

Short Communication

Impact of an icy winter on the Pacific oyster (*Crassostrea gigas* Thunberg, 1793) populations in Scandinavia

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Abstract

The Pacific oyster (*Crassostrea gigas*) is an invasive species that has dispersed into Scandinavia during the last few decades. The objective of this study was to evaluate the effects of extreme winter conditions on the mortality of the Pacific oyster in Scandinavia. The study was done by compiling mortality data from independent surveys in Denmark, Sweden and Norway. Winter mortality of the oysters increased with latitude, which can be explained by the colder climate experienced at higher latitudes. Mortality was also found to be affected by site specific conditions such as water depth at the sampling sites of oyster populations. Despite the severe winter conditions of 2009/2010 causing high mortality, the Pacific oyster still exists in large numbers in Scandinavia. The present investigation indicates that extreme winter conditions may result in a temporary reduction of the density of the Pacific oyster, but that the species can be expected to continue its invasion of Scandinavian coastal areas.

Key words: *Crassostrea gigas*, invasive species, winter mortality, Scandinavia

Introduction

The Pacific oyster (*Crassostrea gigas* Thunberg, 1793) is an invasive species that was recently observed in large quantities in Scandinavia (Wrangle et al. 2010). The species originates from the western Pacific Ocean (Drinkwaard 1999) but has been introduced in many different regions of the world both unintentionally (Andrews 1980) and intentionally (Andrews 1980; Drinkwaard 1999; Ruesink et al. 2005). In several regions the Pacific oyster now forms a bio-invasion, and may change the structure and function of invaded ecosystems significantly

(Andrews 1980; Ruesink et al. 2005; Diederich 2006; Markert et al. 2010). In Europe, the Pacific oyster was first introduced in the 1960s for aquaculture (Andrews 1980; Drinkwaard 1999) and soon after dispersed along coastlines (Drinkwaard 1999; Nehring 2003). At present, the species forms reproducing sublittoral and littoral populations, from France (Andrews 1980; Nehring 2003; Büttger et al. 2008) to the west coast of Sweden and southern part of Norway (Bodvin et al. 2010; Nyberg 2010; Wrangle et al. 2010). In Denmark, low densities of Pacific oysters were observed in the Wadden Sea in the 1990s. In other Danish areas as well as in

Sweden and Norway the main invasion event occurred in 2006/2007. The species distribution in Scandinavia is described in detail in Wrangé et al. (2010).

As an intertidal species, the Pacific oyster is very tolerant to varying abiotic conditions. The temperature span for survival ranges from subzero (Quayle 1969; Diederich et al. 2005; Diederich 2006) to approximately +30°C (Le Gall and Raillard 1988; Bougrier et al. 1995). Summer and winter water temperatures in the North Sea (Danish west coast) and Skagerrak (Swedish west coast and Norwegian south coast) are in general 15-20°C and 0-5°C, respectively, although more extreme temperatures (>25°C and <-1°C) may be experienced locally. Normal climatic conditions in Scandinavia thus seem to be within the species survival range. This is further supported by winter mortality of the species not being high enough to limit the population expansion in the Wadden Sea (Reise 1998; Diederich 2006) or in the Skagerrak (Bodvin et al. 2010; Nyberg 2010).

The winter 2009/2010 was one of the coldest and harshest in Scandinavia in many years. The ice and snow cover was more extensive than in the previous 15 years, and long lasting periods of very low temperatures prevailed. Mean air temperature was 5-6°C below average winter temperatures in Denmark, Sweden and Norway, and minimum temperatures of -10, -15 and -12°C were measured in Denmark (Hanstholm; The Danish Meteorological Institute DMI), at the Swedish west coast (Koster; Swedish Meteorological and Hydrological Institute SMHI) and at the Norwegian south coast (Arendal; The Norwegian Meteorological Institute MET), respectively. At many sites in Scandinavia entire Pacific oyster populations were reported to have gone extinct.

The objective of this study was to evaluate the effects of extreme winter conditions on mortality of Pacific oysters along Scandinavian coasts ranging from the Danish Wadden Sea to the Norwegian south coast. This was done by extracting and combining winter mortality data from independent national surveys performed in Denmark, Sweden and Norway.

Methods

In this study, mortalities of Pacific oysters were recorded at sheltered sites ranging from the Danish Wadden Sea, Danish estuaries, to fjords

and estuaries at the coastline in western Sweden and in southern Norway (Figure 1). The data is a compilation of independent surveys performed at each country. As the environment where the oysters are found and the densities of oysters varies widely between the three countries, different survey techniques adjusted to local conditions have been used in the separate studies to estimate the winter mortalities at each site. In Denmark, Pacific oysters are found at variable densities over vast soft bottom tidal areas confined to existing blue mussel (*Mytilus edulis* Linnaeus, 1758) beds. In Sweden and Norway such an environment is very rare. The Pacific oyster population therefore displays a more patchy distribution and can be found at varying densities in small bays, narrow sounds and other environments with good water circulation, using everything from hard to soft bottoms as substrate. Some common traits among all visited sites were, however, identified. All sites had limited wave exposure and had soft bottom (mud or sand). At all sites, Pacific oysters were sampled from squares (0.25-4 m²) and depth and numbers of dead and alive Pacific oysters were recorded for each square. Oyster shells were classified as oysters dead during the winter 2009/2010 if the shells were hinged and the inside of the shells were clear white and without any sediment, algae or fouling organisms. All sites were visited just after ice break, during April and May 2010 (Appendix 1). General information from all sites i.e. sample size (Appendix 1), maximum and average depth at each location, tidal amplitude, mortalities and oyster densities (Appendix 2) is presented in Appendix 1 and 2. Oyster densities after the winter 2009/2010 is calculated as number of live oysters/m² at each site and oyster densities before the winter 2009/2010 is calculated as the number of live and newly dead oysters/m² at each site.

In Denmark three areas were surveyed; the Danish Wadden Sea (N 55°16.6'; E 08°37.3'), the Isefjord (N 55°40.6', E 11°48.7') and the Limfjord (N 56°43.3', E 08°15.4'). In the Wadden Sea one sample square of 0.56 m² (0.75 × 0.75 m) and one sample square of 4 m² (2 × 2 m) were randomly placed at the oyster bank and mortality of the oysters was calculated. In the Isefjord, a transect inventory performed in spring 2007 (unpublished results, B.W. Hansen) confirmed that the overall density of oysters at the site was very low. Therefore 5000 m² were systematically scanned by two observers for

Figure 1. Location of the study sites for evaluation of winter mortality of the Pacific oyster (*Crassostrea gigas*) after the winter 2009/2010 in Denmark (DK), Sweden (SE) and Norway (NO).



Figure 2. Sampling site at the Tjärnö area, Sweden, and application of aquascope (Photograph by Johan Wingborg, University of Gothenburg).

approximately 20 person hours using aquascope to estimate the oyster density (Figure 2). In the Limfjord two different surveys took place. In one study, three sections of the oyster bank were sampled using a 0.25 m^2 ($0.5 \times 0.5 \text{ m}$) square frame which was randomly put at ten locations at each section and in the other study, eight 4 m^2

sampling squares were randomly placed at the same bank and number of live and dead oysters was recorded for all frames and squares.

Two areas along the Swedish west coast were surveyed; Kristineberg (N $58^{\circ}15.0'$, E $11^{\circ}26.7'$) and Tjärnö (N $58^{\circ}56.2'$, E $11^{\circ}10.4'$). 17 sites (nine from the Kristineberg area and eight from the Tjärnö area) were visited. At each site, two or three transects were laid out, depending on the size of the site. All transects at each site were parallel and started in level with the point of the first oyster at the shoreline and continued in a straight line towards deeper water until no more oysters could be detected or in the case of narrow sounds, until it ended up on the opposite shore. For every meter of each transect a 0.25 m^2 metal frame was put in place and both live and dead oysters inside were recorded.

In Norway five sites on the southern coast were visited, of which two sites were located in the Oslofjord. At each site a 1 m^2 ($1 \times 1 \text{ m}$) metal frame was randomly placed between 8 and 48 times depending on size of the locality so that the entire depth distribution range of the oysters at each site was covered.

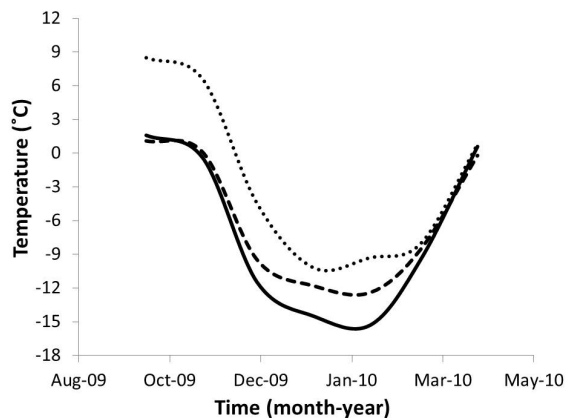


Figure 3. Minimum air temperature per month during the winter 2009/2010 in Denmark (···), Norway (- - -) and Sweden (—).

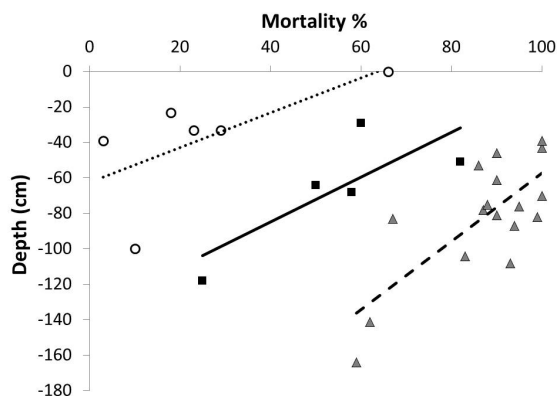


Figure 5. Mortality (%) of Pacific oysters (*Crassostrea gigas*) recorded from counts of newly dead individuals at sites in Denmark (white circles, n=6), Sweden (grey triangles, n=17) and Norway (black squares, n=5) after the winter 2009/2010 related to maximum depth (cm) at each sampling site.

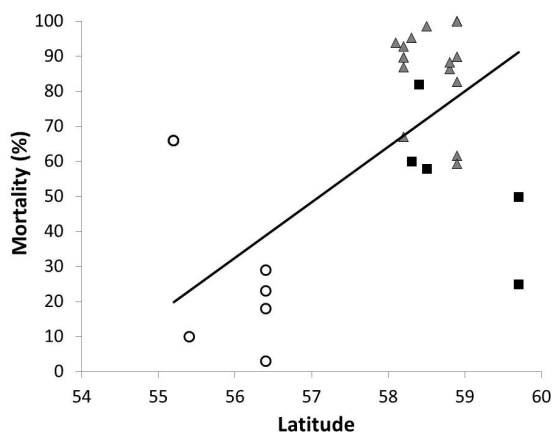


Figure 4. Mortality (%) of Pacific oysters (*Crassostrea gigas*) recorded from counts of newly dead individuals at sites in Denmark (white circles, n=6), Sweden (grey triangles, n=17) and Norway (black squares, n=5) after the winter 2009/2010 related to latitude.

The winter mortality (M_1 , %) of Pacific oysters at all study sites was estimated as:

$$M_1 = N_D / (N_D + N_A) \quad (\text{Equation 1})$$

where N_D is number of dead individuals and N_A is number of alive individuals. Minimum air temperatures for the winter period in Denmark (Hanstholm), Sweden (Koster) and Norway (Arendal) was collected from DMI, SMHI and MET, respectively (Figure 3). Proportions

(mortalities) were arcsine square root transformed before analysis. Depth data from each site was adjusted according to average water level at sampling and average water depth was calculated using the depth registered for each sample square or frame. Maximum depth was calculated as the deepest sample square or frame obtained at each site. Linear regression analysis was used to test the effect of latitude on mortality (M_1) and the effect of maximum depth on mortality for each country separately.

Results

The average mortality (M_1) at the study areas ranged from 3% in the Limfjord to 100% in the Tjärnö area (Appendix 2). Average mortalities in Denmark, Sweden and Norway (\pm standard deviation) were 25 ± 22 , 87 ± 13 and $55 \pm 21\%$, respectively. Mortality of the oysters was found to be related to latitude (Linear regression, $R^2=0.31$, $df=26$, $P=0.002$, Figure 4) with increasing mortalities at higher latitudes. Mortality decreased significantly with increased maximum depth in Sweden (Linear regression, $R^2=0.50$, $df=15$, $P=0.002$). Although not significant, the same trend was clearly visible in mortality-depth data from Denmark (Linear regression, $R^2=0.40$, $df=4$, $P=0.177$) and Norway (Linear regression, $R^2=0.61$, $df=3$, $P=0.120$; Figure 5).

Discussion

In this study, winter mortality of the Pacific oyster was found to be related to latitude. Lowest overall mortality was observed at low latitudes (Denmark, 25%) and mortalities then increased with latitude to 87 and 55% for Sweden and Norway, respectively. These findings are in accordance with climatic data, as Denmark has a milder climate with warmer temperatures compared to Sweden and Norway. The latitudes of the sample locations are also correlated to a number of other abiotic factors such as tidal range, salinity and ice formation. The observed mortality patterns may thus be a complex function of these factors combined. The lower average mortality experienced in Norway compared to Sweden may be explained both by climatic conditions and by site specific conditions. The minimum temperature in Norway was higher throughout the winter season compared to temperatures in Sweden, a factor which may have affected mortality of the oysters. Furthermore, both sites located in the Oslofjord in Norway demonstrated very low mortalities. At one site this may have been due to a rapid incline of the bottom and a larger depth range compared to the other sites. The other site is located at an exposed position and no individuals were found above 28 cm depth. This may have limited the effect of ice cover and increased survivability of the oysters at both sites.

After the winter 2009/2010, Büttger et al. (2011) found mortalities of 60% in March at Sylt in the German part of the Wadden Sea. This is well in accordance with the mortality measured at the northern part of the Danish Wadden Sea in this study (66%). Previously, winter mortality of adult oysters in the Sylt area of the Wadden Sea was found to be moderate (33%) after 66 days of ice cover in 1995/1996 (Reise 1998) and to be low around 0°C (Diederich et al. 2005; Diederich 2006). There is no quantification of the winter conditions experienced in the area in 1995/1996. However, our data seem to be well within the mortality range that can be expected in the region during harsh winter conditions.

Previous records of winter mortality of Pacific oysters in Sweden demonstrate a small effect of winter conditions on the oyster populations. Even with minimum air temperatures of -10°C, winter mortalities have been less than 10% since the major settling event in 2006 (own

observation, Å. Strand). This indicates that normal climatic conditions do not constitute a severe obstacle for continued survival and development of the Pacific oyster populations in Scandinavia. The species could, however, be close to its tolerance range, which may explain the substantial increase in mortalities when exposed to extreme climatic conditions. This proposition is further strengthened by Carrasco and Baron (2010), who conducted an ecological niche model of distribution of Pacific oyster as a function of surface seawater and air temperature. The model predicted that the Pacific oyster could be distributed in a thermal regime with a surface seawater temperature of -2 to 29°C, and an air temperature between -23 and 31°C. In general, water temperatures in Scandinavia range between -1 to 24°C and -12 to 30°C for surface seawater and air temperature, respectively (DMI, SMHI, MET). According to this model, neither surface seawater nor air temperature in Scandinavia should cause any problems for survival and continued dispersal of the species under normal conditions. However, at extreme situations as the one experienced during the winter 2009/2010, the temperatures are approaching the species lower thermal distribution limits. Climatic conditions in the region may thus temporarily reduce the Pacific oyster populations but a general elimination of the species from the region by natural events is highly unlikely.

Mortality in all three countries varied greatly between regions, i.e. from 3-66% in Denmark, 59-100% in Sweden and 25-82% in Norway. It is clear from the collected data that both depth distribution of the oysters and site specific conditions (for example local ice formation, currents and inclination of the bottom) will affect survivability of the oysters. Oysters located in the deeper part of the depth-distribution range are likely to escape the stress, both physical and physiological, caused by ice formation and exposure to low air temperatures during winter due to low water levels. This was also evident in Sweden where the lowest mortality was observed at sites with the greatest maximum depth. Although not significant, the same trend in depth dependence of mortality could be seen in Denmark and Norway. The lack of significance for the regressions from these countries is most likely caused by the low number of replicates and low depth range at study sites. The effect of local conditions is especially evident in the Swedish dataset where

sites with similar maximum depth displayed different mortalities.

In Denmark, future winter mortality is unlikely to affect the development of the oyster populations significantly due to the large populations and the relatively low observed mortality also in extreme conditions. Furthermore, in Sweden, despite the high winter mortality observed 2009/2010, very large oyster populations still exist (although not yet as extensive as in Denmark), thus the probability of further dispersal of the species is still high. In Norway the oysters have not yet formed dense populations. A loss of over 50% of the population under such circumstances may affect possibilities of recruitment and thus future development of the populations. However, any future effects remain to be evaluated. It is, nevertheless, unlikely that the oysters can be eliminated even from Norway due to the high risk of drifting larvae arriving from the Swedish populations.

At present there have been no decisions to develop management strategies in Denmark, Sweden or Norway on how to control the Pacific oyster as a bio-invader. Simberloff (2003) argues that eradication of invasive species should be performed early, before the species start to disperse. Manual destruction as a method for reducing the development and dispersal of Pacific oyster populations at very low densities ($<1 \text{ m}^{-2}$) has been tried successfully in Ireland (Guy and Roberts 2010). In Scandinavia, the oyster densities are in general much higher, thus this approach may not be suitable for limiting the oyster populations in most parts of this region. The method may however be considered a possibility at a few sites, like Isefjord in Denmark, and after the winter 2009/2010 for some locations in Sweden and Norway. Those extreme winter conditions may have reduced the oyster density at some sites to a level where it can be effectively handled through manual removal, thus offering a unique opportunity for management of Pacific oyster populations, which before winter 2009/2010 had already reached moderate densities less easy to control.

In conclusion, this study demonstrates that high winter mortalities were experienced by populations of Pacific oysters in Scandinavia during the winter 2009/2010. Winter mortality was related to latitude with increasing mortality at higher latitudes, explained by the colder climate experienced at higher latitudes. Mortality was also found to be highly affected by site

specific conditions such as depth of the oyster population. Despite the severe winter conditions of 2009/2010 causing high mortality, the Pacific oyster still exists in large numbers in Scandinavia. The present investigation indicates that extreme winter conditions may result in a temporary reduction of the number of individuals of the Pacific oyster, but nevertheless the species can be expected to continue the invasion in Scandinavia.

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References

- Andrews J (1980) A review of introductions of exotic oysters and biological planning for new importations. *Marine Fisheries Review* 42: 1-11
- Bodvin T, Norling P, Smit A, Jelmert A, Oug E (2010) Mulige effekter av etablering av stillehavsosters (*Crassostrea gigas*) i Norge. Norwegian Directorate for Nature Management, DN-utredning 1-2010, Trondheim, Norway, 19 pp (in Norwegian)
- Bougrier S, Geairon P, Desolus-Paoli J, Bacher C, Jonquières G (1995) Allometric relationships and effects of temperature on clearance and oxygen consumption rates of *Crassostrea gigas* (Thunberg). *Aquaculture* 134: 143-154, [http://dx.doi.org/10.1016/0044-8486\(95\)00036-2](http://dx.doi.org/10.1016/0044-8486(95)00036-2)
- Böttger H, Nehls G, Witte S (2011) High mortality of Pacific oysters in a cold winter in the North-Frisian Wadden Sea. *Helgoland Marine Research* 65: 525-532, <http://dx.doi.org/10.1007/s10152-011-0272-1>
- Böttger H, Asmus H, Asmus R, Buschbaum C, Dittmann S, Nehls G (2008) Community dynamics of intertidal soft-bottom mussel beds over two decades. *Helgoland Marine Research* 62: 23-36, <http://dx.doi.org/10.1007/s10152-007-0099-y>
- Carrasco M, Barón P (2009) Analysis of the potential geographical range of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) based on surface seawater temperature satellite data and climatic charts: the coast of South America as a study case. *Biological Invasions* 12: 2597-2607, <http://dx.doi.org/10.1007/s10530-009-9668-0>
- Diederich S (2006) High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology* 328: 211-227, <http://dx.doi.org/10.1016/j.jembe.2005.07.012>
- Diederich S, Nehls G, van Beusekom J, Reise K (2005) Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? *Helgoland Marine Research* 59: 97-106, <http://dx.doi.org/10.1007/s10152-004-0195-1>
- Drinkwaard A (1999) Introductions and developments of oysters in the North Sea area: a review. *Helgolander Meeresuntersuchungen* 52: 301-308

- Guy C, Roberts D (2010) Can the spread of non-native oysters (*Crassostrea gigas*) at the early stages of population expansion be managed? *Marine Pollution Bulletin* 60: 1059-1064, <http://dx.doi.org/10.1016/j.marpolbul.2010.01.020>
- Le Gall J, Raillard O (1988) Influence de la temperature sur la physiologie de l'huitre *Crassostrea gigas*. *Océanis* 14: 603-608
- Markert A, Wehrmann A, Kröncke I (2010) Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden sea of Lower Saxony, southern German Bight). *Biological Invasions* 12: 15-32, <http://dx.doi.org/10.1007/s10530-009-9425-4>
- Nehring S (2003) Pacific oysters in the European Wadden Sea: An irreversible impact in a highly protected ecosystem. *ALIENS*, Newsletter of the invasive species specialist group of the IUCN species survival commission 17, pp 20-21
- Nyberg C (2010) Japanska jätteostronet (*Crassostrea gigas*) på västkusten 2009. Swedish Environmental Protection Agency, Report, Stockholm, Sweden, 50 pp (in Swedish, English summary)
- Quayle D (1969) Pacific oyster culture in British Columbia. Fisheries Research Board of Canada, Bulletin 169, Ottawa: The Queen's printer, 192 pp
- Reise K (1998) Pacific oysters invade mussel beds in the European Wadden Sea. *Senckenbergiana Maritima* 28: 167-175, <http://dx.doi.org/10.1007/BF03043147>
- Ruesink J, Lenihan H, Trimble A, Heiman K, Micheli F, Byers J, Kay M (2005) Introduction of non-native oysters: Ecosystem Effects and Restoration Implications. *Annual Review of Ecology Evolution and Systematics* 36: 643-689, <http://dx.doi.org/10.1146/annurev.ecolsys.36.102003.152638>
- Simberloff D (2003) How much information on population biology is needed to manage introduced species? *Conservation Biology* 17: 83-92, <http://dx.doi.org/10.1046/j.1523-1739.2003.02028.x>
- Wrangé A-L, Valero J, Harketstad L, Strand Ø, Lindegarth S, Torp Christensen H, Dolmer P, Sand Kristensen P, Mortensen S (2010) Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. *Biological Invasions* 12: 1453-1458, <http://dx.doi.org/10.1007/s10530-009-9565-6>

Appendix 1. Summary information about the study sites in Denmark, Sweden and Norway (sampling date, sample size and number of squares per sample) for evaluation of winter mortality of Pacific oysters (*Crassostrea gigas*).

Country	Area	Replicate	Sampling time	Sample size	
				Square size (m ²)	N. squares
Denmark	Wadden Sea		2010-05-20	0.56 and 4	1 of each
			2010-05-26		
	Limfjord	Section 1	2010-05-31	0.25	10
		Section 2	2010-05-31	0.25	10
		Section 3	2010-05-31	0.25	10
		Section 4	2010-04-08 and 2010-05-17	4	8
Sweden	Kristineberg	Furulund	2010-05-27	0.25	177
		Hälleviken	2010-05-27	0.25	112
		Härmandö	2010-05-26	0.25	38
		Rågårdsvik	2010-05-26	0.25	60
		Smalsundet	2010-04-15	0.25	268
		Årsund	2010-05-26	0.25	62
		Gåsö	2010-05-26	0.25	80
		Skredsvik	2010-04-15	0.25	79
	Tjämnö	Krokesundet S	2010-05-24	0.25	103
		Krokesundet N	2010-05-11	0.25	59
		Långörännan	2010-05-20	0.25	50
		Tjälleskär	2010-05-21	0.25	108
		Utsidan Öddö	2010-05-20	0.25	35
		Kockholmen	2010-04-13	0.25	119
		Kollholmen	2010-05-25	0.25	19
		Svallhagen	2010-04-08	0.25	200
Tenholmssundet	2010-05-21	0.25	125		
Norway		Tromlingene	2010-04-07	1	8
		Nørholmkiln	2010-04-08	1	9
		Hove	2010-04-09	1	13
		Hurumneset	2010-04-30	1	18
		Hallangspollen	2010-05-03	1	48

Appendix 2. Summary information about the study sites in Denmark, Sweden and Norway (depth, tidal amplitude, mortality and densities of oysters) for evaluation of winter mortality of Pacific oysters (*Crassostrea gigas*).

Country	Area	Replicate	Depth (cm)		Tidal amplitude (m)	Mortality (%)	Densities (number of oysters m ⁻²)			
			Av.	Max.			Av. before winter	Max. before winter	Av. after winter	Max. after winter
Denmark	Wadden Sea		Exposed at low tide		0.7-1	66	254	471	86	160
		Isefjord	-50	-100	0.5-0.75	10	0.02			
	Limfjord	Section 1	-14	-23	0.3-0.5	18	30	64	25	48
		Section 2	-20	-33	0.3-0.5	29	64	144	46	128
		Section 3	-23	-39	0.3-0.5	3	94	172	91	164
	Limfjord	Section 4	Exposed at low tide		-33	0.3-0.5	23	22	43	14
Sweden	Kristineberg	Furulund	-36	-82	0.05-0.4	99	291	1344	4.3	80
		Hälleviken	-23	-87	0.05-0.4	94	6	44	0.4	8
		Härmandö	-40	-81	0.05-0.4	90	25	124	2.6	24
		Rågårdsvik	-58	-108	0.05-0.4	93	9	64	0.7	16
		Smalsundet	-27	-76	0.05-0.4	95	8	232	0.4	20
		Årsund	-34	-61	0.05-0.4	90	4	20	0.5	12
		Gåsö	-35	-83	0.05-0.4	67	12	68	4.0	52
		Skredsvik	-22	-78	0.05-0.4	87	9	60	1.2	16
	Tjärnö	Krokesundet S	-29	-141	0.05-0.4	62	66	196	25.5	144
		Krokesundet N	-24	-43	0.05-0.4	100	36	108	0	0
		Långörännan	-25	-39	0.05-0.4	100	6	24	0	0
		Tjälleskär	-36	-53	0.05-0.4	86	2	32	0.3	12
		Utsidan Öddö	-42	-70	0.05-0.4	100	35	128	0	0
		Kockholmen	-28	-75	0.05-0.4	88	5	52	0.6	12
		Kollholmen	-28	-46	0.05-0.4	90	10	44	1.1	8
		Svallhagen	-45	-164	0.05-0.4	59	22	296	8.8	212
Tenholmssundet	-64	-104	0.05-0.4	83	3	24	0.5	12		
Norway		Tromlingene	-44	-68	0.3-0.4	58	3	7	1.4	3
		Nørholmkilen	-19	-29	0.3-0.4	60	7	12	2.7	7
		Hove	-25	-51	0.3-0.4	82	4	6	0.8	3
		Hurumneset	-48	-64	0.3-0.4	50	2	5	1.1	4
		Hallangspollen	-79	-118	0.3-0.4	25	4	8	2.8	7