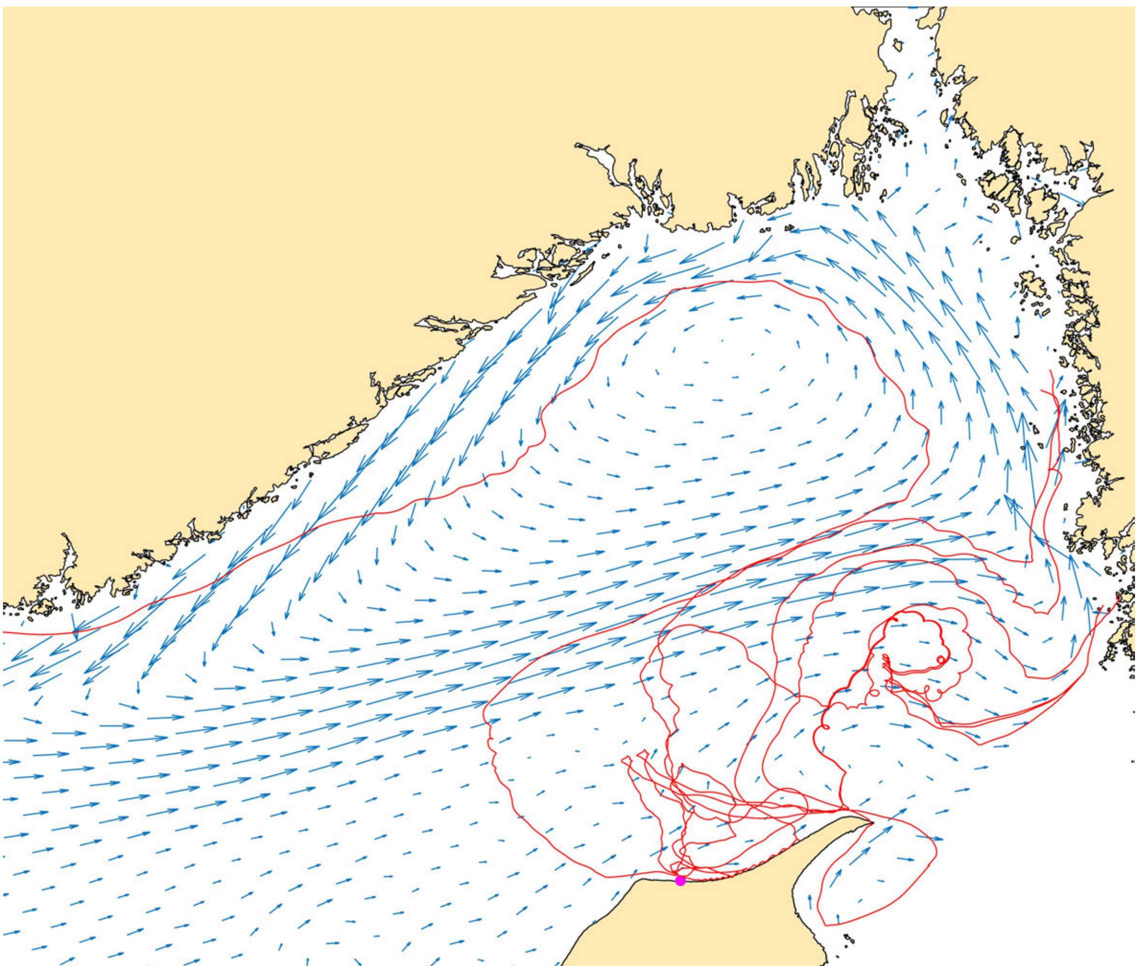
REPORT SNO. 7016-2016

Larvae drift simulations of the Pacific oyster in Skagerrak – influence of climate change on larvae development, survival and dispersal.



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REPORT

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Abstract

We have investigated the extent to which warmer climate in recent years has led to greater opportunities for successful spreading of Pacific oyster (*Crassostrea gigas*) larvae from Danish and Swedish coastal areas to Norway, by simulating larval dispersal and survival using a three-dimensional hydrodynamic model and ocean climate for the years 1990, 1998, 2002, 2006, 2007 and 2010. We have also investigated temporal trends in sea surface temperature in Skagerrak in the period 1990-2014. The main finding is that the temperature increase since 1990 of ca 1.6°C implies adequate temperature conditions for successful larvae development and transport from Danish and Swedish coastal areas and survival at landing sites along the Norwegian Skagerrak coast in warm years following 2000. The 19ºC temperature isocline in August has moved at least 125 km northwards along the Swedish western coast in Skagerrak since 1990.

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Larvae drift simulations of the Pacific oyster in Skagerrak – influence of climate change on larvae development, survival and dispersal

Preface

This work was undertaken within a Strategic Institute Initiative (SIS) project named Klim Alien at NIVA, within the SIS "Climate effects from mountains to fjords". The SIS was funded by The Research Council of Norway. Here we describe the technical details of the three-dimensional hydrodynamic model and the main results of the simulations.

Oslo, 2. April 2016

Eli Rinde

Contents

Summary

We have investigated the extent to which warmer climate in recent years has led to greater opportunities for successful spreading of Pacific oyster (*Crassostrea gigas*) larvae from Danish and Swedish coastal areas to Norway, by simulating larval dispersal and survival using a three-dimensional hydrodynamic model (Norkyst 800) and ocean climate data for the years 1990, 1998, 2002, 2006, 2007 and 2010. We also investigated temporal trends in sea surface temperature in coastal areas along the Skagerrak coast in Sweden in the period 1990-2014 using data from Swedish Meteorological and Hydrological Institutes (SMHI).

The influence of ocean climate on larvae dispersal, survival and settlement of oyster larvae were investigated by setting temperature criteria for larval development and survival based on available published data, and by identifying the larvae who are experiencing the selected temperature criteria along each individual trajectory and thus successfully develop and land in Norwegian coastal areas in the different simulation years. The temperature criterion for larval development was set to 225 degree-days, and minimum sea surface temperature at the landing site for survival ≥ 18ºC. This allowed us to track the dispersal path of every released larva that successfully developed and landed in Norwegian coastal areas, for each of the simulated years. In order to identify any spatial pattern of the successfully landed oyster larvae, number of simulated landed larvae was counted within coastal grid cells (50x50 km).

The main finding is that there has been a 1.6ºC temperature increase in sea surface water along the Swedish Skagerrak coast between 1990 and 2014. This ocean warming has caused sufficient temperature conditions for successful larvae development and transport from Danish and Swedish coastal areas, as well as survival at landing sites along the Norwegian Skagerrak coast in warm years following 2000. The 19ºC temperature isocline in August has moved at least 125 km northwards along the Swedish western coast in Skagerrak since 1990. This also results in a shift of the northern limit of the localities that will achieve favourable summer temperatures for oyster spawning and settlement. Future warmer water will likely increase the potential supply of Pacific oyster larvae from Swedish and Danish Pacific oyster spawning sites to the Norwegian coast.

Sammendrag

Vi har undersøkt i hvilken grad varmere klima de siste årene har ført til større muligheter for vellykket spredning av larver av stillehavsøsters (*Crassostrea gigas*) fra danske og svenske kystområder til norske kystområder, ved å simulere larvespredning og larveoverlevelse ved hjelp av en tre-dimensjonell hydrodynamisk modell (Norkyst 800) og data på havklima for årene 1990, 1998, 2002, 2006, 2007 og 2010. Vi har også undersøkt tidstrender i overflatetemperaturen til kystnære områder langs den svenske kysten av Skagerrak i perioden 1990-2014 ved hjelp av data fra Sveriges Meteorologiska och Hydrologiska Institut (SMHI).

Påvirkningen av havklima på spredning, overlevelse og landing av østerslarver ble utført ved å sette temperaturkriterier for larveutvikling og overlevelse basert på tilgjengelige publiserte data, og ved å identifisere larvene som opplever de valgte temperaturkriteriene langs hver enkeltes drivbane og som dermed lykkes med å utvikle seg og lande i norske kystområder i de ulike simuleringsårene. Temperaturkriteriene for larveutvikling ble satt til. 225 døgngrader og minimum sjøtemperatur på landingsstedet for å overleve ble satt $\geq$ 18ºC. Metodikken ga oss muligheten til for hvert av simuleringsårene, å identifisere spredningsbanen og landingsstedet til hver av de simulerte frislupne larvene som lyktes med å utvikle seg og lande i norske kystområder. For å identifisere eventuelle romlige mønster til stillehavsøsterslarvene som utviklet seg og landet på norskekysten i gitt havklimaet i de ulike simuleringsårene, ble antall landede larver per kystrute(50x50 km) tellet.

Hovedfunnet er at det har vært en temperaturøkning på 1.6ºC i overflatevannet langs den svenske vestkysten, i perioden mellom 1990 og 2014. Denne oppvarmingen har medført tilstrekkelig varmt vann for vellykket larveutvikling og transport av larver fra danske og svenske kystområder, samt overlevelse ved landingsstedene langs den norske Skagerrakkysten i varme år etter 2000. Temperatur-isoklinen for 19ºC i august har flyttet seg minst 125 km nordover langs den svenske vestkysten i samme tidsperiode. Dette medfører også en nordlig forskyvning av grensen for lokaliteter som oppnår gunstige sommertemperaturer for østersgyting og nedslag. Framtidig varmere vann vil øke potensialet for tilførsel av stillehavsøsterslarver fra svenske og danske yngleplasser for stillehavsøsters, til norske kystområder.

1. Introduction

The Pacific oyster (*Crassostrea gigas*) is an invasive marine species that has been introduced to more than 70 countries for aquaculture purposes (Ruesink et al. 2005), including Denmark, Sweden and Norway (Wrange et al. 2010). The species is an "ecosystem engineer" which alters the natural ecosystem in the invaded areas. Hence the Pacific oyster is assumed to be a major threat to the marine biodiversity in shallow coastal areas and to mussel banks and seagrass meadows in particular (Gollasch & Minchin 2009, Wagner et al. 2012, Dolmer et al. 2014).

The rapid expansion of the distribution of the species in Norway, since the first observation of wild specimens in 2003, has been related to ocean warming and supply of larvae from neighbouring countries: i.e. to Sweden from Denmark (Strand et al. 2012) and to Norway (DN 2010, Gederaas et al. 2012). However, DNA analysis reveals that neither of 4 studied Norwegian *C. gigas* populations in southern Norway may stem from larvae drifted from Denmark or Sweden (Anglès d'Auriac et al. Submitted).

In order to investigate the extent to which warmer climate in recent years has led to greater opportunities for successful spreading of Pacific oyster larvae from Danish and Swedish populations to Norway, we have simulated larval dispersal and the influence of ocean climate in the period 1990 until 2010, on larvae development and survival, using a three-dimensional hydrodynamic model.

The Skagerrak coast of southern Norway is at the edge of the Pacific oyster's present distribution limit in Europe. Hence the further northwards spreading potential of the species in this ecoregion is highly relevant for assessing the potential threat of the species for ecosystems in temperate ecoregions in general, due to climate change. Here we describe the technical details of the hydrodynamic model and of the simulations, and the most important trends. The main results linking the simulations to NIVAs DNA studies of Norwegian, Swedish and Danish Pacific oyster populations are included in the studies of Angles d'Auriac et al. (Submitted).

2. Methods

2.1 The NorKyst800 model

2.1.1 Model setup

We have used the three-dimensional hydrodynamic model ROMS (Regional Ocean Modelling System) version 3.5 to calculate the hydrodynamics, current speed as well as salinity and temperature. The model is set up for the entire Norwegian coast with 800 m horizontal resolution. This application of ROMS is called Norkyst 800 (Albretsen et al. 2011). A subset of the full Norkyst domain was used and the model area is shown in **Figure 1**.

For the vertical resolution, the application was set up with 32 vertical layers. The chosen parameters for the vertical coordinate are shown in **Table 1**.

As input on the open boundary of the model domain, the monthly climatology values from the SVIM archive (ftp://ftp.met.no/projects/SVIM-public/; Lien et al. 2013, Melsom and Gusdal 2015) were used. This means that current speed, sea level, temperature and salinity are interpolated to the 800 m grid from a model with 4 km horizontal resolution.

Table 1. Parameters for the vertical coordinate.

Parameter	Description	Value
Nvert	Number of vertical levels	32
Vtransform	Transform equation	2
Vstretching	Stretching equation	2
θ_s	Surface control parameter	5
θ_b	Bottom control parameter	4
Tcline	Width of surface or bottom boundary layer	30

Fresh water input to the model domain is modelled by NVE (Norwegian Water Resources and Energy Directorate) with the HBV model (Beldring et al. 2003), that gives daily fresh water discharge from every main catchment area in Norway.

Atmospheric forcing was taken from a hindcast model run, performed by the Norwegian Meteorological Institute where a model grid with 10 km horizontal resolution was used.

To calculate advection of momentum, temperature and salinity in the model a 3rd order upstream scheme is used in the horizontal dimension and a 4th order cantered scheme is used in the vertical dimension. For more information visit https://www.myroms.org/wiki/cppdefs.h. All calculations were conducted at the supercomputer Stallo that is part of the NOTUR system (www.sigma2.no).

The hydrodynamic model was run for the selected years 1990, 1998, 2002, 2006, 2007 and 2010, representing the climate since the 90s, one cold (2007), two warm (2002 and 2006) and one moderately warm year (2010). The temperature of the individual model runs was corrected as described below.

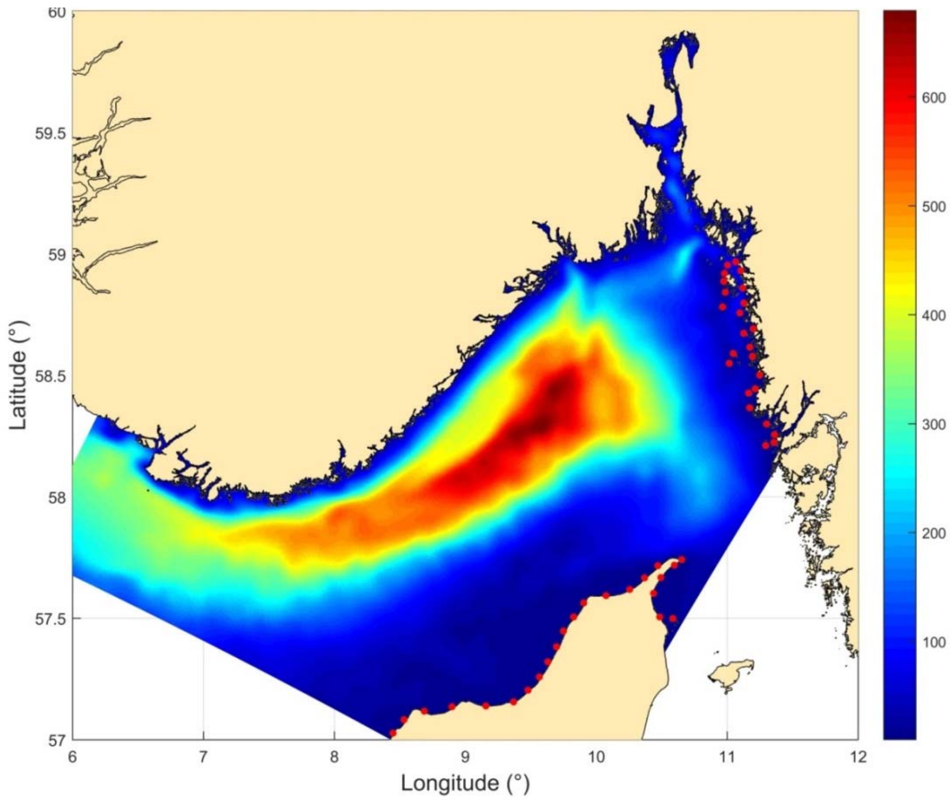

Figure 1. Map of the model domain for the hydrodynamic ROMS model. The bathymetry used in the model is shown on the colour scale. The release points for the oyster larvae are shown as red dots.

2.1.2 Validation of model temperatures

We validated the model by comparing modelled sea surface temperature at 4 oceanographic stations with regular measurements at fixed hydrographic stations (**Table 2, Figure 2**). A plot of modelled and measured temperature for the summer to autumn period for each of the simulated years (**Figure 3**) showed that the modelled temperature is accurate in some locations and years (e.g. Flødevigen in 2007) but that there are several instances where the model deviates from the data. When looking at the temperature bias (i.e. modelled temperature minus observed temperature) over time (**Figure 4**, **Figure 5**) we can see a seasonal pattern in the bias, with a small bias at the start of the summer and with increasing bias as the summer progresses (e.g. 1990, 2002). Hence the temperature in the hydrodynamic model is lower than the measured sea surface temperature, and the difference is increasing towards the end of the summer.

Table 2. Hydrographic stations used to validate the hydrodynamic models surface temperatures (SST). For Flødevigen, temperatures were measured at 0900 in the morning until 2008; from 2009 (when continuous measurements started) we used mean SST for the period 0845-0915. For Ferrybox (Petersen et al. 2003), measurements are done at 4 m depth. For SMHIs (Swedish Meteorological and Hydrological Institutes) stations, sea surface measurements were used.

Station	Institution	Position	Sampling scheme
Å15	SMHI, Sweden	10.85 E, 58.295 N	Ca. monthly
Å16	SMHI, Sweden	10.725 E, 58.2667 N	Ca. monthly
Å17	SMHI, Sweden	10.5133 E, 58.275 N	Ca. monthly
Flødevigen	IMR, Norway	8.7539 E, 58.4260 N	Daily
Ferrybox 58.5	NIVA	10.7526 E, 58.5147 N	Ca. every 3 days
Ferrybox 59	NIVA	10.6489 E, 59.0125 N	Ca. every 3 days

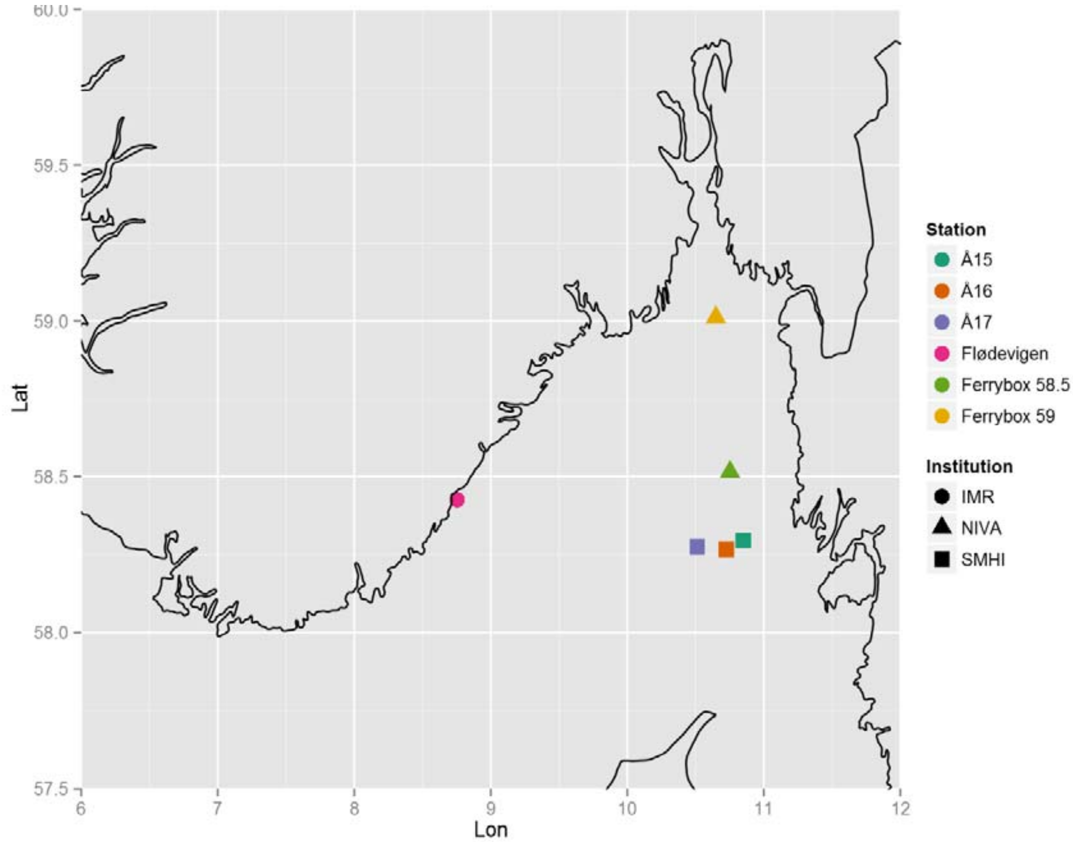

Figure 2. The fixed hydrographic stations used to validate the modelled temperature in the hydrodynamic ROMS model. The symbols shape indicate the data sources (IMR, SMHI and NIVA), and the colour code the individual stations.

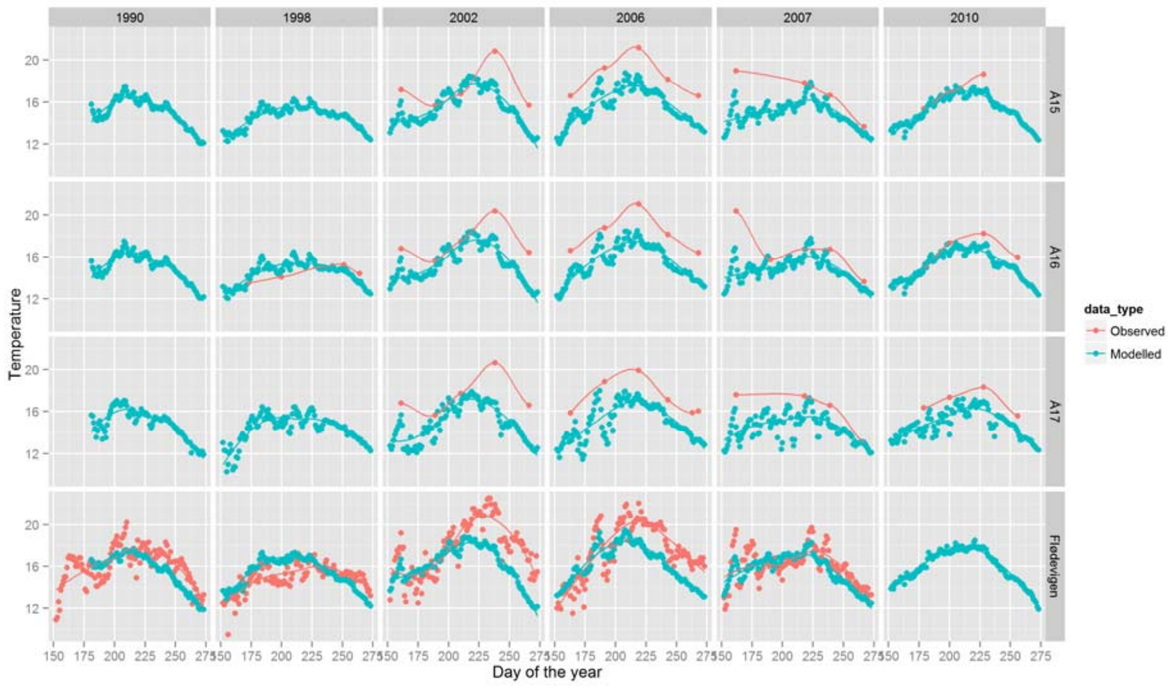

Figure 3. Sea surface temperature in the hydrodynamic ROMS model (blue dots and trend line) and observed temperatures (red dots and trendlines); for the fixed hydrographic stations. The graph shows temperature for the summer and early autumn (day 150-275 of the year = 31 April – 3. Oct). Only selected years, including the simulation years 1990, 1998, 2002, 2006, 2007 and 2010, are shown.

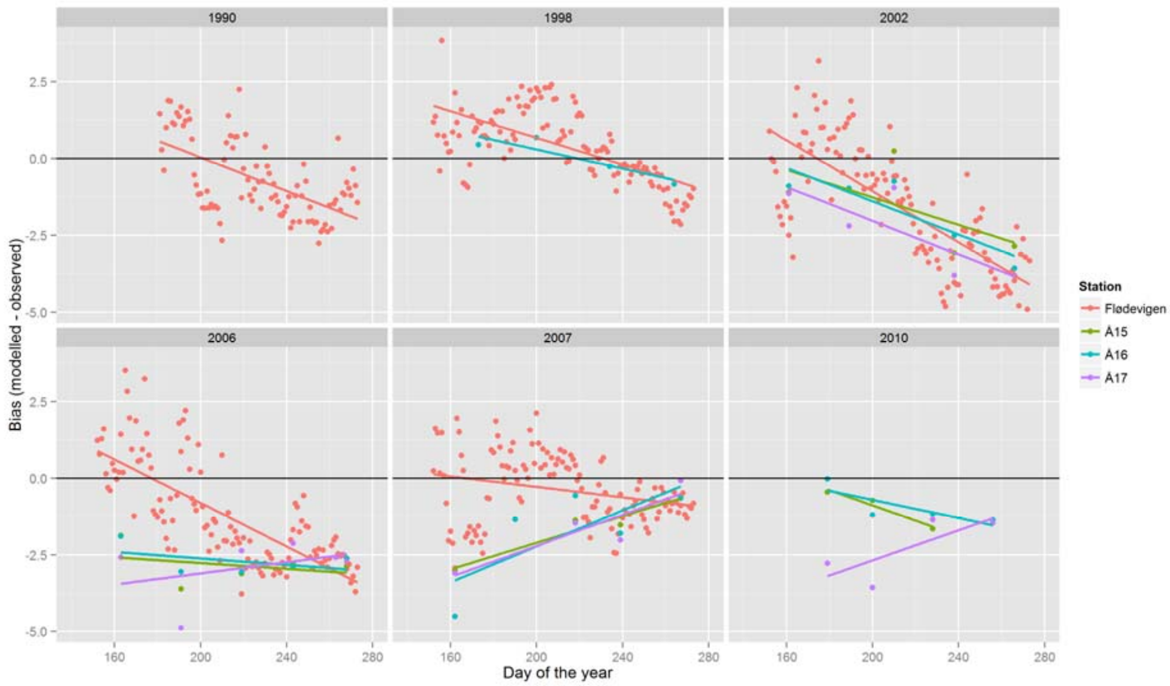

Figure 4. The temperature bias (model temperature – observed temperature) in sea surface temperature at four selected locations; Swedish Meteorological and Hydrological Institutes Å15, Å16 and Å17, and Institute of Marine Research's station Flødevigen, plotted against day number (covering the summer-autumn period) for each of the simulated years.

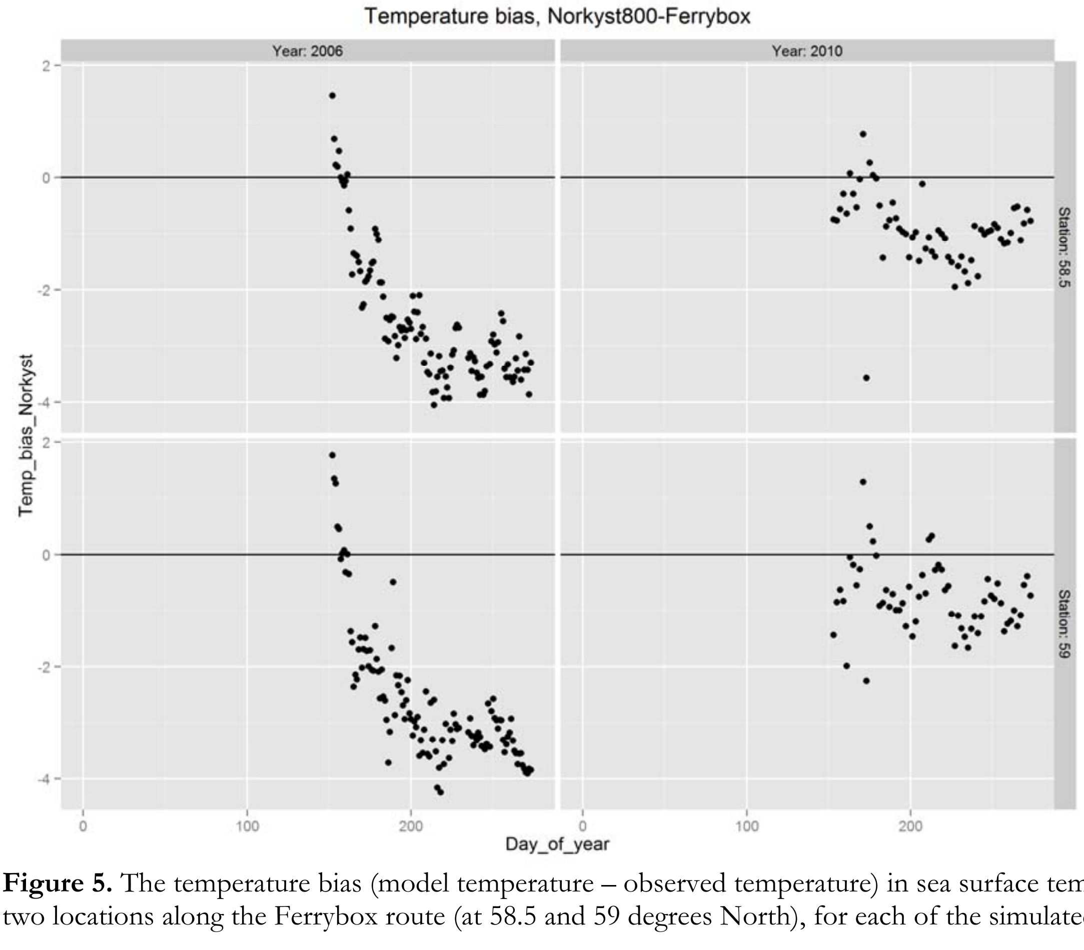

Figure 5. The temperature bias (model temperature – observed temperature) in sea surface temperature at two locations along the Ferrybox route (at 58.5 and 59 degrees North), for each of the simulated years.

2.1.3 Sea water temperature correction

The model validation showed that NorKyst800 runs typically have too weak summer heating compared to the observations in the area (Skagerrak). Inspired by the bias illustrated **in Figure 5** it was decided to perform no temperature correction before Julian day 150, to implement a temperature correction that increase linearly to a maximum correction value between Julian day 150 and 200, and keeping the maximum value (ΔT_{max}) constant after Julian day 200. The temperature correction ΔT can then be written

$$\Delta T = \begin{cases} 0 & ,t < t_1 \\ \Delta T_{max} \cdot (t - t_1)/(t_2 - t_1) & ,t_1 \leq t \leq t_2 \\ \Delta T_{max} & ,t > t_2 \end{cases} \quad (1)$$

where t_1 and t_2 are the Julian days 150 and 200.

Based on the observed bias, the maximum temperature correction value was set to be 1, 0, 2, 2, 1 and 1°C for the simulation years 1990, 1998, 2002, 2006, 2007 and 2010 respectively.

2.2 Temperature criteria for larval development and survival

We based the temperature criteria for larval development and survival on available published data; i.e. 225 degree-days for larval development (Syvret et al. 2008) and the temperature at the landing site ≥ 18ºC (Mann et al. 1991).

2.3 Routines for identifying successful landing or further drift

Particles that represent oyster larvae was released in the surface layer of the model at selected release points which were evenly distributed along the coast of Denmark and Sweden (see **Figure 1**). The tool FLOATS incorporated in ROMS was used to release and track the particles using the hydrodynamics from each of the simulated years. Due to the high reproduction capacity (several millions larvae per spawning individual), true individual-based modelling was impossible. Hence we used the super-individual approach suggested by Scheffer et al. (1995), where each modelled individual represents a large number of actual individuals. From each of 44 locations equally distributed along the Danish and Swedish coastline, 7 larvae were released between 1 and 14 August (1 larvae every second day, i.e., 7*44=308 larvae per year) and their floating path, experienced degree days and temperature at the landing sites were recorded. To identify larvae with successful landings (i.e. the larvae has experienced at least 225 degree-days and has landed at a site that was warmer than 18ºC) the search routine shown in **Figure 6** was used. First, the trajectory paths for all released larvae were calculated with the hydrodynamic model. Then searches were conducted along each of the particle trajectories to calculate the larva's experienced sum of daily temperature values (the degree-days) and to identify if the larvae was close to land. For each position along the trajectories, the first test was to check if the position was close to land. If not true, the next position along the trajectory was tested. The next step was to check if the larvae was mature (>225 experienced degree-days). If not true, the next position along the trajectory was tested. If the larvae was mature, it was checked if the sea temperature at the site was warmer than 18°C. If colder, the larvae were defined to die. If sufficiently warm, the larvae has successfully survived and landed.

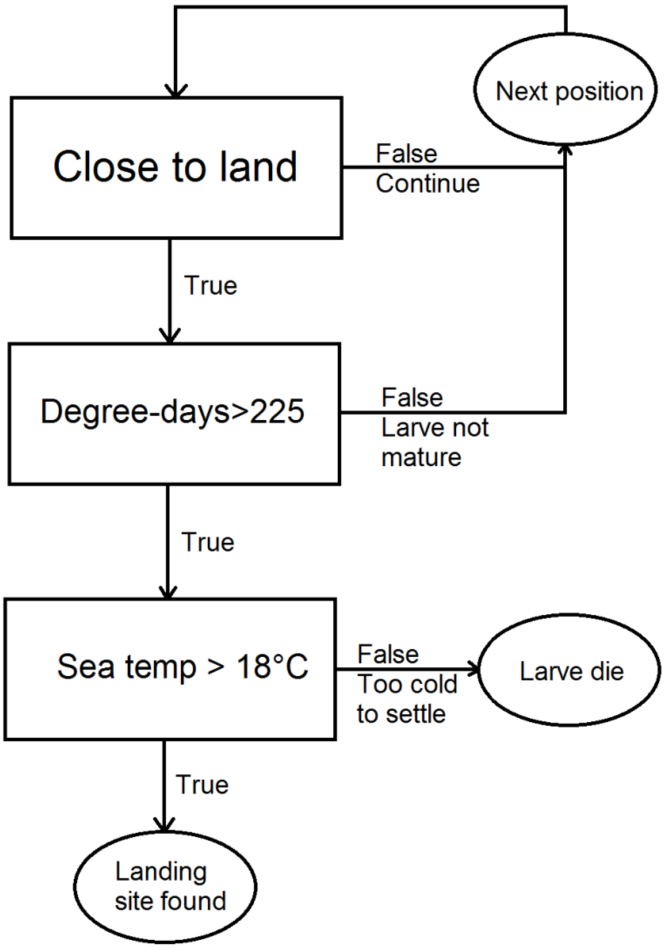

Figure 6. The search routine for finding possible landing sites for the oyster larvae.

2.4 Identification of larval dispersal patterns

To identify any spatial differences in the dispersal pattern of the Pacific oyster larvae between years and possible trends in time, we divided the coastal zone area into equally sized grid cells (50x50 km), and calculated number of successfully landed larvae per cell per year. To identify cells with significantly more than 1 landed larvae per year along the Norwegian and Swedish coastline, we used the exact binomial test (the larvae that survive and land on this coastline per year have a probability equal to 1/25 to land in any of these 25 grid-cells). The analysis were performed in the statistical programme R (R Core Team (2014), and the GIS-analysis in ArcGIS 10.1 by ESRI (http://www.esri.com/).

2.5 Trends in ocean warming

In order to detect any trends in ocean warming within the study area we analysed temperature data available from the Swedish Skagerrak coast; through Swedish Meteorological and Hydrological Institutes (SMHIs) monitoring of several oceanographic stations (http://opendata-catalog.smhi.se/explore/). We used sea surface temperature (SST) from 7 of SMHI's stations in wave exposed areas. A multi-variable GAM analysis, including (possibly non-linear) effects of year, day number of the year (i.e. time of year to detect any seasonal pattern) and latitude was performed to discover how summer temperatures (July-August) has changed and isotherms have moved over time (i.e. from 1990-2014). The analysis were done in R version 3.2.2 (R Core Team 2015), using the R-package *mgcv* version 1.8.7 (Wood 2004) for the GAM analyses.

3. Results

3.1 Ocean circulation

The mean flow in the surface layer for the period August 1st to August 12th is calculated for each year and is shown in **Figure 7**. The flow patterns are very similar from year to year, but there are some differences. The dispersal pathways of released oyster larvae from the Danish coast do respond to small changes in the current field. Some years (1990, 1998 and 2007) the coastal current along the Danish coast is very stable, leading to an effective transport of larvae toward the Swedish coastline. In some other years (2002, 2006 and 2010) the eddy activity east of Denmark is stronger, and the released larvae are transported far out into the Skagerrak before they finally are transported toward Sweden. In this case the transport of larvae is less effective.

When the larvae reach the Norwegian coast, they are transported along the coast in the coastal current. Unlucky larvae can be caught in a current that takes them far out into Skagerrak again. If this happens it is very unlikely that any of these will find a landing site before it is too late, and they will die. This can probably be related to the wind conditions, where on-shore wind is favourable for the larvae.

The border of the hydrodynamic model domain towards the Baltic Sea is not optimal (**Figure 7**), and the larvae paths seem to be effected by spurious boundary currents. As result of this many larvae finds a landing site in the area of the Swedish coast that is close to the border of the model domain. This is regarded as a boundary effect.

To summarise the ocean circulation pattern, it can be stated that the Norwegian coastline is downstream of the Swedish coastline that in turn is downstream of the Danish coastline. There is a fair chance that released larvae from positions both along the Danish and the Swedish coastline, will be transported to the Norwegian coastline within a timespan short enough for the larvae to survive. Temperature is therefore a crucial parameter that determines the survival of the drifting Pacific oyster larvae and their chances to survive at the landing site.

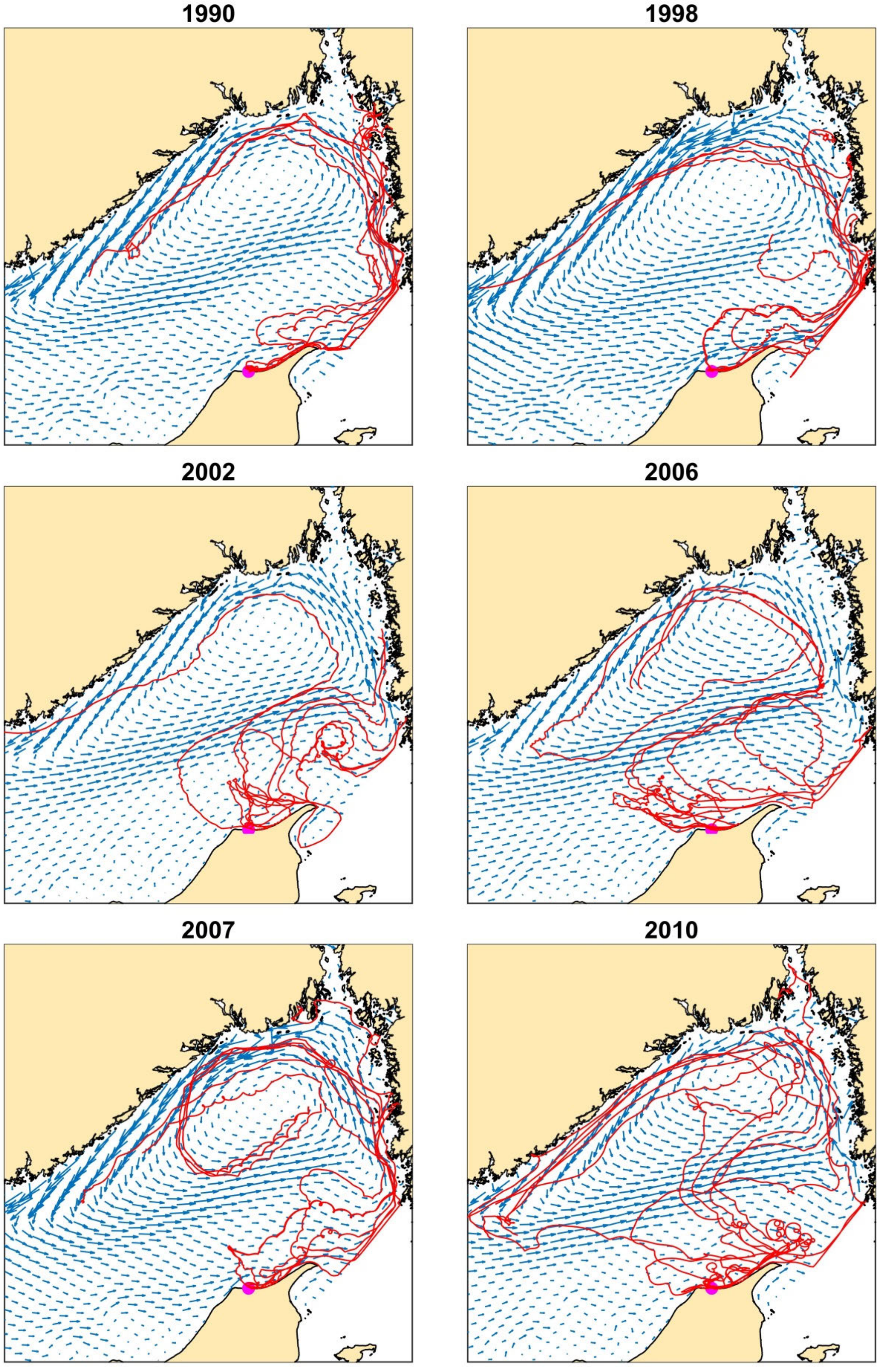

Figure 7. Ocean circulation in the surface layer for the period Aug. 1st – Aug. 12th for each simulated year in the hydrodynamic ROMS model. The dispersion of released larvae from a location on the Danish coast is shown as red paths.

3.2 The influence of climate on larvae dispersal and settlement pattern

The sea water temperature in the 90s was too cold to imply Pacific oyster larvae development and settlement / survival along the Norwegian coastline. None of the simulated released larvae using 1990-climate survived to settlement. The summer temperature conditions after 2000 allowed survival and settlement in various degree, and in warm years (2002 and 2006, in particular 2002) the larvae were able to reach the southernmost region (Mandal) at the Norwegian coast in Skagerrak (**Figure 5**). In the warmest year, 2006, one larva managed to reach Lista, the westernmost of the colonised grid cells along the Norwegian coast, situated in the ecoregion North Sea. In cold years in this century, so far (2010), the larvae only managed to reach Kragerø/Jomfruland in Telemark county (**Figure 5**). The area Sandefjord-Tjøme in the county Vestfold emerged as the area that received most successful landings of released larvae from Swedish and Danish locations in total, for all simulated years.

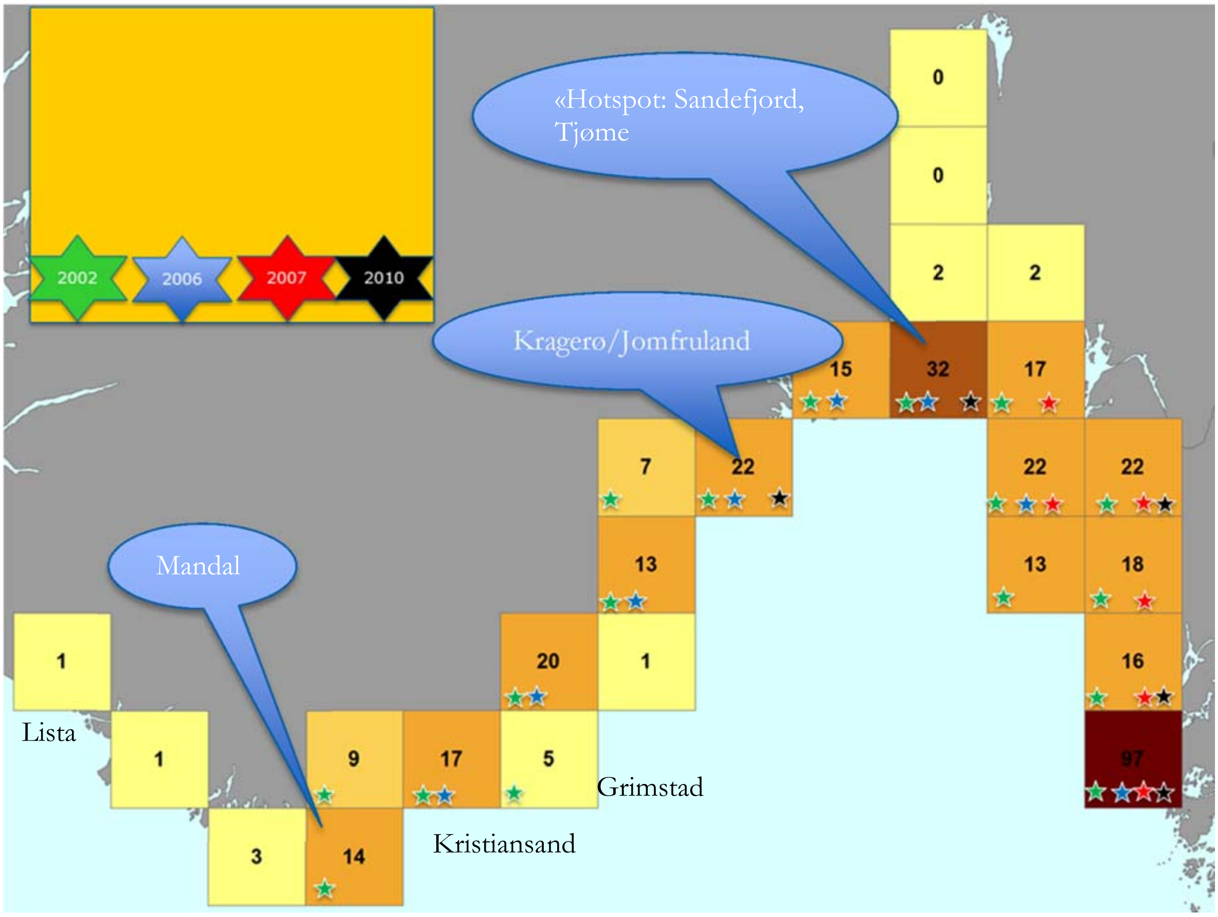

Figure 5. Overview of the spatial distribution of the landed Pacific oyster larvae in total along the Swedish and Norwegian coastline, among the 25 50x50 km coastline cells that were colonised in the simulated years 2002, 2006, 2007 and 2010. Total number of landed larvae per cell is provided. The asterisks indicate for which year the numbers of landed larvae were significantly more than 1. The high number (97) in the cell at the boundary of the hydrodynamic models domain in Sweden, is due to a boundary effect.

The first of the sites along the Danish coastline that experienced sufficient temperature conditions to produce successful landings of the oyster larvae along the Norwegian coastline was the release point at Løkken in Jammerbugten, between Brønderslev and Hjørring (i.e. release point nr 10 counting from the westernmost point along the Danish coastline in **Figure 1**). From this site 2 larvae managed to reach

Kristiansand and Grimstad at the Norwegian Skagerrak coast in the 2002-simulation. The release points at the eastern side of Løkken towards Skagen in Denmark, only achieved sufficient temperature conditions to successfully produce Pacific oyster landings in the warm simulation year 2002 (**Figure 8**). The release points at Skagen also achieved sufficient temperature conditions in 2010, a medium warm year, to produce successful oyster larvae landings at the Norwegian coast.

A plot of the percentage of days with sea surface temperature above 18°C (**Figure 8**) shows that the simulation years (2002, 2006, 2007 and 2010) includes both two of the warmest summers since 2000 (2002 and 2006), one of the coldest years (2007) and a medium warm year (2010).

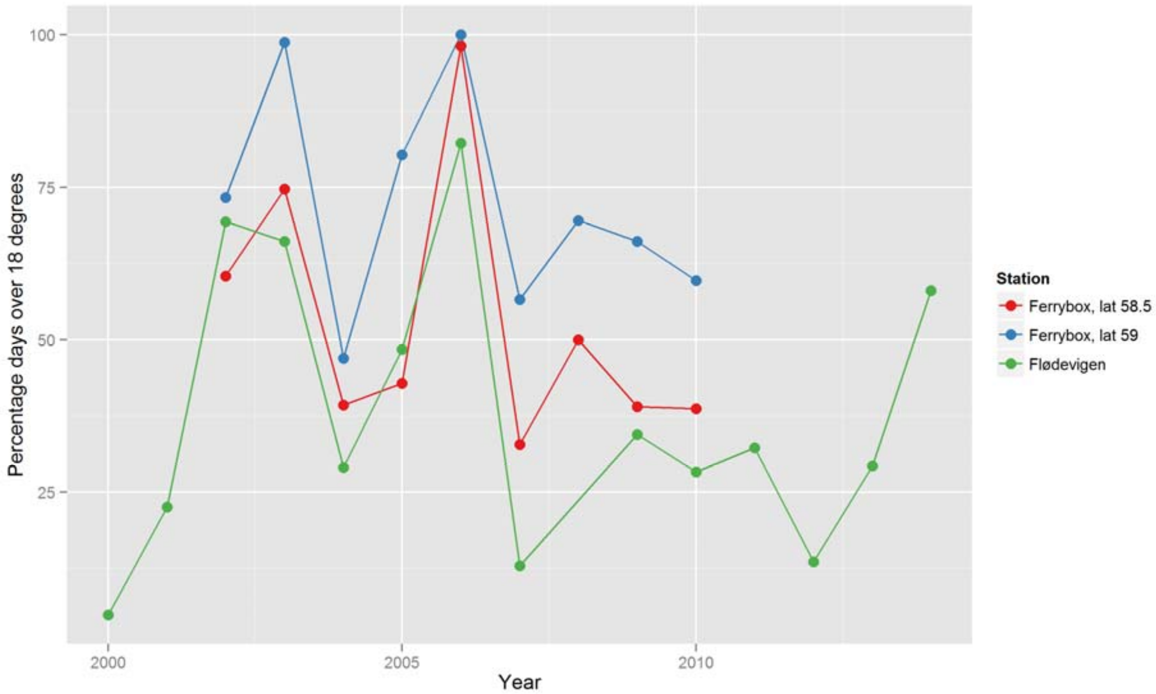

Figure 8. Percentage of days with sea surface temperature above 18 degrees in July-August, at two Ferrybox stations (58.5 and 59 degrees North) and at Flødevigen (see **Figure 2** for geographical positions). Measurement times were at 0900 in the morning at Flødevigen. The ferrybox data are for both night- and daytime (no effort has been done to correct for time in this graph).

3.3 Trends in ocean warming

The analysis of sea surface temperature data along the Swedish Skagerrak coast showed that there has been a substantial temperature increase in summer in the period 1990-2014 (**Figure 9**). For the northernmost station, the estimated temperature at 1st August increased 1.62 °C, from 18.22 °C (SE 0.27) to 19.85 °C (SE 0.22), Drawing isotherms for the 1st of August based on this model (**Figure 10**) indicates that the northernmost station is somewhat warmer now than the southernmost station used to be in 1990. Since the distance between these stations is about 125 km, the 19°C temperature isocline in August has moved at least 125 km northwards during this period.

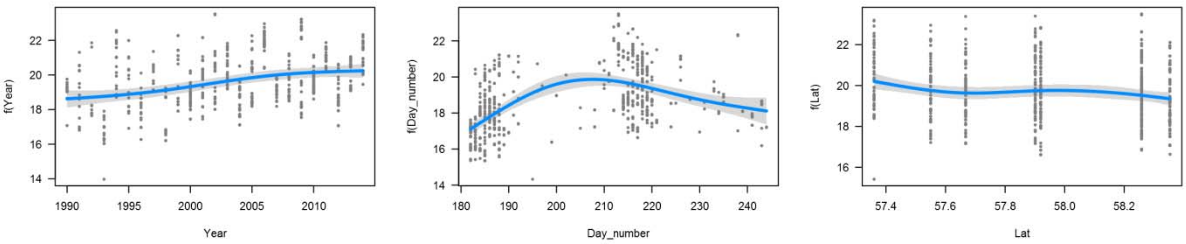

Figure 9. Result of a GAM analysis of measured summer temperatures (July-August) along the Swedish Skagerrak coast.

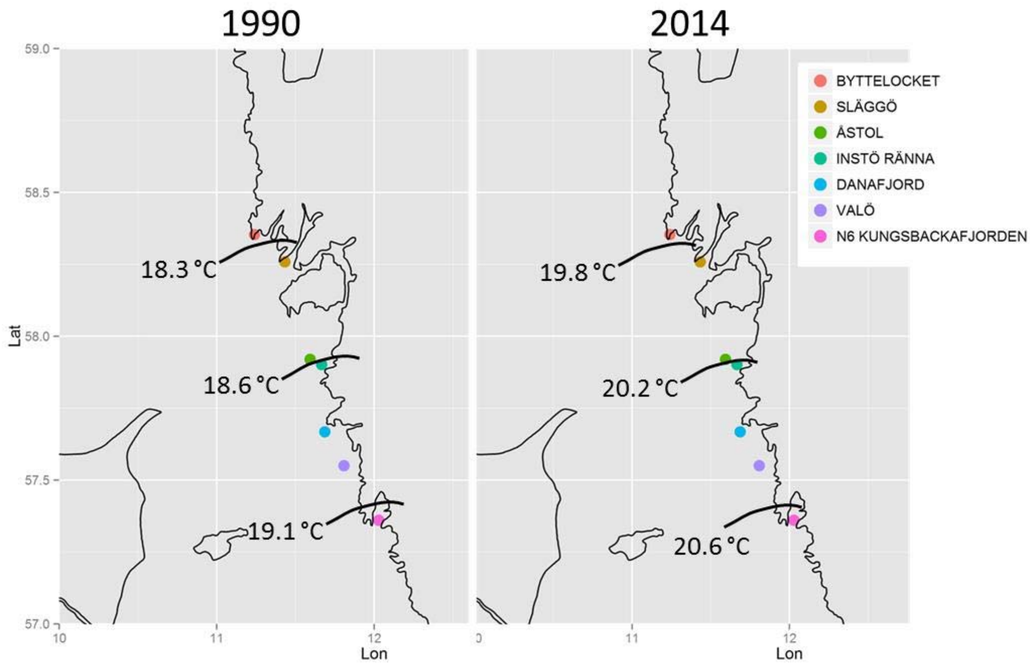

Figure 10. Isotherms for the 1st of August from the GAM model shown in **Figure 9** for the start and end of the 1990-2014 period.

4. Discussion and concluding remarks

The simulation study indicates that the increase in water temperature in Skagerrak between 1990 and 2010, of about 1.6ºC along the Swedish Skagerrak coast, has caused increased possibility for development, survival and hence dispersal of Pacific oyster larvae from Danish and Swedish coastal areas to Norwegian coastal waters. The anti-clockwise ocean circulation pattern facilitates larvae dispersal from Denmark and Sweden to Norway, and the length of the free-floating larval stage, 2-3 weeks, is more than long enough for the larvae to reach the Norwegian coast. Transport of water from Danish and Swedish coastal areas to the Norwegian Skagerrak coast is well documented. Among others; Aure and Magnusson (2008) showed that the coastal waters from 0 to 30 m depth close to Arendal, was a mixture of water from the southern and central North Sea (approximately 57%), surface water from Kattegat (approximately 26%) and water from the German Bight (about 17%). The water transport towards the Norwegian coastal areas is wind dependent and highest in years dominated by southern winds (Aure and Magnusson 2008). By predominant westerly and northerly winds in the Skagerrak (spring - summer), water from the upper layers in Skagerrak is often recycled and periodically able to block the inflow of water from the west coast of Jutland and the German Bight (Aure et al. 2010).

Based on the description above, the larvae may be transported to the Norwegian Skagerrak in every year. However, larvae development and survival depend on temperature, and the simulation study showed that temperature was too cold for successful development and survival in the 1990s. Since 2000, the simulations indicate successful dispersal of the larvae to Norway in warm and moderately warm years. Only in the warm years 2002 and 2006, the temperature was high enough for enabling dispersal and survival of landed larvae to most of the Norwegian Skagerrak coast. In the moderately warm year (2010), the temperature conditions only allowed a restricted successful dispersal to localities in the northeastern part of the Norwegian Skagerrak coast. The two warm years, 2002 and 2006, have the highest sea temperatures recorded in Flødevigen station since measurements started in 1924.

The study does not include any other mortality factors than the influence of temperature on the larvae's possibility to develop successfully during the planktonic phase, and sufficient temperature for the larvae to survive at the landing site. A number of other mortality factors will influence the larvae's possibility to actually survive the planktonic phase (e.g. having sufficient food supply and survive predators) and to survive after settlement (including spatial competition with other species, and other biotic and abiotic factors). In total, 342 localities with Pacific oyster occurrence exist along the Norwegian coast today (information from Artsdatabanken; www.artsdatabanken.no, March 2016). To what extent the observed oyster populations along the Norwegian coastline) stem from reproduction in locally established Norwegian populations, or from larvae drifted from Swedish and Danish populations, need to be further analysed by means of DNA-analysis.

Analysis of the oceanographic model results showed some bias in the simulated temperatures. When compared with continuously measured data, i.e. Flødevigen station and Ferrybox data, most years indicate that the model is quite accurate at the start of the summer, while showing insignificant heating as the summer progresses. This is indicated both by Flødevigen data in 1990, 2002, 2006 and 2007 (**Figure 4**) and by Ferrybox data in 2006 and 2010 (**Figure 5**). In 1996 the model starts out too warm, but also in this year it ends up too cold at the end of summer. Although the SMHI data at stations Å15, Å16 and Å17 shows a different picture in some years (2006, 2007 and 2010; **Figure 4**) we put more faith in the continuous measurements and corrected the model using a bias-correction that increases continuously until a certain date, and we think the resulting modelled temperatures are very close to the real ones. One reason for the deviance between modelled and observed temperatures could be that the study area is in the outskirts of the hindcast model used for atmospheric forcing.

The release points along the northern coast of Jutland in Denmark are north of the published distribution limit of the Pacific oyster in Denmark (Dolmer et al. 2014). However, observations of shells of the species at Løkken (pers. comm.. Kersten Hansen, Denmark) in Jammerbugten, and of live individuals at Hirsholm close to Fredrikshavn, the easternmost of the Danish release points (**Figure 1**, pers. comm. Karin Lise Krabbe, Denmark), shows that the species is also present in northern Jylland. Marine alien species are often found on artificial substrates, such as found in harbours (Minchin 2007). Hence, harbours within the coastal area in northern Jutland, represent areas that might house the species. Artificial substrates in coastal areas can also be found in aquaculture and ocean wind mill sites. The occurrence of such sites within the included Danish coastal area is not investigated in this study. Some of the release points along the Danish coast are probably not, at present, housing wild Pacific oysters. However, the low number of successfully landed larvae in Norwegian coastal areas of the larvae released from the Danish release points, reduce any lack of realism of using these release locations.

Recent climate change has caused an approximately 125 km northwards movement of the 19°C temperature isocline in August along the Swedish coastline. This implies a shift in the northern limit of localities that will achieve favourable summer temperatures for oyster spawning and settlement in Sweden, implying reduced distance between Swedish oyster populations achieving spawning conditions, and Norwegian coastal areas. The analysed temperature data are from wave exposed coastal sites, hence this shift represents a shift of the temperature isocline at regional rather than local scale. In shallow enclosed areas north of this limit, such as found in archipelagos and fjords in both Sweden and Norway, sufficiently warm conditions for oyster spawning occur already given today's climate (unpublished NIVA data from semi-enclosed bays close to Drøbak in the Oslo fjord). Other studies supports a northward expansion of marine biota in Scandinavia, e.g., Brattegard (2011) found that 35% of marine benthic species expanded their range northwards (on average 750-1000 km) during the period 1997 to 2010.

The simulation study indicates that one grid cell in Vestfold County stands out as a hot spot for receiving successful landings of the released Pacific oyster larvae from the Danish and Swedish coastal areas. This is a consequence of both the ocean circulation patterns and the temperature conditions within this area. The area houses one of the localities with highest observed densities of the Pacific oyster in Norway (the locality Hui in Vestfold, Bodvin et al. 2014). Also Brattegard (2011) found this area to be a hotspot for establishment of new marine benthic species; between 1997 a 2010, 8 new species established in this area (i.e. area 3 in Appx. 5 of Brattegard 2011) compared to 0-4 species in the other areas along the Norwegian Skagerrak coast. The 8 new species were assumed to have arrived from Sweden and Denmark along a western immigration route.

A further increase in ocean water temperature, as predicted by IPCC (2013), and longer periods of warm water, will likely increase the potential of supply of Pacific oyster larvae from Swedish and Danish spawning sites to the Norwegian coast. Their chances to succeed in establishing populations will, however, in addition to temperature rely on factors as competition for space and food with other species, predation and diseases.

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