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1 **Increased spreading potential of the invasive Pacific oyster (*Crassostrea gigas*) at its**
2 **northern distribution limit in Europe due to warmer climate**

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13

14 **Abstract**

15 The Pacific oyster, *Crassostrea gigas*, is an invasive species with a large expansion in
16 prevalence globally, and with the potential for spreading increasing due to climate change
17 effects. We examined how future climate might affect its potential for spread at its northern
18 distribution limit in a temperate ecoregion, by simulating spawning, larval dispersal, larvae
19 settlement and adult survival given different climate scenarios. The simulations were
20 performed using a three-dimensional current model (GEMSS) and a specially designed oyster
21 module, applied at the study site in the Oslofjord, Norway. The simulations showed that the
22 expected climate in the middle and latter part of this century, with warmer summers and
23 winters, very likely will lead to increased prevalence of the species within northern Europe.
24 The warmer summers will more often provide favorable temperature conditions for oyster
25 spawning and settlement, and warmer winters will more seldom cause high winter mortality.
26 The simulations gave a realistic picture of the relative frequency and the main distribution
27 pattern observed given current climate. The future climate scenario simulations indicated
28 influence of local differences in temperature on the dispersal pattern. The study indicates
29 increased dispersal and successful establishment at the outer edge of the species present
30 distribution in the future, and hence increased risk to native species and habitats in temperate
31 regions.

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Introduction

Invasive species are one of the major threats to biological diversity and ecosystem services (Millennium Ecosystem Assessment, 2005). Their threat involves competition with native species for food and/or habitat, alteration of the habitat in which they live, transfer of diseases or parasites, hybridisation with native species, and increased risk for native species to become extinct or displaced (Mack et al. 2000, Katasanevakis et al. 2014). Although not all alien species are harmful, some species, and in particular the ones categorized as "engineering species" due to their ability to influence the structure and function of ecosystem (Jones et al. 1994, Sousa et al. 2009), may have a major influence on native species and habitats and their ecological functions and services (Katsanevakis et al. 2014). The threat from invasive species is considered to increase in the future due to global change (Dukes and Mooney 1999) and ocean warming (Stachowicz et al. 2002, Sorte et al. 2010). The predicted success of invasive species in a future warmer climate is attributed to higher survival and greater increase in growth rate relative to the native species (Sorte et al. 2010), that invasive species in general are more generalists than specialists and more likely to adapt to new climate than the native species (Dukes and Mooney 1999), and that global warming may facilitate all stages involved in the invasion process; introduction to new areas, colonisation, establishment and spread (Walter et al. 2009).

The Pacific oyster (*Crassostrea gigas*, **Figure 1**) is identified as one of the most important marine invasive species globally (Molnar et al 2008). This "engineering species" comes originally from Japan (Drinkwaard 1998) but has been spread worldwide due to active introduction for aquaculture (Shatkin et al. 1997, Molnar et al. 2008) and accidental introductions (Andrews 1980). The species was introduced to USA as early as 1902, to South America in 1982 (Orensanz et al. 2002), to southern Europe in the 1960s (1964: the Netherlands, Drinkwaard 1998; and 1966: France, Andrews 1980), and to Scandinavia in the 1970s (Wrange et al. 2010). The Pacific oyster has spread from the aquaculture sites worldwide where it has been introduced (Andrews 1980) and has gradually established wild populations in several countries in northern Europe (France, the Netherlands, Germany, Denmark, Sweden and Norway, Wrange et al. 2010).

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66 Important traits that can explain the species successful spreading are high fecundity, rapid

67 growth rate, long-lived planktonic larvae (2-3 weeks) and long life expectancy (40 years,

68 Pauley et al. 1988). The Pacific oyster becomes sexually mature as a yearling (Pauley et al.

69 1988) and it has high egg production (50-200 million eggs per individual per spawning is

70 estimated for individuals greater than 8 cm, Quayle 1988). The long planktonic larval stage

71 allows the offspring to spread far from the spawning area (Shanks 2009), and makes the

72 species able to recolonize new areas (Pechenik 1999). Another important trait is that the

73 larvae can settle on almost any kind of hard substrate, including rock, stone and shells

74 (Dolmer et al. 2014). Kochmann et al.'s (2013) studies of the species occurrence in Ireland

75 indicate a positive influence of the presence of hard substrata or biogenic reef, long residence

76 time of the water in the embayment, and the size of the intertidal width. They also found

77 disproportionately more oysters in bays with aquaculture.

78

79 Future climate, which entails higher sea water temperature globally (IPPC 2013), is likely to

80 promote the species to further move at its present distribution limit northwards, into areas

81 previously too cold for the species. When the species was introduced to Europe, it was

82 erroneously assumed that the coastal waters in these areas were too cold for the species to

83 become sexually mature (Drinkwaard 1998). In recent years it has become evident that hot

84 summers can facilitate spawning in northern Europe (Drinkwaard 1998, Wrange et al 2010).

85 The first observation of wild individuals in Norwegian waters, the northern distribution limit

86 in European waters, was in 2003 (Bodvin et al. 2014), and since 2007 the number of oyster

87 localities along this distribution limit in Europe has increased dramatically (Bodvin et al.

88 2014). On the other hand, the extreme winter of 2009/2010 resulted in excessive mortality of

89 the species in Scandinavia, particularly in the northernmost and shallowest localities (Strand

90 et al. 2012). Thus, the milder winters expected in the future climate (IPCC 2013) will cause

91 lower risk of winter mortality. The expected future climate entails increased frequency of

92 warm days (IPCC 2013), increasing the number of days with suitable temperature for oyster

93 spawning (16-20ºC, Ruiz et al. 1992 and Dutertre et al. 2010). Warmer water also involves

94 shorter maturation time and a higher proportion of successfully metamorphosed larvae (Rico-

95 Villa et al. 2008), as well as increased larval growth (Kheder et al. 2010). Hence, future

96 warmer water is likely to enhance spawning, recruitment and survival in established

97   populations at the outer edge of its present distribution, further accelerating the proliferation

98   rate and spread to new areas.

99

100   At high density, the Pacific oyster forms reefs which completely changes the naturally

101   occurring habitat and its species diversity and ecological functions. This is a typical trait of

102   invasive bivalves (Sousa et al. 2009) that act as "engineering species". Establishment of oyster

103   reefs can outcompete blue mussels (*Mytilus edulis*, Nehring 2003) and represents a threat to

104   the native oyster (*Ostrea edulis*, Dolmer et al. 2014) and other naturally occurring species,

105   making soft bottom areas inaccessible to both man and birds. Also at low densities, the

106   species can alter the community structure in shallow areas with soft sediment by increasing

107   the habitat diversity and number of species (Norling et al. 2015). Biotic interactions can play a

108   key role in promoting or inhibiting spread of the species (Troost 2010, Kochmann and Crowe

109   2014). Poor oyster recruitment beneath algal canopies has been observed by Diederich (2005),

110   suggesting that fucoids may provide native mussels with a refuge from the invading oysters.

111   Birds, crabs, gastropods (especially the Atlantic oyster drill, *Urosalpinx cinerea*) and sea stars

112   are predators that might control the distribution of particularly juvenile and small Pacific

113   oysters. Kochmann and Crowe (2014) suggest a higher influence of pre-settlement processes

114   and/or post-settlement processes upon juvenile oysters, than biotic interaction involving larger

115   individuals.

116

117   Based on the high dispersal potential and the severe ecological consequences, the species is

118   considered to be a high-risk species (e.g. Hayes et al. 2005, Gederaas et al. 2007), and

119   measures to prevent establishment of high densities of the species in areas that have important

120   ecological functions (e.g. flat oyster and blue mussel banks, conservation areas for shorebirds

121   and seagrass beds) or that are important for outdoor recreation have been suggested (e.g.

122   Bodvin et al. 2014). The chance of succeeding at preventing oyster reef formation depends on

123   how early removal is initiated (Simberloff et al. 2013), and to what extent the population are

124   formed by local reproduction or external supply of larvae. Recent genetic studies

125   (unpublished NIVA data) indicate that the origin of the Norwegian populations are a mix of

126   larvae drifted from established populations in Sweden and Denmark as well as dispersal from

127   more local sources such as previous aquaculture, individual stocking for own consumption, or

128   transfer of larvae or adults by shipping. Also in Ireland the species was found to establish self-

129 sustaining wild populations that differ genetically from adjacent aquaculture systems

130 (Kochmann et al. 2012). Brandt et al. (2008) found a strong influence of external supply of

131 larvae in the early stage of the invasion of the German Wadden Sea. However, they also

132 found indications of local reproduction in the eastern part of the area.

133

134 In this study we investigate how future climate is likely to affect *C. gigas* spawning, larval

135 dispersal, larvae settlement and adult survival in a study area close to its present northern

136 distribution limit in Europe. We have applied three different climate scenarios, one

137 representing the conditions before wild specimens of the Pacific oyster was observed in the

138 study area (1961-1990) and two future climate scenarios, 2021-2050 and 2071-2100. The

139 simulations were performed using a three-dimensional hydrodynamic model (GEMSS) with a

140 newly developed Oyster module for simulating both biological and physical processes

141 involved in dispersal and establishment of the Pacific oyster.

142

143 **Material and methods**

144 Inner Oslofjord in Norway was selected as model area (**Figure 1**). This fjord section is

145 situated in northern Skagerrak, a temperate ecoregion representing the outer edge of the

146 species distribution in the NE Atlantic. It is also an important recreation area and the spread of

147 the Pacific oyster within the area is therefore of particular interest. The fjord is approximately

148 50 km long and 49 m deep, and is separated from the outer Oslofjord by a narrow, shallow sill

149 (700 m wide, 20 m deep). The maximum depth is 157 m. Tide levels are small, with typical

150 water level changes during a tide cycle around 0.5 m. During 2008-2009 (the test simulation

151 period, cf below), maximum water level difference was 1.65 m. The first Pacific oyster

152 populations in the area was established in the two enclosed bays (Hallangspollen and

153 Sandspollen), just inside the fjord sill in south (**Figure 1**). These two populations still have

154 the highest density of the species within the study area (Norling and Rinde 2011, and recent

155 observations).

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159 *The hydrodynamic model*

160 The 3D modelling system GEMSS (Generalized Environmental Modeling System for Surface

161 waters) developed by ERM's Surface water Modeling Group in Exton, USA

162 (http://gemss.com) was applied. The core of this system is a hydrodynamic model, and

163 modules for utilising the dynamics to simulate sediment transport, water quality, etc. The

164 system has been used in a variety of Environmental Impact Assessments (Kolluru and Prakash

165 2012, Kolluru et al. 2012, Prakash et al. 2012) and research projects (Albertson et al. 2009,

166 Kim and Park 2013). The hydrodynamic module provides 3-D spatially and temporally

167 variable currents, temperature and salinity for simulating the fate and transport of larvae and

168 oyster populations in the Oyster module (described below). For the hydrodynamic

169 simulations, the model area (**Figure 1**) was divided into calculation cells of variable size;

170 average horizontal resolution was 0.8 km^2. The vertical layers had high resolution (2 m

171 layers) from 0 to 20 m depth and coarser resolution (10 m layers) from 20 m depth and down

172 to the seafloor. The hydrodynamic model calculated current speed and direction, temperature

173 and salinity forwards in time with at maximum 3 minute intervals. Hourly values of these

174 results were stored and used as input to the Oyster module, which was run in separate

175 simulations. A test simulation run using observed input data for 2008-2009 showed good

176 accordance between modelled and observed depth profiles of temperature and salinity in the

177 eastern part of the study area (Tjomsland et al. 2014), except that summer surface

178 temperatures were somewhat too low (see Results section). Good accordance between

179 simulated and observed current speed and direction was also documented through current

180 measurements at different depth levels (8, 14, 20 and 26 m), at one field station (**Figure 1**) in

181 the period 24. July-28. Aug 2014 (Staalstrøm et al. 2014). However, the modelled current

182 speed was systematically a little lower than measured current speed (median current speed

183 measured: 3 cm/s, versus 1.4-2.1 cm/s modelled).

184

185 *The Oyster module*

186 The Oyster module was built on the GEMSS particle transport module which has been used to

187 simulate spreading of sediments and oil spills (Kolluru et al. 1994, Fichera et al. 2003, Fichera

188 et al. 2013). Additionally, the standard GEMSS suite of tools for entering input values and for

189 producing maps and other result files, were used.

190   Table 1 Overview of included parameters and values in the Oyster module. (Growth rate is

191   presently not related to recruitment or mortality in the model.)

Parameter (measuring unit)	Value	Comments
Larvae mortality, lower threshold temperature (ºC)	8	Larvae die at temperatures below the chosen threshold value, which was set to deep water temperature in summer in the study area.
Maximum duration of the larvae stage (days)	30	The larvae die if they do not settle within the chosen maximum duration of the planktonic larvae stage. Pauley (1988) estimates the larval period to 2-3 weeks.
Adult spawning threshold temperature (ºC)	17	Spawning takes place if the threshold value is continuously exceeded by a chosen time period. Dutertre et al. (2010) and Ruiz et al. (1992) estimated the threshold temperature to be between 16 and 20ºC.
Chosen time period with warm water needed for spawning (days)	5	Number of days above the threshold temperature value needed for spawning. Pauley (1988) indicates synchronous spawning above the threshold temperature, 19.5ºC. Guy and Roberts (2010) suggest that14 warm days are sufficient.
Adult winter mortality threshold temperature (ºC)	1	If this threshold temperature is reached, the year is categorized as a cold year with high winter mortality. Cf. the description of calibration/validation of the Oyster module.
Adult winter mortality rate in cold years	0.5	The fraction of the adult oysters that dies at a specific location if the chosen mortality conditions are true. Strand et al. (2012) estimated the winter mortality in a particularly cold winter in Norway, to be about 50%.
Winter period start (MM/DD)	12/1	The start of the selected winter period (month/day) for determining winter mortality rate.
Winter period end (MM/DD)	5/1	The end of the selected winter period (month/day) for determining winter mortality rate.
Adult growth rate (cm/year)	3	Wang et al. (2007).
Adult maximum size (cm)	15	Wang et al. (2007). Maximum length reported in Norway is 20 cm (Bodvin et al. 2014), however as the size is not linked to either reproduction or mortality, this value is not important.
Adult maximum age (year)	20	Pauley (1988) reports 40 years as maximum age of *C. gigas*. We chose a more conservative value.
Number of larvae released by spawning	5	Each of the larvae represents a super-individual consisting of millions of larvae. The number strongly effects how fast maximum number of particles in the model is obtained.
Maximum number of particles in the model, in millions	10	The maximum number is related to the computer capacity. Maximum number =initial oysters+total sum spawned larvae.

192

193

194   Due to the high reproduction capacity (several millions larvae per spawning individual), true

195   individual-based modelling was impossible. Hence we used the super-individual approach

196   suggested by Scheffer (1995), where each modelled individual represents a large number of

197   actual individuals. This implies that one adult model oyster represents one oyster colony. The

198   oysters were simulated to spawn when the temperature within the grid cell became warmer

199   than a chosen threshold value for a given number of days (**Table 1**). Spawning produces a

200   fixed number of oyster larvae, modelled as super-individuals following the currents. The

201   currents change continuously, so small differences in time of release may lead to great

202   differences in spreading. The dispersal process includes turbulent diffusion, which means that

203   particles released from a single site will end up at different locations (as demonstrated in e.g.

204   oil spill dispersal in Kolluru et al. 1994). The larvae were simulated to die if the temperature

205   falls below a given value (e.g. when transported to deep and cold water), or if they do not hit

206   the coastline within a selected time period (representing maximum duration of the planktonic

207   larvae stage). Following settlement, the larvae are transformed to adults who are ready to

208   spawn the following year, if they survive the winter. Winter survival for both newly settled

209   and established oyster populations is controlled by a selected threshold temperature. The

210   choice of this threshold affects the duration of the cold period; the lower the threshold

211   temperature; the longer the duration of the cold period. The most important parameters of the

212   Oyster module are presented in **Table 1**. The values of most of these parameters were set

213   based on values found in literature, as preliminary model runs showed that they had no large

214   effect on the results. The temperature thresholds for spawning and winter mortality, however,

215   were set using calibration (see below) to ensure an appropriate setting of these parameters

216   when studying the influence of future climate scenarios on the proliferation potential of the

217   species. Simulations were run using the same values for the biological parameters for all three

218   climate scenarios (i.e.; the model does not include evolution or adaptation to temperature over

219   time).

220

Calibration and validation of threshold temperatures

222   The temperature thresholds for spawning and winter mortality was set by calibrating the

223   model to explain the observed expansion of the Pacific oyster in the study area from the first

224   observations in 2003 to the observed distribution in 2013 (Norling and Rinde 2011,

225   unpublished data NIVA). This was done by simulating the spread of oyster populations based

226   on the current climate normal period (1961-1990), i.e. by using the modelled climate for the

227   1961-1990 period (cf. below). We used modelled instead of observed climatic values as we

228 are mainly interested in the differences between future and current climate, which we expect

229 to be more consistent using modelled data due to the deviation between observed and

230 modelled values in the 1961-1990 period. We performed a set of simulations where we

231 systematically varied the two parameters to be calibrated (the lower threshold temperature for

232 spawning and the upper temperature threshold for winter mortality). The proportion of the

233 population that dies in every cold winter was set to 50% (i.e. approximately equal to the

234 average mortality in the Norwegian Pacific oyster populations in the cold winter 2009/2010,

235 cf. Strand et al. (2012)). All simulations started with the observed situation in 2009, when

236 only two oyster populations existed in the study area (i.e. in the enclosed bays Hallangspollen

237 and Sandspollen). We selected the values for the two threshold temperatures which resulted in

238 the best accordance with present distribution. We tested the difference between the observed

239 and simulated distribution by dividing the study area into a square grid, counting the number

240 of occurrences in the grid cells for both the observed and simulated case, and used a chi-

241 square test to test whether distributions were significantly different. This was done for

242 different grids, varying from a fine-scaled grid (1x1 km grid cells) to a course-scaled grid

243 (8x8 km).

244

245 *Climate scenario simulations*

246 The model was run using meteorological climate scenarios for three 30-year periods as input:

247 1961-1990, 2021-2050 and 2071-2100. The scenarios were produced by the Norwegian

248 Meteorological Institute (NMI) using a regional climate model, HIRHAM, covering the

249 Nordic Arctic with an accuracy of 25x25km. This regional model was driven by data from a

250 global model, HadCM3 (Hadley Centre, UK) with the emission scenario SRES A1B (a

251 moderate scenario for greenhouse gas emissions). The models are described in Førland et al.

252 (2009, 2011). The input to the hydrodynamic calculations from the three scenarios was 1)

253 hourly meteorological data, i.e. air temperature, dew point temperature, wind speed and

254 direction, global radiation and air pressure predicted at MNI's station Ås (**Figure 1**), 2) hourly

255 water level at the southern open boundary and 3) daily water flow in rivers. The GEMSS

256 hydrodynamic model calculated water temperatures in the rivers as the equilibrium

257 temperatures from the heat balance. The air temperatures in the climate scenario for 1961-

258 1990 were somewhat lower than the observed values at the meteorological station Blindern

259 (**Figure 1**) in the same period. The difference between the annual mean values was 1.5˚C. To

260   evaluate the difference between predicted and measured sea water temperature, the modelled

261   sea surface temperature for the period 1961-1990 was compared with field measurements

262   from two monitoring stations for the same period, Dk1 (59.815°N, 10.569°E) and Ep1

263   (59.786°N, 10.728°E) (**Figure 1**, Berge et al. 2013).

264   To uncover the dispersal pattern given the two future climate scenarios, we have divided the

265   study area into 7 sub-areas (2 outer, 2 middle and 3 inner areas, covering the latitudinal and

266   the longitudinal gradient, as well as both sides of the fjord) and calculated number of settled

267   larvae and established populations per km coastline within each sub-area, for every simulated

268   year.

269

270   **Results**

271
272   *Calibration and validation of threshold temperatures*

273   The model was calibrated against the observed distribution in 2013 (**Figure 1**) by varying the

274   threshold temperatures for spawning and winter mortality. When the lower threshold

275   temperature for winter mortality was set to 0°C, winter mortality never occurred at present

276   climate conditions, while a threshold of 2°C resulted in high winter mortality every year and

277   no oyster populations established, even when the threshold temperature for spawning was

278   lowered to 14ºC, allowing spawning every year (**Figure 2**, 1961_Sp14C_Mo0C). By setting

279   the winter threshold temperature to 1°C, winter mortality occurred in particularly cold winters,

280   which were in accordance with the observed pattern of winter mortality (Strand et al. 2012).

281   For spawning, the resulting establishment of oyster populations with threshold temperatures

282   equal to 16.5 and 17°C (**Figure 3**, 1961_Sp17C_Mo1C), both gave more or less equally good

283   accordance with present distribution. This was not achieved with lower or higher threshold

284   values (e.g., a threshold of 18°C resulted in no increase in the abundance at all). Thus, future

285   scenarios were ran with a 1°C threshold temperature for winter mortality and the spawning

286   threshold temperature set to either 16.5 or 17 $^{\circ}$C (some figures show only results for the 17 $^{\circ}$C

287   run). The observed and modelled distribution based on the 1961-scenario were significantly

288   different ($P \leq 0.05$) when counting occurrences in grid cells of 4x4 km or smaller, and not

289   significantly different ($P > 0.05$) when we used courser grids (5x5 km or coarser). Thus, the

290   simulations achieved an adequate agreement, although the fine-scaled distribution of oysters

291   was different from the observed pattern.

292

Predicted and observed air and water temperature in the 1961-1990 period

According to the climate scenario for 1961-1990, the mean air temperature was 3.8˚C. In the period 2021-2050 the mean air temperature is predicted to be 2˚C warmer, while in the last period of this century (2071-2100) mean air temperature is predicted to be 4˚C warmer than today's normal temperature based on the 1961-scenario. When these climate scenarios are used as input to the hydrodynamic model, the corresponding mean temperature increase in the surface waters of the Oslofjord was equal to 0.8˚C and 1.5˚C for the two future climate scenarios respectively (2021-2050 and 2071-2100). Based on the simulations, the temperature increase in the future scenarios will be the greatest in the period August to February. The typical increase in maximum temperature in surface waters during summer was close to 1˚C for the period 2021-2050 and almost 3˚C for 2071-2100. The corresponding increase in minimum temperature in surface waters during winter, increased by approximately 0.5˚C and 1.5 ˚C, respectively. Regression between observed and predicted daily means (averaged over all years) of sea surface temperature showed generally good agreement for the period 1961-1990, at the two monitoring stations Dk1 (R^2=0.86) and EP1 (R^2=0.81). However, the predicted temperatures were significantly lower than observed during spring (Mar-May) and summer (June-Aug); maximum predicted sea water temperature in the 1961-1990-period was 19.2˚C, i.e. 3.3°C lower than the maximum observed temperature. During autumn (Sep-Nov) and winter (Dec-Feb), predicted and observed temperatures were not significantly different at the monitoring stations Dk1 ($P > 0.42$) and Ep1 ($P > 0.11$).

313

Predictions given future climate scenarios

The climate in the latter part of this century caused a quicker colonization than the other two climate scenarios (**Figure 3**). The maximum number of populations that the model could handle (10 mill. super-individuals) was reached in 10 years for the 2071-2100 scenario and in 20-30 years (depending on spawning threshold temperature) with the 1961-1990 and 2021-2050 scenarios. Further, the 2071-2100 caused colonisation of a larger part of the available coastline than the two other climate scenarios (**Figure 4**). Both of the future climate scenarios caused a gradual colonization of the coastline by oysters from the outer area and inwards during 10 years of simulation, and with higher levels of both recruitment and colony

323   establishment in the 2071-2100 scenario (**Figure 5**). However, this common pattern becomes

324   to a certain extent concealed by the large recruitment and colony establishment in the outer

325   areas (sub-areas 1-4) and the conversely low recruitment and colonisation in inner areas (sub-

326   areas 6-7) during the last few years in the latter period. This is caused by an opposite spatial

327   pattern of summer and winter temperatures in the inner and outer areas in the 2071-2100

328   scenario. In order to understand the different spatial patterns, it is important to distinguish

329   between the simulated temperature at a coarse spatial scale (i.e. in open water) and the

330   temperature experienced at local scale by the survived oysters. In open waters (in the middle

331   of the fjord basins), the inner areas are warmer than the outer areas in summer for both

332   scenarios (**Supplementary Figure 1**). However, in the 2071-2100 scenario, the outer

333   coastline where the predicted (and real) oysters establish, become faster warmed in summer

334   than the coastline in inner areas, probably due to the presence of shallow bays. Thus, the

335   pattern of high and low recruitment and colonisation in the outer versus the inner areas in the

336   2071-2100 climate scenario correlates with higher experienced temperature in July by the

337   oysters in the outer area. In winter, the outer areas are in general warmer than the inner areas

338   (**Supplementary Figure 1**), causing higher winter survival in these areas, as well as higher

339   recruitment. Although summer temperature in open waters in general are warmer in the latter

340   climate scenario, the July temperature experienced by the oysters (i.e. the temperature within

341   the oyster populations) in the middle part of the century, displayed the opposite spatial pattern

342   as for the latter period: the innermost areas was warmer than the outermost areas, causing

343   higher reproduction and recruitment in the inner area (**Figure 5**). According to the March

344   temperature experienced by the oysters, the winter survival should be higher in the outer areas

345   than in the inner areas in both future climate scenarios, due to warmer water. However,

346   because of the low recruitment in the outer areas within the limited simulation period, this

347   cannot be reflected in increased abundance of populations in the middle part of the century.

348   The chosen threshold temperature for winter mortality (1°C) caused similar or less loss of

349   adults/populations in the last period as in the middle period of the century for 5 of the 7 sub-

350   areas (i.e. number of years in which the proportion of dead adults are $\geq 50\%$, is higher or

351   equal given the middle period climate as given the latter period climate for 5 of the 7 sub-

352   areas). For the warmest month, August, the established oyster populations experienced

353   warmer water in all sub-areas in the 2071-scenario compared to the 2021-scenario, except for

354   sub-area 3. Hence, despite the local differences in temperature between the two scenarios, the

355   temperature on average is warmer in the latter climate scenario. Consequently, according to

356 the simulations, the Pacific oyster will spread substantially faster given future climate

357 conditions.

358

359 **Discussion**

360 The study indicates a dramatic increase in the spreading potential of the Pacific oyster

361 (*Crassostrea gigas*) at its present northern distribution limit towards the end of this century

362 due to warmer climate. As the sea temperatures of the study area are comparable to other

363 temperate ecoregions, the study indicates that the future climate will reinforce the spread of

364 the species in temperate regions in general. This is in accordance with Syvret et al.'s (2008)

365 predictions that i.e. most moderate risk areas in UK and with similar climate as the study site

366 (including northern Ireland, Wales, and southwest England), with intermittent recruitment

367 potential for *C. gigas* at the time of the study, 2004, are likely to suffer regular recruitment

368 before 2040. Southern England and southeast England was considered to have a high level of

369 risk for potential settlement on a regular basis, even given 2004 climate. The applied

370 temperature criteria for spawning and winter mortality gave a distribution that agrees well

371 with the observed distribution of the species with current climate (i.e. the climate for the last

372 30-year normal period based on data from the Norwegian Meteorological Institute). We have

373 not taken into account other factors, but the experience from other countries indicates that the

374 species is flexible e.g. with regard to what kind of habitat it needs for establishment (Troost

375 2010).

376

377 Because of the model's simplicity, we do not expect that the future distribution will

378 correspond to the modelled distribution in detail. Moreover, the model has too coarse

379 resolution to include most of the islands in the inner part of the Oslofjord where the Pacific

380 oyster already has established populations. Additionally, parts of the true current distribution

381 of the species may be unknown to us. Despite the simplicity, the simulated distribution of the

382 Pacific oyster showed a reasonably good accordance on a coarse spatial scale with the present

383 distribution of the species, and the relative frequency within the area. Moreover, the

384 sensitivity test showed that a small difference in the threshold temperature for spawning

385 (0.5˚C increase from 16.5 to 17˚C) had very little impact on the spreading rate given the two

386 future climate scenarios in terms of number of years needed to achieve the maximum

387 attainable number of populations. The models accuracy could be improved by increasing it's

388   the spatial resolution and by linking larvae settlement to habitat suitability (e.g. sediment type,

389   shore width, and retention time of the water, Kochmann et al. 2013), however this will not

390   change the main findings of increased spreading potential of the species in the future. Genetic

391   adaptation, biotic interactions and disease outbreaks are likely to have large influence on the

392   future distribution, but the study indicates that the potential for *C. gigas* spawning and

393   spreading to new areas increases dramatically.

394

395   There were discrepancies between observed and predicted temperature values for the current

396   climate scenario (i.e. 1961-1990). This means that there is a bias in the spawning temperature

397   threshold of 16.5-17 ˚C "estimated" in our study. For the innermost part of the Oslofjord

398   (Bunnefjorden) temperatures of 18 to 19˚C occurs in surface waters in the fjord in most

399   summers with current climate, but in the model based on the 1961-90 climate scenario, these

400   temperatures are very rarely achieved. Thus, the real threshold temperature for spawning is

401   probably slightly higher than the applied threshold values (17 ˚C), and probably above 18˚C

402   as indicated by Dutertre et al. (2010). Despite this deviation from the assumed real threshold

403   temperature for spawning, we consider our simulations of future proliferation potential to be

404   realistic, and that the conclusions are robust in spite of the imperfections in the modelling of

405   climate and biology. We used modelled temperatures, not real temperatures, for simulations

406   with current conditions. Thus, if the discrepancies between observed and modelled

407   temperature also applies for the future scenarios, this will not cause a bias in the predicted

408   future spreading potential. The essential result is the difference between future temperatures

409   and current climate. An increased mean air temperature at the end of this century of 4°C and a

410   corresponding increase in surface temperature of about 1.5°C will generate a larger number of

411   summer days with good conditions for spawning and fewer cold winters with high mortality.

412   Temperatures in shallow and confined areas such as shallow inlets and bays, especially in

413   shallow water (<50 cm) where the Pacific oyster so far in particular has established

414   populations, will probably even more often achieve favourable temperature conditions for

415   spawning than our simulations indicates.

416

417   The increased proliferation rate does not exclude that some extreme winters in the future may

418   knock out large parts of the populations, but the warmer climate will make it easier for the

419   remaining individuals to re-establish populations with high oyster density and accompanying

420   severe ecological consequences (Nehring 2003, Dolmer et al. 2014, Norling et al. 2015). The

421   future climate scenario simulations also indicate influence of local differences in temperature

422   on the dispersal pattern. However, the combination of future warmer summers and warmer

423   winters, especially towards the end of this century (IPPC 2013), will increase the probability

424   of getting more localities with high densities of the Pacific oyster along its present distribution

425   limit in Europe if no combating measures are taken. It will particularly be important to

426   prevent reef establishment in areas that are suitable for the species, such as embayment's with

427   long residence time and in areas with wide intertidal areas (as indicated by Kochmann et al.

428   2013), because reefs will further enhance recruitment success by providing a suitable

429   substrate (Nehls et al. 2006), and by increasing the chance of fertilization of spawned eggs. In

430   warmer water, *C. gigas* will to a greater extent than at present, be able to maintain populations

431   in temperate ecoregions through own larval production. Pacific oyster may be particularly

432   threatening for blue mussels, since they utilize the same habitats (Nehls et al. 2006). Since

433   blue mussel is a cold water species, it can be expected that a warmer climate will reduce their

434   competitive ability relative to the Pacific oyster, for habitat and food (Nehls et al. 2006).

435

436   Some researchers, such as Troost (2010), argue that the Pacific oyster may have positive

437   ecological impacts, e.g. by building complex structures that allow hiding places for many

438   species, and by increasing habitat heterogeneity and species diversity by introducing hard

439   substrate in mud flats. Troost (2010) also emphasizes the species ability to capture sediment

440   when they occur in high densities, and thus the ability they have to reduce erosion of tidal

441   flats. It has also been argued that the blue mussels can be positively affected by the invasion

442   of the Pacific oyster because small mussels can hide between the much larger oysters and thus

443   be protected from predation by for example crabs and sea birds. Despite lower growth rate

444   due to reduced supply of food particles, these mussels could have a greater chance of survival

445   than individuals who do not find habitats with similar protection (Eschweiler and Christensen

446   2011). This positive effect will however only apply at relatively low densities of the Pacific

447   oysters.

448

449   Successful colonisation of the Pacific oyster in new areas will depend on competition with

450   other species, the presence of predators, access to food (i.e. plankton) and the extent to which

451   they are exposed to diseases. Direct and indirect effects of ocean acidification (e.g. on the

452   solubility of aragonite and calcite) on reproduction and growth, may reduce future occurrence

453   of *C. gigas* and cause shifts in the competitive dynamics between calcareous species and

454   fleshy seaweeds (Kroeker et al. 2013). Future changes in salinity due to more freshwater run

455   off, may not be an important issue, as the Pacific oyster is tolerant to a wide range of salinity

456   (Mann et al. 1991). Warmer water in the future may lead to more frequent events of oxygen

457   depletion in shallow eutrophic areas (Rabalais et al. 2009), causing death of bivalves and

458   other benthic fauna. Summer mortality in *C. gigas* is a relatively widespread phenomenon that

459   is associated with warm water, reproductive effort and stress, e.g. anoxic conditions (Samain

460   2011). The warm summer of 2014 caused high mortality of *C. gigas* in outer parts of the

461   Oslofjord, especially in shallow (< 1 m depth), enclosed bays (Bodvin et al. 2014). In deeper

462   water, and in more exposed areas, the warm summer caused high settlement of *C. gigas* in

463   areas previously not colonised, and high survival during the summer mortality event

464   (unpublished observations). Although the species has managed to establish itself in high

465   densities in tidal areas in the Wadden Sea, other conditions, such as minor tidal differences,

466   nutrient limitation, the presence of predators etc., can make the species less dominant

467   elsewhere (Troost 2010). The low density of the species within Limfjorden (Denmark)

468   compared with the Wadden Sea, have for example been associated with low tidal difference

469   and nutrient limitation (Dolmer et al. 2014). Similarly, there may be some conditions in newly

470   colonised areas that may reduce recruitment and survival of the species.

471

472   This study indicates increased spawning, recruitment and survival in established populations

473   at the species northern distribution limit in Europe, in a future warmer climate. Considering

474   that the species still has not reached its maximum potential distribution range according to its

475   eco-physiological limits and reproductive capacity (Cardoso et al. 2007), this will further

476   accelerate the proliferation rate and spread of the species northwards in Europe and in other

477   comparable ecoregions where the species is currently present, in the future. The increased

478   possibility of reef formation due to increased recruitment and survival in future warmer

479   climate, also impose a higher risk to native biodiversity and ecosystems in invaded ecoregions

480   globally.

481

482

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681

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684

685 **Captions**

686

687 **Figure 1**

688 The model area, inner Oslofjord, in southern Norway. The grid shows the demarcation of the
689 area, the islands included, and the horizontal spatial resolution of the hydrodynamic model.
690 The photo shows some specimens of *C. gigas*, about 15 cm long (Photo: Eli Rinde, NIVA).
691 Field observations of *C. gigas* presence (filled circles) and absence (open circles) are
692 indicated. The two source locations in the simulation studies (Hallangspollen and
693 Sandspollen) are marked with circles. The localities for field measurements of current speed,
694 sea water and air temperature, are also included (asterix), as well as the position of NMIs
695 station (Ås) for the climate scenarios.

696

697 **Figure 2**

698 Development of Pacific oyster (*Crassostrea gigas*) populations in inner Oslofjord, Norway,
699 given the climate scenario for the period 1961-1990 and various threshold temperatures for
700 spawning (S) and winter mortality (M): S = 14˚C and M = 1˚C (grey unbroken line); S =
701 16.5˚C and M = 1˚C (thick black unbroken line); S = 17˚C and M = 1˚C (dashed line); and S
702 = 14˚C and M = 2˚C (dotted line). The thin, black unbroken line shows the development for a
703 very low S (the value is exceeded and spawning happens every year) and a very low M
704 (winter mortality never happens).

705

706 **Figure 3**

707 Development of Pacific oyster (*Crassostrea gigas*) populations in inner Oslofjord, Norway,
708 given the climate scenario for the periods 1961-1990 (dotted lines), 2021-2050 (solid lines)
709 and 2071-2100 (dashed lines). Line thickness indicates whether the summer threshold
710 temperatures for spawning was set to 16.5˚C (thin lines) or 17˚C (thick lines). The winter
711 threshold temperature for mortality was 1˚C in all cases.

712

713

714 **Figure 4**

715 Simulated distribution of the Pacific oyster (*Crassostrea gigas*) in inner Oslofjord (Norway),

716 given climate scenarios for the periods 2021-2031 and 2071-2081. Field observations of *C.*

717 *gigas* presence are shown as filled circles. The division into sub-areas is shown.

718

719 **Figure 5**

720 Number of established oyster populations (adults) within 7 sub-areas of the study site (outer

721 sub-areas: 1 and 2, mid sub-areas: 3 and 4, inner sub-areas: 5-7) over a 10 year period given

722 climate scenario 2021- (a) and 2071 – (b) and number of settled oyster larvae per year within

723 the same sub-areas and simulation period given climate scenario 2021- (c) and 2071 – (d).

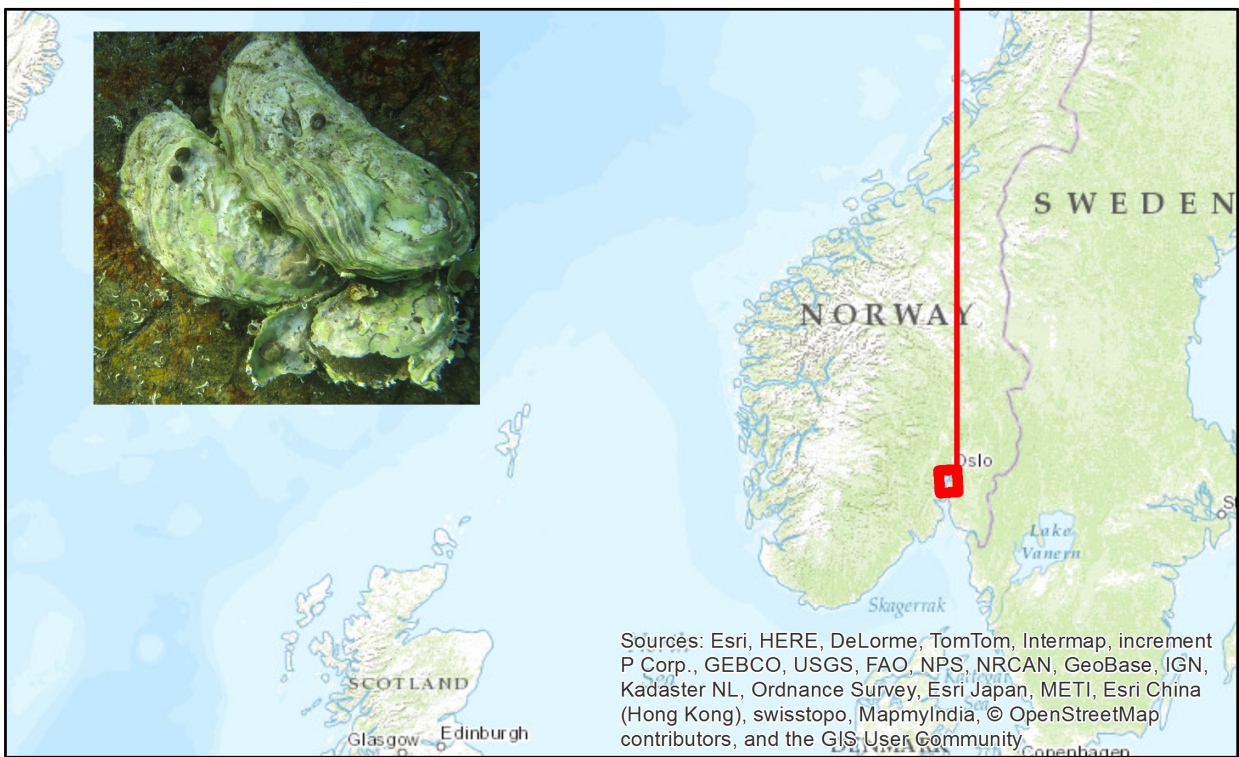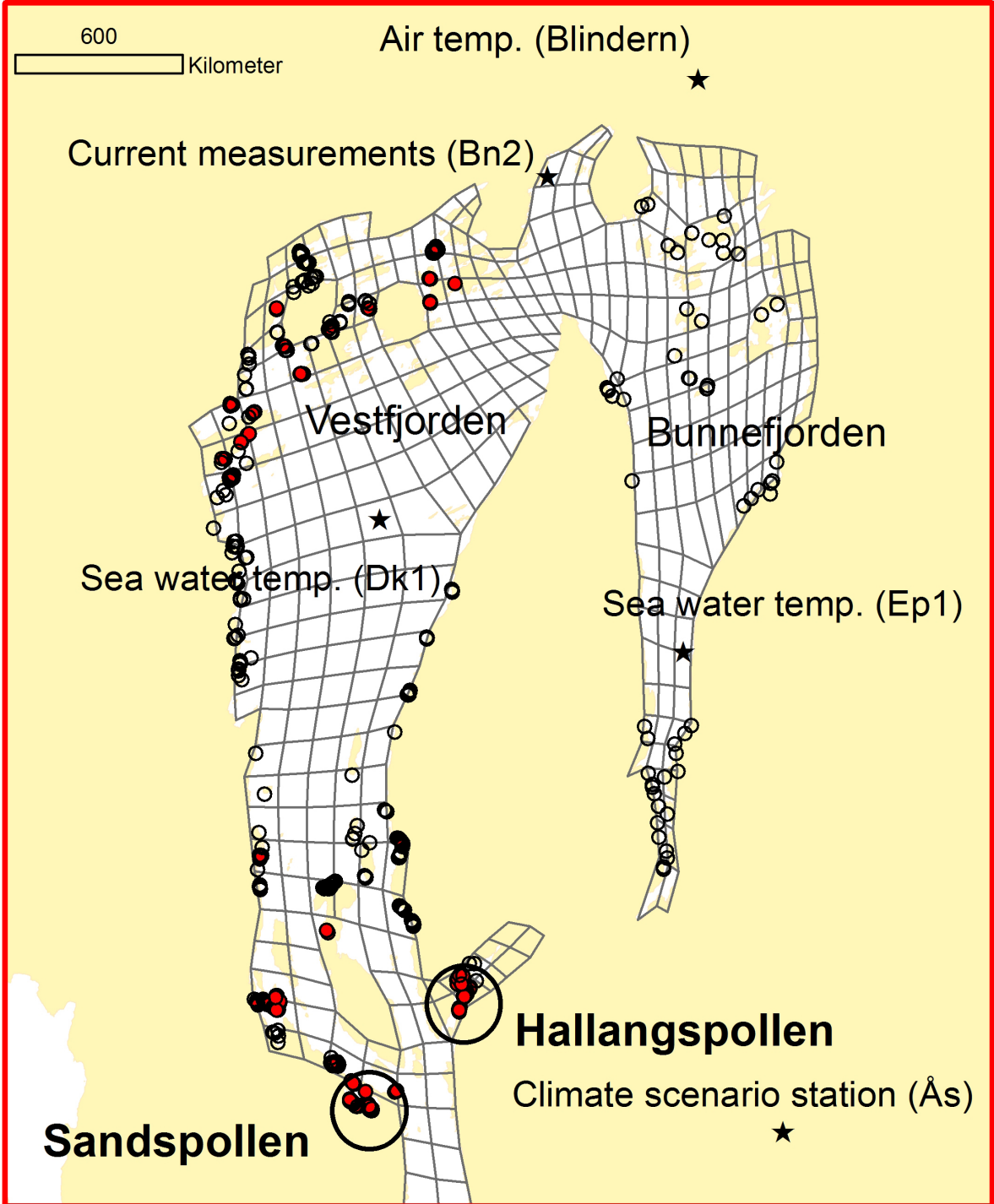724 The numbers are standardized per km coastline.
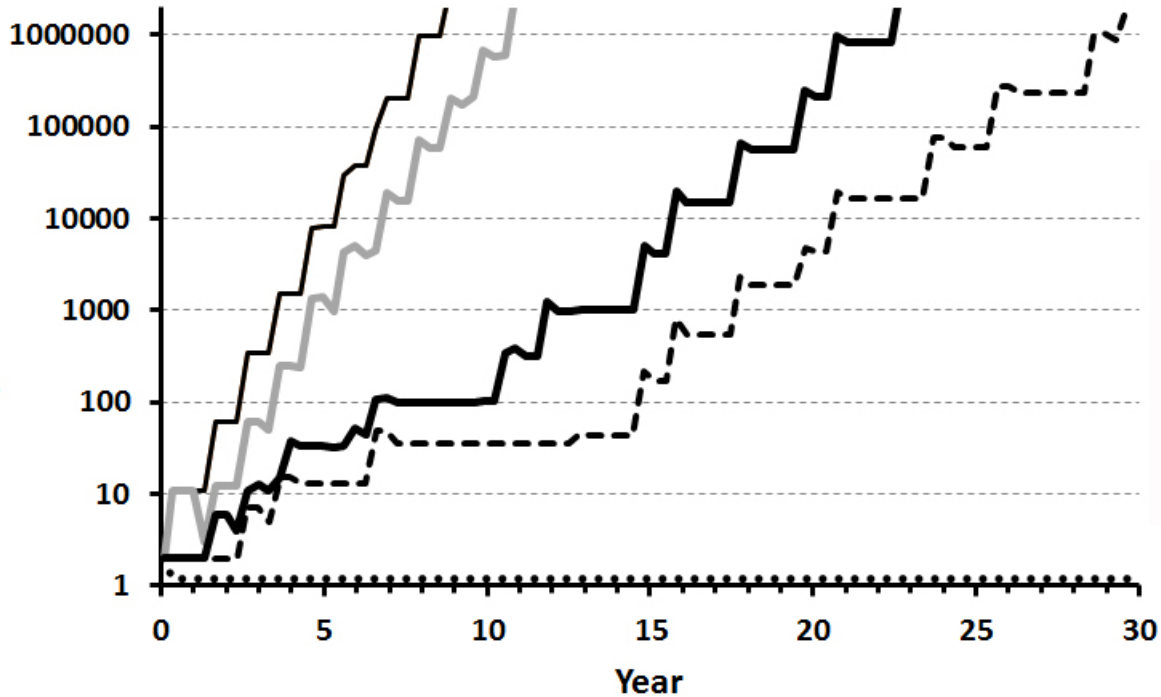
725

726 **Supplementary Figures**

727

728 **Supplementary Figure 1.** Fraction of warm summer days and cold winter days at open mid-

729 fjord stations, i.e. DK1-Vestfjorden, Bn2-Oslo and Ep1-Bunnefjorden, for the two climate

730 scenarios 2021- and 2071-. For geographical position, cf Figure 1.
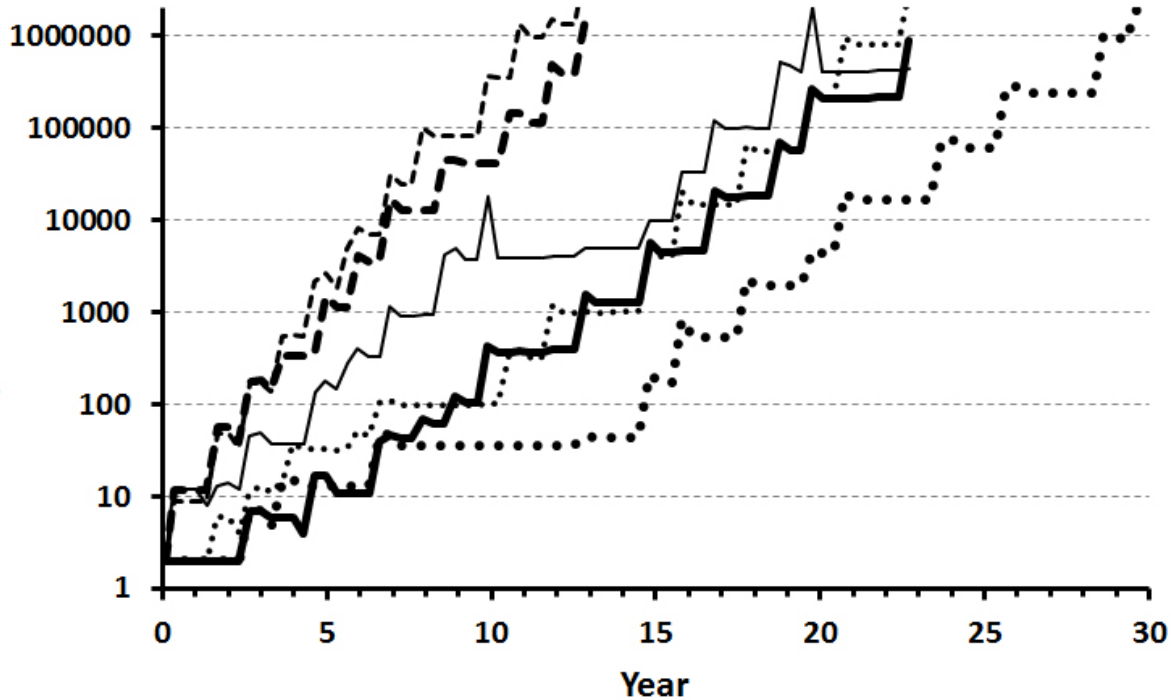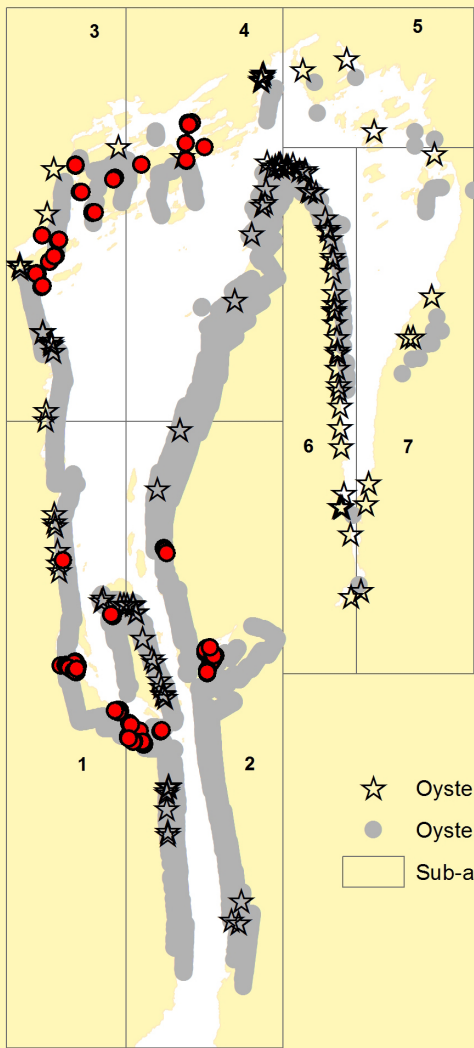
731

Air temp. (Blindern)

Current measurements (Bn2)

600 Kilometer

Vestfjorden

Bunnefjorden

Sea water temp. (Dk1)

Sea water temp. (Ep1)

Hallangspollen

Sandspollen

Climate scenario station (Ås)

☆ Oyster colonies 2021-2031 climate

● Oyster colonies 2071-2081 climate

☐ Sub-areas