Assessment of dietary patterns and prey consumption of marine mammals

Grey seals (*Halichoerus grypus*) in the Baltic Sea

Thesis for the degree of Doctor of Philosophy

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2012

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ISBN 91-89677-49-8

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Printed by Kompendiet, Gothenburg, 2012

Cover illustration by Karl Lundström, smoothened by Marie Svärd
Works of art by Anja Lundström Svärd

Till Farmor

som var med från början
som alltid var intresserad och undrade hur det gick
som funderade på vilken klänning hon skulle ha på disputationsdagen

“When we take seals from the ocean, what holes are left?”
(Victor Scheffer)

“... en warg i Siön, håller sig alltid framme wid Strömmings och andra fisklekar; äter och ofta då för mycket, att han ger det åter, som då kommer fiskmåsarne till godo”
(Carl von Linné)

“Utan tvivel är man inte klok”
(Tage Danielsson)

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Abstract

The Baltic Sea has been severely affected by pollution and resource overexploitation during the last centuries. The grey seal (*Halichoerus grypus*) is a good example of how a species can be affected by such changes. In the early 1900s grey seals were common, but hunting and environmental contaminants caused a rapid decline to the verge of extinction in the 1970s. Since the 1980s the population is increasing. This has intensified the conflicts between seals and fisheries, and resource competition between seals and the fishing industry is a matter of debate. This thesis examines dietary patterns and prey consumption by grey seals collected in the Baltic Sea in 2001-2005. It is the first comprehensive study of the Baltic grey seal diet since the early 1970s.

Dietary studies of marine mammals generally suffer from a number of possible biases, both concerning the methodology and how the samples are collected. This thesis applies different methods to increase the accuracy and quantifies the uncertainties of the dietary estimates. Conventional analysis of prey remains in the digestive tracts showed that the diet differed between seals from the Gulf of Bothnia and the Baltic Proper, and also between young-of-the-year animals and older animals. Herring (*Clupea harengus*) was the main prey in all areas and age groups, followed by sprat (*Sprattus sprattus*) in the south, and common whitefish (*Coregonus lavaretus*) in the north. Furthermore, the digestive-tract contents of seals collected from certain fishing gear was different from seals collected away from fishing gear. Size and numerical correction factors were used to compensate for biases introduced by digestive erosion of prey otoliths, and additional prey hard parts, other than otoliths, were used to increase the detection level of prey items.

The intake of prey biomass by the Baltic grey seal population was estimated using a bioenergetic model and data on population size and diet composition. On a larger spatial scale, the total fish removal by grey seals was negligible. Nevertheless, the predation by seals can have impact on individual prey species and local fish stocks. Concerns for competition between seals and fisheries were augmented by overlapping length distributions of seal prey and commercial catches.

The use of fatty acid signature analysis (FASA), which provides long-term dietary information, irrespectively of identifiable prey remains, to a large extent manifested the results from the conventional analysis. However, the application of FASA indicated different feeding habits between male and female grey seals, which were not found using conventional methodology. Application of FASA on marine top predators relies on the background data of the FA signatures of prey species. Grey seal prey species in the Baltic Sea showed a relatively large overlap in FA composition. The intra-specific variation in some species even exceeded the inter-specific variation, which needs to be considered when applying FASA in ecological assessments of fish predators in the Baltic Sea.

This study presents a compilation of techniques applicable to assessments of dietary patterns and ecological roles of marine mammals. The results suggest that a combination of different methods, each with its own unique potential as well as limitations, is advisable. Efforts should be made to develop and refine these methods and use them in combination with additional techniques to advance the understanding of the ecology of grey seals in the Baltic Sea.

Svensk sammanfattning

Östersjön har under de senaste århundradena genomgått storskaliga ekologiska förändringar, i takt med samhällsutvecklingen i de omkringliggande länderna. Havsområdet har drabbats hårt av miljöförstöring och resurserna har överexploaterats genom storskaligt fiske och omfattande jakt. Gråsälen är ett bra exempel på hur en art kan påverkas kraftigt av sådana förändringar. Från att ha varit mycket vanliga under början av 1900-talet påverkades sälbestånden så kraftigt av jakt och miljögifter att bara en spillra återstod på 1970-talet. Sedan mitten av 1980-talet tillväxer sälbestånden kontinuerligt, vilket har lett till ökande konflikter med fisket. Dels i form av skador på fångst och redskap, men också genom konkurrens om resursen eftersom sälarna äter samma fiskarter som människan fiskar. För att förstå Östersjöns ekosystem och ge underlag för en ekosystembaserad förvaltning behövs kunskap om födovävens utseende och vilka faktorer som påverkar den. Sälarnas roll i ekosystemet och vilka effekter de har på sin omgivning, och vice versa, kräver information om sälarnas födovanor. Denna avhandling presenterar flera metoder som är användbara för att undersöka sälars och andra marina däggdjurs val av föda och påverkan på fiskbestånd. Arbetet omfattar material insamlat under 2001-2005 och utgör den första undersökningen av gråsälens diet i Östersjön sedan början av 1970-talet.

Kort kan sägas att resultaten visar att gråsälarna i Östersjön till stor del äter samma arter och storlekar på fisk som yrkesfisket fångar. Även om sälarnas totala fiskuttag i relation till fisket är försumbart i ett större geografiskt perspektiv kan sälarna ha betydelse för enskilda arter och lokala fiskbestånd.

Ett vedertaget sätt att studera födoval hos marina däggdjur är att undersöka bytesrester från mag- och tarminnehåll från skjutna och bifångade djur. Delstudie I och II beskriver hur man kan minska de felkällor som uppstår i samband med matsmältningen i sälmagarna, samt hur man kan ta reda på hur dieten varierar. Uppskattningarna visar att gråsälarnas diet skilde sig mellan Bottniska viken och egentliga Östersjön, och yngre sälar hade en annan dietsammansättning än äldre sälar. Strömming var det viktigaste bytet bland alla åldersgrupper, i alla områden, följt av sik i Bottniska viken och skarpsill i egentliga Östersjön. Mag- och tarminnehållet från sälar som samlats in från ål- och laxfångande fiskeredskap skilde sig från de sälar som inte samlats in från fiskeredskap.

För att få en uppfattning om möjlig konkurrens mellan sälar och fiske beräknas i delstudie 3 hur mycket Östersjöns gråsälar äter av olika fiskarter och detta jämförs med yrkesfiskets och fritidsfiskets fångster. I gråsälarnas huvudsakliga utbredningsområde var sälarnas uttag av torsk, sik, lax, öring och ål i samma storleksordning som fiskefångsterna. Detta kan ses som möjliga tecken på konkurrens mellan sälen och fisket. Sälens påverkan på fiskbestånden är därför något som bör undersökas vidare.

Sammansättningen av fettsyror i sälarnas späck beror till stor del på fettsyrasammansättningen i sälarnas byten. Fettsyrorna i späcket kan därför användas som dietmarkörer, som ger information om födointaget under en längre tid, oberoende av identifierbara bytesrester i sälarnas mag-tarmkanal. I delstudie IV undersöktes hur sälarnas fettsyrasammansättning varierar och resultaten jämfördes med den korttidsbild man får från undersökningar av mag- och tarminnehåll. Variationerna i fettsyrasammansättning bekräftade till stor del de dietmönster som vi såg i analyserna av mag- och tarminnehållet, men genom att använda fettsyror upptäckte vi även skillnader i födovanor mellan hanar och honor. Detaljerade födoekologiska undersökningar baserade på fettsyror kräver bakgrundsinformation om bytesdjurens fettsyrasammansättning. I delstudie V undersöktes därför hur sammansättningen av fettsyror varierar inom och mellan olika fiskarter i Östersjön. Hos vissa arter skilde sig fettsyrasammansättningen mellan Bottniska viken och egentliga Östersjön, och skillnaderna kunde till och med vara större inom en art än mellan olika arter.

De beskrivna metoderna kan och bör vidareutvecklas och kombineras, antingen med varandra eller med andra metoder, för att ytterligare förbättra kunskapen om Östersjöns gråsälar.

List of papers included in the thesis

I Lundström, K., Hjerne, O., Alexandersson, K. and Karlsson, O. 2007.Estimation of grey seal (*Halichoerus grypus*) diet composition in the Baltic Sea. *NAMMCO Scientific Publications* 6: 177-196.

II Lundström, K., Hjerne, O., Lunneryd, S.G. and Karlsson, O. Understanding the diet composition of marine mammals: grey seals (*Halichoerus grypus*) in the Baltic Sea. *Ices Journal of Marine Science* 67: 1230-1239.

III Lundström, K., Hjerne, O. And Karlsson, O. Grey seal (*Halichoerus grypus*) prey consumption in the Baltic Sea. *Manuscript*.

IV Lundström, K., Lind, Y. and Karlsson, O. Assessment of the use of blubber fatty acids as a complement to conventional dietary analysis to study foraging ecology of grey seals (*Halichoerus grypus*) in the Baltic Sea. *Manuscript*.

V Lundström, K., Lind, Y., Walton, M. and Karlsson, O. Distinction and characteristics of fish species in the Baltic Sea based on fatty acid composition. *Manuscript*.

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Additional papers

List of related papers with contributions from the author, not included in the thesis

Gårdmark, A., Östman, Ö., Nielsen, A., Lundström, K., Karlsson, O., Pönni, J. and Aho, T. 2012. Does predation by grey seal (*Halichoerus grypus*) on Bothnian Sea herring affect herring stock estimates? Submitted to *Ices Journal of Marine Science.*

Königson, S., Hemmingsson, M., Lunneryd, S.G. and Lundström, K. 2007. Seals and fyke nets: An investigation of the problem and its possible solution. *Marine Biology Research* 3:29-36.

Königson, S.J., Lundström, K.E., Hemmingsson, M.M.B., Lunneryd, S.G. and Westerberg, H. 2006. Feeding preferences of harbour seals (*Phoca vitulina*) specialised in raiding fishing gear. *Aquatic Mammals* 32:152-156.

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Lundström, K., Lunneryd, S.G., Königson, S. and Hemmingsson, M. 2011. Interactions between harbour seals (*Phoca vitulina*) and coastal fisheries along the Swedish west coast: an overview. *NAMMCO Scientific Publications* 8:329-340.

Introduction

Information about the structure and function of an ecosystem is fundamental for responsible management and sustainable resource use. Knowledge of the feeding habits of top-level predators is essential for understanding their predatory role. This thesis examines different methods applicable to the assessment of foraging ecology of marine mammals. The work is focused on the dietary patterns and prey consumption of the grey seal (*Halichoerus grypus*), an essential top predator in the Baltic Sea.

Diet and foraging ecology of marine mammals

Marine mammals are major consumers of prey, feeding to a large extent at the ecosystem top-level (Pauly et al., 1998), and understanding of their feeding patterns is fundamental for quantitative assessments of trophic interactions. Being predators at the top of the food web, marine mammals are also integral components and important indicator species in the ecosystem. For example, dietary data can be used to monitor changes in commercial as well as un-exploited fish stocks.

Ecosystem assessments

Understanding of the dynamics in most marine ecosystems is limited, causing increasing demands on ecosystem based assessment and multi-species based fisheries management. As a consequence, the so-called ecosystem approach has been introduced in several ecosystems lately. Marine top-level predators may have impact on the structure of marine ecosystems (Paper III and references therein). However, the adequacy of including the impact of a predator, e.g. the grey seal, in a multi-species model, such as a fisheries management model, will depend on the quality of the estimated consumption of prey species. From a general point of view, better data on the feeding patterns of top-level predators are needed in multi-species ecosystem models. Examples of removals of top-level marine predators show that the predatory impact of marine mammals is more evident in simple, short-chain, food webs than in more complex, long-chained food webs (e.g. Beddington and May, 1982, Estes and Duggins, 1995, Trites, 1997, Roppel, 1984, Parsons, 1992). This motivates assessments of the predatory role of grey seals in the relatively simple Baltic food web further.

Interactions with fish stocks

Data on diet and prey consumption of a predator are needed in order to estimate the predatory impacts on various species, e.g. whether a predator population can prevent an over-exploited species to recover. Information about the prey preferences and feeding patterns is also of relevance for understanding of the responses of the predator population to environmental changes. For example, dietary variation in response to fluctuations in abundance, species composition, sizes and energy contents of prey items provide insights into how the populations of predators are influenced by changes in quality and availability of prey. Even though predatory fish are generally considered as one of the largest consumers of fish, consumption by marine mammals can be substantial, even exceeding commercial catches, and has been suggested to have impact on commercial fish stocks (e.g. Li et al., 2010, Power and Gregoire, 1978, Hollowed et al., 2000, Overholtz et al., 2008, Beverton, 1985, Yodzis, 2001, Trites et al., 1997). Nevertheless, the interactions with other top-level predators and environmental factors are complex and often unknown (Bax, 1998, Furness, 2002, Overholtz and Link, 2007, Christensen, 1996). *Vice versa*, relationships between population parameters (e.g. population size, body condition, breeding success) of marine top predators and changes in abundance and quality of food have been found in many regions, including the Baltic Sea, reviewed by Österblom et al. (2008). Reduction in food quality and nutrient deficiency have been suggested as critical factors to the population decline of Steller sea lions (*Eumetopias jubatus*) in the North Pacific (Rosen and Trites, 2005, Merrick et al., 1997, Trites et al., 2007b, Wolf et al., 2006, Calkins et al., 1998, Rosen and Trites, 2000).

Not only can the concerns of resource users and conservationists come into conflict, but also can the conservation and management objectives of both a predator and its prey species be incompatible. An example of this may be the issue of grey seals and cod in the Baltic Sea (Österblom et al. 2007, Hansson et al. 2007). Quantitative information on the removal of fish by top-level predators is thus essential for assessments of the mutual relationships between predators and their prey stocks. Even prey species that do not constitute the bulk of the diet may be affected by a predator if the predation is focused in small areas or on depressed species (Wright et al., 2007, Yurk and Trites, 2000, Butler et al., 2006). Inclusion of fish removal by marine mammals may also benefit fish-stock assessments (Tyrrell et al., 2011, Hollowed et al., 2000, Overholtz et al., 2008, Tjelmeland and Lindstrom, 2005).

Interactions with fisheries

Marine mammals are large and visible predators in the top of the food web, sometimes feeding on the same fish species that are exploited by commercial fisheries. The conflict between man and seals has thus been inevitable and has existed for a long time. Interactions between marine mammals and fisheries are reciprocal and can be divided into operational and ecological interactions. An operational interaction arises when a marine mammal cause damage to fishing gear, destroy or remove fishes from the catch, but also when a marine mammal is incidentally caught in a fishery operation. Ecological interactions arise when marine mammals and fisheries compete for the resource, either directly or indirectly via food web dynamics. Dispersal of fish parasites that use marine mammals in their cycles, e.g. the anisakid nematodes *Pseudoterranova decipiens* (sealworm) and *Anisakis simplex* (whaleworm), may reduce the commercial value of fish catches (McClelland, 2002) and is another example of indirect ecological interactions.

Seals in the Baltic Sea

Seals belong to the monophyletic group of marine carnivores entitled Pinnipedia. The pinnipeds consist of 34 extant species from three families: Phocidae (true or earless seals); Otariidae (sea lions and fur seals); and Odobenidae (walruses). Different species of phocid seals have successively colonised the Baltic basin since the deglaciation of the last ice age. Grey seals, together with the other two present species, ringed (*Phoca hispida*) and harbour (*Phoca vitulina*) seals, co-existed during a long period (thousands of years) with harp seals (*Pagophilus groenlandicus*) (Forstén and Alhonen, 1975, Ukkonen, 2002, Schmölcke, 2008, Härkönen et al., 2005). The harp seal declined rapidly during the end of the Stone Age, probably due to extensive hunting, climatic changes, low genetic diversity and inter-specific competition, and then vanished from the area (Stora and Ericson, 2004, Bennike et al., 2008).

The three species of seals inhabiting the Swedish Baltic coastline today have rather limited spatial overlaps. Harbour seals exist as one isolated population off the southeast coast (Kalmarsund) and one larger population in the South Western Baltic extending into the

Skagerrak. Ringed seals are limited to waters providing suitable ice conditions in the Gulf of Bothnia, Gulf of Finland and Bay of Riga. Grey seals are present in the entire Baltic Sea, but the majority of animals are found north of latitude 58°N (Hiby et al., 2007).

The Baltic grey seal

Besides the Baltic population two other grey seal populations inhabit the north Atlantic. One in the northwest (Labrador to New England) and one in the northeast (from the Kola Peninsula to France, via Iceland, Norway, UK and Holland). The Baltic grey seal population is separated from the Atlantic populations not only spatially, but also in behaviour, genetics and morphology (Curry-Lindahl, 1970, Biuw and Karlsson, 2003, Graves et al., 2008, Boskovic et al., 1996, Davies, 1957).

The grey seal is the most numerous and largest of the Baltic seals. The species exhibit sexual dimorphism where males grow larger than females and can reach a weight of almost 300 kg and 200 kg, respectively. The size of the Baltic grey seal population has fluctuated greatly, from an estimated number of about 88,000-100,000 animals in the early 1900s to a few thousand in the late 1970s (Hårding and Härkönen, 1999).The decrease in population size was a result of intense hunting and reduced reproduction caused by environmental toxins (Helle et al., 1976b, Helle et al., 1976a). The Baltic ringed seal decreased in a similar way during the last century, from about 200,000 to 5,000 animals (Hårding and Härkönen, 1999). Protective measures and bans on hunting and use of PCBs and DDTs during the 1970s and 1980s had positive effects on the seal population, causing a recovery in health and number of animals during the last decades (Bergman, 1999, Bäcklin et al., 2011). In 2004 the population size was estimated to 20,875 seals (Hiby et al., 2007). The population size of both grey and ringed seals in Swedish waters have continued to increase the last years. The number of counted animals during the annual survey in 2010 was about 23,000 grey seals in the entire Baltic Sea, and about 6,500 ringed seals in the Gulf of Bothnia (Härkönen et al., 2011).

Life cycle and behaviour

Grey seals spend much time in open water, with regular visits to certain haulouts for rest (McConnell et al. 1992, Goulet et al. 2001, Sjöberg and Ball 2000, Sjöberg et al. 1999). Prolonged times ashore or on ice only occur during the reproduction and moulting periods. Grey seals exhibit large degree of site fidelity, generally returning to the same haulout area after time at sea, and may even return to the same breeding place year after year (Pomeroy et al., 2000, Karlsson et al., 2005). Baltic grey seals generally breed in late February and early March, on ice or on land. The pups are nursed 2-3 weeks. Mating takes place at the end of lactation and thereafter the mother abandons the offspring. Moulting generally occur in late May and early June, when the animals spend much time on land to maintain a high skin temperature (Bonner, 1981, Feltz and Fay, 1966, Boily and Lavigne, 1996). It is during the moult, when the majority of the animals haul out, that the annual counting surveys occur to monitor trends in population size and distribution. The food intake is limited during breeding and moulting (Bonner, 1981, Mellish et al., 2000, Lidgard et al., 2005). After reproduction and moult the seals spend much time foraging at sea, to replenish their food reserves and rebuild the blubber layer until next season (McConnell et al., 1999, Sjöberg and Ball, 2000, Breed et al., 2011).

Despite their capacity of long-distance movements (Bjorge et al., 2002, Goulet et al., 2001, Sjöberg et al., 1995, McConnell et al., 1992, McConnell et al., 1999, Thompson et al., 1991, Thompson et al., 1996), Baltic grey seals seem to spend most of the time in the vicinity of their haulouts (Sjöberg and Ball 2000). Baltic grey seals have been shown to carry out most dives less than 50 m, and prefer certain areas (Sjöberg and Ball 2000), i.e. they do not seem to use areas around halouts symmetrically, as typical central place foragers.

Interactions and conflicts with fisheries
Interactions between seals and fisheries have probably occurred for as long as fishery operations have been carried out. Documented records of conflicts between seals and fisheries from the Baltic Sea date from as early as the 17th century (Broman, 1954). However, seals have historically been considered as an important resource as much as a nuisance. Products from seals generated oil, pelt, food and tools to coastal inhabitants in the Baltic region since pre-historic times (Clark, 1946). The seals have also been regarded as an important income. Bounty payments for killed seals were handed out by Swedish authorities already during the 19^{th} century until the 1970s. However, during the 20th century the profitability of seal products decreased and commercial fisheries became more effective and intense. As a consequence the view of seals in the coastal communities shifted, from being a resource to a pest, during the latter part of the last century. Although nowadays limited in both size and financial importance, the Swedish coastal fishery has been important for many coastal communities. However, following declining fish stocks, decreased profitability, changed consumer behaviour, increasing seal-induced damage to catch and gear and increasing seal stocks, the conflicts with grey seals has been considerable during recent decades (Bruckmeier and Larsen, 2008, Westerberg et al., 2000, Kauppinen et al., 2005, Jounela et al., 2006, Suuronen et al., 2006, Königson et al., 2007, Fjälling, 2005, Varjopuro, 2011).

Study area, the Baltic Sea
The Baltic Sea is a semi-enclosed shallow body of brackish water, consisting of several sub-basins, with an approximate surface area of 4 x 10^5 km^2. Large quantities of freshwater from discharging rivers mix with sea water entering the basin through the Sound (Öresund) and the Danish Belts (Ojaveer et al., 2010). As a consequence, the species diversity is limited with a mixture of marine and freshwater aquatic organisms adapted to the brackish conditions. The number of species decrease consequential with the salinity gradient from the more saline (less than 10 PSU) southwestern region to the freshwater-like (about 2 PSU) conditions in the north, and the inner parts are generally characterised by freshwater species (Kullenberg, 1981, Ojaveer et al., 1981).

The Baltic Sea has undergone large-scale environmental changes during the 20^{th} century, Beginning as an oligotrophic ecosystem, dominated by marine mammal top predators, there was a shift from seal to cod domination during the first half of the century, and yet another shift to a clupeid (sprat and herring) dominated ecosystem in the late 1980s (e.g. Österblom et al., 2007). The sizes of commercial fish stocks responded to drastically decreased marine mammal populations, eutrophication, changing oceanographic conditions and intense fisheries (Hårding and Härkönen, 1999, Elmgren, 1989, Thurow, 1997, MacKenzie et al., 2002, Alheit et al., 2005).

Aims of the thesis

The purpose of this thesis is to elaborate applicable methods for assessments of feeding habits and prey consumption of marine top-level predators, and to present the prey consumption of grey seals in the Baltic Sea. Based on the results, implications and recommendations for future work are suggested. The main topics are: (i) Accounting for biases caused by digestive erosion and unrepresentative sampling to be able to describe the diet adequately; (ii) Implementation of a consumption model for assessments of the predatory role of Baltic grey seals; (iii) Quantification of the uncertainties in the estimates of diet composition and prey consumption; (iv) Assessment of the use of additional methodology (fatty acid signature analysis) to improve the data on feeding ecology.

Estimating feeding patterns of marine mammals

Different methods can be used to collect dietary data from marine mammals. Foraging typically takes place below sea surface at different spatial and temporal scales. Due to difficulties in direct measurements of feeding patterns and prey consumption, indirect methods are used to produce quantitative estimates. The following section describes the basis of the methods used: analysis of prey remains in digestive tracts (Papers I and II); analysis of fatty acids (Papers IV and V); bioenergetic modelling and estimation of prey consumption (Paper III). In addition, complementary methods using stable isotopes, prey-DNA remains and biotelemetry are also described briefly.

Robust prey remains from faecal scats and digestive tracts

Traditional studies of the diet of marine mammals rely on analysis of undigested prey remains identified in faecal scats or digestive tracts (e.g. Pierce and Boyle, 1991). Provided that suitable haulout sites are accessible, collection and analysis of faecal scats can be an effective method to analyse dietary patterns of pinnipeds. However, this method lacks individual data connected to the examined samples (e.g. age, sex, health status and number of individuals that were the cause of the collected scats), and may be biased towards animals that forage close to the haulout and/or visit the haulout site more frequently. On the contrary, analysis of digestive tract contents provides individual information about the examined animals, but this method can be limited by obtainable sample size and impact on the population (in forms of dead animals). Additionally, animals collected from fisheries operations may be biased towards the target species of particular fisheries (Pierce et al., 1991). Nevertheless, the use of hard parts of prey, such as otoliths and vertebrae, facilitates estimation of species and size of ingested prey items. Skeletal prey remains can to a varying degree be determined to species or a higher taxonomic level by means of identification keys and reference material, whereas prey size can be estimated by the use of regression equations that convert the size of the prey remain to the length and weight of the consumed fish (e.g. Härkönen, 1986, Watt et al., 1997, Leopold et al., 2001). Limitations of the use of undigested prey remains in dietary assessments is that only a snapshot picture of the last meals is provided and that the methodology is dependent on ingestion of identifiable robust hard parts, i.e. cases when no hard parts are eaten are not considered. Moreover, digestive erosion affects both the sizes and numbers of obtained prey remains, which may lead to biased estimates of diet composition and prey consumption (e.g. Jobling and Breiby, 1986, Christiansen et al., 2005, Harvey, 1989, Tollit et al., 1997, Bowen, 2000, Grellier and Hammond, 2006).

Fatty acid signature analysis

Fatty acid signature analysis (FASA) is a relatively new technique that can be used to overcome some of the limitations of conventional dietary analysis (e.g. Iverson, 1993, Budge et al., 2006). FASA is applicable irrespective of identifiable robust prey remains, i.e. also cases when only soft tissues are consumed will be regarded. In fact, this method does not depend on the collection of digestive tracts or faecal scats, which is of particular interest for studies of free-ranging animals at sea (e.g. whales). The basis of FASA is the diversity of long-chain (between 14 and 24 carbon atoms) FAs available in the marine ecosystem and the characteristic FA patterns of different organisms. Specific prey FAs enter the circulation intact and are incorporated in the blubber of marine mammals with little modification. Hence, the blubber FA composition in the predator will depend on the FA composition of its diet (e.g. Kirsch et al., 1998, Iverson et al., 2004, Budge et al., 2006, Iverson et al., 2007, Iverson et al., 1995). The method provides dietary information integrated over space and time, and can be used both qualitatively and quantitatively. Qualitative information is gained by analysing the FA variability for comparison of patterns in foraging ecology among species, population segments, areas or time periods (e.g. Budge et al., 2008, Thiemann and Iverson, 2007, Thiemann et al., 2008, Beck et al., 2007b, Walton and Pomeroy, 2003, Walton et al., 2000, Käkelä et al., 1993, Strandberg et al., 2011, Cooper et al., 2009, Meynier et al., 2008). The quantitative application is to get more specific dietary information, by comparing the blubber FA composition to the FA composition of potential prey species (Iverson et al., 2004, Beck et al., 2007a, Nordstrom et al., 2008, Iverson et al., 2007, Tucker et al., 2008, Meynier et al., 2010, Tucker et al., 2009, Wang et al., 2010). However, FASA reveals less detailed dietary information than conventional hard-part analysis and quantitative interpretation of the complexity of the FA signatures demands statistical modelling, in combination with knowledge on predator FA metabolism and the FA signatures of prey species (Iverson et al., 2004, Käkelä et al., 2009, Käkelä et al., 2010).

Bioenergetic modelling and estimation of prey consumption

Knowing the diet composition and energy contents of comprised prey species, the prey consumption of a predator can be estimated from its energy balance. Combined with the size and structure of the population, the energy requirement and prey consumption of individuals can be extended to the population level by using bioenergetic modelling. Consumption models, ranging from simple to more detailed equations, are commonly used in studies of marine mammal prey consumption and ecosystem dynamics (e.g. Boyd, 2002, Folkow et al., 2000, Hammill and Stenson, 2000, Mecenero et al., 2006, Mohn and Bowen, 1996, Nilssen et al., 2000, Noren, 2011, Olesiuk, 1993, Winship et al., 2002, Trzcinski et al., 2006).

Additional methods

Similar to FASA, results from stable isotope analysis are integrated over space and time. This technique can be applied to obtain information about the trophic relationships in an ecosystem as well as foraging habitat and region of the predator, but detailed information about the species composition of the diet is more limited (e.g. Hobson, 1999, Cherel et al., 2008, Hobson et al., 1997, Huckstadt et al., 2007, Zhao et al., 2004, Lesage et al., 2001, Angerbjorn et al., 2006, Bearhop et al., 2004). Genetic analysis of prey remains from digestive tracts and faecal droppings can be used to reveal information about consumed prey species. The advantage of using DNA technique to identify prey species is that it provides objective information and, just as FASA and stable isotope analysis, is independent of consumed prey hard parts. However, this technique does not give any information of the size of the consumed prey items (e.g. Marshall et al., 2010, Bowles et al., 2011, Deagle et al., 2007, Deagle and Tollit, 2007, Parsons et al., 2005, Tollit et al., 2009). Telemetry systems using acoustic tags, radio transmitters or the global positioning system (GPS) in combination with data loggers can provide essential data on the movement patterns and foraging habitats of free-ranging marine mammals. Systems can be developed to collect also physiological and oceanographic variables and even visual observations (e.g. Simpkins et al., 2001, McConnell et al., 1999, Sjöberg and Ball, 2000, Le Boeuf et al., 2000, Thompson et al., 1996, Suryan and Harvey, 1998, Bowen et al., 2002, Davis et al., 1999, Parrish et al., 2008, Hooker et al., 2002, Hooker and Boyd, 2003, Austin et al., 2006, Greaves et al., 2004, Biuw et al., 2007). Direct visual observations (Stanley and Shaffer, 1995, Jeffries et al., 2000, Wright et al., 2007) and serological methods (Pierce et al., 1990b, Pierce et al., 1990a, Boyle et al., 1990) have also been used in dietary assessments of marine mammals.

Papers in brief

Dietary data were obtained from 299 grey seals collected in the Baltic Sea between year 2001 and 2005. The diet composition and fish removal by Baltic grey seals was estimated from digestive tract contents and bioenergetic modelling (Papers I, II and III). Feeding patterns obtained from conventional dietary methodology were compared to the variability in blubber FA composition, and the FA characteristics of important prey species were examined (Papers IV and V). The studies and their outcomes are presented briefly in the following paragraphs.

Accounting for the digestive erosion of prey remains (Paper I)

Using a material consisting of the digestive tract contents of 145 grey seals collected between 2001 and 2004, we evaluated the use of different dietary methods to estimate the diet composition and compensate for biases introduced by digestive erosion. We used additional hard-part structures other than otoliths to increase the detection level of prey items. Species- and erosion-class specific numerical and size correction factors (NCF; SCF) were used to compensate for digestive erosion of numbers and sizes of otoliths. The SCFs were calculated from the average size ratio of otoliths from the different erosion classes, whereas the NCFs were generated from a relationship between otolith size and recovery rate from feeding studies of captive seals. We estimated both numerical and biomass contribution of the different prey species, either by weighting each seal in proportion to the total prey biomass in its digestive tract (pooled data), or by giving each seal the same weight independently of its total content (seal weighted).

The differences in diet composition between estimates with and without numerical correction were relatively small, but the proportion of prey species with small otoliths (and large numerical correction factors) increased, in relation to species with larger otoliths. When pooling the data the estimated diet composition will be dominated by seals containing large quantities of consumed prey, whereas in the seal-weighted model each seal contributes equally which seems to smooth out the diet composition, making rare species more important. By using all hard parts the number of identifiable prey items increased, and resulted in higher estimates of the number and biomass contributions of cyprinids, salmon, trout and sculpins. For large prey items (e.g. salmon), if the seals do not eat the head of the fish, using other structures than otoliths will improve the estimated diet composition. The application of SCFs had impact on the size distribution of consumed prey, with a shift towards larger, and consequently older, individuals and an increase in size overlap with commercially important fish.

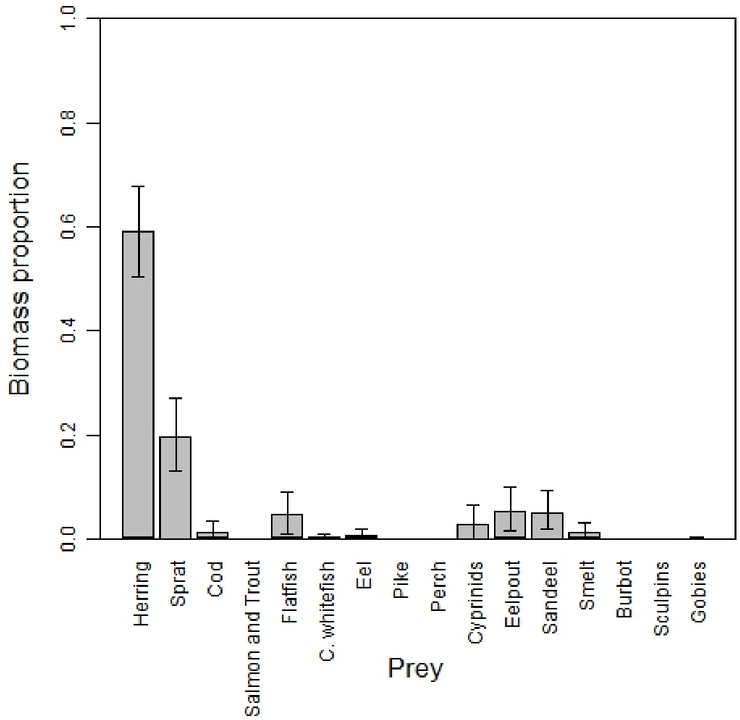
This was the first description of the diet of grey seals in Swedish waters since the 1970s (Söderberg, 1972, Söderberg, 1975). Although the results differed, dependent on the choice of dietary estimation method, the general pattern was that herring dominated the diet, followed by common whitefish, sprat, cyprinids, salmonids (*Salmo* spp.), eelpout and flounder. In addition, the results indicated dietary differences both between age groups and between the Gulf of Bothnia and the Baltic Proper.

Assessing how the estimated diet relates to extrinsic and intrinsic factors (Paper II)

Besides digestive erosion of digestive tract contents (Paper I), other important sources of error in dietary assessments of marine mammals are linked to sampling schemes. Random sampling is often hard to achieve, which may lead to skewed sample distribution among, for example, age groups, areas and seasons. We assessed the effects of various external factors that could affect dietary estimates, using multivariate ordination techniques. The diet was estimated based on the mean of the biomass values obtained from the two different methods in Paper I, using all hard parts and application of correction factors, respectively. For more appropriate estimations of length and weight of prey items we generated regression equations for cod, common whitefish, herring and sprat based on fish specimens collected in the Baltic Sea.

The diet differed significantly between the northern and southern Baltic (Figures 1 and 2), probably to a large extent caused by the distinct salinity gradient and accompanying changes in prey species composition. Herring dominated the diet in all areas, followed by sprat in the south and common whitefish in the north. The diet composition of pups was characterized by more small, non-commercial species such as sandeels and viviparous blenny, and differed significantly from the diet of juveniles and adults. The diet of juveniles and adults, on the other hand, was characterized by more cod, cyprinids, salmon, and trout (Figures 1 and 2). Herring, common whitefish, and sprat were common prey among all age groups. The diet composition of seals not collected from fishing gear differed significantly from the diet of seals collected from both eel traps and salmonid gear. Hence, the sampling condition actually does seem to affect the estimated diet. The main differences found seemed however to be the relative increase in the abundance of herring in samples not collected from fishing gear, rather than which species the gear was primarily targeting. No support for dietary differences related to season, sex was found. Together with Paper I, this study established an increased importance of herring and sprat in the diet of Baltic grey seals since the late 1960s and early 1970s, while the importance of cod had decreased.

A



B

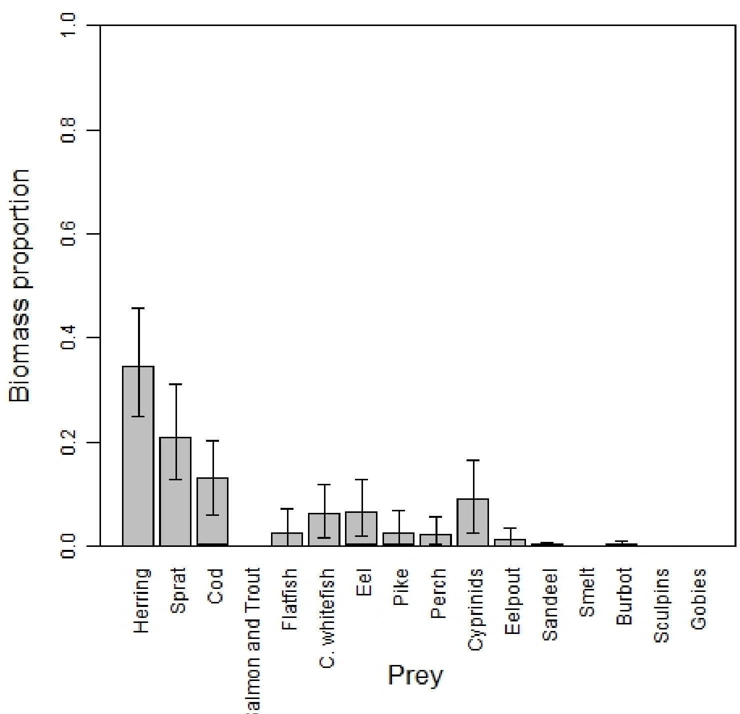
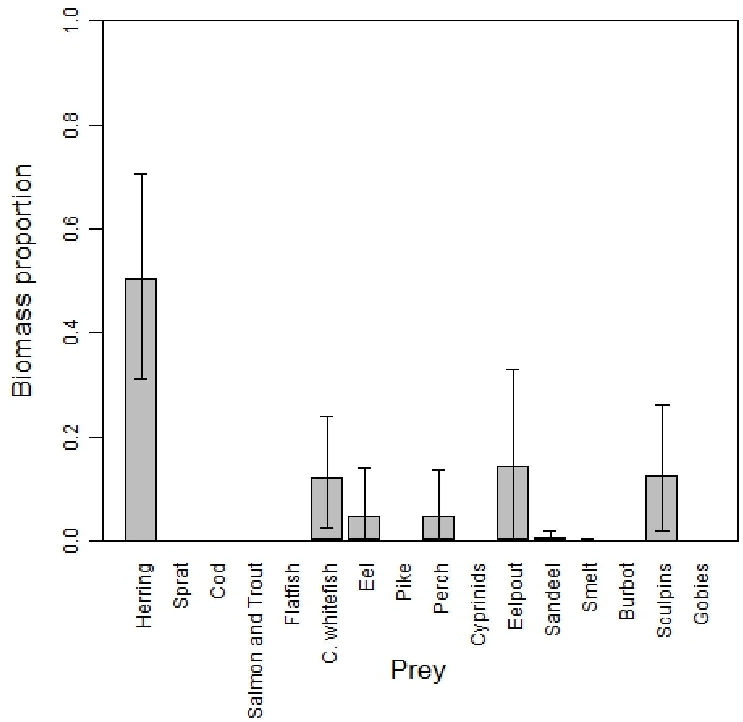


Figure 1. Estimated biomass proportions of prey species in the grey seal diet in the Baltic Proper in 2001-2005, in relation to age groups. A: pups; B: juveniles and adults.

A



B

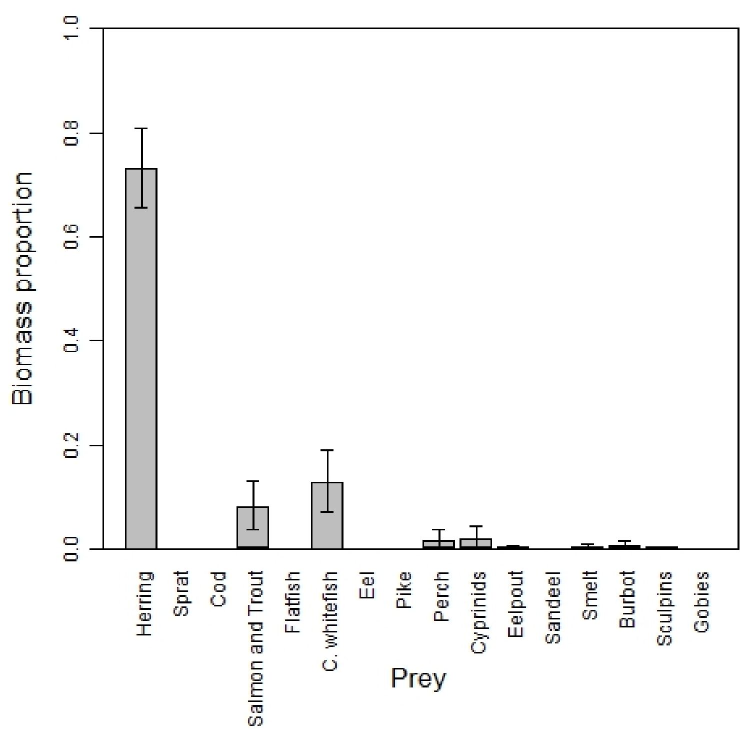


Figure 2. Estimated biomass proportions of prey species in the grey seal diet in the Gulf of Bothnia in 2001-2005, in relation to age groups. A: pups; B: juveniles and adults.

The uncertainty of the estimated dietary composition was quantified by bootstrap calculation of confidence intervals. The limited sample size and consequential large uncertainties in the estimates of more rare prey species indicate that more material is desirable to achieve a more detailed description of the diet. We propose that efforts are made to achieve a balanced and representative sampling of seals in terms of age group, area, and sampling condition, taking into account both latitudinal and inshore–offshore gradients.

Estimation of energy requirement and prey consumption (Paper III)

The conflicts between grey seals and fisheries have become more intense during the last decades, mainly because of damaged catch and fishing gear, but also because of potential competition for the fish resource. Based on estimates of diet composition, energy requirement, population size, population structure and prey energy contents, we quantified the magnitude of grey seal predation in terms of biomass of different prey species in the Baltic Sea in 2004. We also calculated uncertainty limits of the consumption and compared the length distribution of prey items in the seal diet with length distribution of commercial catches.

On a larger spatial scale (the Baltic Sea), the seal consumption was negligible to commercial catches. Regionally, however, the consumed fish biomass seemed to be of the same magnitude as fishery catches, or even larger, for some species. The estimated consumption of common whitefish, salmon, trout, cod and eel indicated potential competition with fisheries and possible effects on the fish populations that should be investigated further.

In terms of length distribution there was an evident overlap between commercial landings and grey seal predation, especially for herring and sprat, of which the grey seal predation was directed towards larger prey items. The similar magnitudes of fish removal by fisheries and seals, in combination with overlap in preferred prey sizes, indicate a competition between grey seals and the fishing industry. However, uncertainty levels were large and more data are needed to be able to generate a refined consumption model and more detailed quantification of prey consumption. We recommend continuous monitoring of size, distribution, structure and feeding habits of the Baltic grey seal population. In combination with additional information on activity budgets and energy requirements of grey seals, as well as prey energy contents, a more detailed prey consumption model could be applied.

Nevertheless, the consumption model presented in this study constitutes a starting point for further assessments of the predatory role of Baltic grey seals, and possible competition between grey seals and fisheries in the Baltic Sea.

Foraging ecology of Baltic grey seals assessed by fatty acid signature analysis (Paper IV)

Fatty acid signature analysis (FASA) can be a useful tool in assessments of foraging ecology, particularly in wide-ranging animals where dietary data generally are limited and hard to obtain. In this study we examined the FA composition in grey seal blubber samples from 154 animals collected in the Baltic Sea between 2001 and 2005. We compared the feeding patterns assessed from FASA with results obtained from conventional analysis of prey remains found in digestive tracts (Paper II). The differences in FA composition related to area, age and sex were statistically significant, supporting to a large extent the feeding patterns that have been found using conventional methodology (Paper II). No differences related to season or method of collection were found. The general blubber FA composition differed from that of marine seal populations and could be related to brackish and freshwater environments. Our results support the high proportion of herring in the grey seal diet as has been shown using conventional analysis of prey choice (Papers I and II).

Due to the small number and unbalanced geographic age distribution of samples in this study, we stress the importance of collecting and analysing a larger material, particularly from the intermediate central areas, to study geographic differences in diet and foraging ecology in more detail. Nevertheless, this study supports the application of FASA to obtain a long-term picture of the feeding habits of marine top-level predators, not relying on identifiable prey remains. Results based on FA signatures need, however, to be combined with conventional methodology as well as additional techniques, such as DNA, stable isotopes, QFASA and biotelemetry, to obtain a more comprehensive picture of the diet and foraging ecology.

Distinction and characteristics of fish species in the Baltic Sea based on fatty acid composition (V)

This study presents the FA composition and fat content of 21 fish species that are potential prey species of grey seals (Papers I and II) and other top-level predators in the Baltic Sea. We examined how different fish species could be distinguished based on their FA composition and how the intra-specific FA variation related to different areas within the Baltic Sea. The overlap in FA composition among species was relatively large, but inter-specific differences became more evident when the data were transformed. Within-species differences between the Gulf of Bothnia and the Baltic Proper were significant and even exceeded the inter-specific variation in some species. The distinct geographic differences in FA composition in the analysed fish specimens manifest the importance of considering feeding areas and spatial movements of fish eating predators in ecological assessments based on FASA in the Baltic Sea.

For a more detailed interpretation of FA patterns of Baltic piscivores and application of FASA in quantitative estimates of the diet composition (QFASA), additional background data on the variability of FA signatures are needed. A FA library of prey species consisting of a larger material from a wide range of species and size classes, including temporal and geographic variation, is needed for better understanding of the FA patterns in the Baltic Sea.

Future perspectives

The results of this study can be regarded a basis of grey seal diet in the Baltic Sea in the early 2000s, available for future comparisons. Studying the diet of over time increases the understanding of not only the seal population, but also the Baltic Sea ecosystem. Dietary studies are one way to monitor environmental changes and large-scale ecosystem transformations at different spatial and temporal scales, e.g. alterations in prey-species abundances, quality of food, climate effects and health status. Monitoring fish stock fluctuations and environmental changes in marine ecosystems has been suggested and used for seabirds (e.g. Iverson et al., 2007, Robinette et al., 2007, Piatt et al., 2007, Montevecchi, 2007, Bost et al., 2008, Mallory et al., 2010, Cairns, 1992) as well as marine mammals (Trites et al., 2007a, Riemer et al., 2011, Bredesen et al., 2006, Sinclair et al., 2008, Sinclair and Zeppelin, 2002, Laidre et al., 2008). Thus, long-term monitoring of dietary patterns of a top-level predator may provide early warning signals of large-scale environmental changes affecting the predator population as well as fish stocks. Grey seal is a suitable indicator species of the Baltic Sea, and a relatively large number of animals are collected on annual basis.

Conclusion

I present a comprehensive use of dietary information from grey seals collected from hunt and fishery operations in the Baltic Sea. The methods used constitute a useful compilation of techniques that can be applied in assessments of dietary patterns and ecological roles of marine mammals. Each method has its limitations, but also potential for improvement. As the Baltic Sea ecosystem has undergone large-scale changes during the last decades, in combination with high fishing pressures and fluctuating seal populations, I recommend continuous assessments of the diet and foraging ecology of Baltic grey seals. A strategic scheme should be developed to include collection and analysis of long-term dietary data in the regular monitoring of health-status of Baltic seals coordinated by the Swedish Museum of Natural History. With additional collection of samples (e.g. faecal scats in areas of particular interest) and the combination of conventional dietary analysis with biochemical methods and biotelemetry studies, a more detailed picture of the feeding patterns of grey seals as well as changes in the ecosystem could be acquired, at different spatial and temporal scales.

Acknowledgements

Arbetet med den här avhandlingen låg under en längre tid vilande. Av olika anledningar, och inte enbart i väntan på bättre tider. Att avhandlingen till slut blev färdig har jag, förutom mig själv, främst Olle Karlsson och Teija Aho att tacka för. Olle, min handledare, bidrog med sin framåtdrivande lugna vänskap, uppmuntrande förståelse och inspirerande kunskaper. Du väckte också avund med dina strapatser söderöver och överraskade som postpunkkonnässör. Synd att vi inte träffas oftare, tur att vi fortsätter arbeta tillsammans. Teija, du lyssnade på mina idéer, insåg vikten av feedback och långsiktighet samt försåg mig med GD, motivation, förtroende och tid. Tack även för förträffligt sällskap bland norrländska kluriheter och Helsingfors bakgator. Synd att vi inte träffas oftare, tur att vi fortsätter arbeta tillsammans. En annan Olle som betytt mycket är dito Hjerne. Du har bidragit med assisterande handledning, förbättrande analyser och kommentarer samt nattlig programmering. Du tog dig tid till engagerade granskningar och lyckades alltid se på våra arbeten med kritiska och konstruktiva ögon. Utan dig hade arbetet inte nått lika långt. Synd att vi inte träffas oftare, men jag hoppas att vi fortsätter vårt samarbete. Sven-Gunnar Lunneryd bidrog till arbetet med avhandlingen i ett tidigare skede och underlättade kontakter med fiskare och insamling av prover. Jag vill även tacka Håkan Westerberg för att du beredde en väg in till arbetet med sälfrågor, via ålar, teknisk kringutrustning, reconciliation action plans och Goran Bregovic.

I samband med vistelserna på Tjärnö marinbiologiska laboratorium bättrades tillvaron på av bland andra Lars, Lena, Helena, Mia, Tuuli, Sara, Totte, Hans G, Bertil, Benno och Göran. Karin och Maria muntrade upp och effektiviserade genomgången av alla sälmagar.

På Fiskeriverkets huvudkontor i Göteborg livades världen upp av Stig, Charlott, Ingvar, Malin A, Patrik, Åsa, Karin & Martin, Elle, David, Ingmar, Fredrik och Anna. Deltagare som kom och gick, och till och med stannade, inom alla Sälar&Fiske-projekt. Ni hjälpte till med att skapa roliga vistelser i fält, samt en och annan nattklubbseskapad. Även om detaljerna bitvis är suddiga minns jag er väl: Sara, Malin, Arne, Maria, Fredrik, Mikael, Dan och David.

Personalen på Naturhistoriska riksmuseets enhet för miljögiftsforskning var alltid välkomnande och trevlig att träffa och samarbeta med. Dessutom bidrog ni med alla sälprover och ovärderlig bakgrundsinformation. Lotta, Britt-Marie, Ylva, Anna, Maria, Annika och Tero, jag tror att vi har skapat förutsättningar för ett långvarigt samarbete.

I och med att jag så smått börjar lära mig konsten att sitta på två kontorsstolar på samma gång vill jag tacka alla kollegor för den inspirerande, vänliga, uppsluppna och lindrigt befängda atmosfär ni skapar, både på Havsfiskelaboratoriet i Lysekil och på Kustlaboratoriet i Öregrund. Tack till Jocke för att du tog emot mig på Hlab. Tack till Mikaela för att du gav mig möjlighet att färdigställa avhandlingen, och att du dessutom förgyllde junimorgnarna på potatisupptagaren på Bjärehalvön i slutet av 80-talet.

Jag uppskattar även all den hjälp jag fått av Britta Carlström, Eva Sers samt universitetsbiblioteken på GU och SLU för att få fram alla gamla vetenskapliga artiklar. Tack till familjen Westlund i Skärså för lärorik, god och väldigt trevligt bemötande och sällskap. Tack till mina examinatorer Rutger Rosenberg och Kristina Sundbäck. Ni bidrog med uppmuntran och

Kristina tog sig an min avslutande termin och guidade mig genom universitetsvärldens disputationspraxis, vilket underlättade betydligt.

Det allra största stödet och den mesta uppmuntran har emellertid kommit från min familj. Detta kunde visa sig på olika sätt. Marie, du gav mig möjlighet att jobba ostört under slutskedet och utan din förståelse och ditt tålamod hade det aldrig gått. Dessutom förbättrade du text och layout. Anja, Signe och Hillevi, ni undrade varför jag i hela fridens namn skulle sitta och jobba ostört när jag istället kunde komma en trappa upp och leka. Fortsätt så, jag älskar er.

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