DEPARTMENT OF BIOLOGICAL AND
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The effect of inbreeding in small populations of Harbour seals (*Phoca vitulina*)

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Abstract

The Harbour seal (*Phoca vitulina*) is a common pinniped species on the west coast of Sweden. However, only one population exists in the Baltic proper. The Baltic population in Kalmarsund has been isolated for several thousand years and a recent study shows that they have lower levels of heterozygosity and genetic diversity compared to any other European population. Historically the population has undergone severe population bottlenecks which in turn have led to higher degrees of inbreeding. Inbreeding is known to influence fitness negatively however, it has been ignored in current ecological risk assessments for harbour seals. In order to fill this knowledge gap, the current study present a literature overview and maps different fitness traits reported to be affected by inbreeding depression in pinnipeds. We run multiple population viability analyses (PVAs) to estimate the effects from inbreeding depression on small, isolated harbour seal populations. The inbreeding depression was applied in the units of lethal equivalents commonly found in mammal populations and the amount of inbreeding (F) was based on recently available values from the Kalmarsund population. Several scenarios were investigated by simulations of an age structured, stochastic population model including the combined effects from epizootic events and reduced fecundity due to endocrine-disrupting pollutants. The simulations also elaborated effects from various initial population sizes and carrying capacities to gain better understanding of how population sizes as such mitigate the effect of inbreeding. The results showed that inbreeding depression at the currently detected level can be expected to have an overall negative effect on the population viability of the Kalmarsund harbour seal population and other isolated seal populations. High levels of inbreeding depression also increased the probability of extinction (34% risk of extinction in 300 years) compared to low levels (5% risk of extinction in 300 years). Populations were severely affected by inbreeding depression in scenarios which simultaneously accounted for reduced fecundity and epizootics, highlighting the need for animal conservation to account for multiple stressors. Understanding how inbreeding affects isolated marine mammal populations can be important for the design of effective conservation programs and to ensure stable and healthy populations.

Keywords:

Phoca Vitulina; Population Viability Analysis; VORTEX; Inbreeding depression; Lethal equivalents; Extinction risk

Sammanfattning

Knubbsäl (*Phoca vitulina*) är en vanlig sälart på västkusten i Sverige, däremot finns det endast en population i Östersjön. Den baltiska populationen i Kalmarsund har varit isolerad i flera tusen år och en nyligen genomförd studie visar att de lider av lägre nivåer av heterozygositet och genetisk mångfald jämfört med andra europeiska populationer. Historiskt sett har populationen drabbats av flera allvarliga populationsminskningar vilket i sin tur lett till högre grad av inavel. Inavel påverkar fitness negativt och kan därav också påverka populationens långsiktiga överlevnad. Förståelsen för hur inavel påverkar isolerade marina däggdjurpopulationer är avgörande för bevarandet av arten och för att säkerställa stabila och hälsosamma populationer.

Baserat på en litteraturöversikt kartlägger denna studie olika fitness-egenskaper som rapporteras vara påverkade av inavelsdepression hos olika sälarter. Vi genomförde även flera populationsviabilitetsanalyser för att uppskatta effekterna av inavelsdepression i små, isolerade knubbsälpopulationer. Inavelsdepressionen inkluderades i enheter av dödliga ekvivalenter som vanligtvis återfinns i däggdjurpopulationer och mängden inavel (F) baserades på nyligen publicerade värden från Kalmarsundpopulationen. Flera scenarier undersöktes genom simuleringar av en åldersstrukturerad, stokastisk populationsmodell som inkluderade kombinerade effekter av epizootiska virus och reducerad fertilitet på grund av hormonstörande ämnen. Simuleringarna inkluderade även olika initiala populationsstorlekar för att få bättre förståelse för hur effekten av inavel varierar. Resultaten visar att inavelsdepression kan förväntas ha en övergripande negativ effekt på livskraften hos Kalmarsundpopulationen och andra isolerade sälpopulationer. Populationer påverkas allvarligt av inavelsdepression i scenarier som samtidigt tar hänsyn till minskad fertilitet och epizootier, vilket visar på behovet av att analyser tar hänsyn till flera stressfaktorer.

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1. Introduction

The Harbour seal (*Phoca vitulina*) is a widespread pinniped species with populations distributed across a variety of climatic zones in the Northern Hemisphere (Teilmann & Galatius, 2018). Based on several criteria, it is a successful species found in a wide range of habitats and in significant numbers (Liu et al., 2022). Harbour seals form structured populations with several subpopulations with genetic differences (Silva et al., 2021). The assessment and identification of population structure is challenging but crucial for the evaluation of effects from harvesting and other stressors in order to estimate the risk of population declines (Olsen et al., 2013). Along with a large number of marine mammals worldwide, seals share a history of overexploitation due to hunting (Silva et al., 2021). Until the second half of the 20th century, hunting was the main threat to seal populations. Though harbour seals population development has also been impacted by various other stressors, including Phocine distemper virus epizootics affecting reproduction and survival rates (Brasseur et al., 2018) and reduced fecundity due to endocrine-disrupting pollutants (Silva et al., 2021).

A small population of harbour seals were descended from seals entering the Baltic sea approximately 8000 years ago and ever since, the Kalmarsund population in the Kalmarsund is believed to have been isolated from other harbour seals geographically. (Härkönen & Isakson, 2010). The population differs genetically from populations on the Swedish west coast and is closer related to harbour seals in Svalbard, and also show significantly lower levels of heterozygosity (Reinholdt, 2024) compared to other European populations (Härkönen et al., 2005). Historically, the population has been listed as endangered (EN) (SLU Artdatabanken, 2000, 2005) due to its small population size, but is now, based on more recent values listed as vulnerable (VU) (SLU Artdatabanken, 2020). A combination of long-term isolation and historically severe population bottlenecks seem to explain the low genetic diversity and low variation within the population (Härkönen et al., 2005).

Inbreeding depression refers to the decreased fitness observed in the offspring of closely related individuals (Charlesworth and Willis, 2009). A reduced population size (population bottlenecks) could lead to loss of genetic diversity, which in turn could influence population viability. It is possible that a decreased amount of genetic diversity could increase the chances of inbreeding depression - therefore, the study of small populations and genetic diversity is crucial in evaluations of conservation status (Andersen et al., 2011, Weber et al., 2004). There is conclusive evidence for inbreeding depression (Brook et al., 2002; O'Grady et al., 2006), but little is known about fundamental features such as strength of inbreeding depression and the variation across different life stages (Stoffel et al., 2021). Measurements of an individual's inbreeding coefficient (F), i.e. how inbred an individual is, can be done through estimation of molecular marker data. Obtained F measurements can then be used to estimate inbreeding depression (Caballero et al., 2020). Though it is still unclear which estimator of inbreeding depression is most suitable and correct when studying natural populations due to generally poor pedigree information (Bérénos et al., 2016). The quantification of inbreedings impact on survival can be done in units of lethal equivalents (LEs). Each lethal equivalent represents a collection of harmful alleles that would result in death if the alleles are identical (homozygous). A lethal equivalent might denote a single lethal allele at one locus or multiple mildly harmful alleles throughout several loci (Nietlisbach et al., 2018). Decreased heterozygosity can result in lower fitness as the fraction of the genome that is homozygous increases (Stoffel et al., 2021) and the fitness value for traits controlled by dominant loci may be reduced. This increases the risk of expressing lethal equivalents (Coltman et al.,1998; Billing et al., 2012). Although, when increased expression of lethal equivalents occur, the natural selection (purging) increases as well, limiting the reduction in fitness (García-Dorado, 2012).

Population Viability Analysis (PVA) projects the population size into the future based on life history data for the species using stochastic computer simulations (Brook et al., 2002). PVA is a standard heuristic tool in population biology (O'Grady et al., 2006), where the investigation of the effects of inbreeding depression on extinction risk has been made (Brook et al., 2002) Inbreeding depression has been predicted to affect the risk of extinction in small populations of rhinoceros (Dobson et al., 1992). It has also been shown that species with slow initial population growth will be especially impacted by inbreeding (Mills & Smouse, 1994). Vital traits affected by inbreeding in earlier studies on mammals are fecundity, lifetime reproductive success, first year survival (0-1), survival to sexual maturity (1 year - age of first reproduction) and adult survival (O'Grady et al., 2006; Stoffel et al., 2021). Due to the impact of inbreeding on individual fitness, effects can be transferred to populations, species and communities (Billing et al., 2012). Earlier models to estimate harbour seals population viability did not include decline in fitness due to inbreeding (Silva et al., 2021).

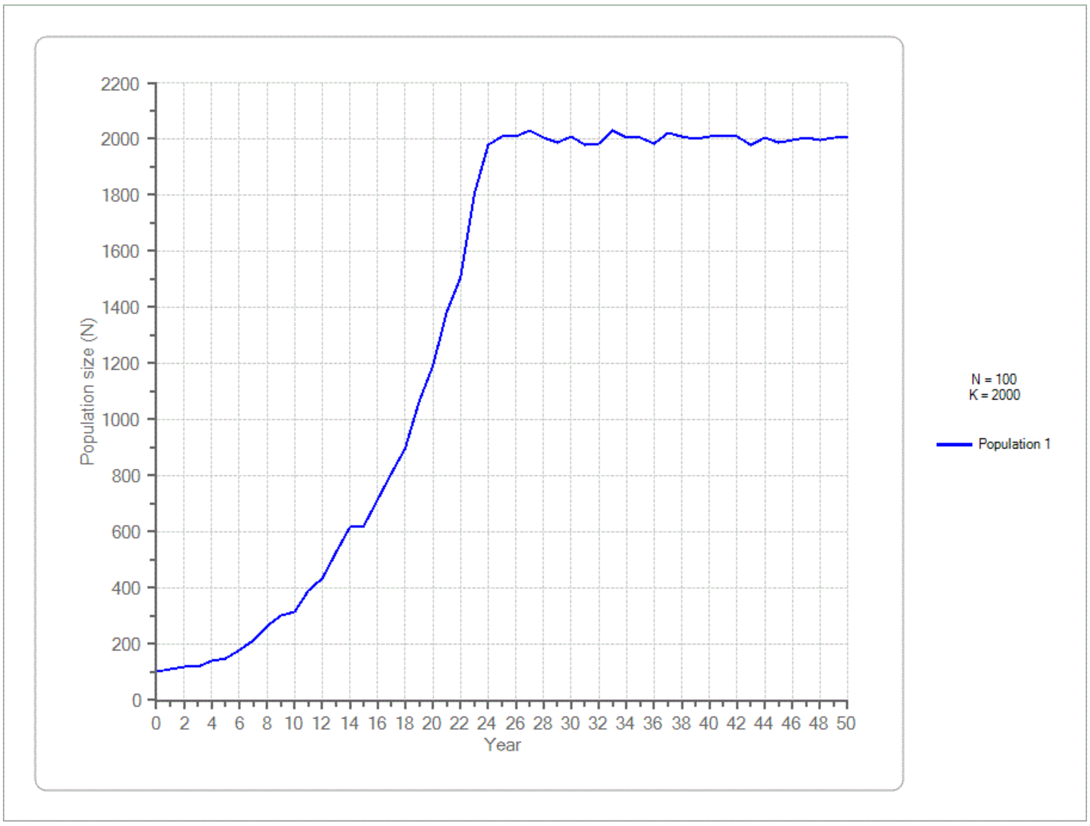

Figure 1. An example of one simulation of the model for harbour seals assuming no disturbances over a time span of 50 years, initial population size (N) = 100 and carrying capacity (K) = 2000. Growth rate during the exponential phase is here at the biological maximum for harbour seals, 11,4%.

1.1 Aim of the study

The aim of this study is to, through a literature review (1) investigate how inbreeding in seals affect specific fitness traits; and (2) determine the contribution of inbreeding depression on the population growth over time and the risk of extinction in small isolated populations, by using realistic PVA models with different theoretic initial population sizes and inbreeding coefficients (*F*) based on the Kalmarsund population.

2. Methods

2.1 Literature review of the effects of inbreeding depression

Search tools used for finding relevant literature for this study were Scopus, Supersök and Google Scholar. The different search words used to pinpoint essential information includes: *Phoca vitulina, harbour seal, pinniped, inbreeding, inbreeding depression, fitness, genetics* and *extinction risk.* Some of the scientific articles used were found through other articles, either through references or citations. Data and results from various sources were gathered and reviewed. Studies on fitness related to inbreeding depression are common but have mostly been done in captive populations and controlled environments. Studies on wild mammals and especially pinniped species are more limited. Methods of measuring effects from inbreeding vary and even though there are divided opinions about the credibility of the various methods, this study does not include a detailed comparison, but instead collected a broad overview of what the literature of today states on the certain issue. A compilation of used articles can be found in Appendix S1: Table S1.

2.2 Population viability analysis

The program VORTEX v.10.6.0 was used for the stochastic population modeling and simulated the effect inbreeding depression has on population size over time and/or how the risk of extinction is affected with the use of various theoretical values of lethal equivalents (LE) and inbreeding coefficients (*F*) across different initial population sizes.

The models integrated the effects of environmental, demographic and catastrophic stochasticity. Most of the data needed for the simulations were obtained from Silva *et al.* (2021), including: survival rates; age 0-1: 75%, ages 1-4: 89%, age 4+: 95%, age-specific fertility rates; age 3: 17%, age 5: 33%, ages 6-27: 47%, ages 28-38: 35%. All used parameters can be found in Appendix S1: Table S2. The initial population sizes (N) were set to 100, 200 and 500, corresponding to IUCN Red List categories (IUCN, 2024) and what are considered as small population sizes. Based on a current study (Reinholdt, 2024) on genetics of the Kalmarsund population, three values of inbreeding coefficients (*F*) were chosen and included in the projections (*F*=0,05, 0,1, 0,15). Two levels of inbreeding depression were modeled for the different population sizes respectively; and these were (1) the effect of 3,14 diploid LEs and (2) the effect of 6,29 diploid LEs (50% due to recessive lethal alleles (Lacy et al., 2021)). The selected LE-values were based on earlier studies on inbreeding depression and applied on juvenile survival (O'Grady et al., 2006, Lacy et al., 2021). Each scenario was simulated 100 times each with a time span of 300 years. Scenarios also included effects from environmental stressors such as increased mortality rates and reduced reproduction due to epizootic outbreaks (phocine distemper virus) and reduced fecundity due to endocrine-disrupting pollutants (e.g. xenobiotics).

3. Results

3.1 Literature review assessing the effect of inbreeding on specific traits

3.1.1 Parasite infections

By examining genetic variation across 27 microsatellite loci in deceased harbour seals in the Wadden Sea, Rijks et al. (2008) discovered a negative correlation between individual heterozygosity and lungworm burden in young seals. Hoffman et al. (2014) later found a stronger fitness correlation by measuring the genome-wide heterozygosity by RAD-sequencing. The study revealed that the variation in heterozygosity among 14,585 Single Nucleotide Polymorphisms (SNPs) accounted for 49% of the variability in lungworm infection levels, indicating that heterozygosity serves as a reliable indicator for inbreeding. Studies on parasite burden have also been seen in other pinniped species. Acevedo-Whitehouse et al. (2006) reported on a correlation between heterozygosity and resistance to hookworm infection in the California sea lion (*Zalophus californianus*). A correlation in genetic diversity and different types of helminth parasites in *Zalophus californianus* was also shown by Acevedo-Whitehouse et al. (2003), where individuals with higher levels of inbreeding are more likely to host a wider range of parasites.

3.1.2 Neonatal fitness & survival

The relation between survival to weaning, birth weight and microsatellite heterozygosity in harbour seals, based on individual's mean d^2 (squared distance between microsatellite alleles), were examined by Coltman et al. (1998). Pups that died before weaning were found to be more inbred compared to pups that did survive. In a similar way, a positive correlation was also found between birth weight and genetic variation. A study on the isolated Saimaa ringed seal (*Pusa hispida saimensis*) (Sundell et al., 2023) analyzed heterozygosity and genome sequencing and uncovered evidence of inbreeding. The study concluded that stillborn pups showed a tendency for higher levels of runs of homozygosity (RoHs), compared to pups born alive, suggesting inbreeding depression. Results from Bean et al. (2004) provided evidence that grey seal (*Halichoerus grypus*) pups with higher levels of internal relatedness (IR) have a significantly lower chance of survival, using heterozygosity measures of IR and standardized mean d^2. Hoffman et al. (2006) found no significant association between heterozygosity and the fitness traits of birth weight and survival in the Antarctic fur seal (*Arctocephalus gazella*), despite a relatively large sample size and several measures of genetic variation. Another study on Antarctic fur seal (Paijmans et al., 2024), using microsatellite and SNP array data, showed clear absence of inbreeding depression on the fitness traits of birth mass or survival, though also implying that this is in contrast to harbour seals, grey seals and californian sea lions where neonatal survival have been strongly associated with microsatellite heterozygosity.

3.1.3 Reproductive success

Hoffman et al. (2004) studied several traits contributing to male reproductive success, including competitiveness and time spent on territories, related to heterozygosity in the Antarctic fur seal. Internal relatedness correlated with competitiveness, time spent ashore and reproductive longevity - resulting in a strong heterozygosity correlation. Males with higher values of heterozygosity showed to be more successful compared to males with lower heterozygosity. With the use of molecular data Powell et al. (2023) estimated the association between reproductive success and inbreeding in antarctic female Weddell seals. They were not able to reject the null hypothesis stating no inbreeding depression, though their data suggest that if inbreeding were to affect the success of reproduction, the overall effect is minor. Amos et al. (2001) found a significant relationship between parental relatedness and reproductive success (measured as internal relatedness (IR) and standardized heterozygosity (SH) in grey seals, indicating that individuals with more distantly related parents become more successful as adults.

3.2 Population viability analysis in VORTEX

3.2.1 Initial population size (N=100)

Each simulation scenario included three different populations with various degrees of inbreeding *(F*) (0,05, 0,1, 0,15) based on the Kalmarsund population. Higher values of *F* indicate more inbreeding within the population. All scenarios showed a trend of decreased population size over a time span of 300 years when exposed to the various levels of inbreeding depression applied to juvenile survival. In the theoretical best case scenario with the low value of inbreeding depression (3,14 LEs) and in the absence of reduced fecundity (90%), the three populations did not differ remarkably and remained relatively stable over time (Figure 2). In the scenario with higher values of inbreeding depression (6,29 LEs) and no reduced fecundity (90%), all population sizes reduced over time and the three populations differed (Figure 3). The population affected the least (*F* = 0,05) had a mean population size of 95 individuals, (*F* = 0,1) 78 individuals and (*F* = 0,15) 58 individuals after 300 years. The probability of extinction also varied within the three populations; 0,11, 0,22, 0,34 (Table S3). In the scenarios where reduced fecundity (70%) was included, all populations in both scenarios (LE = 3,14 ; 6,29) were negatively impacted (Figure 4; Figure 5). The difference between the three populations were noticeable in both cases, but more severe in one scenario (Figure 5), where the population with high inbreeding coefficient (*F* = 0,15) showed a remarkably negative trend over time and had a mean population size of 19 individuals and the population with the lowest inbreeding coefficient (*F* = 0,05) had a mean population size of 49 individuals after 300 years. Supporting information of all values of mean population size, mean growth rate (r) and probability of extinction (PE) for all simulations (N=100, 200, 500) can be found in the Appendix S1: Table S3; S4; S5.

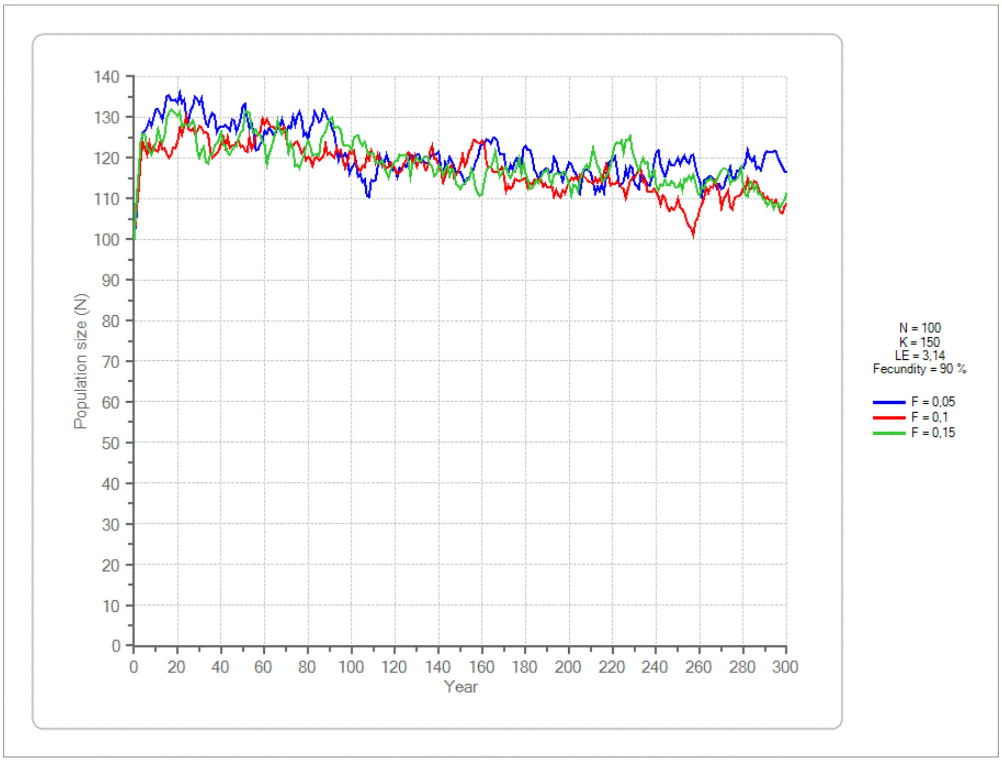

Figure 2. Scenario 1 - Population growth curve simulating the impact of inbreeding depression in the units of lethal equivalents (recessive deleterious alleles). The simulation includes 3,14 LEs along with different inbreeding coefficients (*F* = 0,05, 0,1, 0,15), where a high value of *F* indicates more inbreeding. The values are based on the Kalmarsund harbour seal population over a time span of 300 years with 100 iterations each. The initial population size was set to 100 individuals (N) with a carrying capacity of 150 individuals (K). The simulation also includes effects from sporadic Phocine distemper virus (PDV) outbreaks (mortality 65% and probability of occurrence 7%).

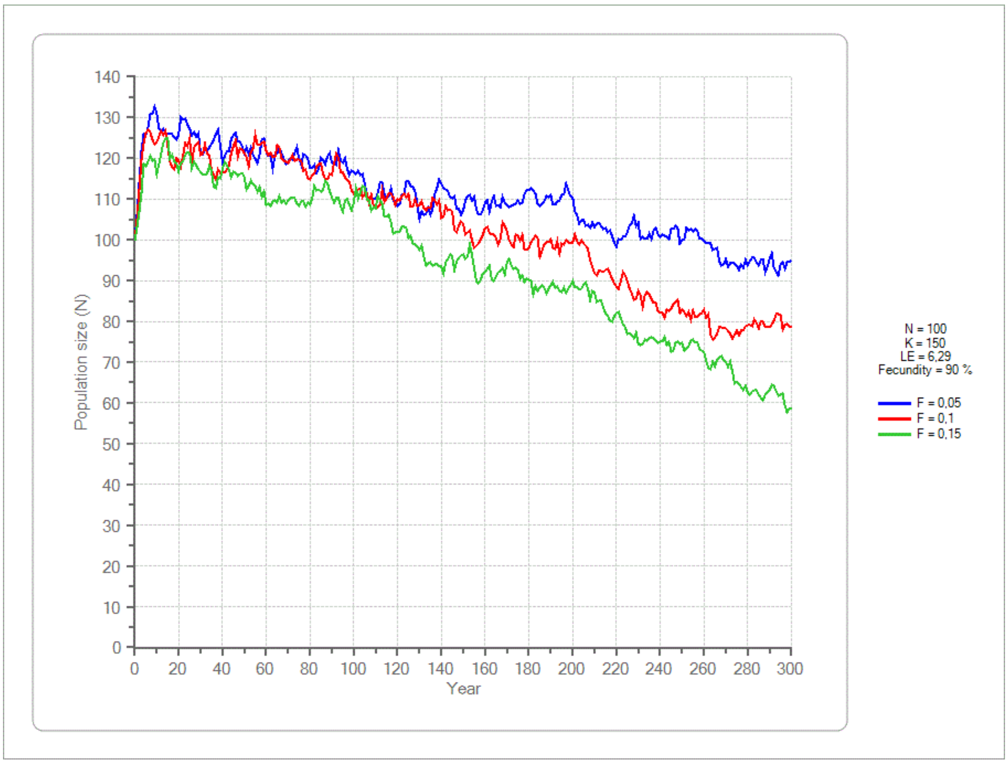

Figure 3. Scenario 2 - Population growth curve simulating the impact of inbreeding depression in the units of lethal equivalents (recessive deleterious alleles). The simulation includes 6,29 LEs along with different inbreeding coefficients (*F* = 0,05, 0,1, 0,15), where a high value of *F* indicates more inbreeding. The values are based on the Kalmarsund harbour seal population over a time span of 300 years with 100 iterations each. The initial population size was set to 100 individuals (N) with a carrying capacity of 150 individuals (K). The simulation also includes effects from sporadic Phocine distemper virus (PDV) outbreaks (mortality 65% and probability of occurrence 7%).

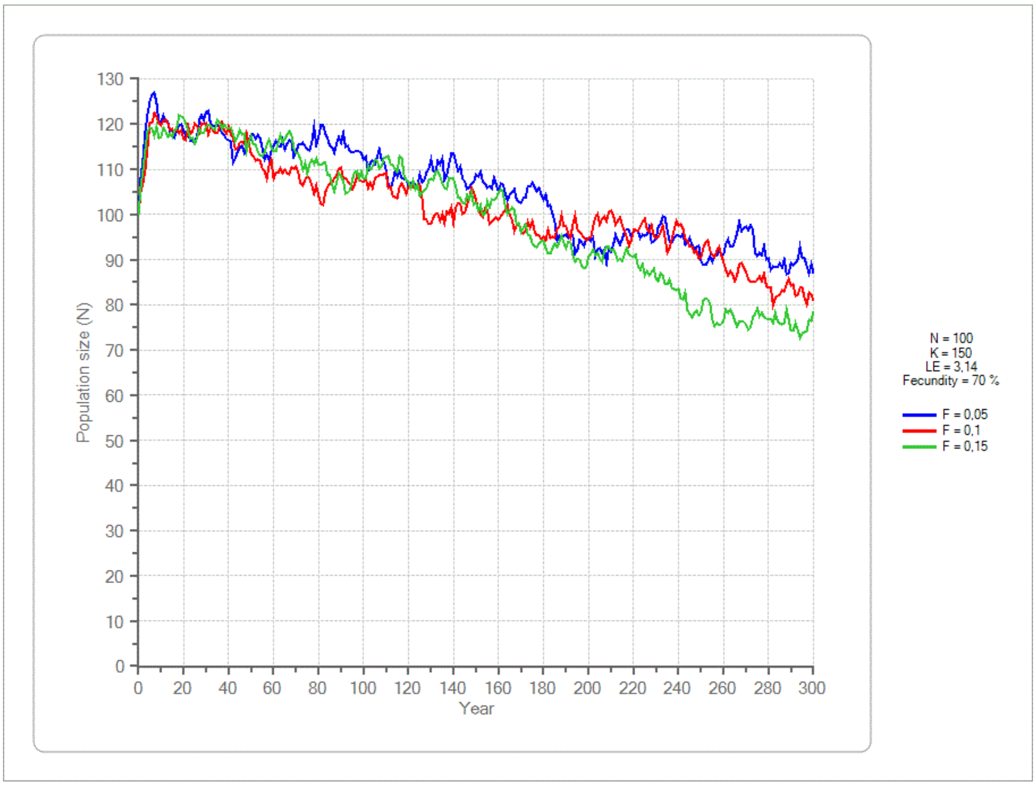

Figure 4. Scenario 3 - Population growth curve simulating the impact of inbreeding depression in the units of lethal equivalents (recessive deleterious alleles). The simulation includes 3,14 LEs along with different inbreeding coefficients (F = 0,05, 0,1, 0,15), where a high value of F indicates more inbreeding. The values are based on the Kalmarsund harbour seal population over a time span of 300 years with 100 iterations each. The initial population size was set to 100 individuals (N) with a carrying capacity of 150 individuals (K). The simulation includes effects from sporadic Phocine distemper virus (PDV) outbreaks (mortality 65% and probability of occurrence 7%) along with reduced fecundity (70%) due to endocrine-disrupting pollutants.

Figure 5. Scenario 4 - Population growth curve simulating the impact of inbreeding depression in the units of lethal equivalents (recessive deleterious alleles). The simulation includes 3,14 LEs along with different inbreeding coefficients (*F* = 0,05, 0,1, 0,15), where a high value of *F* indicates more inbreeding. The values are based on the Kalmarsund harbour seal population over a time span of 300 years with 100 iterations each. The initial population size was set to 100 individuals (N) with a carrying capacity of 150 individuals (K). The simulation includes effects from sporadic Phocine distemper virus (PDV) outbreaks (mortality 65% and probability of occurrence 7%) along with reduced fecundity (70%) due to endocrine-disrupting pollutants.

4. Discussion

Assessing the possible effect inbreeding has on various fitness traits in mammals have previously been done in a wide range of studies. Though the effect of inbreeding depression on both fitness traits and population abundance is complex and in some ways controversial, compiling several sources with various methods gives an overview of already existing research. The controversy mainly arises from critics on the various methods of estimating effects from inbreeding depression and the often relatively small sample sizes. Simulating several scenarios with various degrees of environmental impact is complex and it is in some cases hard to mimic reality, as environmental conditions change over time. Including effects from inbreeding in small, isolated populations could help create more realistic simulations.

This study contributes to a better understanding of inbreeding and its effect on fitness traits, population viability and the possible risk of extinction, over a long period of time.

4.1 Fitness traits affected by inbreeding depression

In this study, the summarized fitness traits affected by inbreeding includes neonatal survival, birth weight, parasite infection and reproductive success. The common denominator among the traits is the reduction in fitness if they were to be negatively affected. Exploring the way inbreeding depression affects pinniped species provides insight to the possible ways small, isolated populations might be affected over a longer period of time.

The correlations between various infections and increased homozygosity point to a possible weakening of the immune system as one of the effects from inbreeding. A healthy and well-functioning immune system is vital for individual health as a protection towards infectious diseases (Sonne et al, 2020). Due to increased levels of contaminants in the Baltic sea, marine mammals there would possibly also have suppressed immune systems due to exposure to those. If seals with higher degree of inbreeding have a more impaired immune system and are more susceptible to various infections and parasites, a negative trend throughout the population could occur. Jensen et al (2017) stated that the risk of epidemics could also increase due to inbreeding, possibly affecting the population viability greatly.

Harbour seals weight dependent survival has been reported in earlier studies (Zatrak et al., 2022; Adachi et al., 2014; Harding et al., 2005), where the significance of blubber thickness most likely affects the maintenance of buoyancy during foraging, along with the ability to thermoregulate. The negative effect from inbreeding on birth weight and reproductive success can possibly affect population viability. If the reproduction success is suppressed, fewer individuals would contribute to population reproduction, thereby reducing population growth rate. Interestingly, effects from inbreeding on several fitness traits could create an overall negative effect on population viability and the risk of extinction in more exposed populations. Effects on traits combined with other environmental factors, e.g. climate change, competition and disturbance, could pose even further risks.

4.2 Population viability analysis

Even though the harbour seal population in Kalmarsund today is rather stable and has been growing steadily since the 1990s (Härkönen & Isakson, 2010), acknowledging threats such as inbreeding depression combined with other environmental stressors on hypothetically small and isolated populations with slow growth rates is important when implementing conservation measures. A study on the Bengal tiger (*Panthera tigris tigris*) (Khan et al., 2021) provided evidence of higher levels of inbreeding depression in small, isolated populations, compared to more large-connected populations, possibly affecting population viability negatively. In our simulations with an initial population size of 100 individuals, we could see an overall negative trend in growth rate and population viability when applying inbreeding depression and various environmental effects. In the worst case scenario (Figure 5) with the higher value of inbreeding depression (6,29 LEs) and reduced fecundity (70%) the population with the highest degree of inbreeding (*F* = 0,15) had a mean population size of 19 individuals after 300 years. In scenario 1 and 2 (Figure 2 & 3), with fully obtained fecundity (90%) the populations remained more stable over time and were not as severely affected compared to scenario 3 and 4 (Figure 4 & 5) where reduced fecundity were applied. This shows the importance of healthy levels of female fecundity and well-functioning reproduction in order to maintain long-term population abundance, something that was also reported in Silva et al. (2021).

We can also see an overall increase of the probability of extinction between the three populations (Table S3), where the most inbred population (*F* = 0,15) obtained higher probability of extinction in all scenarios with one exception (scenario 1). In scenario 1, two populations (*F* = 0,05 & 0,15) had the same probability of extinction (PE = 0,05) and the last population (*F* = 0,1) a slightly higher value (PE = 0,06). There was also a difference in response comparing various initial population sizes. Small population sizes tend to be more vulnerable to stochastic effects, including inbreeding and environmental effects, possibly also affecting the risk of extinction (Kunnasranta et al., 2021). In our simulations, the bigger population (N=500) (Figure S2) remained more stable over time and was not as affected by the lower LE-value compared to the small population (N=100) (Figure 2 & 4). Overall, the bigger population was more resilient and remained more stable in all scenarios despite the various inbreeding values.

The more inbred populations (higher *F*-value) were on an average more negatively affected. Though it is important to have in mind that inbreeding degrees within a population can vary, meaning all individuals might not sustain equal levels of inbreeding. In these simulations, the inbreeding coefficients were based on individually measured levels of inbreeding in the Kalmarsund population (Reinholdt, 2024). This means that the population as a whole does not currently exhibit these levels of inbreeding; instead, individuals within the population have shown these values. Through these simulations, we can theoretically quantify the consequences of high levels of inbreeding throughout the whole population.

4.3 Individual stressors affecting population viability

The LE-values used in this study are default input values in VORTEX applied to juvenile survival, which is based on reported values from 40 captive populations of mammals (O'Grady et al., 2006) and on studies made on wild populations of mammals. Some claim that LE-values can vary from 0 to more than 30 over all fitness traits, but more realistically from 0-10 (Lacy et al., 2021). Using the most accurate and realistic responding LE-values is difficult, as the number of LEs only has been closely examined in some species. In future simulations, using LE-values based specifically on harbour seals would perhaps give more precise and optimal values and results.

Silva et al. (2021) reported on the importance of including multiple environmental and anthropogenic stressors in PVAs due to the possible severe consequences affecting the risk of extinction and causing declining trends in population abundance. In our simulations we included effects from both PDV and reduced fecundity and the results showed that scenarios affected by both factors obtained higher risk of extinction and a more affected population abundance compared to the scenarios that only included effects from PDV.

The interspecific competition with grey seals has most likely affected the Kalmarsund population (Reinholdt, 2024) along with by-catch, exposure to various contaminants and other human-related disturbances (Blanchet et al., 2021). Although there is currently no licenced hunt of the Kalmarsund population, it cannot be ruled out that misidentification of grey seals and harbour seals may occur, causing accidental shootings of harbour seals, possibly affecting the population viability. Acknowledging the state of the Baltic sea and the various ongoing environmental challenges (Svedäng et al., 2022; Kõuts et al., 2021), other factors could also be included in future simulations to gain better understanding of the population viability of Baltic based mammals and for conservation measures.

5. Conclusion

In conclusion an overall negative effect from inbreeding on several fitness traits throughout various pinniped species has been reported in the literature. Exactly how severe and how much damage inbreeding contributes to a species' fitness is hard to estimate but crucial to take into account when studying population viability. Our simulations provide an insight on how inbreeding depression in the units of lethal equivalents affect small populations of harbour seals with different degrees of inbreeding in various scenarios. In all scenarios with initial population sizes of 100 and 200 individuals, a negative trend in population size over a time span of 300 years could be seen. All populations were more negatively affected in the scenarios where reduced fecundity were applied. The populations with an initial size of 500 individuals were more resilient and remained more stable in all scenarios, though when exposed to 6,29 LEs and reduced fecundity they too underwent a significant decrease in population size over time. There was also a noticeable difference in effect when comparing inbreeding coefficients (F). The populations with the highest value of inbreeding ($F = 0,15$) were more negatively affected compared to the ones with lower values ($F = 0,05, 0,1$). The study contributes to ecological risk assessment methodology for marine mammals and highlights the importance of including inbreeding in long term population projections, something that earlier studies have ignored.

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7. Appendices

Appendix 1 - Literature review, supporting information.

Author	Article - title	Species	Fitness trait affected by inbreeding
Rijks et al. 2008	Heterozygosity and lungworm burden in Harbour seals (*Phoca vitulina)*	Harbour seals (*Phoca vitulina)*	Parasite resistance
Hoffman et al. 2014	High-throughput sequencing reveals inbreeding depression in a natural population	Harbour seals (*Phoca vitulina)*	Parasite resistance
Acevedo-Whitehouse et al. 2006	Contrasting effects of heterozygosity on survival and hookworm resistance in California sea lion pups	California sea lion (*Zalophus californianus*)	Parasite resistance
Acevedo-Whitehouse et al. 2003	Disease susceptibility in California sea lions	California sea lion (*Zalophus californianus*)	Parasite resistance
Coltman et al. 1998	Birth weight and neonatal survival of harbour seal pups are positively correlated with genetic variation measured by microsatellites	Harbour seals (*Phoca vitulina)*	Birth weight and pup survival
Sundell et al. 2023	Genomic evidence uncovers inbreeding and supports translocations in rescuing the genetic diversity of a landlocked seal population	Saimaa ringed seal (*Pusa hispida saimensis*)	Stillborn pups
Bean et al. 2004	Patterns of parental relatedness and pup survival in the grey seal (Halichoerus grypus)	Grey seal (Halichoerus grypus)	Pup survival
Hoffman et al. 2006	No relationship between microsatellite variation and neonatal fitness in Antarctic fur seals, *Arctocephalus gazella*	Antarctic fur seal (*Arctocephalus gazella)*	Birth weight and pup survival
Paijmans et al. 2024	Little evidence for inbreeding depression for birth mass, survival and growth in Antarctic fur seal pups	Antarctic fur seal (*Arctocephalus gazella)*	Birth mass, pup survival and growth
Hoffman et al. 2004	Exploring the relationship between parental relatedness and male reproductive success in the Antarctic fur seal Arctocephalus gazella	Antarctic fur seal (*Arctocephalus gazella)*	Reproductive success

Powell et al. 2023	Evidence of an absence of inbreeding depression in a wild population of Weddell Seals (Leptonychotes weddellii)	Weddell Seal *(Leptonychotes weddellii)*	Reproductive success
Amos et al. 2001	The influence of parental relatedness on reproductive success	Grey Seal (Halichoerus grypus)	Reproductive success

Table S1. Table of selected articles used for the literature review.

Parameter	**Setting**	**Reference**
Scenario settings		
Iterations	100	
Years in simulation	300	
Extinction criterion	Only one sex remains	
Species description		
Environmental variation	0.5	Assumption
Lethal Equivalents	Variable: 3.14, 6.29	O'Grady *et al.* 2006, Lacy *et al.* 2021
Percent due to recessive alleles	50	Lacy *et al.* 2021
Reproductive system		
Mating type	Monogamous	Coltman *et al.* 1998
Age of first offspring female	3	Silva *et al.* 2021
Age of first offspring male	4	Silva *et al.* 2021
Maximum lifespan	38	Silva *et al.* 2021
Maximum age of reproduction	38	Silva *et al.* 2021
Maximum number of broods per year	1	Silva *et al.* 2021
Maximum number of progeny per brood	1	Silva *et al.* 2021
Sex ratio at birth (males:females)	1:1	Silva *et al.* 2021
Females breeding at low density	90%	Härkönen *et al.* 2005

Parameter	**Setting**	**Reference**
Scenario settings		
Females breeding at K	45%	Olsen *et al.* 2014
Allele parameter, A	0	Olsen *et al.* 2014
Steepness parameter, B	1	Härkönen *et al.* 2007
Reproductive rates		
Adult females breeding	Variable: 90%, 70%	Härkönen *et al.* 2005
EV in adult females breeding	5%	Olsen *et al.* 2014
Mortality rates		
Mortality from age [0;1]	25%	Silva *et al.* 2021
Mortality from age [1;3]	11%	Silva *et al.* 2021
Mortality from age [3;35]	5 %	Silva *et al.* 2021
Catastrophes		
Type of catastrophe	PDV epizootic	Silva *et al.* 2021
Frequency	7.14 %	Silva *et al.* 2021
Effect on reproduction	100%	Silva *et al.* 2021
Effect on survival	65 %	Silva *et al.* 2021
Mate monopolization		
% males in breeding pool	90%	Coltman *et al.* 1999
Population size		
Initial population size		
Population 1	100	Assumption
Population 2	200	Assumption
Population 3	500	Assumption
Age distribution	Stable	Assumption
Carrying capacity		
Population 1	150	Assumption

Parameter	**Setting**	**Reference**
Scenario settings		
Population 2	250	Assumption
Population 3	550	Assumption
Standard deviation of K	10% of K	Olsen et al. 2014
Genetics		
Inbreeding coefficient (*F*)	Variable: 0.05, 0.1, 0.15	Reinholdt (2024)

Table S2. Parameter settings for the demographic simulations.

Scenario	**Inbreeding coefficient (*F*)**	**Inbreeding depression (LE)**	**Epizootic frequency (%)**	**Fecundity (%)**	**N_{300}**	**Mean (r)**	**Probability of population extinction (PE)**
Scenario 1	0,05	3,14	7,14	90	116	0,052	0,05
	0,1	3,14	7,14	90	109	0,048	0,06
	0,15	3,14	7,14	90	111	0,046	0,05
Scenario 2	0,05	6,29	7,14	90	95	0,038	0,11
	0,1	6,29	7,14	90	78	0,03	0,22
	0,15	6,29	7,14	90	58	0,023	0,34
Scenario 3	0,05	3,14	7,14	70	87	0,031	0,13
	0,1	3,14	7,14	70	81	0,023	0,16
	0,15	3,14	7,14	70	79	0,025	0,17
Scenario 4	0,05	6,29	7,14	70	49	0,016	0,31
	0,1	6,29	7,14	70	39	0,011	0,46

Scenario	Inbreeding coefficient (*F*)	Inbreeding depression (LE)	Epizootic frequency (%)	Fecundity (%)	N300	Mean (r)	Probability of population extinction (PE)
Scenario 1	0,05	3,14	7,14	90	116	0,052	0,05
	0,1	3,14	7,14	90	109	0,048	0,06
	0,15	6,29	7,14	70	19	0,003	0,63

Table S3. Population 1 (N=100). Table containing used values in the VORTEX simulations and output values of population size after 300 years (N300), mean growth rate (r) and probability of population extinction (PE) based on 100 iterations.

Scenario	Inbreeding coefficient (*F*)	Inbreeding depression (LE)	Epizootic frequency (%)	Fecundity (%)	N300	Mean (r)	Probability of population extinction (PE)
Scenario 1	0,05	3,14	7,14	90	202	0,057	0,03
	0,1	3,14	7,14	90	193	0,055	0,01
	0,15	3,14	7,14	90	200	0,051	0,01
Scenario 2	0,05	6,29	7,14	90	196	0,046	0,02
	0,1	6,29	7,14	90	181	0,04	0,03
	0,15	6,29	7,14	90	160	0,03	0,08
Scenario 3	0,05	3,14	7,14	70	165	0,035	0,07
	0,1	3,14	7,14	70	189	0,037	0,04
	0,15	3,14	7,14	70	148	0,027	0,08
Scenario 4	0,05	6,29	7,14	70	149	0,026	0,09
	0,1	6,29	7,14	70	120	0,018	0,21
	0,15	6,29	7,14	70	93	0,012	0,25

Table S4. Population 2 (N=200). Table containing used values in the VORTEX simulations and output values of population size after 300 years (N_{300}), mean growth rate (r) and probability of population extinction (PE) based on 100 iterations.

Scenario	**Inbreeding coefficient (*F*)**	**Inbreeding depression (LE)**	**Epizootic frequency (%)**	**Fecundity (%)**	**N_{300}**	**Mean (r)**	**Probability of population extinction (PE)**
Scenario 1	0,05	3,14	7,14	90	460	0,063	0
	0,1	3,14	7,14	90	462	0,06	0
	0,15	3,14	7,14	90	468	0,057	0
Scenario 2	0,05	6,29	7,14	90	455	0,057	0
	0,1	6,29	7,14	90	426	0,05	0
	0,15	6,29	7,14	90	421	0,04	0,02
Scenario 3	0,05	3,14	7,14	70	453	0,04	0,02
	0,1	3,14	7,14	70	404	0,037	0,04
	0,15	3,14	7,14	70	383	0,033	0,01
Scenario 4	0,05	6,29	7,14	70	354	0,03	0,02
	0,1	6,29	7,14	70	340	0,024	0,08
	0,15	6,29	7,14	70	299	0,018	0,05

Table S5. Population 3 (N=500). Table containing used values in the VORTEX simulations and output values of population size after 300 years (N_{300}), mean growth rate (r) and probability of population extinction (PE) based on 100 iterations.

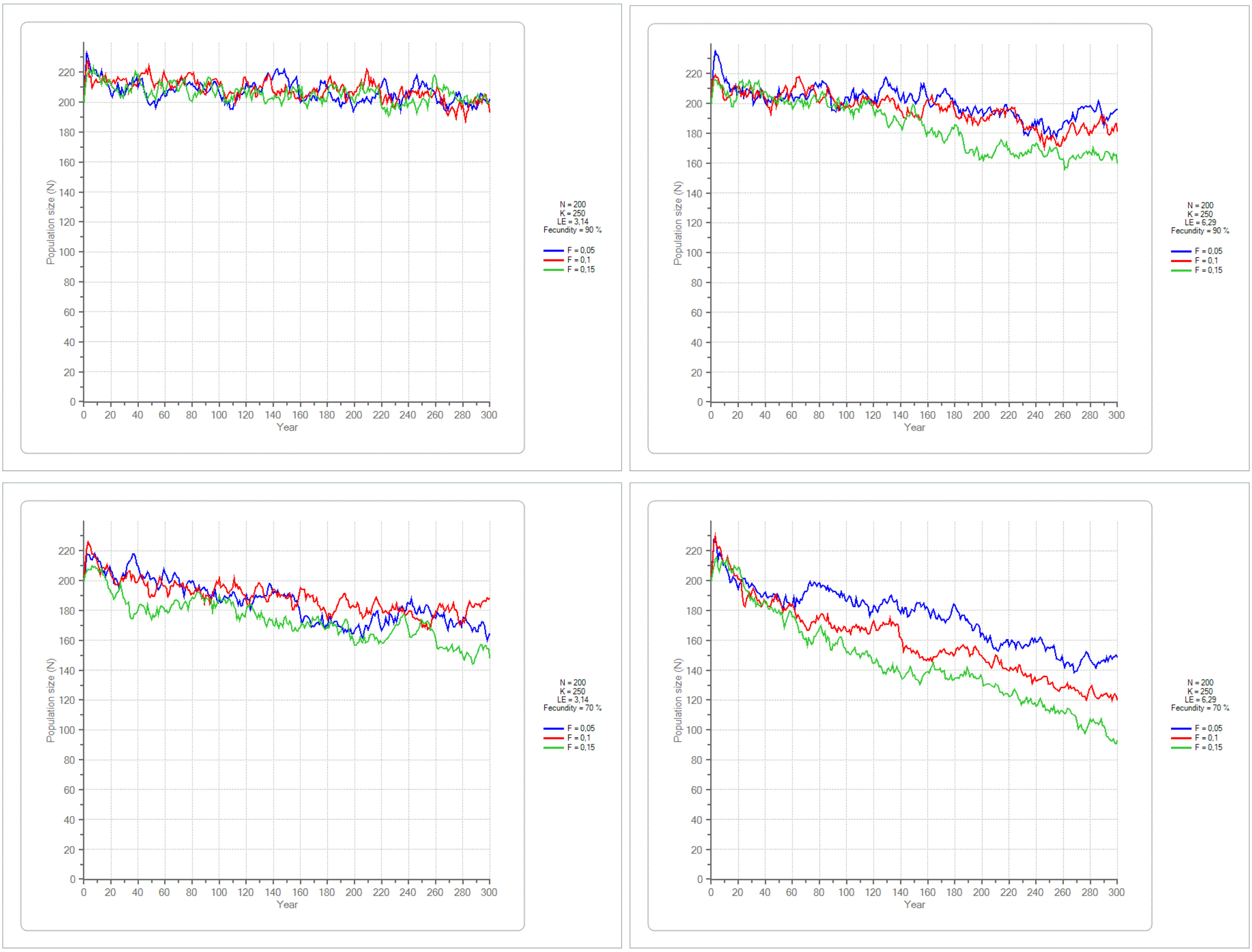

Figure S1. Population 2 (N=200). Population growth curve simulating the impact of inbreeding depression in the unit of lethal equivalents (recessive deleterious alleles). The simulation includes 3,14 and 6,29 LEs along with different inbreeding coefficients (*F* = 0,05, 0,1, 0,15), where a high value of *F* indicates more inbreeding. The values are based on the Kalmarsund harbour seal population over a time span of 300 years with 100 iterations each. The initial population size was set to 200 individuals (N) with a carrying capacity of 250 individuals (K). The simulation includes effects from sporadic Phocine distemper virus (PDV) outbreaks (mortality 65% and probability of occurrence 7%) along with reduced fecundity (70%) due to endocrine-disrupting pollutants.

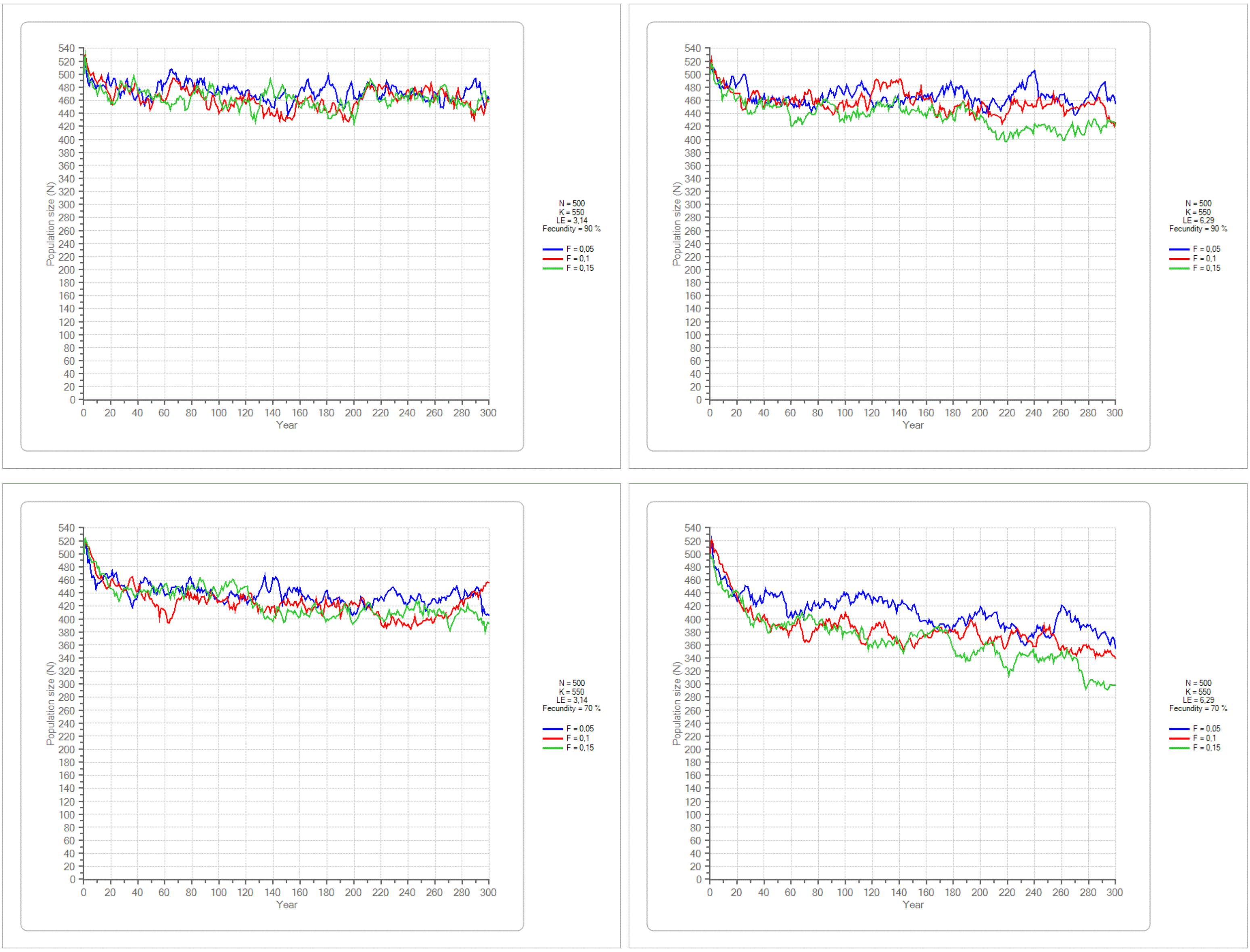

Figure S2. Population 3 (N=500). Population growth curve simulating the impact of inbreeding depression in the unit of lethal equivalents (recessive deleterious alleles). The simulation includes 3,14 and 6,29 LEs along with different inbreeding coefficients (*F* = 0,05, 0,1, 0,15), where a high value of *F* indicates more inbreeding. The values are based on the Kalmarsund harbour seal population over a time span of 300 years with 100 iterations each. The initial population size was set to 500 individuals (N) with a carrying capacity of 550 individuals (K). The simulation includes effects from sporadic Phocine distemper virus (PDV) outbreaks (mortality 65% and probability of occurrence 7%) along with reduced fecundity (70%) due to endocrine-disrupting pollutants.