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Living on an edge:
land-locked seals in changing climate

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Living on an edge: land-locked seals in changing climate

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LIST OF ORIGINAL PUBLICATIONS

This thesis is a summary of the following scientific publications, which are referred to in the text by the Roman numerals:

I Jüssi, M., Härkönen, T., Helle, E., and Jüssi, I. 2008. Decreasing ice coverage will reduce the breeding success of Baltic grey seal (*Halichoerus grypus*) females. Ambio. 37(2):80–85.

II Härkönen, T., Stenman, O., Jüssi, M., Jüssi, I., Sagitov, R. and Verevkin, M. 1998. Population size and distibution of the Baltic ringed seal (*Phoca hispida botnica*). Heide-Jörgensen M and Lydersen C (eds). NAMMCO Scientific Publications 1: 167– 180.

III Härkönen, T., Jüssi, M., Jüssi, I., Verevkin, M., Dmitrieva, L., Helle, E., Sagitov, R. and Harding, K. 2008. Seasonal Activity Budget of Adult Baltic Ringed Seals. PLoS ONE. 3(4): e2006.

doi:10.1371/journal.pone.0002006.

IV Härkönen, T., Jüssi, M., Baimukanov, M., Bignert ,A., Dmitrieva L., Kasimbekov, Y., Verevkin M., Wilson S. and Goodman S.J. 2008. Pup production and breeding distribution of Caspian seal (Phoca caspica) in relation to human impacts. Ambio 37: 356–361.

Original publications are reproduced with the permission of The Royal Swedish Academy of Sciences (**I, IV**) and the North Atlantic Marine Mammal Commission (**II**).

I contributed to planning the work, developing methodology and collecting field data for all the four publications. I was fully responsible for data analyses in paper **I** and partly in all other papers. I wrote the first draft of paper **I** and contributed to the completion of all papers.

1. INTRODUCTION

Marine mammals are claimed in legends to be of human origin, would it be then fingers of Inuit girl Sedna, mariners lost to the sea, Faroese *selkies* or pharaoh's perished army. Evolutionists place them among descendants of terrestrial mammals who have, after dwelling in a diversity of terrestrial habitats, returned to the marine environment (Arnason et al. 2006). The modern seals, whales and sirenians are molded by ages of life in the sea. The elements are putting up new challenges for them to face, leading the extant species to new forms or alternatively, extinction. *Panta rhei*.

We can not describe the details of species' evolution. The process, as a rule, exceeds significantly human life span or even the length of the modern science history. Experiments in this area are perhaps possible with quickly reproducing invertebrates in the controlled conditions of laboratories (see e.g. Blount et al. 2012). Manipulations with wild species and environments are not only challenging in a physical or material sense, but also questionable in ethical contexts – history has shown that many attempts to interfere with nature have brought about irreversible catastrophes (e.g. Clavero and Garcia-Berthou 2005). Still, knowledge of the key determining factors in the ecology or evolution of animals in their natural habitats can be used to detect changes over spatial or temporal limits that we otherwise can not look beyond. We can measure and compare indicators like behaviour, health and population dynamics to understand the ecological challenges, adaptive responses and consequences to fitness of an individual, population or a species.

Adaptation is also seen as a process, where these reactions cause changes over time. Individuals of many generations contribute to the development of behavioural, physiological or other traits in populations and species (e.g. Futuyma 1979). As a result of the complexity of contributing factors, different forms of life evolve with their specific adaptations to the environment they live in.

Detection of power and direction of a single factor in the complexity of the natural environment is, as a rule, impossible. But by choosing relevant spatiotemporal scales and optimal study objects many questions of evolution and adaptation can be still addressed, and eventually, possible answers can be described.

Large, long living mammals are in the wide range of mediators which can provide information on the evolutionary aspects in the complex end of the scale. But their value as a research tool lies namely in their complexity – they have a plentiful record of reactions to a great variety of environmental challenges over evolutionary time scales. So they can provide researchers with data from physiological processes on a molecular level to global distributions of species and populations, and relations therein.

The main problem I see in using large mammals in ecological studies is the complexity of the environment they inhabit and the difficulty to follow free ranging individuals for prolonged time periods to measure their behaviour and reactions to changes in their habitats. Large mammals tend to have extensive ranges and intricate behaviour patterns to fulfil their vital requirements. Experimental manipulation of these ranges is mostly beyond our material possibilities, so picking up the right signal in the ecological "polyphony" is often a challenge.

In terrestrial ecosystems the natural and man-made mosaic of habitats and physical barriers can often disguise the behavioural reaction of a species to changes in the environment (Hanski 1998) while avian and aquatic life forms are less influenced by those restrictions. Facilitated by relatively low energetic cost of transport and freedom of movement they undertake, for example, long migrations between breeding, wintering and foraging areas (Gregr et al. 2006)

Yet, the wide distribution of marine mammals, large populations and the global scope of the oceanic habitats render detection of the influence of environmental factors often difficult. Extraction of key factors that mould the main biological features of modern seals from the complex of ecological interrelations requires control over the physical environmental conditions and sufficient amplitude of oscillations to make measurements possible. As the features are related to the environment at large and statistically significant numbers of individuals have to be involved, laboratory experiments have substantial limitations for such studies. So we need to rely on the free-ranging populations and let the regional and seasonal differences in environmental conditions create the conditions for experimenting, or at least recording and comparing the different states of seals and their environment over periods of time.

Fortunately, geomorphologic and zoogeographic changes during the past thousands of years have locked several seal populations into fully or partly isolated , thus creating natural "laboratories" where physical barriers of distribution force the seal populations to adapt and react to the specific features or changes of the local environment.

1.1. Note on evolution of seals – shifts in time and space

In an evolutionary time scale progeny of several species of mammals which tested their endurance in the terrestrial environment have returned to the sea as their primary habitat.

Water is a relatively hostile environment to most terrestrial mammals. They merely can swim enough to rescue themselves from disaster or cross at the surface. In many cases water can be a natural barrier for distribution or movements. Few species of terrestrial mammals may wade in shallow water to forage, but exploiting the three dimensions of the marine environment is available only for the aquatic and semi-aquatic species which have adapted to live in the water.

Ancestors of the true seals (*Phocidae*), according to Howell (1930) and Berta et al. (2006), entered the tropical waters in Oligocene 29–23 Mya.

Adaptation to the aquatic way of life has molded both the anatomy and the physiology of marine mammals to increase their fitness and survival in this element. Over long evolutionary time and through several intermediate stages, modern pinnipeds have gone through significant modifications to meet the physical demands of long diving to high hydrostatic pressure, high thermal conductivity of water, buoyancy and drag of swimming. All the modifications are a result of long time evolution, being also ecologically convergent and conservative in all modern taxa of marine mammals (Williams and Worthy 2002).

Over the millions of years marine mammals have explored the full range of climatic and geographic latitudes of the Earth developing optimal distribution and activity patterns fitting the best to the variety of habitats found in those latitudes. Combination of climatic, physical and biotic factors have led to present patterns of distribution where all genera, except the monk seals (sub-fam. *Monachinae*) (Repenning et al. 1979) have migrated from the tropics to high geographic latitudes and are adapted to those conditions to a greater (e.g. Antarctic pinnipeds, arctic ringed seals *Phoca hispida*, harp seals *Phoca groenlandica*) or lesser degree (e.g. common seal *Phoca vitulina*, grey seal *Halichoerus grypus*). The range is often wide – for example ringed seal and harp seal show circumpolar distributions in the Northern Hemisphere, and all the true seals of Antarctica in the Southern Hemisphere.

Seals are mostly migratory mammals. Ease of transport in the aquatic environment facilitates active use of the entire range of distribution. Mark recapture using photo-identification (Karlsson et al. 1995), flipper tagging (Jüssi unpubl.) and telemetry studies show, that all the species in focus of this thesis are capable of free movement within the whole distribution range. Those movements allow utilization of the whole ecological scale of the area resulting in spatiotemporal activity patterns of diving and resting behaviour Those patterns are molded by life history events such as mating pupping and moulting. (**III**).

General life history theory predicts that individuals tend to optimize their behaviour to accomplish their biological requirements (Stearns and Koella 1986, McNamara and Houston 1996), and seals prefer certain parts of their wide distribution ranges depending on variations in habitat quality. This quality can be described both in term of habitat availability (e.g. places to haul out) and quantity of the resource (e.g. abundance of food) (Ray 1976). Such diversity is often higher in fragmented habitats of archipelagoes or borders between marine and freshwater ecosystems (Ray 1991). Consequentially, seals move inshore and forage in river estuaries, follow narrow fjords and rivers inland and reach separated gulfs or lakes (e.g. Thompson et al. 1996). With post-glacial rebounds or other geo-morphological changes over long periods of time those fjords, estuaries and lakes can partially or fully separate from the sea. If the water system can provide sufficient habitat and resource, landlocked seals can survive over multiple generations and go through substantial genetic selection. Today, at least four fully landlocked true seal populations are determined as the Baikal seal (*Pusa sibirica*), the Caspian seal (*Pusa caspica*), the Ladoga Seal (*Pusa hispida ladogensis*) and the Saimaa seal (*Pusa hispida saimensis*) (Palo 2003). Harbour seals (*Phoca vitulina*) are known to inhabit freshwater Iliamna lake in Alaska (Hauser et al. 2008) and East Canadian lake and river system (Ungava seal, *Phoca vitulina mellonae*) (Mansfield 1967). In addition, the Baltic grey seal (*Halichoerus grypus*) and the Baltic ringed seal (*Pusa hispida botnica*) inhabit waters of the Baltic Sea, which are linked to the Atlantic Ocean by the Danish Straits. The core distribution area of those two species is found in the Central and Northern parts of the Baltic Sea while, according to telemetry studies (Sjöberg et al. 1995, Dietz et al. 2003, Karlsson 2003, Jüssi unpubl.) and recoveries of tagged individuals (Jüssi unpubl.), the exchange of individuals with Atlantic population is very limited. So, those seals can also be considered to meet the general criteria of geographic isolation.

Seals of the landlocked water bodies are adapted to live in seasonally changing environments where physical conditions can change dramatically over the year. The air temperature at sea surface can range from +30°C in hot summers to –30°C over ice during winter months. Seasonal changes in water temperatures together with variation of day length cause locally quantitative changes in oxygen concentration, bio-productivity and hence pray availability for the top predators. Such wide fluctuations in one hand provide diverse habitat but in the other hand challenge the adaptivity of the seals.

All the mentioned species and subspecies are to greater or lesser extent ice-related as their distribution ranges freeze over partially or wholly during the winter months.

Regularly forming ice as a hard surface creates temporary habitats, providing the seals with an ecological option to be considered when a platform is needed for, e.g. reproduction. On the other hand, ice forms a physical barrier in many sea areas which can be used by seals in the ice free seasons, forcing the animals to change their distribution patterns (e.g. Reeves 1998).

Behavior is a reaction of organisms to the challenges of their living environment to increase survival. Over generations the ability to respond adequately will be inherited and mould the biological characteristics of individuals composing populations or species. For understanding of the ecological and evolutional limitations of landlocked seals in historic and present timescales it is important to focus on behavioral traits as adaptations to specific environmental condition: seasonality, oceanography and spatiotemporal availability of critical habitats.

In the context of this thesis the most important adaptations are related to foraging and reproduction as the main factors for survival over several generations, as also concluded by Harwood and Rohani (1996). Survival is thus dependant on the availability of critical habitats for accomplishment of those biological requirements in seals' life cycle (Ray 1976). The resources are distributed unevenly over the distribution range, so location and optimal use of those ecological units is fundamental of maximizing individual and population fitness over time. Behavior, related to foraging and breeding are a reaction to optimize energy expenditure, avoid predation and maximize breeding success and fitness (e.g. Partridge and Silby 1991). Named features, *inter alia*, are adaptive to specific environmental conditions and change of those conditions will cause shift from an established optimum resulting in selection towards a new optimum. In open environments, the distribution of individuals will follow the gradient of habitat quality, matching the core to the spatial shifts of optimal habitat. For land-locked seals those shifts have physical barriers where the optimum may not be achieved any more.

1.2. The study

My practical work with the Baltic seals started in late winter of 1989 when sea level rose during a storm that brought tens of ringed seal pups to the streets and parks of the coastal town Pärnu in Estonia. Although seals were known to inhabit the ice in the Pärnu Bay and occasionally haul out on beaches, they had never been seen in the town in so large numbers before. The event was considered to be extraordinary, and according to Seina and Palosuo (1996) it was the winter with smallest recorded ice coverage in the Baltic since 1720.

In the following spring, 1990, field studies began with an inventory of grey seal breeding islands in the West Estonian archipelago – summer survey of 1989 had revealed breeding of grey seals on land as several tens of pup carcasses were reported from the islets South of Saaremaa by ornithologists (Veljo Volke, pers comm.). Breeding of grey seals on islands in warmer winters was historically known but rare event.

In 2004 an international scientific consortium the Caspian international Seal Survey (CISS, administered through the Zoological Society of London and subsequently the University of Leeds) was formed by seal biologists from the UK, Estonia, Sweden and Russia to carry out scientific research and assess the conservation status of the Caspian seal. In following seasons aerial surveys flown over the breeding ice of the species in the North Caspia showed wide variability of ice conditions and exposed several climate related processes which potentially affect the species over a longer time scale.

The period since 1989 is characterized by mild winters in Baltic and Caspian regions in comparison to several historic timelines (Seina and Palosuo 1996, Jevrejeva 2001, Kuoraev 2004). The changes in nature are obvious, whether measured by availability of ice roads in the West Estonian Archipelago or frequency of land-born seal pups on islands in the past two decades. The measured extremes in physical environment and biological characteristics of marine mammals were outstanding, but their impact was not broadly discussed in the scientific literature. The significance of the climate change came into the focus of marine mammal research community worldwide only in mid-2000's (see e.g. Kovacs et al. 2011 and references therein). So most of the papers included in this thesis are based on studies, which were carried out in period 1990–2006 and are thus not focused on the effects of changing global climate *per se* but interactions of seals with their physical environment.

All the studied populations of seals are pagophilic (ice-lovers) in their reproduction strategies. Ice is critical breeding habitat, but also ice-cover extent and durability may affect e.g. predation risk, exposure to weather or prey availability (Bluhm and Gradinger 2008, Laidre et al. 2008). Among the physical characteristics describing a seal habitat, like e.g. area or temperature, sea ice shows the widest annual variation while it has a distinctive and fundamental role in several processes of seal biology. For assessment of possible effects of changing climate to seals, sea ice is suitable descriptor and determinant.

1.3. The objective

The objective of this thesis is to analyze the possible impacts of climate change on the fitness and survival of the land-locked seal populations in the Baltic and Caspian Seas in the light of the following key questions:

How does winter severity influence the distribution of seals?

In papers **I**, **II**, **III** and **IV** we discuss the general patterns of distribution of seals in frozen seas, but also in open water periods. The material allows to assess the role of ice as determinant of seal distribution during one of the fundamental biological events – breeding and assess the breeding success in both annually varying ice conditions and in course of one season. Unpublished observational and telemetric data is used to append and compare the published results in the Discussion.

How do ice physical characteristics determine breeding strategies of seals?

Ice is the breeding substrate to all three study species and has, as temporary habitat, in evolutionary process designed the breeding strategy. Measurable elements of the strategy are discussed in papers **I**, **II** and **IV**, with implications of habitat to birth and nursing period timing in paper **III**.

How does climate change reflect in the breeding success of seals?

The breeding success can be measured both directly by registering the mortality and morbidity of offspring, or by comparing e.g. the states of pups in different breeding conditions. In paper **I** we have measured the body condition of Baltic grey seal pups, in **I** and **IV** we have made observations on general breeding conditions and factors contributing to breeding success such as presence of potential predators in breeding areas. The published data is supplemented in the Discussion by recent telemetry results and material collected on expeditions to Baltic and Caspian ice after the publication of included papers.

2. MATERIAL AND METHODS

2.1. Study species

In my thesis I focus on the grey seal and the ringed seal in the Baltic Sea and Caspian seals. Given their common condition – inability to leave the home water-body, I believe the general processes discussed in the thesis apply to all land-locked seal species of the Northern hemisphere.

The ringed seal

The Baltic ringed seal (*Pusa hispida botnica*) is a regonized sub-species of the circumpolarly distributed Arctic ringed seal (*Pusa hispida hispida*). The ringed seal has entered the current geographical region of the Baltic Sea from the Arctic Ocean from North in the Yoldia Sea phase (Lõugas 1999). Later the post-glacial land uplift isolated the Baltic basin from the White sea approximately 10900 years ago and further, approximately 9000 years ago segmented the already isolated population into Saimaa and Ladoga lakes (Ukkonen 2002). The landlocked populations have developed distinct behavioral and morphological differences and are considered to be subspecies of the ringed seal (Sipilä and Hyvärinen 1998).

The ringed seals are among the smallest seals in the world. Their asymptotic adult weight is 65 kg and asymptotic standard length 127 cm with very small sexual dimorphism (Krafft et al. 2006). In the Baltic the seal is distributed predominantly in the Northern and Central parts with the main distribution range closely associated to regions where the sea is covered by ice in average winters (**II**).

Of the three study species the ringed seal has the strongest association to ice as it can breed successfully only on ice. As a small seal it has adapted to dig lairs in the snow piles on ice to hide its offspring, weighing only 4–5 kg at birth, from low temperatures and predators during the lactation period of up to six weeks (Smith et al. 1991, Reeves 1998).

The grey seal

The grey seal is divided geographically into three sub-populations – West Atlantic (Gulf of St.Lawrence, Nova Scotia, Newfoundland), East Atlantic (Iceland, British Isles, Scandinavian West coast up to White Sea) and Baltic Sea. These sub-populations are traditionally treated as geographically isolated populations (Davies 1957), which is also confirmed by genetic evidence (Boskovich et al. 1996). The separation of East and West Atlantic populations has taken place one million years ago while the Baltic population is considered to be approximately 350 thousand years old (ibid.). According to archaeological data and hunting statistics, the grey seal occupied the Baltic basin during the Yoldia Sea stage from South-West although the highest densities have been in the central and northern areas ever since the Mesolithic some 8000 years before present (Lepiksaar 1986, Lõugas 1999, Ukkonen 2002). Recoveries of marked grey seal pups in the Kattegat (Jüssi unpubl.) serve as evidence of contacts between the Baltic and the East Atlantic grey seals.

The grey seal is sexually dimorphic with males approximately 1.2 times longer and 1.5 times heavier than females (Beck et al. 2003). The Baltic grey seals are the smallest grey seals in the world. Measured maternal weights can not be found in literature, but birth weights of pups are smaller (11–12 kg, **I**) than the published values for other grey seal populations (15.6–16.6 kg, Shulz and Bowen 2004).

The grey seal is considered to be capital breeder with a relatively short lactation period which lasts in average 17 days (Kovacs and Lavigne 1986). The West Atlantic population breeds from December to March with breeding peak in January (Mansfield and Beck 1977). Ice breeding is prevailing in Gulf of St.Lawrence (Bedard 1993) and land-breeding in the other parts of this distribution area. The East – Atlantic population, holding two thirds of world grey seal population (Bonner 1972), breeds from September to January with breeding season varying largely within localities (Coulson and Hickling 1964, Boyd and Campbell 1971, Lorentsen and Bakke 1996, t'Hart et al. 1988, B.M. Jenssen unpubl.). Land-breeding is common to all grey seals in this population. Population surveys in the 1960s indicated the Baltic grey seal to be a typical ice-breeding pinniped, giving birth in February-March on the drift ice in the central and northern Baltic. Seals keep close to natural openings and cracks in ice cover and are not known to establish systems of breeding and haul-out holes in fast ice (Aruste 1962, Hook and Johnels 1972). Location of breeding areas are varying yearly according to extent of ice-cover and in warm winter with insufficient ice-cover to provide breeding habitat, seals breed on land (**I**).

Current main distribution area of the species is in the Central Baltic while according to the photo ID and telemetry data (Karlsson et al. 2005, Sjöberg et al. 1995, Dietz et al. 2003, Jüssi unpubl.) individual seals are able to move in the whole Baltic Sea.

The Caspian seal

The enigmatic zoogeography and phylogeny of the endemic Caspian seal has been widely discussed (see review in Arnason et al. 2006:352). The modern molecular methodology places them phylogenetically to close sister group of modern grey seals (Palo and Väinölä 2006) or ringed seals (Fulton and Strobeck 2010a). The species was trapped in the Caspian Sea in Pliocene (1–3 Mya, Palo and Väinola 2006), their white pup lanugo and ice-breeding as main reproductive strategy confirm their Arctic origin (Fulton and Strobeck 2010b).

The Caspian seal is a small seal with 105–130 cm of body length and average weight of about 70 kg, where both sexes are of the same size (Chapskii, 1976). The Caspian seals are predominantly ice-breeders. Krylov (1990) also reports breeding females from the ice-free East coast of the Caspian Sea where they give birth to their pups on sandy islets and shores. Although such alternative breeding system exists for the species, the reported numbers are relative low – around 50 – compared to the total number of seals – 15 000, counted in the area.

The seals use ice in the Northern Caspian Sea as their main breeding ground while the distribution and ice types used depend on the severity of winter (**IV**). The pup weighs 5 kilograms at birth and lactation lasts for 23 days according to Schulz and Bowen (2004). Given the maternal and offspring size and severe climatic conditions the energetic costs of lactation are high while the continental climate in the region does not provide thick snow cover on ice surfaces. So the seals are seeking shelter in ridged ice (**IV**, P. Kalashnikov, pers. comm.). Although the preferred habitat in close drift ice provides natural access to water, the seals are able to create and maintain holes in thick ice. Kidney shaped cavities in snow containing seal pups have been observed during aerial surveys (original observations, M.Verevkin pers. comm.). The species showns diverse breeding strategies, which are similar to both grey and ringed seals in the Baltic. It is knot known whether the Caspian seals feed during lactation, but small maternal size, relatively long lactation period and preference of stable ice types for breeding all point towards income breeding to some extent, as also seen in the ringed seals (Sinisalo et al. 2008).

According to the observations and telemetric data the species inhabits all parts of the Caspian Sea with seasonal shifts of the highest concentrations of seals to North during breeding on ice and South during ice-free period (Krylov 1990, CISS unpubl.). In earlier periods, seals inhabited the Central Caspian shores (Apsheron archipelago in Azerbaijan, Ogurchinskii island in Turkmenistan), hauling out in thousands (Krylov 1990). In recent decades the seals are rarely seen in those areas (CISS unpubl., T. Eybatov pers. comm.). This distribution pattern may be an effect of decrease in population size due to mass mortalities (Kennedy et al. 1999) unsustainable harvest (**IV**) and human-induced changes in environment (Hall et al. 1999, Ivanov et al. 2000, Härkönen et al. 2012).

2.2. The seas – hydrology and climate

The Baltic Sea

The Baltic Sea is almost enclosed water body in North Europe (latitudes 53°58 – 65°50 N) with area of 415 266 square kilometers and maximum depth of 459 meters in the Baltic Proper. Still, the average depth of the sea is only 50 meters. The sea is, due to influx of several large rivers a brackish water sea with the salinity ranging from <1 ppt in the North (Gulf of Bothnia) to 32 ppt in the South (Danish straits). Such wide salinity gradient influences the biota – oceanic communities in the South are gradually replaced by fresh water species in the Northern parts and river estuaries.

The Baltic Sea freezes over partially in the winter with the maximum ice cover up to 217 000 square kilometers while the inter-annual variability is large – from 10–100% of the recorded maximum (Granskog et al. 2006). Several studies have been commenced on the ice history of the sea with long time series of various ice characteristics like ice cover extent, thickness and duration recorded over two to five centuries (Seinä and Palosuo 1996, Jevrejeva 2001). In the milder ice-winters the sea ice can be found only in the North-Eastern parts of the Baltic Sea due to their exposure to low Arctic temperatures and cold continental air of the areas East from the Baltic Sea. In the Eastern part of the sea shallow waters and sheltered bays support formation of annual ice cover. Duration of ice cover varies significantly in the freezing parts of the Baltic Sea, from six months in the Gulf of Bothnia (Leppäranta and Seinä 1985) to three months in the Gulf of Riga (Jevrejeva 2000). In very mild winters, like 2007–2008 the open sea areas of Gulf of Riga and Gulf of Finland can be ice-free with very limited ice cover, both in time and space, forming in shallow bays and straits (FIMR 2008). As the ice is forming on the frontal line between cold continental air masses and moist air from North Atlantic, snow cover on ice is often thick.

The general freezing pattern of the sea provides seals with suitable habitats in the Arctic conditions of the northern part of the Bothnian Bay. Eastern cold continental airstreams combined with shallow and sheltered seas lead to frozen seas in the North-Eastern part of the Gulf of Finland, Northern part of the Gulf of Riga and the Moonsund archipelago.

Analyses of long term sea ice conditions and meteorological measurements have indicated increase in the winter temperatures in the Baltic Sea area over the past two decades which is expressed in ice cover extent and duration. One Celsius degree of average temperature rise would reduce the winter ice cover by 45 000 square kilometers and four degrees of rise would result in ice-free winters in the whole sea area (see review in Granskog et al. 2006).

The Caspian Sea

The Caspian Sea is the world's largest salt-water lake situated between Europe and Asia (latitudes 36°33' N – 47°07' N) with area of 392 600 square kilometers. Oceanography of the different parts of sea is very contrasting: the Northern Caspia (area North of the Saddle area, a threshold at approximately 45° N) is shallow with average depth of 5–6 meters and it holds only about 1% of the Caspian water, Middle and Southern Caspian are deep parts of the sea with the maximum depths of 788 meters and 1025 meters respectively. Water salinity varies from 1.0 in the North to 13.5 ppt in the Southern Caspian (Dumont 1998). The sea surface temperature varies also seasonally and regionally. Mean water temperature for Northern part is +12.5°C (from –0.5°C to +26°C), for Middle Caspian – +14.1°C (from +2°C to +24°C) and for

Southern part +16.8°C (from 9°C to +26.8°C). Caspian flora and fauna consists of 46% endemic species including one marine mammal (Panin et al., 2005).

Annual ice cover with maximum area of 88500 square kilometers forms in the Northern part of the sea. The area is limited by the greater depths and warm water upwelling South of the Saddle area. The ice season last normally from 80 to 120 days (Kuraev et al. 2008). Temperatures on ice can be as low as –30°C. Due to the continental climate snow cover on ice is usually very limited. Still, snow can be abundant in times when warmer and moist air masses enter the area in winter. The ice conditions vary annually, mild and severe winter conditions normally alternate with 2–3-year intervals. Kouraev et al. (2004) assessed the ice conditions from historical observations compared with satellite-derived data and found a decreasing trend of both duration of ice-season and ice extent since the winter 1993/1994.

In spite of different geographic latitudes the two seas have much in common: they are of similar size and have quite wide range of hydrographical and meteorological conditions – e.g. general bathymetry patterns, North-South salinity gradient and shallower parts freezing annually in the North. So, as seal habitats the seas have similar ecological conditions with spatiotemporal changes of habitat quality (prey density) and availability (breeding ice). Both seas are on the verge of ice-free winters if the global temperature rises further.

2.3. Habitat changes

Human influence

In past century the environment of the Baltic and Caspian seas have undergone very notable change, mostly due to the human influence. In the context of my thesis it is important to account this influence as additional stressor to the seal populations in the conditions where natural conditions are becoming biologically unfavorable on both individual and population level. The ecological situation in both seas is substantially altered from natural by human activities and the application of natural selection mechanisms can be significantly amplified by those changes.

We can assume, that some 150 years ago the habitats of the studied seal species were in pristine natural state, as human technological development did not allow to disturb the marine environment and overexploit aquatic resources (Österblom et al. 2008). Steam and combustion engines were seldom used for propelling ships and absence of refrigerating technologies limited fishing to sustainable amounts. Chemical industry, oil and gas extraction or agriculture had not yet exceeded the threshold of significant impact to marine environment. The state of ecosystem in the landlocked water bodies was very likely maintaining historically evolved balance of habitat use by the residing seal populations.

Yet, with onset of the 20^{th} century human influence on marine ecosystem escalated – the seal habitat quality became under substantial anthropogenic pressure in form of overfishing by highly mobile and destructive fishing equipment, anorganic and organic pollutant load and influx of nutrients from sewage disposal and agriculture. The availability of critical habitat was deteriorating due either direct human disturbance or increased aquatic noise coming from motorized vessel traffic. Fragmentation of habitat for the Baltic seals started in the Baltic in 1894, when dam building started between islands Saaremaa (Ösel) and Muhu (Moon) in West Estonian archipelago, cutting away passage from Moonsund area to Gulf of Riga through a 5 km wide strait. In the Caspian sea, similar history started in 1878 when Nobel brothers launched in Baku the worlds first tanker *Zoroaster*. By the way, later one of their ships in the tanker fleet carrying petrochemicals from the Caspian Sea through rivers, Lake Ladoga and Baltic Sea to the Western markets was called *Darwin* (Tolf 1976). Today the Baltic Sea has become one of the busiest shipping corridors in the World with intensive fishing and eutrophied environment. The Caspian Sea contains one of the World largest reservoirs of oil and has recent history of seal mass mortalities (Forsyth et al. 1998) and ecological crisis caused by invasive comb jellyfish *Mnemiopsis leidyi* (Ivanov et al. 2000).

Environmental pollution, particularly by heavy metals is suggested as a cause of high neonatal mortality in Saimaa ringed seals (Hyvärinen and Sipilä 1994, Sipilä 2003). This anthropogenic factor may increase neonatal mortality and worsen pup condition also in the Baltic Sea, where the ringed seals suffered significant reproductive disorders in 1970ies. In 1974–79 in the Bothnian Bay ringed seals the proportion of pregnant mature ringed seals was only 27% vs. normal 80–90% (Eero Helle pers. comm., Helle 1981). Improvement in gynaecological health of female ringed seals have been observed in later studies (Helle and Stenman 1990, Olsson et al. 1994), but there is still a possibility that pollution affects neonatal survival and juvenile health of the Baltic seals and the natural mortality values are higher than those of the true seals inhabiting pristine environments.

Humans have also influenced the seal habitat quality through eutrophication and overfishing (Österblom et al. 2007). Seals in both studied seas have been affected also directly by unsustainable hunting in the first half of the 20^{th} century (Harding and Härkönen 1999, Härkönen et al. 2012), which in turn probably influenced the marine habitats through reducing the predation factor in the food web (Baum and Worm 2009, Härkönen et al. 2012).

Pollution, eutrophication, fisheries impact on prey species, bycatch, energy extraction infrastructures (oil installations and wind power plants) and under-water noise are present and growing concern in these seal habitats (Härkönen et al. 2012).

Climate change

Shifts in climate during the geologic time scale have altered the availability of habitat and food, thus influencing the distribution and abundance of seals in different geographic regions. Earlier (a million years ago till the end of the last glaciation in the Baltic region, 10 000 ybp.) period of cooling had strong effect on the general distributions of seal species, as most of the Northern hemisphere was covered with ice. The glacial cycles influenced among other aspects of physical environment sea level fluctuations which brought about separation of marine basins (Anderson and Borns 1997). This process has altered both the species composition of and molecular diversity of the species (Palo et al. 2003, O'Corry-Crowe 2008). Still the shifts in climate and habitat during the named early period have been slow enough to involve hundreds of generations of seals.

The recent history is different. The planets temperature is increasing in an unprecedented pace with consequent reduction of sea ice and rise in sea levels (IPCC 2007). In the past half a century the marine environment at high latitudes has shown changes, which exceed the range of natural variability over the past 1000 years (Walsh 2008). The rate of this warming is so high, that it involves only some generations of seals, thus severely challenging their capability to adapt to the changes in the environment (Moore 2008, Moore and Huntington 2008). Climatic conditions are reflected in the nature of annual ice cover of the freezing , influencing maximum ice area, ice thickness and duration of ice seasons. Ice, in turn, is a critical habitat for the land-locked seal species under observation. Its fundamental role is expressed and discussed in the context of such vital biological traits like distribution (see e.g. **I,II** and **IV**) habitat use (**III**) and reproduction (**I**,**IV**).

2.4. The methodology

Measuring ecological features in the open sea in changing climate is challenging due to the vast spatiotemporal nature of the processes and responses. This means that often there are no direct methods to apply. In most cases standard methodology of marine mammal ecology research have to be used and allow time to assist with natural inter-annual and seasonal variability, providing series of samples. To get a conclusive amount of empirical data may take a decade. Experimentation and result verification are often dependant on events provided by the nature so the methodology has to be robust and flexible to off-shore challenges. This comes with the price of data precision and repeatability. Many studies and practical field tests have shown, that increased effort has the most notable effect on the costs of the research while the confidence limits of the measurement remain largely in the same range. So when the methodology of seal research is discussed or questioned, one has to bear in mind that there are reasons why seals do not tolerate human presence or boats do not get to the sea or shore even when the sun is shining.

For studies of habitat preference, abundance and distribution alternatives are to cover the maximum proportion of the population in relatively short time to "snapshot" the patterns or to follow individuals over longer periods. In the first case, aerial surveys are the most cost effective approach, covering seal habitats in short time. We used systematic transect observation method for determining distribution and abundance of seals on ice (**II,IV**). The standard method described in Härkönen and Heide-Jørgensen (1990) has been slightly modified as advances in geo-locating technologies and digital photography allow to collect data on substantially higher detail than it was earlier done by eye. The shortage of the method is, that in the Baltic Sea breeding ringed seals use snow lairs to hide their pups and direct determination of breeding distribution is complicated. Still, in the late season collapsed snow caves and mothers with young pups basking on ice reveal the range and preferred breeding habitat for the species. Also additional data on the physical environment, interactions with e.g. humans, birds and predators was collected and geo-tagged by the observers.

Following movements of individual grey seals has been possible by using flipper tags for pups (Jüssi, unpubl.) or the individually recognizable pelage patterns of females (e.g. Karlsson et al. 2005). Still, those marking methods are mostly restricted to warm season as seals bearing artificial or natural markings can be seldom "caught" during the winter season. Fishing (i.e. by-catch) and visual identification chances are very limited in the freezing parts of the Baltic Sea. Mark-recapture methods provide only very limited data on the migration patterns. Recovery of a flipper tag is predominantly related to the death of the animal in fishing gear and re-sighting of a known pelage pattern is a result of special observation or photography session. Occasionally I have observed two albino grey seals and one female with identifiable scar on breeding islands in Estonia during several seasons and read a flipper tag of breeding female. So for several animals there are some repeated observations in space and time. Joining those points reveal some of the movements, but direct line between the points does not describe sufficiently most of the grey seals' seasonal behaviour.

In open water seasons most of activities take place below the sea surface and seals are concealed from the observers eye. To look beyond the visible and measure behavioral traits telemetric data loggers are preferred. Paper **III** is based on diving data collected with Satellite Linked Time Depth Recorders (SLTDR, Argos) which use orbital satellites to relay information on various activities like dive depth and duration, time spent at surface and hauled out. Geo-location of the devices has an estimation error of several kilometers due to methodological restrictions, so the data can be used mainly for generalization within a sub-region. Still the telemetry information has provided data to assess ice relatedness of the seals in papers **II** and **III**. Advances in technologies have significantly improved the data collection precision and amounts of relayed information. Yet, catching the "right" animals for study depend on chance. Most of the grey seals, equipped with telemetry tags in the Baltic Sea have been juvenile or sub-adult as larger specimen are relatively difficult to catch due to their body size and experience with nets.

Seal movement information for the species of this thesis has been gathered by telemetry devices in frames of several research projects as reference data. Given the logistic and financial cost of the method, pooling of different projects, national and international, are needed to increase the spatiotemporal coverage or sample size. This has not been done yet for majority of the recent datasets and so the telemetry data is referred to as unpublished in this thesis while the lead researcher of a project or CISS has been used as the source of unpublished information.

In measurement of breeding processes on individual, group and population level, multiple catching or following of same individuals throughout the breeding season and beyond would be the preferred method. Although in drift ice environment this is almost impossible as recapturing breeding females or even finding whole colonies after a week takes an unreasonable logistic effort. So a set of assumptions together with data gathered during a single capture is what the conclusions in the paper **I** are based on. Those assumptions can be used with the reservation that certain basic biological characteristics like individual pup birth mass or health condition at birth are not related to the birth substratum and the measured mean values in studied spatial and developmental stage groups reflect post-partum exposure to variable environmental conditions.

3. RESULTS AND DISCUSSION

The study seal populations are pagophiles. In general it can be said that they are ice-dependant as this breeding platform is a basic survival prerequisite for them. One may argue, that grey seals breed successfully on land in North America, around Britain and Eastern Scandinavia for thousands of years, but as we show in I, land breeding comes with higher cost when compared to the ice-breeding conspecifics in the Baltic. That cost may be bearable in the undisturbed nature where e.g. climatic conditions shift gradually over tens of generations, but in the modern world with anthropogenic pressure on natural resources, predator removal and dramatic glacial "meltdown" we can not be sure that the natural survival of the species in far future is secured also without the modern conservation efforts. The research results from the other Eurasian ice breeders (e.g. Sipilä 2003, Härkönen et al. 2012, IV) have shown that even in cool climates the anthropogenic interference may push seal species to the verge of extinction.

As many of my works with seals have been related to and largely facilitated by the absence of ice where it is expected to be according to centuries of measurement, I chose to discuss the role of ice in distribution, habitat use and reproduction of the landlocked seals. In following I focus on the processes contributing to survival in conditions where one critical habitat has become unpredictable and physical borders set limits to evolutionary alternatives.

3.1. Ice related distribution.

The distribution of hauled out seals can vary significantly over the year as the ice forms temporary hard platforms off shore. At the same time ice can restrict access to certain parts of the summer distribution range as the seals' ability to cross firm ice-sheets or dive under is spatially limited. For the Baltic seals, average extent of winter ice cover can probably influence summer distribution of the ringed seal and winter distribution of the grey seal. General distribution pattern of the ringed seal overlaps largely with the areas where sea freezes in winter, leading to conceptual understanding of four isolated sub-populations in the Baltic (**II**, Nordström et al. 2011) although recent telemetry studies have shown exchange of individuals between those subpopulations (Jüssi and Kunnasranta unpubl.). Also the main grey seal land-breeding colonies can be found in areas where their preferred ice-type – drifting pack ice occurs in normal winters (**I**). Those evidence indicate strong spatial conservatism of the Baltic seals regarding the regions where favourable breeding habitat occurs in the winter months regardless of the ice conditions elsewhere. Grey seals do not go to breed in the Bothnian Bay in large numbers in years with mild winter and the ringed seals keep close to their breeding areas in the summer and specially during the onset of winter.

Ice type preference is specific to the studied seals and hence I have divided the paragraphs accordingly.

The ringed seal

The modern ringed seal population of the Baltic Sea can be divided into four regional sub-populations, location of which overlap with the freezing patterns of the sea in the Northernmost part of the Gulf of Bothnia, in the Eastern part of the Gulf of Finland and in the archipelagos of South-West Finland and West Estonia. Almost total freezing of the sea, as well as absence of ice in the Central Baltic have been rather exceptional cases in the known ice-history (Seinä and Palosuo 1995). Those irregular events have not probably influenced the general, long time ice-related distribution patterns of the species.

Breeding distribution of the Baltic Ringed seals can be related to the location and extent of suitable breeding habitat – ridged ice with snow cover (Reeves 1998). As the seals hide their pups in snow lairs and spend excessive time in lairs and in water, their distribution range can not be detected by visual observation of seals on ice. The special survey trips to ice in the Gulf of Riga in years 2004– 2006 provided data on the breeding habitat preference in general as the presence of seals could be verified by observation of young pups, breathing holes, lairs with lanugo fur and presence of adult seals. Still, estimation of habitat range or breeding densities is almost impossible with the current methodology under normal ice conditions.

In general, breeding distribution can be described through location of suitable ice habitats. The preferred ice fraction-ridged pack ice forms first along edges of fast ice and seals settle there before the breeding season. This is also confirmed by observations from seal hunters in the Gulf of Riga – most of the ringed seal lairs were found on the edges or in the ridges of “old dirty” ice regardless of the location and extent of “new white” ice which formed in the second half of ice season (Soosaar 1976).

Inter-annual variation of the Baltic ice cover is also reflected in the ringed seal breeding habitat and related seal breeding distribution. Comparing a normal (1996, see **II**), mild (2012) and very mild (2008) ice winters in the Baltic reveal notable differences in seal breeding habitat and observed seal distribution in the Southern populations of the ringed seals. Major difference from “normal” in mild years was the presence of seals closer to the mainland both in the Eastern part of the Gulf of Finland (M.Verevkin pers. comm.) and in the West Estonian Archipelago (Jüssi unpubl.). In normal ice winters those areas are covered by flat fast ice where lack of access to the air or water and absence of structures to build lairs provide poor breeding conditions to ringed seals. Extremely mild winter conditions in 2008 forced the ringed seals to opportunistically haul out and breed on any type of ice. The ice cover reached the winter's maximum only on 24th of March 2008 with 49,000 square kilometres, the all-time low (Anon. 2008). Ice in the Gulfs of Riga and Finland reached only some kilometres from shore while stormy and warm weather in the end of March made the ice to melt quickly. Annual differences in the Bothnian Bay are smaller as the sea area is relatively less sensitive to winter severity (Meier et al. 2004a). There is no recent data on the breeding ringed seal distribution in the icefields of the bay but given the geographical scale of the area and population size, regardless of the location of ice-fields breeding habitat has been abundant in all winters of recorded ice history.

An aspect worth attention in the context of breeding distribution of the ringed seals in the Baltic is use of ice habitat by non-breeding seals. Given the harsh conditions of the pack ice habitat and potential antagonistic territorial behaviour of the breeding individuals (Lydersen and Gjertz 1986) it is probable that non-breeding segment of the population is not using the same areas in ice habitat as the breeding seals. This hypothesis is indirectly supported by behaviour of two adult female ringed seals in the Gulf of Finland in 1998 and 1999 (Härkönen unpubl.) that stayed in the unfrozen part of the sea for the whole winter. As they weighed 74.5 and 80 kilos, respectively, when caught for telemetry in early summer, they were considered to be non-breeders in the previous season. Possibly those individuals had permanent reproductive disorder which is known to affect the Baltic ringed seals (Helle et al. 1976, Bergman and Olsson 1985) as they skipped breeding also in the season when the seals were followed with telemetry devices. Likely the non-breeding animals do not follow the spatial and temporal regularities of the breeding cycle, thus optimising expenditure during the energetically unfavourable season.

Late winter distribution of the species in the Baltic is presented in **II**. In the Gulf of Bothnia, independently from the severity of winter and ice extent, highest concentrations of ringed seals occurred in the central northern drift ice in 1988–1996 (Fig 2. page 171). This distribution pattern is in concordance with earlier data of spatial distribution of the catch from seal hunt, (Olaffson 1933 in **II**, Figure 4, page 177). Historic hunting data also confirm persistent distribution of overwintering seals in the North-Eastern part of the Gulf of Finland (**II**). In the Gulf of Riga central and northern part of the sea area have been known as rewarding seal hunting areas for centuries (Vesik 2005), while areas south of island Ruhnu (Runö) were less popular amongst the seal hunters of Kihnu (ibid.). A journal article on the visit of the first Estonian President, Konstantin Päts to Ruhnu in 1921 contains also a remarkable detail describing indirectly the seal distribution in the gulf in those days. Namely, after the political re-division of Europe after the First World War this historically rather autonomous border island, inhabited by a Swedish population had to choose between newly established Estonian and Latvian states. Substantial livelihood of the community came from seal hunt and one of the fundamental arguments, presented to the President for consideration was location of seals – the seals were mostly, according to the experience of the hunters, in Estonia i.e. North from the island (Neggo 1926). The islanders chose Estonia to maintain access to the seal stocks.

The historical hunting information does not often specify the hunted species, so it is important in the context of the ringed seal distribution to note that the species was sought for and hunted in certain types of ice sea which was usually located in the Northern part of the Bay.

Duration of the ice season shows significant annual variation in the southern part of the distribution range of ringed seals in the Baltic Sea. Break up of ice occurred before completion of the moulting period in one year out of four as an average in period of 1930–1995 (Hook and Johnels 1972, Seinä and Palosuo 1996). Since 1996, less in than half ice seasons ice extent has reached the long term average ice area while the duration of ice season has been shorter than the long time average (Granskog et al. 2006, pers. obs.). In such springs, rapid decomposition of ice force the seals to leave their breeding grounds and gather to moult on the last ice or stones in the in-shore areas. Then ringed seals are often seen on leads in groups moving towards land or more stable ice fields. Observed density "hot spot" in the Gulf of Riga in 1996 (Figure 2 in **II**) is a result of such spring migration rather than reflection of the breeding distribution. With the advance of ice decomposition seals move towards inshore waters, but ice floes are preferred haul-out surfaces as long as they exist.

In the ice-free period ringed seals move in wide sea areas, staying at the open sea for long periods and hauling out on shallows and rocks for shorter intermediate periods. The long-distant movements off-shore are most probably related to foraging as several target species (sprat, Baltic herring) leave the coastal shallow waters when sea water temperature rises in shallow areas and stay in cold, deep parts of the Baltic Sea for the most of the ice-free period (**III**).

The grey seal

The main distribution areas of the species in the Atlantic today occurs far form the annually forming ice edge. The retreat of ice in Pleistocene was relatively rapid and the shift of the freezing zone to North left behind a geographically wide area of grey seal distribution. Todays range of the species in the East Atlantic from latitude of Brittany, France (48°N) to Finnmark, Norway (71°N) is 2500 kilometres with continuous distribution along the whole range. The Southern limit of polar ice reaches to the North Iceland and the White Sea (deVernal and Hillaire-Marcel 2000), the Baltic Sea is situated more South but freezes due to lower salinity. Only the northernmost East Atlantic grey seals and the Baltic population are distributed in the freezing seas. In the Baltic grey seals are distributed mainly in the central parts of the Baltic Sea between latitudes of 58 and 61 degrees North where 85% of the hauling-out individuals can be counted during annual molt (Harding et al. 2007). The West Atlantic population is distributed in the latitude of the Gulf of St.Lawrence whereas approximately 90% of the seals breed on the beaches of Sable Island, 290 kilometres East from Halifax, Canada (Hammill et al. 2007)

Freezing seas limit grey seal distribution significantly, as the species is known to avoid hard ice conditions in the fast ice and dense pack ice (Hook and Johnels 1972, **I**, E.Helle pers. comm.). Although the grey seal is capable to make and maintain breathing and haul-out holes in those ice habitat types

(Smith et al. 1990, E.Helle pers. comm), they prefer ice areas with natural cracks and openings, which provide easy access to the water. As the species is breeding on open ice where the pups are exposed to low temperatures, pup survival in severe frosts of the winter may also limit the species distribution in the Baltic Sea (Hansen and Lavigne 1997). Numerous tag recoveries and telemetry indicate, that sexually immature specimens avoid freezing seas and spend their winters in the Southern part of the Baltic Sea (Jüssi unpubl, Dietz et al. 2003). So winter distribution of sexually mature grey seals is mostly related to frozen parts of the Baltic Sea, drift ice or pack ice fractions where optimal breeding habitat is formed (**I**). In the Bothnian Bay, where ice cover lasts almost up to the end of seals' annual moult in May, grey seals can be found hauling out on ice till then. Elsewhere sea ice melts by April, shortly after the breeding season and seals gather on offshore skerries, reefs and islands in groups up to several thousand individuals.

Observations have shown, that the adult seals leave for sea to replenish their energy reserves spent during the breeding event and prepare for the annual moult, another energetically expensive period in the annual cycle when the seals tend to spend most of the time out of the water. Gradually, the observed numbers on summer haul outs in the main distribution area – archipelagos in South West Finland, Aland and Stockholm areas start to increase (Helle and Stenman 1990) while seals numbers in areas, where majority of pups were observed during the breeding season remain thinly populated by the grey seals (Jüssi and Jüssi 2001). This change in observed distribution between breeding and summer haul-outs indicates mass migration of grey seals between different sea areas shortly after breeding.

Grey seals are described to undertake seasonal migrations to the different parts of the Baltic Sea already from the observations of the seal hunters (Soosaar 1976 , Ylimaunu 2000). Soosaar (1976, p. 313) describes a case from early 1900's where a grey seal, bearing a harpoon in its head, was hunted on ice close to Kronstad (Island of Kotlin), Gulf of Finland. The harpoon could be identified to belong to Kossu Endrek, a hunter from Kihnu, Estonia, where it had been used in a seal hunt some months earlier. This rare early observation is significant addition to recent studies of seal movements, as there is very little data on grey seal behaviour in relation to location of breeding ice. Recent telemetry results have also shown, that seals can travel long distances to find suitable breeding platform. The female grey seal marked at Rodsand, Denmark, bred on Allirahu close to Saaremaa, Estonia, 820 kilometres away, in 2002 (Dietz et al. 2003). Two individuals, one male and one female marked in West Estonian Archipelago in 2007/2008 when ice conditions were the poorest in recorded history moved to the Eastern Gulf of Finland, 390 kilometres from the Estonain West coast just before the breeding period (Jüssi unpubl.). The adult male stayed in the area until 11th of March. The transmitter of the female (probably subadult, 89 kg when caught in end of July) failed on return route in 28th of January.

Combining of the knowledge obtained by different available methods leaves still the colder periods relatively under-represented and data to judge upon site fidelity of breeding or regularity of return to certain ice or land breeding areas is limited. The available measured and observational data still indicate, that females return to breed to the same sea areas over seasons and recovery of flipper tagged individual shows that this conservatism can exceed generations. Also there are indications from the telemetry and anecdotal evidence, that the grey seals are actively moving between different Baltic Sea areas in the winter season so the distribution patterns of breeding seals do not represent overlaps of seasonal habitat use of individuals but rather indicate habitat preference on the population level.

The Caspian seal

Krylov (1990) describes the general seasonal distribution pattern of the Caspian seal with its main distribution shifting to the ice when the Northern part of the sea freezes. The shift is related to the breeding season and involves mostly sexually mature specimens. The description contains still one quite questionable statement: "Flocks of pups and young from the previous year occupy the firmest pack ice in the middle of the ice area whereas the remainder of the immature animals form separate flocks along the edges of the ice cover". Yet, our aerial observations and shipboard studies have produced no evidence of seals older that pups of the year but distinguishable from adults in the pack ice area. Also all 5 juveniles marked with telemetry tags in 2008 stayed away from the frozen sea (CISS unpubl.). Thus, the seals entering the ice fields are most probably related to the breeding event while juveniles stay in the open water areas over winter.

The distribution of the seals in the ice during the breeding season varies with the extent and nature of the annual ice cover (**IV**). Ridged pack ice is preferred when available, but when firm ice forms in most of the Northern Caspian and access to those preferred structures is blocked seals use floes at the ice-edge. Comparison of measured breeding seal distribution (**IV**, CISS aerial surveys 2005 – 2012) to the bathymetry of the North Caspia shows, that on fast ice the seal distribution is limited to approximately 2 meters of depth. Probably the limit is set by ice thickness and water column available for diving. As there is usually very thin layer of snow on the ice, preference of ridged ice fractions for breeding is caused by need of shelter from wind chill in low temperatures. Seal birth sites, observed as stains of blood on ice, are predominantly in close proximity of ridged ice sheets and very rarely in the middle of a flat plate of ice (CISS unpubl.)

Seal breeding on shore in the open water areas form a very small fraction of the total breeding population and the observable numbers of seals in the ice free areas during winters (Krylov 1990). The seals in open water areas are m ost probably juvenile and adult non-breeders, altogether less than five per cent of the population estimate given in the same paper. The land breeding females form only 0.3% of those or about 0.01% of the population. This small proportion probably represent an abnormality in the breeding habitat choice, possibly by primiparous females, rather than remarkable alternative to the main ice-breeding strategy of the species.

It is obvious from the observations, that ice is a key habitat in the context of the general distribution of all the three species. Largely so as breeding platform for the pagophilous seals. Summer distribution patterns of grey and ringed seals in the Baltic overlap largely with breeding areas. Changes in ice cover and types define the annual breeding distribution while quick shifts towards warmer climates would probably, through the climatic or physical limitations make seals to vacate some parts of the present distribution areas. In the open ocean environments this may mean shifts of distribution for several hundreds of kilometres to new areas with potentially suitable habitat (Freitas et al. 2008), but in the land-locked water bodies geographical distribution barriers in combination with biological factors can lead to loss of breeding habitat and consequent reduction of breeding distribution range. The contributors here are lack of ice for the Baltic ringed seal and Caspian seal (Meier et al. 2004a, Granskog et al. 2006, Härkönen et al. 2012, Sundquist et al. 2012) but also flooding of several currently available land-breeding sites of the Baltic grey seals in the Southern and Eastern Baltic by rising sea levels (**I**, Meier et al. 2004b).

3.2. Breeding success

The breeding success can be measured directly for a season or site in terms of pup survival and conditions (**I**, Baker, 1984), but also indirectly for longer time as number of offspring for a female in far future (McNamara and Houston 1996). The first method describes the outcome of a breeding event but for long living animals one season is representing only a fraction of lifetime breeding effort. Still, recurring reduction of offspring quality in unfavourable breeding conditions can have adverse cumulative effects on population or species level. The study species differ in their habitat requirements and plasticity, so they are discussed separately in this context.

The ringed seal

The Baltic ringed seal pups are very difficult to find and catch in the breeding habitat in statistically significant numbers, so there is no data on lair mortality and pup conditions which would enable to measure breeding success using those parameters. High, close to 20% pup mortalities given for Saimaa seal (*Phoca hispida saimensis*) by Sipilä et al. (1990) can not be applied directly to the Baltic as the Saimaa seal is establishing subniveal breeding lairs on the shoreline where extensive water level fluctuations can cause lair collapse with fatal consequences to the pup (ibid.). The Baltic ringed seal preferred breeding habitat – old ridged ice structures are rather stable even when the ice moves with waves or currents. Considering the physical factors that secure survival of the offspring through the lactation period – stability and duration of ice cover, sufficient layer of snow to cover the lair – winters around and above average severity should yield low pup mortalities and normal growth of pups from birth to weaning. Ice also provides a platform for weaned pups during early period of independent life thus enhancing the fitness of individuals (**I**). It can be assumed, that in such conditions the survival of foetuses to weaning is close to 95% as shown in many other phocid seal species (Harding et al. 2005, Hastings and Testa 1998, **I**). There is no published information on conditions of weaned ringed seal as an analogue to used measurement of breeding success of grey seals **(I).** There are some specific differences which allow to assume that the pup conditions with consequent variation in female breeding success are more influenced in ringed seal. It is a small seal inhabiting a cold environment which leads to relatively higher energetic costs during lactation (Smith et al. 1991, Lydersen 1995). Female ringed seals feed during the six week lactation period to compensate for some of the energetic expenditure (Sinisalo et al. 2008), their pups are found to be significantly more active than the offspring of other true seals. The neonates spend up to half of their time in cold water and take long dives in early age (Lydersen 1995). All those factors combined contribute to the total energetic expenditure of the nursing period and are probable causes of the relatively long lactation through lower energy transfer efficiency. The optimal breeding ice habitat provides a platform for breeding and foraging for females and shelter to the pup during the lactation period. Role of stable ice in lowering breeding costs of ringed seal is obviously more substantial than in grey seal.

Changes in physical conditions in direction of reduced snow cover, ice duration and stability would bring about reduced breeding success through exposure to predators and low temperatures, loss of platform and interruption of normal lactation. Ferguson *et al.* (2005) show detrimental effects of early spring breakup, reduced snowfall and rain to ringed seal recruitment in Hudson Bay, Canada. In the Baltic, reduced breeding success in the Gulfs of Finland and Riga areas have been observed during the warm winters of 2007 and 2008. Year 2008 serves an example of extreme habitat instability when the ice extent was moderate due to a mild winter. Seals occupied offshore breeding habitats when ice became available in February but stormy weather in mid-March destroyed the ice-sheet and compressed the remaining ice to inshore areas, relocating breeding ringed seals by tens of kilometres. The event took place in the period when majority of pups are still dependant on their mothers and probably caused significant physical stress and premature weaning. The seals did not lose totally their hauling-out platform, but such a substantial change in habitat quality probably caused significant reduction in breeding success through reduced pup quality, mortality due to environmental stress, premature weaning and exposure to avian and terrestrial predators.

The grey seal

Paper **I** is fully dedicated to discussion of the species breeding success in alternative breeding habitats in both contexts given above. We show that the species is able to breed successfully in both land and ice habitats. This ability is inherent in the population and also known for the species worldwide. In earlier literature there has been some discussion on the main breeding strategy of the species and the direction of evolutionary shifts between the two habitats (see e.g. Pierotti and Pierotti 1980). Both land- and ice-breeding are extant in the Northern hemisphere over long periods of time and there is population increase regardless of the breeding system, so in the context of survival or evolution the alternatives seem to be of equal weight. The general division of the species between the alternative breeding systems seem even to favour land breeding as it represents over 90% of the world population of the species according to the numbers reported in Haug et al. 2007. I suggest that the current population distribution cannot be used as direct evolutionary evidence. The modern population has been very significantly influence by human activities, both in terms of harvesting and conservation (see e.g. Harding and Harkönen 1999, Ferguson and Higdon 2006). Comparison of factors determining reproductive success together with features like e.g. white lanugo of pups favour theories of polar origin of the modern grey seal rather than shifting to ice-breeding in recent times (Pierotti and Pierotti, 1980, Schultz and Bowen 2005, **I**.) In the limits of constraints defined by e.g. low temperatures (Pierotti and Pierotti 1980, Hansen and Lavigne 1997) or ice cover duration, the cost of reproduction is significantly lower in the ice habitat, and when both alternatives are available ice is chosen for breeding by grey seal females as shown in **I**. So, why still most of the worlds breeding grey seals are found in the temperate waters? Probably the answer is in the complex of ecological limitations and the anthropogenic influence on the species. This was not the case some 80 years ago. Land-breeding grey seals went almost extinct on European shores due to hunting pressure (Härkönen et al. 2007). The West Atlantic grey seals were also severely depleted. (Bowen et al. 2003).

During the Last Glacial Maximum continental ice sheet covered the whole present range of the species distribution. The retreat of ice from the late Pleistocene glacial maximum to current southern arctic ice limit was relatively quick. The interglacial climate was attained in approximately 7000 years (Charbit et al. 2007). During this change in the environment the grey seals had both breeding substrata available along the north-south distribution scale and similarly to today's situation it is likely that both alternatives were used. Probably, similarity to current breeding patterns in the Baltic and the Gulf of St.Lawrence, drift ice and off-shore islands were preferred to reduce the terrestrial predation risk and thus increase the breeding success. The species is known to be philopatric (Pomeroy et al. 2000, Jüssi unpubl.) and the distribution range expanded over variable habitats during the ice retreat. Constraints of habitat availability, site fidelity and migration costs resulted in fragmentation of the species into colonies with variable habitat quality and prevalence of respective breeding strategy. On the metapopulation level futher population spatiotemporal dynamics would depend on intrinsic growth rate for each of the sub-populations (Matthiopoulos et al. 2005). Here we can expect the heterogeneity in breeding success to favour the fragment of the species inhabiting higher quality breeding habitat like shown in **I**.

Yet, the modern global distribution of grey seal numbers shows the opposite, but we have to remember, that the today's situation is very substantially influenced by human activities. Harding *et al.* (2007), Härkönen *et al.* (2007) and Hammill *et al.* (2007) suggest that the modern grey seal distribution and abundance in the Baltic, East and West Atlantic population are strongly and directly influenced by human activities – conservation, hunting and culling. Indirectly the breeding success can also be influenced both by e.g. removal of predators (Aspi *et al.* 2006) or environmental pollution (Bergman and Olsson 1985). Those alterations of environment can shift the balances otherwise dictated by purely natural conditions and they should be born in mind when perspective population effects of breeding success is discussed in the grey seal context or in the land-locked seal populations in general.

The Caspian Seal

Breeding success of the species in terms of pup mortality and conditions at weaning is very poorly studied despite of several decades of seal harvest on breeding ice. There are no recent works on the ice surface and data collected from ships or aircraft do not provide information on this subject. Krylov (1990) reports early neonatal mortality of up to 15% in years 1977–1979 and 1983 but the causes are not specified. A survey report (Krylov et al. 1978) mentions stillbirths to be the cause of death in 1.6%, starvation in 2.4% and ice pressure as factor (in one breeding colony) in 1977. Also it was mentioned, that when the breeding colonies went adrift with wind change, many pups died of exposure after falling into water. It is mentioned, that mortality in 1977 is "lower than in earlier years, but still should be considered as high with relevant implications to hunting quota" (p. 173).

There are several factors to be considered in assessment of the breeding success of the species. Caspian seals pups are the second smallest seals at birth with birth mass of only 3.5 kilograms according to review in Kovacs and Lavigne 1986 (4.9–5.5 in Krylov and Vorozchov 1972). Observations of seal distribution on ice show that the pups are born on flat ice with very thin snow cover and shelter from winds is provided by ice ridges and possibly by mothers. I have experienced temperatures below –30°C in the North Caspian ice fields during the seals' breeding period. The lower 90% percentile of average coldest measured temperatures for February in the period of 2004–2012 is at –23°C (Anon. 2012). Considering the size, temperatures and lack of shelter, low temperatures pose significant environmental and energetic stress and possibly reduce breeding success of the species in cold seasons. In Krylov and

Vorozchov (1972:47) “unfavourable hydrological and meteorological conditions” are mentioned as cause of starvation for many pups who died within first 5–12 days of their life, further in the same report ice pressure and cold are mentioned as mortality factors. So in general the breeding success of the Caspian seal can be considered to be sensitive to ice and winter conditions due to offspring’ exposure to the elements.

Breeding success of the Caspian seal on islands is poorly recorded, but Krylov (1990) mentions delay in the breeding period, early moult of lanugo, commencement of water life in the age of 7–10 days and “somewhat retarded growth” as characteristic features for the land-breeders. The same features are observable in land breeding Baltic grey seal colonies (**I**) and supposedly similar processes and effects contribute to the breeding success of land breeders also in the Caspian Sea.

3.3. Predation

Avoidance of predators is, among others, one of the determining factors why remote islands or drift ice are chosen for breeding by grey and Caspian seals, one function of the ringed seal lair is to hide the pup from “evil eye”. Predation has been, at least historically, a significant determining factor in the breeding ecology of all three study species. Coasts are rewarding foraging habitats for many predators and scavengers. Need to give birth on hard surface made seals and their offspring vulnerable to their attacks, so keeping off shore is an effective way of reducing or avoiding those contacts. One of the advantages of ice as seal habitat is that it does not provide most terrestrial and avian predators with shelter and food. Also the distances and dilution of densities are mostly exceeding the cost-effectiveness of opportunistic foraging trips a terrestrial mammal can afford energy-wise. Birds can cover long distances with low energetic expense but even though the trips to this temporary forming, bare habitat is seldom rewarding.

The ringed seal

Predation by large birds and terrestrial carnivores can be considered non-existent in average and severe ice conditions due to the spatial dilution effect and the fact that the pups spend their vulnerable early age in the lairs far offshore. Pack ice is relatively rarely visited by large gulls (*Larus canus et argentatus*), corvids and eagles as there is seldom food to sustain scavengers or birds of prey. On exploratory expeditions to coastal ice and ferry crossings during the ringed seal breeding season red fox (*Vulpes vulpes*) tracks have been observed in the ice fields with ringed seal breeding habitat. Fox tracks have led the expeditions often to the seal lairs, but I have no record of foxes digging into the lairs or otherwise successfully accessing the pups. Still, as the observations from the Arctic confirm successful attacks of arctic foxes (*Alopex lagopus*) on ringed seal pups (Smith 1976) and there is evidence of red fox attacks on birth lairs from Eurasian lakes (Kunnasranta et al. 2001, Sipilä 2003), red fox can be considered as potential predator also for the Baltic ringed seal.

In 2008 the ice cover had the smallest area in the recorded history of Baltic ice conditions and in the Southern distribution areas there formed only very narrow strip of coastal ice. Snow cover on ice was very thin or absent. In the Gulf of Riga a 1–2 kilometres wide crescent of coastal ice formed only in the Eastern part of Pärnu Bay and in the Gulf of Finland only inner bays of the easternmost parts froze. Ringed seals gathered to breed on that ice. Those frozen areas were at inhabited coasts and the ice was also used by hobby fishermen and feral dogs.

Observations of the ringed seals in that limited breeding area in 20^{th} of March 2008 revealed presence of at least 54 mother-pup pairs and 55 white tailed eagles (*Haliaetus albicilla*). Also a red fox was observed on the ice in the proximity of the breeding seals. Eagles were observed to feed on ice, but due to the long distance of observation it was not possible to determine their food item. A repeated observation a week later revealed that ice area was further reduced and observable seal and eagle numbers had substantially fallen, no pups could be observed on ice.

Behaviour of the female ringed seals showed weak or absent reaction to presence of eagles. When eagles approached, flying or walking on ice against the mother-pup pair, the female seals paid little attention to the potential predator and when the eagles stayed in close range, the female dived into the sea leaving the pup on ice unattended. Such behaviour is controversial to what one would expect from a mother when offspring is exposed to a predation risk. On the other hand, considering the cryptic breeding strategy of the species in normal conditions it is probable, that leaving to water and thus not attracting attention to breeding lair is an adequate evolutionary reaction to presence of predator. Similar behaviour was observed also by Smith *et al.* (1991) in Kongsfiord, Spitsbergen. The ringed seals, breeding on open ice in unfavourable winter conditions left their pups unattended when polar foxes approached. In the same study it is described how polar bears use ringed seal pups as bait to catch adult females. It is possible, that the evolutionary behavioural trait to distract the attention of predators from the birth lair or avoid being caught prevails over the instinct to protect the pup. Still, losing an offspring in exceptional conditions would reduce lifetime reproductive success less than losing life. In recurring unfavourable breeding conditions when the pup is exposed to predators such behaviour is counter-productive and reduce population fitness. Quick changes in environment then exceed the inherent behavioural flexibility of ringed seals.

In the Baltic Sea large gulls are over-wintering in the frozen sea area although in normal winters they are not distributed in the ringed seal breeding habitat. In mild winter, when the ice area is compressed and contain more open water patches, the gulls are frequent where seals breed. Observations of grey seals on land (**I**) and ice breeding colonies (E.Helle, pers. comm.) show that gull attacks can cause severe injuries to young seal pups. Lydersen and Smith (1989) report kills of ringed seal pups by glaucous gull (*Larus hyperboreus*) and attacks to their head and eyes. Consumption patterns of several carcasses revealed also avian rather than terrestrial origin of the scavenger but kill could not be confirmed. The authors suggest, that predation by large gulls can be one of the important factors limiting the southern distribution range of the ringed seal (ibid.).

The grey seal

The Baltic grey seal is out of the three species discussed here the least affected by predators in the modern world. It inhabits areas where there are no sharks and large terrestrial carnivores have become rare. Grey seals demonstrate antagonistic behaviour against intruders in breeding colonies and defend their pups vigorously. Even the pups are already in age of one week tenacious fighters when disturbed, but during the first days of life they are susceptible to avian attacks. During the field works in Estonia we have recorded an event when white tailed eagle attempted to land on a beach where grey seals were nursing their pups. All the females in the vicinity of the landing site jumped up with snarl and successfully scared the bird away. Gulls with broken wings are usual in seal breeding colonies in the Baltic and the Atlantic, and eagles and foxes are frequently observed feeding on carcasses. This observed defensive reaction together with the general aggressive behaviour of the species indicate that grey seals are aware of the danger the predators pose and have adapted to defend themselves. Yet, activities caused by disturbance and defensive behaviour add to the energetic expenditure of the breeding event. Injuries, even minor, may lead to infections and as a result, breeding success will lower compared to undisturbed individuals (**I**). Gull attacks are considered to be a factor which lowers reproductive success in the land-breeding colonies in the Atlantic Ocean also by other authors (Boyd and Campbell 1971, Twiss et al. 2003).

The Caspian seal

Large terrestrial and avian predators are dangerous mainly to young of the study species. The adults are usually not vulnerable to predators' attacks. Still, there are reports and evidence of wolf (*Canis lupus*) attacks to adult Caspian seals. According to V. Terentyev (pers.comm.) wolves have been observed to kill numbers of adult Caspian seals on Kulali Island (NE Caspia) in early spring after the sea ice has melted and to feed on the carcass until nesting seabirds arrive. Observations during ground expeditions in summer 2010 to seal colonies in Komsomolets Bay (NE Caspia) revealed wolf attacks at adult seals hauling out close to reed beds. Wolf tracks, fresh bite marks on seals and panic escape reactions of undisturbed seal groups could be observed (M.Verevkin, pers.

comm.). Large pools of blood on ice with several wolf tracks, lone wolves and packs up to dozen individuals have been observed annually during the aerial survey of breeding Caspian seals in 2005–2012 (CISS unpubl, **IV**). The observations indicate, that wolves are able to cross fresh ship channels and loose ice to reach breeding colonies of seals even hundred kilometres from shore. Inshore ice areas and islets are frequented by those large carnivores. Quite substantial, 17–40% loss of Caspian seal pups is assigned to the wolf by Krylov (1990), he also refers to an earlier report about a colony of 1500 pups having been wiped out by wolves North from the Kulali Island in one season. Those numbers are based on historic seal and wolf abundances and do not necessarily describe current interactions, but it is obvious that locally or in years of mild winters wolf pressure on breeding Caspian seals can be substantial. Given the evidence that wolves are actively hunting on Caspian seals also in ice-free period they can be considered to be a persistent, not opportunistic or seasonal predator, a local analogue to the polar bear in the Arctic food web. The only way to reduce its influence is to stay off shore.

Avian predation pressure to Caspian seal is also a notable disturbance for breeding seals. In **IV** we estimated the number of eagles on Caspian ice to about 2200 specimen and showed distribution of eagles across the seals breeding grounds. Based on the energetic requirements of an adult eagle, we estimated the amount of seal pups consumed by eagles to 10% of the pup production (**IV**). This contradicts with earlier reports (Krylov and Vorozchov 1972, Krylov 1990) where predation by eagles is estimated to be 0.3–0.7% of the observed mortality. Very likely our estimate describes consumption rather than direct predation. Natural mortalities and presence of starving pups presented by Krylov and Vorozchov (1978) show that there is substantial amount of dead and dying pups, also placentas, to meet the energetic needs of numerous eagles and not all the consumed pups are killed by birds. At the same time large number of eagles and falling numbers of breeding seals (**IV**) would decrease the amount of available carcass and increase frequency of taking living seal pups. The presence of eagles also poses increased energetic costs to the females when they protect their offspring.

In the light of the whole complex of ecological factors, predation can today be considered of low significance as the average natural conditions mostly allow avoiding predators. Yet, the key to successful avoidance is availability of habitats with low predator abundance in the form of offshore ice. With warming climate the ice area, ice season duration and consequently the distance from the predators would be reduced (Meier et al. 2004a, **IV**). As the seals are mostly seasonal and opportunistic prey to the present terrestrial and avian predators of the study area, the reduced ice area would cause increased pray density with proportionally increasing predation, a situation known as “predator pit” (see. E.g. Pech et al. 1995). Increased losses of offspring to predation can jeopardize future of all the land locked seal species (Sundqvist et al. 2012).

3.4. Nursing period

Seasonal fluctuations in the environment affect a wide spectrum of ecological factors, which contribute to the natural selection process. Successful organisms have the capacity to cope with those factors by adequate behavioural responses. One major ecological delimiter for seals is the need to reproduce on hard surface. Nursing the offspring takes place in an environment where marine mammals cannot feed so energy has to be brought along from the sea. True seals are to a large degree capital breeders whose annual reproductive allocation is delimited to energy stored during the preceding foraging period. Both mother and offspring have to survive on this energy during the breeding event (Kovacs and Lavigne 1986). In seasonal environments timing of this event is one of the core survival factors, as there are energetically more and less favourable periods in the annual cycle. Those periods are reflected in the seasonal activity patterns where periods of active energy accumulation are distinguishable from passive periods when accumulated reserves are maintained or invested into reproduction. Those differences are clearly demonstrated in a telemetric measurement of seasonal activity patterns of the Baltic ringed seal in paper **III**.

We discuss spatial effects of habitat quality on breeding success in **I**, showing that variable physical and biological characteristics of alternative breeding platforms or geographic sites contribute to the pup survival and quality of offspring. We also show, that grey seal females prefer a habitat with lower breeding costs when alternatives are available. Change of habitat quality in time poses similar challenge providing a range of choices, which lead to variable consequences on individual and population level. True seals have wide ranges of distribution from moderately seasonal tropical waters up to high latitudes, where the amplitude of extremes can be dramatic in freezing seas (Ferguson and Higdon 2006). The range also reflects in breeding seasonality. According to Adam and Garcia (2003) the recently extinct West Indian or Caribbean monk seal (*Monachus tropicalis*) had rather an irregular or very long breeding season as pregnant female and young of variable size were observed during a short period of an expedition in summer 1900. The Mediterranean monk seal (*M. monachus*) has almost no breeding seasonality due to low variance in the physical environment and constant availability of food throughout the year (Gazo et al. 1999). With increasing latitude the variability of environment increases and factors like thermoregulatory requirements (Pierotti and Pierotti 1980, Twiss et al. 2002), formation of breeding habitat (**I,II,IV**), or seasonal fluctuations in food availability (Bluhm and Gradinger 2008, **III**) will differentiate temporal qualities of habitats to more and less favourable breeding conditions. Effectively, seals develop distinguishable breeding seasons with late winter and early spring birth timing in the ice-related species of both polar hemispheres (Pierotti and Pierotti 1980).

The species discussed in this thesis are ice-breeders with birth timing to the late phase of ice season. The breeding event is highly synchronized on the population level as shown by cumulative counts of breeding females of the Caspian seal (Krylov and Vorozchov 1972, **IV**) and grey seals in breeding colonies (**I**). Due to the cryptic nature of the species Baltic ringed seals, there is no data on the duration of the breeding season and shape of the birth curve. Anecdotal data from the historical seal hunt indicate, that the hunting yield improved after certain calendar dates in late February or early March (Ylimaunu 2000), but those dates indicate probably times past the birth peak when the probability of finding prey was the highest for the hunters. Given the high cost of the seal hunt, earlier trips were rarely undertaken. Occasional observations and exceptional events, like stranding of numerous ringed seal pups of different age in Pärnu Bay after a storm in end of February 1989, indicate that first pups are born already in early February or even late January. Phenological differences of the breeding season are possible in different distribution sub-areas with earlier births in the southern and delayed season in the north. Aerial surveys of ringed seals have indicated two weeks difference in annual molting season, which follows shortly the breeding, in the Gulf of Riga and the Bothnian Bay (**II**).

Nursing period of the study seals is approximately three weeks for grey seals (Kovacs and Lavigne 1986, **I**), four to five weeks for Caspian seal (**IV**) and six weeks for ringed seals (Lydersen 1995). For successful weaning, a favourable habitat is required during the whole length of the nursing period. Pierotti and Pierotti (1980) link the timing of breeding to the end of ice season with trade off between thermal regulation in low winter temperature and availability of stable breeding habitat. Bluhm and Gradinger (2008) represent ice retreat related changes in productivity and marine food web which provide food for adults as well as weaned pups for replenishment of their energy reserves after fast. Thus it can be said, that all three species have optimised their nursing period according to their seasonal environmental and nutritional conditions to maximise the reproductive success while ice cover has a key role in this complex adaptation.

The timing of reproduction of East Atlantic grey seal provides an opportunity to further assess the role of ice in development of the breeding season. The different populations of grey seal breed in different times. Atlantic grey seals from September to December with different peaks in different colonies (Bonner 1972), Baltic grey seals give birth to their young from late February till April (Hook and Johnels 1972, **I**). Pups born in January and early February are reported from Amrum area, Germany (Abt and Koch 2000) and Terschelling, Netherlands (t'Hart *et al.* 1988). Such a distinctive difference in regional breeding seasons is most probably caused by formation of ice in the Baltic. The annual energetic cycle of the species would suggest onset of breeding when energetic reserves of the females are the highest, i.e. shortly after favourable season in terms of foraging (summer). Further, the thermal stress for the female and offspring are the lowest during the winter. The energetic reserves of female must sustain both the mother and offspring during the breeding event which takes, if the post-weaning fast of pup is included, notable proportion of the unfavourable foraging season (winter). Relatively low variability in environmental conditions during this season would allow wide spatial and individual variability in timing of birth. This is true for the grey seals in the East Atlantic as we see from Bonner (1972), Boyd (1984) and Twiss et al. (2002), but the assumption does not fit to the Baltic population where breeding is significantly delayed from the described optima. The delay is most probably caused by an ecological constraint: birth of offspring in the beginning of cold season would be energetically very costly for both the female and the pup despite of the fact that the female has maximised her energy reserves prior to the onset of winter. The energy reserves of female and offspring after the nursing period would be low in regard to the thermoregulatory and foraging demands in the frozen sea. This in turn would lead to high mortality or energetic cost of survival of offspring. Both are negatively selective factors in the evolutionary perspective as shown in **I**. Delay of breeding to the late phase of ice season increases energetic maintenance costs for females in winter but will eventually increase fitness through increased pup survival and availability of high quality breeding habitat – the drift ice (**I**).

The timing and high synchronicity of births of the study species correspond with the availability of specifically optimal breeding habitat. The true seals breeding cycles are annually fixed, contain an embryonic diapause and placental gestation lasts several months before birth of the young (Coulson 1981, Atkinson 1997). Thus the environmental conditions at birth influence the birth timing through pup survival and quality, i.e. over generations. Change in average environmental conditions of the breeding season can cause temporary shifts in availability of optimal breeding condition with consequences to breeding success. Hence, inheritable conservatism in birth timing can be considered as a negative factor in rapidly changing environmental conditions.

4. CONCLUSIONS

In this thesis I have used the seals trapped in the natural laboratories – the Baltic and the Caspian Seas to explore effects of changing climate on marine mammals. The studies are mere “snapshots” in an evolutionary time scale. In the library of scientific literature vast numbers of papers have been written about marine mammals and climate. Yet, the seals in land-locked aquatic habitats have their particular contributions to the knowledge and history. The ringed seals and grey seals I have worked with are cut away fraction of the globally abundant species, and the Caspian seal is an enigmatic species on its own. They have survived over thousands of generations in isolation by inhospitable environments, being still exposed to the same elements and global changes as the other seals of the world. So observations and findings in those natural laboratories render it possible to assess the role of several environmental factors, their contribution to behavioural responses, fitness and long time survival which are less evident in the open ocean populations.

The original publications included in the thesis provide unique insight into ecology of the land-locked seal populations. Paper **I** is the only comparative study of the grey seal in alternative pupping habitats, ice and land, with an emphasis on measuring the factors contributing to the breeding success. Although globally present, the alternative breeding systems are geographically separated which renders direct comparisons difficult. Our study is carried out in location where the alternatives are available in different extents according to inter-annual variation in winter severity. In this situation the seals reaction to the specific climatic conditions can be measured, which in turn allows to assess and project the possible impacts of climate change, both locally and in the context of the species in the World.

Papers **II** and **IV** present the results of aerial surveys of the Baltic ringed seals and the Caspian seals in their captive ice habitats. Both studies are based on multiple systematic aerial surveys covering the whole seal distribution area. This has not been done for either of the seals before. Paper **II** also reviews the historic knowledge and earlier studies on the status of the species in the Baltic Sea. The review and field studies date back to times before late 1990ies and since the publication, the comprehensive aerial survey effort has failed due to poor ice conditions in some or all ringed seal core distribution areas. If the process is continuous, there is doubt that several earlier studies may have become methodologically unrepeatable due to the climate change. In this light the study, in seals’ respect, is probably describing the environmental status in the end of an era in the Baltic ice history. Similar changes are observable in the Caspian environment (**IV**) and although we introduced the methodological aerial surveys to the area only in 2005 I hope the results serve as a reference or starting point for following the possible changes in the Caspian environment. Regardless of the future climate scenarios, the data collected during those aerial surveys allow to supplement several earlier works and design future studies on the ice surface.

Paper **III** is the first instrumental measurement of the Baltic ringed seal behaviour. It covers the whole year and has relatively high resolution of measurement both in time and space. Also, it is the only study so far which involves individuals from all of the three core distribution areas. Although small in sample size, the results allow to decide upon the diurnal regularity and seasonality of ringed seal behaviour and project the impact of potential changes in the seasonal environment. As discussed in this thesis, the Baltic ringed seal is highly sensitive to the ice conditions and due to its small size, reproduction is energetically very challenging. Measurement of behaviour in various environmental conditions allow to assess the energy budgets in the changing climate. The spatial restrictions of Baltic are potentially emphasising aspects, which are less measurable in the vast complexity of the main habitat for the species – the Arctic Ocean. The research is ongoing, the resolution of apparatus is improving and the study gathers value as reference point in the past.

Equipped with the results from the research, it is possible to look beyond the present state of the study species and the other ice related seals in the world. The seasonally forming critical breeding habitat, ice, is today in fragile balance with the seals' biological requirements. Ice forecast models show that change of the climatic conditions would bring about changes in seal habitat availability. The balance would change towards stability when it gets cold. Warming in an average of only some Celsius degrees would bring about critical conditions for the southern populations of the Baltic Ringed seal and the Caspian seals. In light of questions addressed in this study, I can say that deficit of ice will restrict breeding seal distribution to areas where the habitat quality, measured by both physical and biological parameters is lower compared to the present situation. On the scale of general population distribution this would probably mean a shift of the core to the North in both seas with probable loss of permanent ringed seal occurrence in the southern part of today's range. The Caspian seal breeding area will become restricted too. The conservative, ice related breeding strategy of the ringed and the Caspian seals appears to become a major negative factor during changes, which take place during only some generations. The grey seal would be less affected due to plasticity in breeding strategies, but loss of the ice platform and access to several current land breeding sites in the South and Central Baltic, due to sea level rise (Meier *et al.* 2004 b) would also restrict the breeding range of the species. All the three species would lose in breeding success through reduced offspring quality on unstable ice. The biological restrictions and geographic limitations of the habitats make the seals vulnerable to terrestrial and avian predation. As the predators are not specialists and take seals opportunistically, the remaining ice fields may turn into "predator pits" with increasing proportional predation loss rates of offspring. For the Baltic grey seal, terrestrial predators set geographical barriers for its breeding distribution.

The seals of this thesis challenge mankind. On the top of their struggle to survive is a substantial load of anthropogenic stress to the seals and their environment. Many of the factors outlined here have impact on all long-living and slowly reproducing mammals. While debating over the roots of the current rapid changes in the world climate and ecological health status we should recognize the signals from these top predators on how to survive in a complex ecosystem. How to become a part of the Earths mammalian history and not the end of it.

SUMMARY

Over the millions of years marine mammals have explored the full range of climatic and geographic latitudes of the Earth, at present several seal species show circumpolar distribution ranges. Post-glacial rebounds or other geomorphological changes have locked several seal populations into fully or partly isolated water bodies. They are adapted to live in seasonally widely fluctuating environments which in one hand provide diverse habitat but in the other hand challenge the adaptivity of the seals. This thesis is discussing the landlocked seals in their captive habitats and ecological implications therein.

I analyze the possible impacts of climate change on the fitness and survival of the land-locked grey seal (*Halichoerus grypus*) and ringed seal (*Pusa hispida botnica*) in the Baltic Sea and the Caspian seal (*Pusa caspica*). The four original publications form a firm basis to approach this analysis, as they are covering spatially, temporally or topically several key aspects relevant to the climate change. In the context of probably ongoing global warming they provide reference to the times when the change was not expressed yet (**II, III, IV**) or focus on ecological challenges, which will gather force with warming Earth (**I**, also **II–IV**).

All the involved species and subspecies are to greater or lesser extent ice-related as their distribution ranges freeze over partially or wholly during the winter months. Ice forms a temporary critical habitat to the study species so winter severity and its potential changes are discussed in the context of seal distribution, breeding strategy and success.

The current ecological balance is determined by long term average ecological conditions while climatic models show increasing temperatures in close future. Change of the ice conditions in warming climate would bring about critical conditions for the southern populations of the Baltic Ringed seal and the Caspian seals. Deficit of ice will lead to change of seal distribution to areas where the habitat quality, measured by both physical and biological parameters is lower compared to the present situation. The seals' breeding area will become restricted and thus the conservative, ice related breeding strategy of the seals appears to become a major negative factor during changes, which take place during only some generations. The grey seal would be less affected due to plasticity in breeding strategies, but loss of the ice platform and access to several current land breeding sites would also restrict the breeding range of the species. All the three species would lose in breeding success through reduced offspring quality on unstable ice. The reduced ice cover makes the seals vulnerable to terrestrial and avian predation.

Climatic changes in the environment are amplified by the anthropogenic factors like pollution, intensive fishing and disturbance which add to the stress and challenge further the survival of the land-locked seal populations.

SUMMARY IN ESTONIAN

Elu ääre peal: sisemerede hülged muutuvas kliimas

Miljonite aastate jooksul on mereimetajad asustanud kogu Maa geograafiliste ja klimaatilised piirkondade mitmekesisuse, paljud tänapäevased hülgeliigid on levinud ühtlaselt kogu polaarmerede ulatuses. Samas on jääaja järgne maatõus või teised muutused vangistanud mitmed hülgeasurkonnas osaliselt või täiesti maailmameredest eraldatud veekogudesse kus nad on kohastunud elama aasta-ajaliselt väga laialt vahelduvates tingimustes. Ühest küljest pakub selline olukord mitmekesiseid elupaiku kuid teisalt esitab tõsise väljakutse nende hüljeste kohastumisvõimele.

Käesolevas väitekirjas analüüsitakse kliimamuutuste võimalikke mõjusid Läänemere hallhülgele (*Halichoerus grypus*), viigerhülge (*Pusa hispida botnica*) ning Kaspia hülge (*Pusa caspica*) kohasusele ja elujäämisvõimalustele. Väitekirja osaks olevad neli teaduspublikatsiooni moodustavad sellele analüüsile tugeva põhja, kuna nendes uuringutes on kaetud ajalisel, ruumiliselt või sisuliselt mitmed kliimamuutustega seotud võtmeteemad. Võimaliku üleilmse soojenemise jätkudes pakuvad nad viiteid aegadesse kui see muutus end veel ei ilmutanud (**II, III, IV**) või keskenduvad ökoloogilistele väljakutsetele mis Maa soojenedes jõudu koguvad (**I**, ka **II–IV**).

Kõik käsitletud hülged on enamal või vähemal määral jääga seotud, kuna nende levilad külmuvad talvekuudel täielikult või osaliselt. Jää moodustab uuritud liikidele ajutise kuid kriitiliselt olulise elupaiga. Käesolevas töös on hüljeste levikut, sigimisstrateegiaid ja edukust käsitletud talve karmuse ning selle võimalike muutuste valguses.

Tänapäevane looduslik tasakaal on kujundatud pikaajaliste keskmiste ökoloogiliste tingimuste poolt, samas näitavad kliimamudelid lähiajal temperatuuri tõusu. Jääolude muutused soojenevas kliimas toovad kaasa kriitilise olukorra Läänemere lõunapoolsetele viigerhüljestele ja kaspia hüljestele. Jääpuudus suunab hüljeste leviku aladele kus keskkonnatingimused, mõõdetuna nii füüsiliste kui ka bioloogiliste näitajate kaudu, on praegusest ebasoodsamad. Hüljeste sigimisalad surutakse kokku ning konservatiivne, jääga seotud sigimisstrateegia võib osutuda oluliseks negatiivseks teguriks kiirete, vaid mõnd põlvkonda hõlmavate muutuste keerises. Hallhüljes võib tänu oma paindlikumale poegimisviisile olla vähem mõjutatud kuid ka nende puhul ahendab jää puudumine ning merepinna tõus selle liigi tänast poegimisaegset levikuala. Kõigile kolmele vaadeldud hülgeliigile mõjub pärssivalt jää ebastabiilsusega kaasnev järglaste madalam kvaliteet. Jääpindala kahanemine teeb hülged haavatavaks ka maismaakiskjate ja rööveluviisiliste lindude poolt.

Kliimast tulenevaid keskkonnamuutusi võimendavad inimtekkelised tegurid, näiteks reostus, intensiivne kalapüük ning häirimine. Lisandudes keskkonnast johtuvale stressile kahandab inimtegevus oluliselt sisemeredes elavate loivaliste tulevikuväljavaateid.

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ACKNOWLEDGEMENTS

It was a morning in March, 1990 when a small inflatable boat took to the sea from South Saaremaa. The vessel carried a team of determined people to the first ever scientific field study of land breeding grey seals in the Baltic. Our destination was Allirahu, a sandy islet seven kilometers off shore. We expected to be there in less than an hour. Three hours later, after several attempts and application of various but useless navigation methods we turned around in the fog. This early expedition was led by Eero Helle whose minuscule pocket compass, the only navigation instrument on board of that boat, brought us back from the sea that day. We did not get to the island then, but we kept returning there every spring, ever since that foggy voyage, with various research projects and teams from all over the Baltic and further. Eeros "compass", as I remember it from that trip, has helped me to find my course to many islands in the seas and research, out of the fog and reach of the surf.

It was an evening in late November in Moonsund when a small boat, heavily loaded with seal catching expedition gear, four crouching adults and a baby was cutting through the breakers into the darkness of rising icy storm. We had started the field works without a slightest knowledge of how to catch ringed seals in that sea area. We started with tying rope into a net for anchor stones. Then, returning from the weeks full of experimental approaches we left behind three seals with telemetry tags to fathom the seas for us. The expedition was led by Tero Härkönen, his "hand-woven net" has helped me to set and anchor the gear and ideas on soft and hard bottoms of the seas and research. To retrieve whatever you are out there to catch.

It was a sunny day of early 1999. I was sitting in the office of Alar Karis in Tartu University, trying to formulate answer to his question why am I not dedicating my time to science, not fulfilling my obligation as researcher to share the knowledge I have gathered. Well, it was easier then for me to write the Masters thesis than to come up with a plausible answer. There is none. Over the years since, regardless of my whereabouts or commitments, I have had those irregular calls, letters and greetings from Alar. All ending with the same question. *Carthago delenda est*.

It takes two to get a boat into water and out. From the first exploratory trips to grey seal breeding island back in 1991, with inflatable and paddles axed from a simple plank, to flights with hi-tech survey aircraft there has been my brother Ivar with me. While arguing on meaningless details sometimes through the night we do not need words to make the boat turn the right way. Enough salty water of seas and research has been swallowed over the years together to know, that if the engine does not start, we will paddle the boat with oars, axed from a simple plank, until it gets to the shore.

It has been a long journey from foggy Allirahu to here. The two decades have put me on different shores of the Baltic Sea, Scotland, Scandinavia and Caspia. The people, from years spent in all the boats, field stations and research aircraft would make a crew of a tall ship. Yes, a tall ship it is, with friends helping each other to master the navigation, steering and sails, to take turns in the watch and have all those intellectual conversations in the mess when the Sun is over the yardarm.

Thank you, mates!

For all the ships, imaginary and real, there is a home harbor. I thank Janika, Martin and Inger for keeping always an eye on the horizon to spot the sail.

I thank my father for leaving irresponsibly his natural history library unattended when I was in vulnerable age and I dearly remember my late mothers sigh when she was sewing me my first waterproofs from a waxed table cloth canvas.

PUBLICATIONS

CURRICULUM VITAE

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2007–2011 Member of Estonian Parliament
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Publications:

Graves, J. A., Helyar, A., Biuw, M., Jüssi, M., Jüssi, I., and Karlsson, O. 2009. Microsatellite and mtDNA analysis of the population structure of grey seals (*Halichoerus grypus*) from three breeding areas in the Baltic Sea. Conservation Genetics, 10:59–69.

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