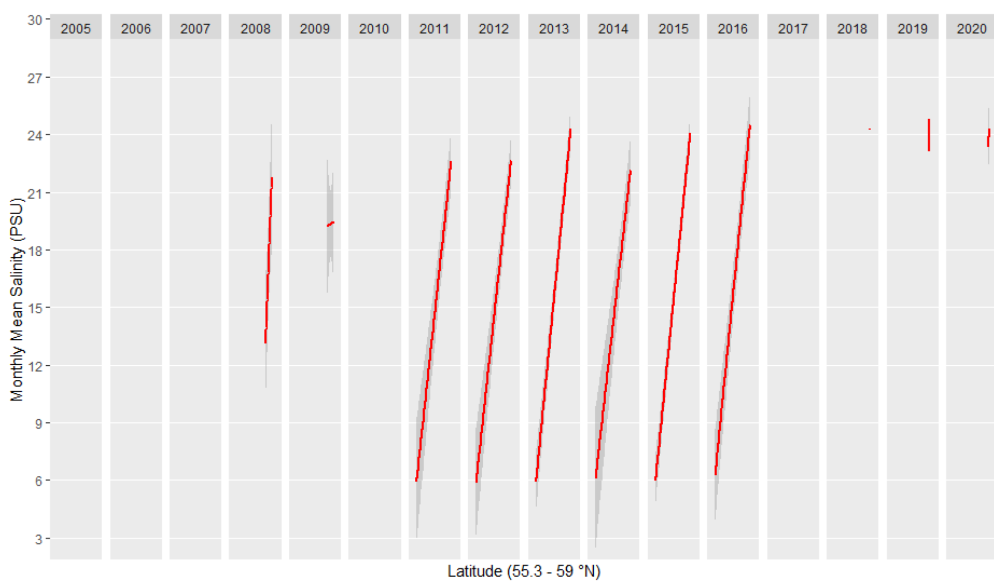

Figure 16: Salinity data from field stations on the west coast of Sweden. Average monthly values plotted against latitude, smoothed by linear regression and faceted by year.

As with the Danish data, annual maximum and minimum temperatures and also salinity readings were plotted against latitude (*Figure 17*). Temperature maximums do not appear to have increased or decreased significantly, but a slight decrease can be seen in temperature minimums. Salinity maximums appear to be increasing over the years and minimums have a less clear relationship.

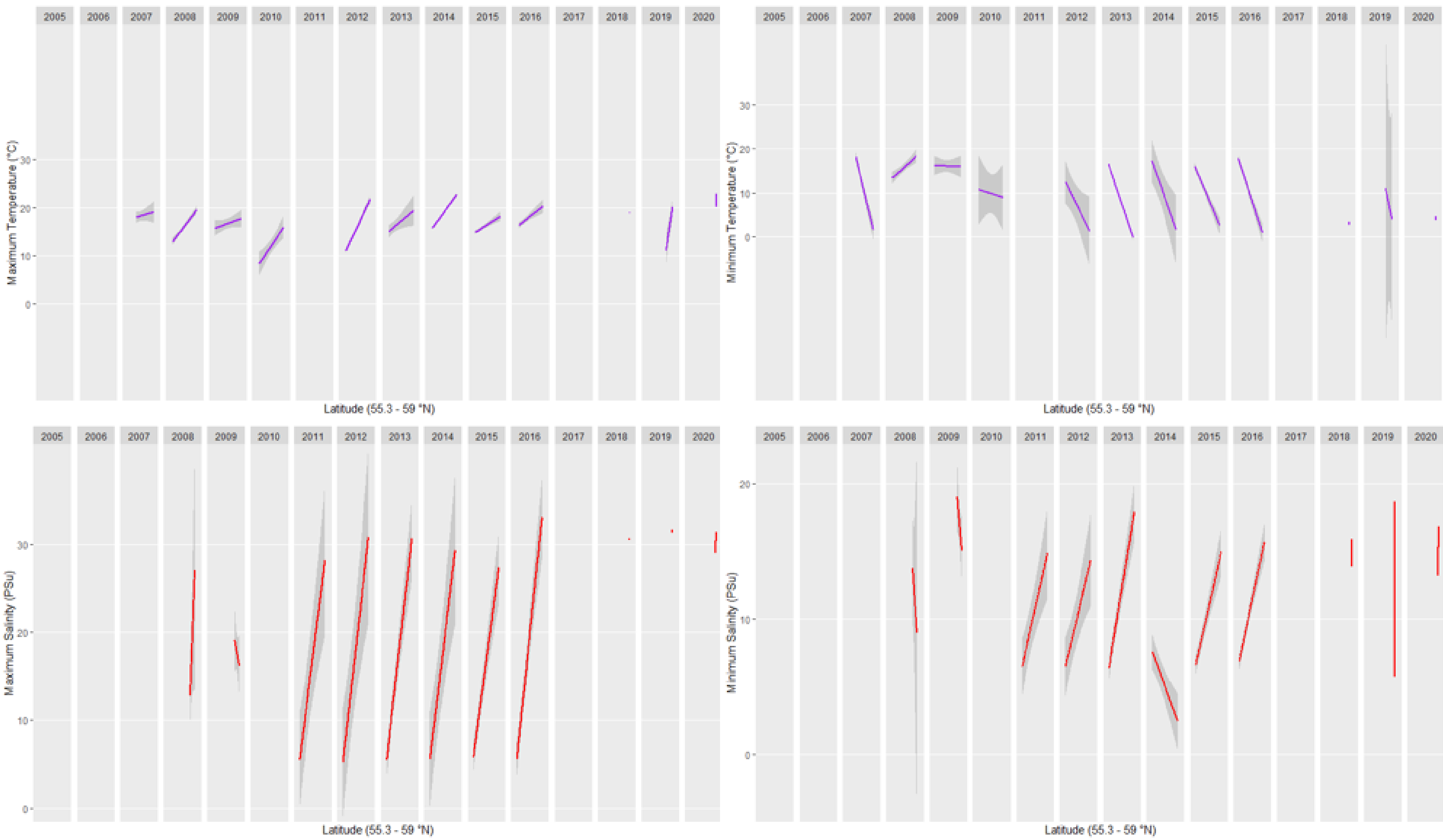

Figure 17: Maximum and minimum yearly temperatures and salinity readings plotted against latitude, smoothed using a linear regression and faceted by year.

3.2.3 Norway

The data on temperature and salinity in Norway was obtained from CTD data and averaged by month in each year. Linear regressions were applied to both temperature and salinity data and then plotted. *Figure 18* shows average monthly temperatures against latitude, faceted by year. There is less variation from 2013 onwards, and there appears to have been an increase in temperatures up to 2014, after which there has been a gradual decrease. A wide range in temperature can be seen in 2013.

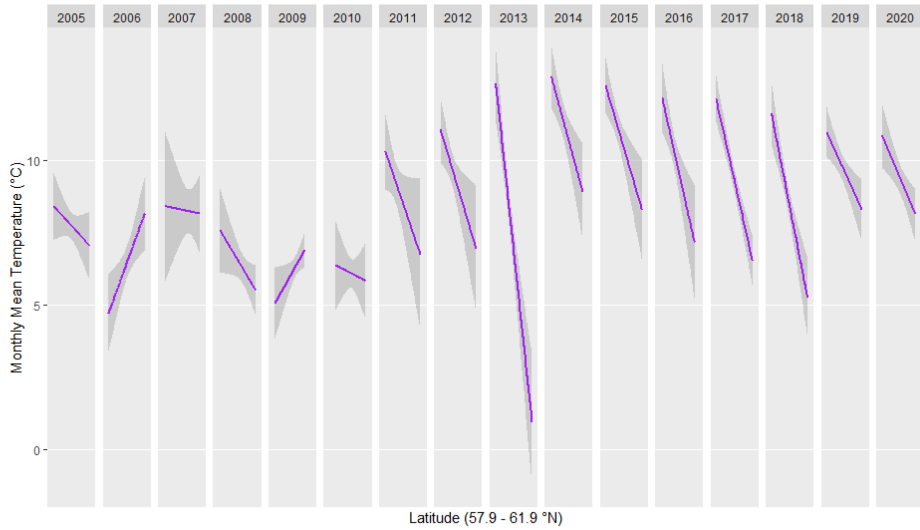

Figure 18: Temperature data from CTD readings on the Norwegian coastline. Average monthly values plotted against latitude, smoothed by linear regression and faceted by year.

In *Figure 19* is the salinity data from the same CTD readings, again with monthly averages and a linear regression analysis. A drop in salinity can be seen from 2010 to 2011, followed by an increase and then another drop from 2015 to 2016. Salinity averages increased for the next two years before beginning to decrease.

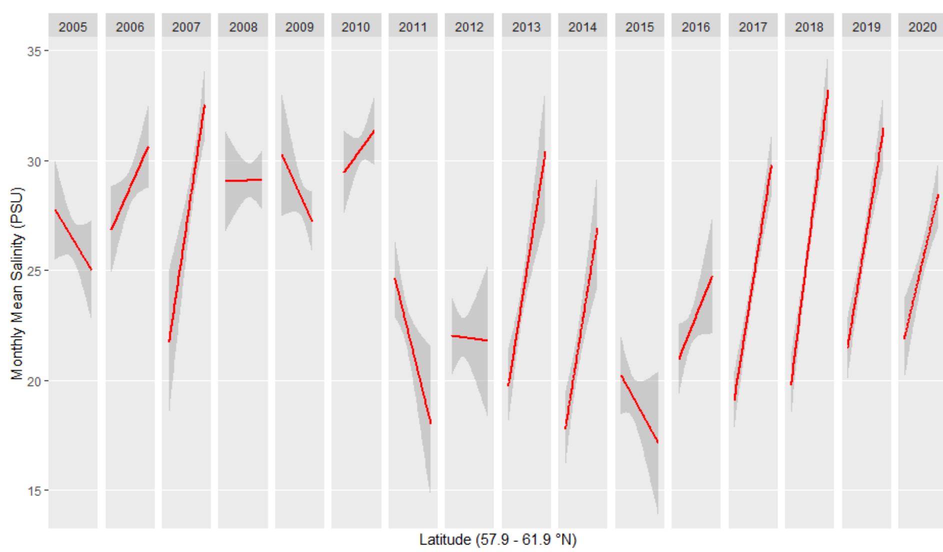

Figure 19: Salinity data from CTD readings on the Norwegian coastline. Average monthly values plotted against latitude, smoothed by linear regression and faceted by year.

Lastly, maximum and minimum temperature readings and salinity readings were calculated and plotted against latitude (*Figure 20*). While the increase in both temperature figures is not steady, there are still higher averages being reported in 2020 than there were in 2005. From 2014 to 2020 there is a gradual decrease in both maximum and minimum water temperatures, while 2015-2020 shows an increase in salinity maximum and minimum readings. In both the temperature and salinity plots there is a similar relationship occurring within the variable's max and mins.

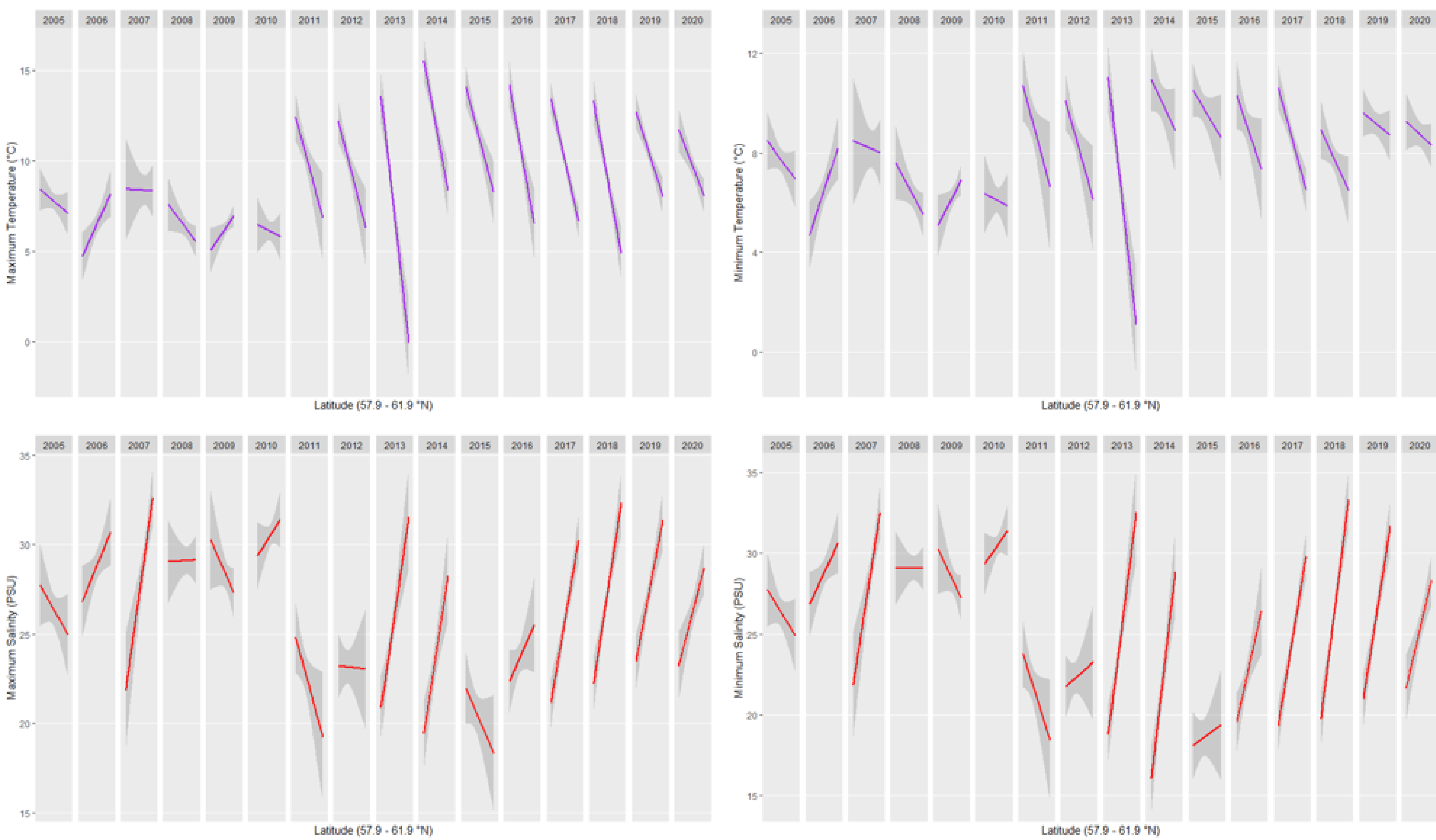

Figure 20: Maximum and minimum yearly temperatures and salinity readings plotted against latitude, smoothed using a linear regression and faceted by year.

4. Discussion

This study collected historical and current data on Pacific oyster populations in Denmark, Sweden, and Norway and mapped their distribution over space and time. It serves as an important step towards developing a Scandinavian protocol for surveying and tracking oyster populations, as well as informing their future management. The results after mapping the oysters suggest that populations are increasing over time in Denmark and showing both increase and decrease in Sweden and Norway (area-dependent). Having areas of growth in the number of Pacific oysters was expected, as it follows trends that have been observed in the spread of Pacific oysters into the colder waters of Scandinavia in recent years (Wrange et al., 2010). The areas that demonstrated decreasing numbers of oysters could be attributed to fluctuating conditions year-to-year.

This study also examined two variables relevant to Pacific oyster growth, salinity and temperature, and plotted that data against latitude for each year. The findings demonstrate an increase in average temperature and salinity levels in Denmark over time, a decrease in average temperature and increase in average salinity in Sweden (although there is some data missing), and both positive and negative short trends in Norway.

4.1 Oyster populations

There were only two available datasets of Danish oyster populations, one being a bachelor's thesis from the University of Copenhagen (Andersen et al., 2019), and the other a collection of verified citizen science observations over the timeframe of this study (2005-2020; https://www.naturbasen.dk/) The densities mapped around Zealand from the bachelor's thesis revealed higher numbers of oysters on the eastern coast and smaller populations on the western coast. This could be a result of the geographical closeness between the east coast of Zealand and the Swedish west coast, with populations from each side contributing to a larger volume of spat from spawning oysters. Analysis within this study showed that there has been an increase in temperature and salinity levels over the last fifteen years in Denmark, which could also explain the larger populations, however this is difficult to separate from the general process of invasion which sees more offspring as a result of more individuals (Geburzi & McCarthy, 2018). The citizen science data showed a very clear increase in the number of oyster observations submitted over the fifteen years, with large numbers recorded all along the east coast of Denmark by 2016-

2020, compared to just a few individuals recorded in 2005-2010. There is of course the potential risk with citizen science data that observations are not done systematically each year, and so a lack of data points in earlier years could be due to lack of public knowledge on Pacific oysters or a lack of interest in submitting sightings.

In Sweden there were several datasets available, but a few of these were only one-year surveys. The three years of data from the Strömstad-Helsingborg survey (2007, 2013, and 2019) were analyzed with maps to get a clear picture of any trends. The finding that all locations saw a decrease in the number of oysters between 2007 and 2019 was very interesting, as these sites run from the Norwegian border right down to the area around Helsingborg. This could be explained by the unusually warm temperatures that occurred in Sweden in the summer of 2007, which led to a boom in oysters (Wrange et al., 2010). It would be natural if, when the next year was not as warm, the numbers would not increase in the same way and may even decrease. The 2017 survey from the Ringhals-Falsterbo area gave information on oyster presence in the area closest to Zealand in Denmark, and over half of the locations had no Pacific oysters at all, most of which were in the more southern range of the survey. Two years of data were used from the Båstad-Malmö survey (2018 and 2020), and while their maps showed an overall increase in the number of oysters, the more northern sites reported less oysters and only a minority of sites had increasing populations. The overarching trend for oyster populations in Sweden was a negative one however there are still large, established populations and so some of these changes could possibly be attributed to smaller fluctuations in suitable conditions for reproduction from year to year. Adult oysters are not as affected by changing temperatures as young spat, which depend on the water temperatures for their survival (Diederich, 2006). The decreasing temperatures plotted from what data was available for the west coast of Sweden could be a reason for these losses.

In Norway there was included the survey that our team conducted in 2020 on the west coast, which was plotted here as a presence/absence survey. Just over half of the locations had Pacific oysters, but many of the sites were very early in their establishment and had as little as one or two oysters. The four years from the Telemark survey (2017-2020) showed an overall decrease in the number of live oysters reported over the four years with a significant (>1000) oyster decrease between 2017 and 2018. When comparing temperature and salinity data between those years there is a decrease in temperatures and an increase in salinity readings. The reports include counts of dead oysters and each year there were hundreds recorded, with mention made of the

2017/2018 winter in which the causes of mortality are estimated to have been ice formation, prolonged exposure at low tide combined with cold temperatures, disease, predation, and picking (Tangen, 2018). There were also more oysters in the more southwest range of the study and less in the northeast range, which contradicts the assumption that as Swedish populations are spreading to Norway there should be more oysters closer to the Swedish border. There is an area here for future research, investigating whether these smaller scale changes in distribution are due to local impacts such as river output or if they are random. The last multi-year study included was from Agder and Vestfold in the Haaverstad survey (2015 and 2016), which showed an increase in the number of oysters. The sites at a higher latitude contained the most oysters but there were still fluctuations at these sites. The most extensive survey in Norway for this study came from IMR in 2017, with sites from the Swedish border to Bergen. Predictably, there were larger and more established sites farther east, with smaller populations on the west coast. Absences were also plotted from this survey and there were many locations without Pacific oysters; the most absences were recorded in the area between Kristiansand and Stavanger.

4.2 Temperature and salinity data

The inclusion of temperature and salinity readings was of interest due to the influence these two factors can have on a Pacific oyster's ability to survive and most importantly – to reproduce. With the oyster's capabilities when it comes to adapting to new ranges and the trends we see with regards to anthropogenic climate change, it is to be expected that settlement in more northern areas of Scandinavia should be occurring more and more as the years pass. The data from Denmark showed a positive trend over the fifteen years studied, and this correlates with the increasing numbers of oysters seen between the two surveys included in this study. The data obtained from Sweden was patchy in that not every field station recorded measurements each year, so there were years where an analysis against latitude were not possible. However with the data we have it appears that average temperatures have been decreasing (at least until 2017) and that average salinity is increasing. Annual temperature highs appear to be increasing, but lows are decreasing, and salinity maximum and minimum values are both increasing. Again, the last three years did not have clear data available, so it is very possible that there are different trends occurring in recent years. The data from Norway showed an increase in temperatures until 2013/2014, after which there has been a slight negative trend. For the salinity values the results were less clear, with a dip in 2011/2012 and another dip in 2015, which was then followed by a positive trend until 2019 when readings have begun to decline again. The dip in 2011 could perhaps be due to the lower temperatures experienced in 2010, which could result in greater amounts of snow that would melt and reduce salinity levels through runoff. The Norwegian oyster data appeared to show an increase in oysters from 2015-2016, followed by a decrease from 2017-2020.

The only European coast that the Pacific oyster has not yet established itself on is in the Baltic Sea, where salinities ranging between 15 and 19 PSU are believed to be too low for larval development (Lennartz et al., 2014). Several oysters were found in the Kiel Fjord in 2019, an area which historically has experienced the typical low Baltic Sea salinity levels, but in late summer of 2018 there were unusually high temperatures and salinities (Ewers-Saucedo et al., 2020). Comparison of the surveys included from Sweden and Denmark reveals that there are oyster populations farther south in Denmark than in Sweden, which could suggest that conditions are more favourable for future expansion along Danish and subsequently German coasts than along the Swedish south and east coasts.

4.3 Habitat and substrate

One of the factors that has aided the spread of Pacific oysters is their ability to establish themselves in different habitats. Though preferring rocks, they can also attach themselves to any small piece of hard substrate, such as stones, living bivalves, and shell fragments (Fey et al., 2010). Sheltered and shallow coastal areas with adequate water circulation is where you can find Pacific oysters in Scandinavia. The 2014 Dolmer et al. risk assessment of Norwegian Pacific oysters for IMR assessed the impact of the invasive oyster on four different habitats and following three different climate scenarios. The four habitats included in the assessment were low energy littoral rock, littoral sand and muddy sand, littoral biogenic reefs, and sub-littoral sediment, all of which were deemed important habitats for Pacific oysters currently. The assessment concluded that the first, second, and fourth habitat types were at limited risk in the short term (next 30 years) and moderate risk in the long term (next 80 years), and that the third habitat type was at moderate risk in both the short and long term. The information from this risk assessment should form the basis of location-dependant management strategies, but it has not been followed up since its publication seven years ago. Choosing locations to conduct a standardized survey in that follow a risk assessment such as this one would make efforts more efficient, by identifying areas of higher risk for large-scale invasion.

4.4 Suggestions for management

As previously mentioned, there are positive effects that Pacific oysters have on the ecosystems they settle in, and these can be framed in the ecosystem services that they provide. Globally, Pacific oysters are one of the most important aquaculture products (Mortensen et al., 2019), so the first and most obvious type of ecosystem service that they provide is as a provisioning one. Commercializing Pacific oysters can also be done on a smaller scale; handpicking, depuration, and selling on local markets is already occurring, and in Denmark Pacific oysters are delivered as by-catch in the blue mussel dredge fishery in Limfjorden (Mortensen et al., 2019). Pacific oysters also provide regulating services, as efficient filter feeders that lower particle concentration and turbidity and by providing habitat through reef building (Smaal et al., 2019). Lastly, the oysters provide cultural services though traditions of oyster picking in communities, collection for decoration and art, and educational programs about marine ecosystems (Smaal et al., 2019). Attaching a monetary value to these services that can be provided by Pacific oyster invasions can help to shape management efforts, instead of potentially wasting money on small scale removal efforts where the oysters are discarded.

Public involvement in wild oyster populations can have its benefits; in Denmark there are oyster safaris where tourists can be taken out, learn about and collect oysters, which they then take home and eat (Mortensen et al., 2019). This is a positive way of handling wild populations, as it gives income to the local community as well as lowering the number of Pacific oysters present. However, Pacific oysters are often difficult to remove from the substrate they have attached themselves to, and so determining where hand-picking by the public occurs becomes influenced by ease of picking as well as the size or shape that the consumer may prefer.

In 2016 the Norwegian Environment Agency (Miljødirektoratet) published a plan for how to handle Pacific oysters, including methods for their removal and areas of priority. One of the two proposed methods for removal was to handpick the oysters. They state that volunteer labour is cost effective and increases public interest, and that the method is environmentally friendly because there is minimal damage done to the surrounding ecosystem when the oysters are removed. However, handpicking is a slow process and has to be often repeated to prevent the population from replenishing itself (Mortensen et al., 2017). This is the only method of the two mentioned in the plan that is currently being used in Norway, with the other being mechanical pumps that suck up the oysters onto ships (which is suggested but not in use), however any potential effects on the environment are not yet well understood. Choosing areas of particular concern is left to local jurisdiction, though they are advised to prioritize recreational areas and important habitats such as eelgrass beds and blue mussel banks (Miljødirektoratet, 2016). By creating a system of classification whereby substrate, current patterns, and existing populations are taken into account there could be standardized procedure for local authorities to follow in choosing where their oyster removal initiatives should occur, which would have a wider impact on the spread of oysters.

5. Conclusions and Future Studies

5.1 Study limitations

An impediment to identifying trends in oyster populations is that there has not been a large-scale and standardized survey conducted each year in each of the three countries involved in this study. The available data is patchy and unstandardized with differing methods and variables involved. This is a major challenge to making predictions on how the populations are going to change in the near future, because the data on which those predictions would be based is not necessarily an accurate representation of the entire area. When putting this study together there were numerous obstacles due to the nature of the data, such as using different GPS systems, different file formats, different variables measured, etc. These kinds of alterations greatly increase the amount of time it takes to collect data together into once resource and could be easily streamlined with proper protocol. Lastly, a few of the surveys included in this study only collected one year of data, which is difficult to draw conclusions from. It can be taken into consideration with the other surveys conducted in different locations, but with limitations.

5.2 Future work

This study has highlighted the areas that need further work, with the main issues being the fragmented information available and the stumbling blocks this can cause for management efforts. Collaboration between Denmark, Sweden, and Norway is crucial in the management of Pacific oysters, because larval dispersal between the three countries has been occurring and will continue to occur. The oysters have no regard for jurisdiction boundaries, so it is in the best interest of all management authorities involved to have open and continuous dialogue. Establishing large-scale surveys that track populations at specific sites each year would be an excellent way of forming a clear picture of how populations are changing over time, but if this is not possible then developing a protocol for surveying that any group participating must follow would help significantly. Standardized procedures and reporting would allow datasets collected by different research groups or authorities to be easily combined to obtain an overview of larger areas.

Future studies could include those variables that were not included in this study, such as substrate, mortality, and individual size data. Including more variables would lead to a more complete picture of population dynamic parameters such as recruitment and size structure. The choice to not include the length data is due to the majority of surveys not including that type of data, combined with aging of wild oysters being an area that is still being researched and so concrete conclusions about age classes could not be reached in this study. Age class analysis has been attempted on the Swedish west coast, however there was no consistent growth trajectory that fit all sites and so age data for now has to be used in a site-by-site basis (Partoft et al., in prep.).

Understanding how invasions occur is a key detail in understanding how populations will grow. The four stages of bio-invasion are first the arrival of the species, next that they occur in low numbers with no altering of the existing habitat, third that the population expands and changes the habitat, and lastly an adjustment phase where predators and disease will reduce the population of the invasive (Reise et al., 2006). If we could apply a classification system to surveys where each location was evaluated and placed into one of these four stages then there could be a much faster process for choosing which locations required which type of management, and also which locations were a high priority for continued surveying.

Through mapping this study has visualized the current and historical populations of Pacific oysters in Scandinavia and has attempted to draw conclusions as to possible trends. Salinity and temperature data has been mapped as possible explanatory variables, with some correlation between readings and oyster presence. Long-term growth was found in oyster populations across all three countries, with some fluctuation that could be explained by short-term changes in conditions and subsequent mortalities. This study is intended to inform the creation and adoption of a Scandinavian protocol for Pacific oyster surveying and highlights the need for trans-border collaboration and consultation as we move forward with management efforts.

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