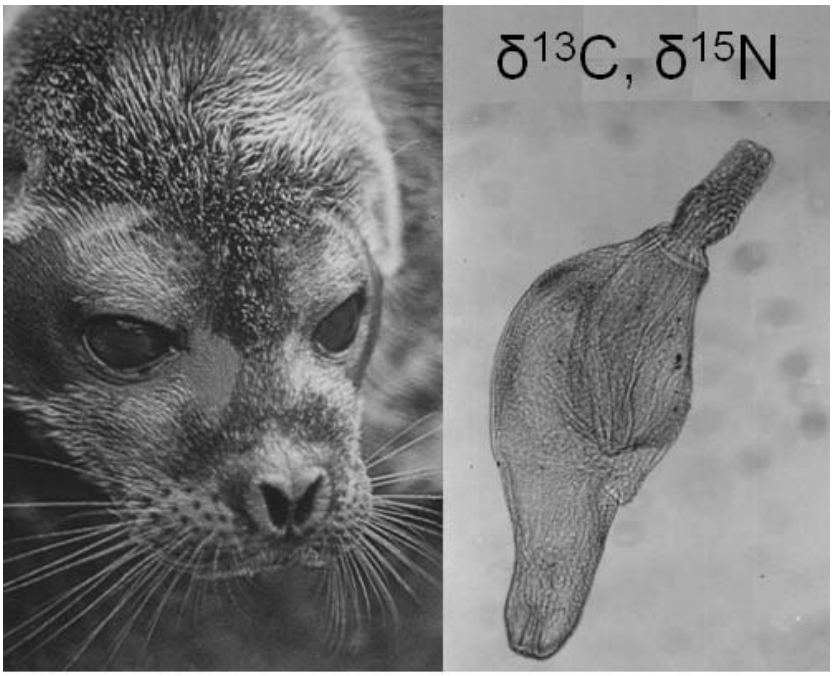
JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE
174

Tuula Sinisalo

# Diet and Foraging of Ringed Seals in Relation to Helminth Parasite Assemblages




JYVÄSKYLÄN YLIOPISTO

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE 174

Tuula Sinisalo

# Diet and Foraging of Ringed Seals in Relation to Helminth Parasite Assemblages

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa YAA303
maaliskuun 24. päivänä 2007 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Science of the University of Jyväskylä,
in the building Ambiotica, Auditorium YAA303, on March 24, 2007 at 12 o'clock noon.

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2007

# Diet and Foraging of Ringed Seals in Relation to Helminth Parasite Assemblages

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE 174

Tuula Sinisalo

# Diet and Foraging of Ringed Seals in Relation to Helminth Parasite Assemblages

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2007

Editors
Timo Marjomäki
Department of Biological and Environmental Science, University of Jyväskylä
Irene Ylönen, Marja-Leena Tynkkynen
Publishing Unit, University Library of Jyväskylä

Jyväskylä Studies in Biological and Environmental Science
Editorial Board

Jari Haimi, Timo Marjomäki, Varpu Marjomäki
Department of Biological and Environmental Science, University of Jyväskylä

Cover picture: Young ringed seal in the Bothnian Bay (photo by Eero Helle)
and Corynosoma semerme cystacanth parasite (photo by Tuula Sinisalo)

URN:ISBN:9789513927905
ISBN 978-951-39-2790-5 (PDF)

ISBN 978-951-39-2782-0 (nid.)
ISSN 1456-9701

Copyright © 2007, by University of Jyväskylä

Jyväskylä University Printing House, Jyväskylä 2007

# ABSTRACT

Sinisalo, Tuula
Diet and foraging of ringed seals in relation to helminth parasite assemblages
Jyväskylä: University of Jyväskylä, 2007, 38 p.
(Jyväskylä Studies in Biological and Environmental Science
ISSN 1456-9701; 174)
ISBN 978-951-39-2790-5 (PDF), 978-951-39-2782-0 (nid.)
Yhteenveto: Perämeren ja Saimaan norpan suolistoloisyhteisöt ja niiden hyödyntäminen hylkeen yksilöllisen ravintoekologian selvittämisessä
Diss.

In this study of Baltic ringed seal (*Phoca hispida botnica* Gmelin) and Saimaa ringed seal (*Phoca hispida saimesis* Nordquist) populations, the main aim was to infer the dietary variation between individual seals living in atypical brackish and freshwater habitats by combining data from intestinal metazoan parasites, from alimentary tract contents analysis, and from stable isotope ratio analysis ($\delta^{13}C$ and $\delta^{15}N$). Three acanthocephalan species, *Corynosoma semerme*, *C. strumosum* and *C. magdaleni* have adapted to the brackish water, but in Lake Saimaa only *C. magdaleni* has survived. Sexual selection plays an essential role in determining the spatial distribution of *C. magdaleni* within the lake seal gut. The combined approach allowed inferences of individual seal feeding behaviour in the Bothnian Bay. Some seals fed on a similar mixture of coastal and benthic fish and isopods (*Saduria entomon*), some foraged mainly on fourhorn sculpin (*Myoxocephalus quadricornis*) and ruffe (*Gymnocephalus cernuus*), and some included mainly herring (*Clupea harengus membras*) in their diets. One seal evidently fed on salmon (*Salmo salar*) and one seal consumed a high proportion of isopods as well as three-spined sticklebacks (*Gasterosteus aculeatus*). The results also indicated that the breeding and moulting period imposes foraging restrictions on all seals but especially on nursing females. The differences between females possibly reflect individual variation in the onset and duration of parturition and lactation. In future stable isotope analysis from non-destructive sampling of seal hair, nail or whisker tissue might be linked to provide further information about the diets of endangered seals without large samples sizes and without causing harm to animals.

Keywords: acanthocephalan; Baltic Sea; *Corynosoma magdaleni*; *C. semerme*; *C. strumosum*; diet; foraging; helminths; Lake Saimaa; *Phoca hispida botnica*; *P. h. saimensis*; ringed seal; stable isotope ratio analysis.

*Tuula Sinisalo, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland*

**Author's address** Tuula Sinisalo
Department of Biological and Environmental Science
University of Jyväskylä
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
Email: tsinisal@bytl.jyu.fi

**Supervisors** Professor E. Tellervo Valtonen
Department of Biological and Environmental Science
University of Jyväskylä
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Professor Roger I. Jones
Department of Biological and Environmental Science
University of Jyväskylä
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

**Reviewers** Emeritus Professor John Holmes
4711 117A St NW
Edmonton AB
T6H 3R9
Canada

Docent Jouni Taskinen
University of Joensuu
Karelian Institute
Department of Ecology
P.O.Box 111
80101 Joensuu
Finland

**Opponent** Dr. Kenneth MacKenzie
University of Aberdeen
Tillydrone Avenue
Aberdeen AB24 2TZ
UK

# CONTENTS

LIST OF ORIGINAL PUBLICATIONS

1 INTRODUCTION ....7
1.1 General introduction ....7
1.2 Previous parasite community studies ....8
1.3 The helminth communities of seals ....9

2 DIETARY STUDIES OF RINGED SEALS ....11
2.1 Identification of prey from the remains in alimentary canal ....11
2.2 Intestinal parasites in dietary studies ....12
2.3 Stable isotope analysis in dietary studies ....12
2.4 Aims of the study ....13

3 MATERIAL AND METHODS ....15
3.1 Ringed seals living in atypical habitats ....15
3.2 Life cycle of *Corynosoma* species ....16
3.3 Samples for parasitological and alimentary tract content studies ....16
3.3 Samples for stable isotope analysis ....17

4 RESULTS AND DISCUSSION ....19
4.1 Parasite community studies ....19
4.2 Dietary studies ....22

*5* CONCLUSIONS ....25

*Acknowledgement* ....27

YHTEENVETO (RÉSUMÉ IN FINNISH) ....28

REFERENCES ....30

## LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-V. I planned and performed large part of the work in each paper, except the intestinal parasites were jointly collected together with Markku Raatikainen from the intestines of Saimaa seals and with Joanne Kitchen from Baltic seals. The co-authors contributed to data analysis and manuscript writing, but I was main responsible for writing all articles.

I Sinisalo, T. & Valtonen, E. T. 2003: *Corynosoma* acanthocephalans in their paratenic fish hosts in the northern Baltic Sea. Parasite 10: 227-233.

II Sinisalo, T., Kunnasranta, M. & Valtonen, E. T. 2003. Intestinal helminths of a landlocked ringed seal (*Phoca hispida saimensis*) population in the eastern Finland. Parasitology Research 91: 40-45.

III Sinisalo, T., Poulin, R., Högmander, H., Juuti, T. & Valtonen, E. T. 2004. The impact of sexual selection on *Corynosoma magdaleni* (Acanthocephala) infrapopulations in Saimaa ringed seals (*Phoca hispida saimensis*). Parasitology 128: 179-185.

IV Sinisalo, T., Valtonen, E. T., Helle, E. & Jones, R. I. 2005. Combining stable isotope and intestinal parasite information to evaluate dietary differences between individual ringed seals (*Phoca hispida botnica*). Canadian Journal of Zoology 84: 823-831.

V Sinisalo, T., Jones. R. I., Helle, E. & Valtonen, E. T. Changes in diets of individual Baltic ringed seals (*Phoca hispida botnica*) during their breeding season inferred from dual stable isotope ratios of multiple tissues. Submitted.

# 1 INTRODUCTION

## 1.1 General introduction

The parasitic way of life is probably one of the most common life forms on earth (May 1988, Windsor 1997, 1998): virtually every species is parasitized at some point during its lifetime (Price 1980). Parasitism is a close association of two coevolving organisms, in which one (the parasite) derives from the other (the host) some benefit (food and shelter). However, in a heavy infection a parasite could cause harm and become pathogenic to a host individual (Anderson & May 1979, May & Anderson 1979).

Parasite communities have proved to be excellent model systems for investigations of general ecological theories (Hamilton et al. 1990, Esch & Fernandez 1993, Moore 2002) and they have been proposed as excellent indicators of the biodiversity both on host species and at the ecosystem level (Huxham et al. 1995, Marcogliese 2002, 2003, Poulin et al. 2003, Chambers & Dick, 2005). Moreover, since many helminth parasites (parasitic worms) have complex life cycles involving several different hosts depending on trophic interactions for transmission, they can also provide valuable information on host migration and diet (Williams et al. 1992, Marcogliese & Cone 1997).

Although a food web typically contains more parasite-host links than predator-prey links (Lafferty et al. 2006), parasites are rarely incorporated into dietary studies (Pascual et al. 1996, Marcogliese & Cone 1997, Marcogliese 2002). In fact data from intestinal parasite communities in the host could highlight many methodological problems and inconsistencies in food webs (Huxham et al. 1995, Thompson et al. 2005), clarify the discrepancies in host diet (Kennedy et al. 1992) and even reveal the individual foraging habits of the hosts (Marcogliese 2002). In this thesis I have studied variations in the helminth parasite communities of two seal populations and used this information as the basis for drawing inferences about the foraging behaviour and diets of individual seals.

## 1.2 Previous parasite community studies

Wisniewski (1958) and Dogiel (1961) first recognized the variation in helminth community structure between fish populations sampled from adjacent lakes. Yet, the actual birth of quantitative parasite community research was marked by Holmes (1961) with his experimental investigation of interactions between cestode and acanthocephalan parasites in the intestine of a rat host. Since then much effort has been put into studies of the patterns and processes underlying the structure of both ectoparasite and endoparasite communities (Holmes 1973, Rohde 1979, Dobson 1985, Holmes & Price 1986, Esch et al. 1990, Koskivaara et al. 1992, Sousa 1994, Poulin 1998, Bagge et al. 2005, Karvonen et al. 2005). However, studies of helminth parasites of ringed seals living in brackish or in freshwater habitats are very limited (Forssell 1906, Delyamure et al. 1980, Helle & Valtonen 1980, 1981, Valtonen & Helle 1988).

Parasite communities are arranged hierarchically, such that each infracommunity (all parasite individuals of all species within a host individual) is a subset of the component community (all parasite individuals of all species within the host population) (Bush et al. 1997). The key questions have been whether those parasite species that form each infracommunity are random or non-random subsets of those parasite species found in the component community, and what are the factors acting within the infrapopulation on the spatial distribution of its members or their mean sizes (Poulin & Valtonen 2001, Poulin 2005).

A large number of factors could contribute to the extensive variation in different parasite communities. The diversity and abundance of the intermediate and definitive hosts in the area (see Valtonen et al. 1997, 2001, 2003, Halmetoja et al. 2000, MacKenzie 2002), host population size or density (Morand & Poulin 1998, Bagge et al. 2004), even environmental characteristics such as pH, water color, temperature or concentration of total phosphorus, could contribute to distinct parasite communities between different populations (Marcogliese & Cone 1991, Valtonen et al. 2003, Goater et al. 2005, Poulin 2006). Moreover, all individual hosts from the same population do not harbour the same parasite species or quantity. Some hosts may harbour most of the parasite species included in the component community, others only one or two species (Poulin & Valtonen 2001). Parasite-related filters determine what subset of the potential pool of parasites comprises a realized infracommunity: hosts that the parasite cannot meet and hosts in which the parasite cannot survive or develop are excluded. Also interspecific interactions within mixed-species infections may affect parasite species from the infracommunities (Sousa 1994).

Some previous studies have indicated that abundant parasite communities could be interactive (Kennedy et al. 1986) and some suggest that infracommunities are often just random assemblages of the available species (Poulin 1998) and that the presence of one species has no influence on the presence of other species (Rohde 1991). It has also been suggested that two or

more parasite species can compete for the same resource and that one parasite could eventually displace other species of the infracommunity by competitive exclusion (Esch et al. 1990). The competition can also be expressed so that parasites specialized to live in different niches (interactive site segregation) or their demands for the resource have genetically differentiated during evolution (selective site segregation) (Esch et al. 1990). Still, regarding the importance of interspecific interactions among parasites in structuring of helminth communities, there is no general underlying rule or process that can be applied to all communities.

In free-living animals, sexual selection is a central force shaping many population features (Andersson 1994). But studies of the influence of sexual selection processes on the structure and dynamics of helminth populations are rare. In dioecious and polygamous taxa such as acanthocephalans, however, sexual selection processes could be important in shaping the structure of the parasite infracommunity: there is some indirect evidence for competition among males for access to females and mate choice by one or both sexes (Lawlor et al. 1990, Sasal et al. 2000).

## 1.3 The helminth communities of seals

Marine mammals worldwide harbour a rich parasite fauna containing single-celled protozoan parasites as well as multicellular organisms (trematodes, hookworms, heartworm and lungworms). Gastrointestinal nematodes (*Anisakis*, *Contracaecum* and *Pseudoterranova*), cestodes and acanthocephalans (*Bolbosoma* and *Corynosoma*) are found in ocean cetaceans and pinnipeds worldwide (Dailey 2005). The Okhotsk ringed seals (*Pusa hispida ochotensis* Pallas, 1811) are reported to be infected with 3 cestodes, 4 acanthocephalan and 5 nematode species (Popov et al. 1980). Twelve species of helminths were found from the spotted seals (*Phoca largha* Pallas, 1811) in the Bering Sea, five of which were acanthocephalans (Shults 1982). Altogether 62 different helminth species have been found from the northern seals belonging to sub-family *Phocinae*, of which ten are acanthocephalan species (Dailey 1975).

The number of parasitic helminth species is greater among the oceanic seals (Dailey 1975, Popov et al. 1980, Measures & Gosselin 1994, Dailey 2005) than among the seals in isolated populations in brackish and freshwater environments (Barysheva & Bauer 1957, Delyamure et al. 1980, Helle & Valtonen 1980, 1981, Valtonen and Helle 1988, Valtonen et al. 1988). Component communities of intestinal metazoan parasites of ringed seals in the northern Baltic Sea are among the most depauperate currently known in any marine mammal: only three *Corynosoma* species (*C. semerme* (Forsell, 1904), *C. magdaleni* Montreuil, 1958 and *C. strumosum* (Rudolphi, 1802) have been recorded (Helle & Valtonen 1980, 1981, Valtonen and Helle 1988, Valtonen et al. 1988, Valtonen et al. 2004). Accidentally also the cestode *Schistocephalus solidus*

(Müller, 1776), unidentifiable *Diphyllobothrium* larvae, and a larval nematode (*Contracaecum osculatum* Rudolphi, 1802) are known to occur (Chubb et al. 1995, Valtonen & Helle unpubl. data) in the Baltic ringed seal (*Phoca hispida botnica* Gmelin, 1785). The intestinal parasites of the freshwater Saimaa seal (*Phoca hispida saimensis* Nordquist, 1899) have been studied previously by Valtonen & Helle (1988), who reported only one *Corynosoma* species, *C. strumosum*, although Forssell (1906) had also noted *C. semerme* from one seal.

# 2 DIETARY STUDIES OF RINGED SEALS

Ringed seals in the Bothnian Bay breed colonially and most pups are born between late February and early March, the majority of parturitions are over by the middle of March. Ringed seals nurse their pups for 4 to 6 weeks. Towards the end of lactation, mating takes place over a period of about a month. Following the nursing and mating periods, seals undergo an annual moult in April-May (Helle 1983). These events might influence the foraging behaviour, and hence the diets of seals leading to differences between individuals.

## 2.1 Identification of prey from the remains in alimentary canal

The diets of the Baltic ringed seal and Lake Saimaa ringed seal are thought to consist mainly of small shoaling fish species such as herring (*Clupea harengus membras* L., 1761), smelt (*Osmerus eperlanus* L., 1758) and perch (*Perca fluviatilis* L., 1758), while demersal fourhorn sculpin (*Myoxocephalus quadricornis* L., 1758) and ruffe (*Gymnocephalus cernuus* L., 1758), migratory salmon (*Salmo salar* L., 1758), and three-spined stickleback (*Gasterouteus aculeatus* L., 1758) are also thought to be important prey of ringed seals (Söderberg 1975, Tormosov & Rezvov 1978, Kunnasranta 2001, Routti et al. 2005, Stenman & Pöyhönen 2005). Differences in diet due to location (Söderberg 1975, Tormosov & Rezvov 1975, Lowry et al. 1980), season (Söderberg 1975, Lowry et al. 1980) and age of seals (Lowry et al. 1980, Holst et al. 2001, Kunnasranta 2001) have been documented in ringed seals, but little is known about dietary variation among individual seals.

Most previous studies of the diet of ringed seals have determined diets from scats and from stomach and intestine contents (Söderberg 1975, Tormosov & Rezov 1978, Lowry et al. 1980, Holst et al. 2001, Kunnasranta 2001). These techniques rely on the identification of prey from the remains of more or less digested food items and are mostly inaccurate, because food quickly passes through the alimentary canal of homothermal seals with varying and largely unknown species–specific rates of digestion. According to Parsons (1977) the

digestive tracts of seals can be empty within 6-8 hours of feeding. Thus it is extremely difficult to build a reliable generalized picture of food composition during longer periods without large sample sizes. Prey remains in the stomach, intestine or faeces represent only the most recent seal food items.

## 2.2 Intestinal parasites in dietary studies

Studies of the intestinal helminth parasites of the seals offer an alternative approach to study the foraging behaviour of individuals (Marcogliese & Cone, 1997). The consistent presence of particular parasites in a host indicates long-term trends in feeding patterns as the worms reside in the host intestine for weeks or months (Curtis et al. 1995). Studies of intestinal parasites provide some information about host diet and individual foraging behaviour since the amount of food and the composition of the diet are factors affecting the abundance of the intestinal parasites passed in the food chain (Marcogliese & Cone, 1997).

In this study I focused on the transmission of intestinal acanthocephalan parasites and a cestode larva in the relatively simple food web of the Bothnian Bay. These parasites proceed through the food web via predator-prey interactions to the seal definitive host and hence are closely linked to the diet of the seals (Valtonen 1983a, b). Acanthocephalan species are good indicators of past diet over a longer term, as they reside in the host for weeks (Valtonen & Helle 1982).

## 2.3 Stable isotope analysis in dietary studies

Stable isotope analyses have been increasingly applied to ecological questions (Peterson & Fry 1987, Koch et al. 1994, Fry 2006). The ratio of heavy to light isotopes is expressed relative to a standard as $\delta^{13}C$ ‰ and $\delta^{15}N$ ‰ (Peterson & Fry, 1987). Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are used to characterize food webs (Kwak & Zedler 1997, Vander Zander et al. 1999) and to determine the contributions of different food sources to animal diets (Hobson et al. 1996, Phillips 2001, Phillips & Gregg 2003).

Changes in the isotopic signatures of components occur at each trophic step because of fractionation of isotopes between animals and their diets during assimilation or excretion (Peterson and Fry 1987). Fractionation occurs because the lighter isotope is more likely to be excreted due to the lower activation energy for bond breakage in reactions. As a result, consumers become enriched with the heavier isotope and have a higher and predictable $\delta$ value than their diet (Fry 2006).

Carbon isotope signatures ($\delta^{13}C$) of food sources have proved a reliable tracer to distinguish the relative contributions of prey items in a consumer's

diet (DeNiro & Epstein, 1978, Fry & Sherr, 1984, Hobson 1999, Phillips & Gregg 2003) or to reveal the foraging location of consumers (Lesage et al. 2001). Nitrogen fractionates to a greater extent than carbon from one trophic level to next and $\delta^{15}N$ has been successfully used to assess the trophic level of species in aquatic food webs (e.g., Vander Zanden et al. 1999, Lesage et al. 2001, Cabana & Rasmussen 2002). The physiological state of an animal can also affect the isotope ratios in its tissues (Hobson et al. 1993). Fasting, starving or stressed animals can become $^{15}N$ enriched due to increased protein metabolism (Ambrose & DeNiro 1986, Hobson et al. 1993, 1996, Gannes et al 1998).

Naturally occurring stable isotopes of carbon and nitrogen of consumers and their food sources have successfully revealed the feeding preferences of various generalist predators (Rau et al. 1992, Oelbermann & Scheu 2002), as well as temporal variations in vertebrate diet (Dalerum & Angerbjörn 2005). Moreover, stable isotope measurements of several tissues with variable metabolic rates from the same individual can provide information on diet integrated over days (e.g. plasma), weeks (e.g. liver) or months (e.g. muscle) (Tieszen et al. 1983, Hilderbrand et al. 1996), since the elements in these tissues have been assimilated during the time scale specific to the turnover rate of the given tissue (Dalerum & Angerbjörn 2005).

## 2.4 Aims of the study

The main aim of this study was to investigate the diet and foraging of individual ringed seals living in brackish and freshwater habitats which are atypical habitats for generally marine seals. I used a new combination of methods by utilizing data from parasitological studies of the intestinal helminths, from alimentary tract contents analysis, and from stable isotope ratio analysis of seal tissues. It was essential first to confirm the *Corynosoma* species in both areas, because the unclear description of *C. strumosum* in relation to *C. magdaleni* has created confusion in previous studies.

In the first paper (I), I examined the stability of the *Corynosoma* infection and the local distribution of the cystacanth stages of *Corynosoma* species in their most common paratenic fish hosts, fourhorn sculpins (*M. quadricornis*) in the Bothnian Bay. In the next two papers (II and III), I studied the intestinal metazoan fauna from lake ringed seals *P. h. saimensis*, and confirmed the single *Corynosoma* species population in Lake Saimaa. Paper II concerned the extrinsic factors affecting the transmission of the helminth to the Saimaa seals via the food web. Paper III addressed the intrinsic factors affecting the structure of *Corynosoma* infrapopulation by testing the influence of sexual selection on the spatial distribution, male body size and female mating success in the acanthocephalan infrapopulations. This paper was an integral part of the characterization of the helminth fauna in Saimaa seals. In paper IV the *Corynosoma* infection data from Baltic ringed seals (*P. h. botnica*) was combined

with data from alimentary tract contents and from stable isotope analysis of the diaphragm muscle tissues of the same seals to evaluate dietary differences between individual seals in the Bothnian Bay. Finally in paper V I used stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of several tissues with variable metabolic rates (plasma, liver and muscle tissues) to elucidate temporal variation in the diet among individual seals during their breeding season in the Bothnian Bay.

# 3 MATERIAL AND METHODS

## 3.1 Ringed seals living in atypical habitats

The Baltic ringed seal (*P. h. botnica*) population was cut off from the stock of the Arctic ringed seal (*P. hispida hispida* Schreber 1775) 11 000 years ago. Three thousand years later as the land rose after the last Ice Age, Lake Saimaa was separated from the Baltic Sea basin causing the further segregation of the ringed seals into two subspecies. Since then the Saimaa ringed seal (*P. h. saimensis*) and the Baltic ringed seal have lived geographically isolated in freshwater and in brackish environment atypical to seals (Hyvärinen & Nieminen 1990).

The occurrence and abundance of both seal subspecies in the Baltic Sea and in Lake Saimaa has varied during recent decades. The number of Baltic ringed seals used to be large, ca. 100 000 - 300 000 individuals (Harding & Härkönen 1999, Kokko et al. 1999) and the maximum size of the Saimaa ringed seal population has been at least 1 000 animals (Kokko et al. 1999). Both seals have suffered from heavy harvesting and from reproductive disorders caused by environmental toxins (Helle 1980, Helle et al. 1985, Hyvärinen et al. 1998, Harding & Härkönen 1999) and the population sizes collapsed in both areas in the mid 1990s. Twenty years ago an estimated haul-out population of ringed seals in the whole Baltic Sea area was 5500 individuals (Härkönen et al. 1998) and only 100-150 ringed seals inhabited the middle parts of Lake Saimaa (Sipilä et al. 1990). Today the populations have recovered and the number of seals has increased. In the Gulf of Bothnia alone 4748 ringed seals was reckoned in 2004 and the stock is increasing by some 5% per year (Härkönen unpubl., The Swedish Museum of Natural History). In the Baltic Sea this has led to conflict between conservationists, who welcome the increase, and commercial fishermen, who accuse seals of causing economic losses for them by damaging their fishing gear and eating the catch (Backman & Helle 1998, Lunneryd 2001, 2005). In Lake Saimaa the current population of ringed seal consists of approximately 280 individuals, mainly in the central parts of the lake (Hyvärinen et al. 1999, Kunnasranta 2001, Hyvärinen et al. 2004, Metsähallitus 2007 www.metsa.fi). Despite strict protection it is still highly threatened (Palo 2003).

## 3.2 Life cycle of *Corynosoma* species

*Corynosoma* species are dioecious and polygamous acanthocephalan parasitic worms that attain sexual maturity and copulate in the alimentary tract of seals (Crompton 1973, 1985). During the copulation of acanthocephalans (Dezfuli & DeBiaggi, 2000), the everted bursa of the male worm wraps around the posterior end of female and the spermazoa are transferred. After insemination the male worm blocks the vaginal region of the female worm by an external cement cap which is lost after a few days. Males can also remove competitors from the population by capping other males (Adele & Gilchrist, 1977).

In the life cycle of *Corynosoma* species in the Bothnian Bay and in Lake Saimaa, acanthocephalan eggs (acanthors) exit with the faeces from the seal intestine. When an acanthor is eaten by the amphipod intermediate host, *Monoporeia affinis* (Lindström, 1855), it hatches and burrows into the haemocoelom of the amphipod. In the amphipod it develops into an infective larval stage called a cystacanth. The amphipod intermediate host is eaten by fish. In fish the cystacanth enters the internal organs and mesenteries and is then transferred to the final host when the fish is eaten by a seal.

In the aquatic realm host populations are often patchy and scattered and thus parasites must adapt to maintain themselves in an environment where the contact between successive hosts in a life cycle may be periodic or rare (Marcogliese 2005). A paratenic or transport host is not required for the development of the acanthocephalan (Nickol 1985) but is often used to increase transmission to the next host in the life cycle (Marcogliese 2005). Paratenic hosts can accumulate large numbers of parasites and a variety of species and thus transmit an entire assemblage of species as a single packet when they are eaten by an appropriate definitive host (Marcogliese 2002). They are acting as a bridge over the trophic or temporal gaps between intermediate and definitive hosts.

Although thirteen fish species can act as a paratenic host for the *Corynosoma* worms in the Bothnian Bay (Valtonen 1983a), they are found most commonly and abundantly in Baltic herring, smelt, eelpout (*Zoarches viviparous* L., 1758), ruffe and fourhorn sculpin (Valtonen 1983a, 1983b, Valtonen et al. 2001).

## 3.3 Samples for parasitological and alimentary tract content studies

Intestinal metazoan parasites were examined from the alimentary tracts from nine Baltic ringed seals and from 61 Saimaa ringed seals. Both seal species are protected, but a few Baltic ringed seal individuals are taken annually for scientific purposes from northwest of Hailuoto Island as ongoing research by the Finnish Game and Fisheries Research Institute (Fig 1). The freshwater seals

were found dead during 1981-2001 in Lake Saimaa (Fig 1). Most of the seals were from Haukivesi, Joutenvesi and Kolovesi (A) and Pihlajavesi (B) basins in central Lake Saimaa (n=53) (Fig 1), which represent the main distribution areas of the ringed seals in Lake Saimaa. Some specimens were also obtained from two other basins used by Saimaa ringed seals (Fig 1). The stomach, small intestine, caecum, large intestine and rectum of the seals were dissected and all parasites were collected. The exact position of each worm in the intestine of Saimaa seals was recorded to the nearest centimeter. All particles other than parasites were collected from the alimentary tract of the Baltic seals.

Additionally, internal organs and mesenteries were examined from 340 fourhorn sculpins and from 42 bull-rout (*M. scorpius* L., 1758) for larval acanthocephalans. The fourhorn sculpins were caught by gill nets from coastal and central areas of the Bothnian Bay (Fig 1). The bull-rout was captured from Tvärminne, the southern part of the Gulf of Bothia (Fig 1). Seven fish species were studied from the Haukivesi basin of Lake Saimaa to trace the possible source of parasite infection in paratenic fish hosts in Lake Saimaa (Fig 1). Detailed descriptions of the material and methods of the parasitological studies are reported in the original papers (I-IV).

## 3.4 Samples for stable isotope analysis

The tissue samples for stable isotope analysis were obtained from the same nine Baltic seals as were examined for their intestinal metazoan parasites. The dual isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) were determined from diaphragm muscle (IV), shoulder muscle, liver and plasma (V) of the individual seals shot as part of ongoing research by the Finnish Game and Fisheries Research Institute from northwest of Hailuoto Island (65°11'N, 24°36'W) (Fig 1). In addition dual stable isotope signatures were determined from 13 fish species and one crustacean species *Saduria entomon* L., 1758. The fish and isopod samples were provided by the staff of the Bothnian Bay Research Station from the by-catches from local fishermen (65° 07'-65°08'N, 24°32'-24°37'W). The salmon samples were caught by gill nets as part of ongoing research by the Finnish Game and Fisheries Research Institute (65°02'N, 24°32'W) (Fig 1). The $\delta^{13}C$ values of all four seal tissues were lipid-corrected using the model of Kiljunen et al. (2006), based on tissue C: N ratios but the $\delta^{15}N$ values were not modified in any way. Detailed descriptions of the sample preparation are reported in original papers IV and V.

FIGURE 1 Map of the research areas: 1= the northern part of Gulf of Bothnia, Bothnian Bay, Hailuoto Island, 2=Lake Saimaa, the hatched areas indicate the location of the study sites A=Haukivesi, Joutenvesi and Kolovesi and B=Pihlajavesi and 3= the southern part of the Gulf of Bothnia, Tvärminne.

# 4 RESULTS AND DISCUSSION

## 4.1 Parasite community studies

Three acanthocephalan helminth species of the seals, *Corynosoma semerme*, *C. magdaleni* and *C. strumosum*, were found in their paratenic fish host, fourhorn sculpins, in the brackish Bothnian Bay (I). The *Corynosoma semerme* infection was shown to be stable when comparing with data from 20 years earlier in the Bothnian Bay. The *Corynosoma* species were shown to be easy to distinguish already at the cystacanth stage (I).

The number of parasitic helminth species is greater among oceanic seals (Dailey 2005) than among seals in isolated populations in brackish and freshwater environments (Barysheva & Bauer 1957, Delyamure et al 1980, Helle & Valtonen 1980, 1981, Valtonen and Helle 1988, Valtonen et al. 1988, Valtonen et al. 2004). The depauperate gastrointestinal helminth assemblages of both ringed seal subspecies were also evident in my studies (II and IV). The stable infection of *C. semerme* in the Bothnian Bay shows that this marine acanthocephalan species has adapted to the brackish water ecosystem and has survived through the very varying history of the Baltic Sea. However, it seems that only *C. magdaleni* has survived during the isolation of the landlocked ringed seal and coevolved with the host in the freshwater environment in Lake Saimaa (II). The absence of *C. semerme* and *C. strumosum* in Lake Saimaa is of particular note because the intermediate amphipod, *M. affinis*, host is common in most basins of the lake (Hynynen et al. 1999). I suggest that the parasite assemblages in Lake Saimaa could have comprised all *Corynosoma* species at the time when seals were isolated from the Baltic basin and founded the Saimaa population. Chance may have influenced the parasite composition of the Saimaa seals or the low intensity of *C. semerme* and *C. strumosum* infection may have led to the extinction of these species. This view is supported among the other land-locked seal populations. Contrary to *C. semerme* and *C. magdaleni*, *C. strumosum* has not been reported from the freshwater populations of seals, except the findings in Ladoga ringed seal (*Phoca hispida ladogensis* Nordquist). However, based on the results of one dissected seal from Lake Ladoga in 1992 in which hundreds of *C. semerme* and

111 *C. magdaleni* were found, but not a single *C. strumosum* (Sinisalo T. unpublished data), it is likely that *C. semerme* and *C. magdaleni* occur in Lake Ladoga. In Lake Baikal *Corynosoma* species are not found at all (*Phoca sibirica* Gmelin 1788) (Dailey 1975). Of course it is also possible that *C. magdaleni* itself or its intermediate or even paratenic host may be better adapted to the freshwater habitat than the other two *Corynosoma* species.

The distribution of a parasite is mostly dependent on the occurrence of the definitive seal host and the intermediate amphipod host (see Brattey et al. 1990, Lunneryd 1991). However, in this study the role of the paratenic fish host species was found to be important in the transmission of *Corynosoma* species carrying the parasite over the ecological barrier to the definitive host, and the stability of *Corynosoma* populations was suggested to be maintained mainly in their paratenic hosts (I). Host specificity of *Corynosoma* species at the paratenic level is thought to be low (Nickol 1985). However, Valtonen (1983a) and Valtonen et al. (2001) have reported all three *Corynosoma* species in ruffe but more sparsely than in fourhorn sculpin. Smelt are thought to be infected with *C. semerme* and *C. magdaleni* and marine herring and eelpout with *C. semerme* and *C. strumosum* (Valtonen 1983a, Valtonen et al. 2001, E. T. Valtonen and T. Sinisalo unpublished observation). Also Nickol et al. (2002) recorded differences in *Corynosoma* assemblages between individual young grey seals indicating segregation of *C. magdaleni* and *C. strumosum* in the piscine host. Differences in infections in different paratenic hosts might be due to differences in altered behaviour of amphipods infected with different species of acanthocephalans. For example Bethel and Holmes (1973) showed that local *Corynosoma constrictum*, *Polymorphus marilis* and *P. paradoxus* did cause different behavioural changes in their amphipod hosts. Different response to light or to disturbance could expose infected amphipods to different fish hosts.

In this study the distributions of *Corynosoma* species were highly aggregated across their definitive host seal population; the majority of ringed seals had few parasites, whereas a few seals had many parasites (see Shaw & Dobson 1995). The well-developed vertebrate immune response could contribute to these differences between hosts (Schad 1966, Kortet et al. 2003); differences in susceptibility to the parasite infection can cause variation in parasite loads between individual hosts (see Wilson et al. 2002). The other main reason for the high intensity of infection in some seals may be an increased amount of infected fish being eaten by these hosts (see Sousa 1994). The amount of food and the composition of the diet is probably the most important factor that contributes to the heterogeneities of worms in the acanthocephalan infracommunities of seals in this study (II and IV)

In Lake Saimaa the uninfected young seals spend more time in shallow waters catching small schooling fish like perch and roach, whereas the adult seals forage mainly in deeper offshore waters (Kunnasranta 2001, Kunnasranta et al. 2002), which are inhabited by pelagic and demersal fish species. The fish species of the deeper areas are most likely to create the higher mean intensity of *C. magdaleni* infection in the adult lake seals (II). The accumulation of parasites over time can not be the main reason for the high intensity of infection in some

seals since *Corynosoma* worms have a short life span maturing after 2-3 weeks in homeothermic animals (Valtonen & Helle 1982).

In this thesis the single *Corynosoma* species population in Lake Saimaa was confirmed. To characterize the helminth fauna in Saimaa seals also the intrinsic factors affecting the structure of *C. magdaleni* infrapopulation was tested. The *C. magdaleni* infrapopulation in the freshwater seal offered a unique opportunity to study the distribution of the acathocephalan worms in the host gut without interactions with other parasite species and effects of overcrowding due to other species (III). Several theories concerning the evolution of parasite communities have been developed from the concepts of competition (Holmes 1961, 1973, Holmes & Price 1986). It has been suggested that two or more parasite species can compete for the same resource and one parasite could remove or replace the other species in the infracommunity (Bush & Holmes 1986, Stock & Holmes 1988). In this study, as in the studies of Valtonen & Helle (1988) and Nickol et al. (2002), the majority of *C. semerme* specimens were located in the rectum and in the large intestine and the distribution of both *C. magdaleni* and *C. strumosum* overlap in the small intestine of the Baltic seal (IV). In the small intestine of the Saimaa seal, the current site preference of the single parasite species, *C. magdaleni*, most likely reflects the influence of past competition with other *Corynosoma* species (see Kennedy 1990) in the Baltic, leading to the selective site segregation (Holmes 1973) observed also in the isolated Saimaa ringed seal (II).

Site segregation has been shown to help the sexes to find a partner for sexual reproduction (Rohde 1979). This mating hypothesis states that in a low density population the intrinsic factors which are responsible for niche restriction exist to increase intraspecific contact of the parasites and their chances of mating. The data from the Saimaa ringed seals show that sexual selection plays an important role in determining the spatial distribution of *C. magdaleni* within the lake seal gut (III). Males have a more active role in copulation than females among acanthocephalans (see also Parshad & Crompton 1981). A single acanthocephalan male can inseminate as many as 17 females (Crompton 1974). My data suggest that copulation occurs mainly in the anterior part of the small intestine of the seal where male and female *C. magdaleni* mate as soon as they arrive in the intestine (III). Large males are commonly favoured by sexual selection (Andersson 1994), as among polygamous acanthocephalans. Male body size seems to be important during mating, as the larger males appear to be the first to approach non-mated females (III). This study shows that the mating success of female *C. magdaleni* covaries with the sex ratio, with a higher proportion of *C. magdaleni* females having copulated in seals with relatively more male worms. The mating success of a female is particularly associated with the availability of males very close to her (III).

## 4.2 Dietary studies

The stomach contents of the Baltic ringed seals showed that seals had been feeding during their breeding period, but most of the stomachs had sparse contents and gave only hints of the most recent food items consumed by certain individuals. This is the problem in the traditional dietary studies. In addition, the remains of hard parts of prey items can be more or less digested and laborious to identify. Therefore, alimentary tract content analysis alone is of limited value to reconstruct the diets of seals without large sample sizes (IV).

The variation in the number of worms in individual Saimaa seals indicated differences in feeding behaviour and in diet of seals (II). However, the intestinal parasite *C. magdaleni* infrapopulation could only reveal the infected prey items on which Saimaa seals had been feeding, not the uninfected ones. In general, a higher mean intensity of *C. magdaleni* infection in the heavier and older seals means that those seals have got more worms when their diet consists more and more of fish once they reach an age of 6 months. In addition, the results showed that seals of different ages forage in different areas. Adult seals forage mainly in deeper offshore waters, which are inhabited by the paratenic fish host (*G. cernuus*) of *C. magdaleni*. In contrast, the young seals spend more time in shallow waters where the uninfected small schooling fish species occur (II).

The infection of Baltic seals by the three *Corynosoma* species provides information about previous food of seals over the longer term, but only about infected fish species in the diet. However, combining data from the intestinal parasite analysis, the alimentary tract contents, and from stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) allowed inferences about diets of individual ringed seals in the Bothnian Bay. This study showed considerable variation in diets between individual seals. All nine seals were infected with *Corynosoma* intestinal worms but besides having different parasite species, the seals also contained different numbers of parasites (IV). The ringed seals become infected with these parasites by feeding on the paratenic fish hosts and hence have different parasite species and different parasite burdens according to their dietary history. The $\delta^{13}C$ values of individual Baltic seals varied from -19.2 ‰ to -21.4 ‰ and $\delta^{15}N$ values ranged from 12.9‰ to 13.9‰, indicating some differences in the diet. The lower $\delta^{13}C$ values in two seals suggest that these individuals foraged more on marine herring. Further, these seals were also infected to a slightly higher degree by *C. strumosum* that is thought to be transported mostly by marine paratenic fish species (Valtonen et al. 2001, Nickol et al. 2002). In contrast, the higher $\delta^{13}C$ values observed in two other seals indicate a greater reliance by these seals on benthic prey (see Hobson et al. 1996, 1997, Hobson 1999). Moreover, one seal must have included salmon in its diet, as its stable isotope ratios fall outside the polygon defined by all other prey items besides salmon (see Phillips and Gregg 2003). My data suggested a more important contribution of invertebrates to the diet of ringed seals than reported in previous studies based on analysis of scats and stomach or intestine contents

only (Söderberg 1975, Tormosov & Rezvov 1978, Stenman & Pöyhönen 2005). Perhaps food availability or food quality is influencing feeding specialization of individuals, or perhaps the individuals become imprinted, when younger, to a specific prey type and will preferentially exploit that prey when available. However, the results of this study also indicated that the breeding and moulting period imposes particular foraging restrictions on all seals and especially on nursing females (V).

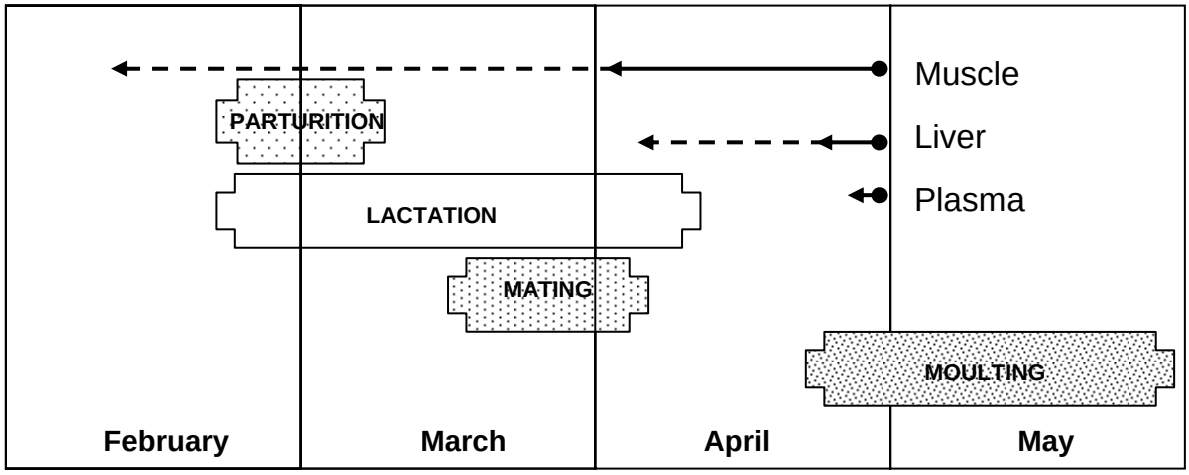



FIGURE 2 The schematic timetable of the ringed seal breeding season in the Bothnian Bay. The sampling point is marked by ●, the approximate turnover time of each tissue is marked by a arrow, and the time period previous to collection when the isotope composition of the given tissue begins to reflect the isotopic signatures of prey sources is indicated by a dashed extension.

Baltic ringed seals breed colonially and most pups are born over a period of about a month between late February and early March. After parturition female seals generally remain with their pup throughout the lactation period (4-6 weeks) and do not make long foraging trips (Bowen et al. 2002). Females which had given birth to a pup could have been more confined to the nursing lair during this period and may rely more on prey items like isopods and benthic fish species that are abundant and easily obtainable in the breeding area (Kuparinen et al. 1996). However, during the weaning period females are again able to move more widely and could forage more on pelagic fish species. The $\delta^{13}C$ and $\delta^{15}N$ from three different tissues with distinct turnover times reflect diet from different time periods: plasma tissue reflect the most recent diet, liver tissue the diet during one month in April, and muscle tissue corresponds with the diet during almost the total breeding season from February to end of April (see Kurle & Worthy 2002, Philips & Eldridge 2006). Hence in principle the restricted foraging period might be traced from the isotope ratio of these different tissues. The differences between females could reflect variation in the onset of duration of parturition and lactation (Fig 2).

Female seals number 6 and 7 had the most $^{13}C$ enriched carbon ratios for liver tissue indicating that the diet included a higher proportion of $^{13}C$-enriched benthic prey in April (see Hobson et al. 1996, 1997, Burns et al. 1998). These seals also had higher $\delta^{15}N$ ratios in muscle than in liver and plasma tissue indicating that the brief fasting (see Ambrose & DeNiro 1986, Hobson et al. 1993, 1996, Gannes et al. 1998) during the parturition period was still evident in the muscle nitrogen values. Female 2 should have had the earliest parturition, since the isotopic value of this seal liver is most depleted in $^{13}C$ suggesting pelagic prey items already in April. Moreover, the muscle, liver and plasma of this female had very similar $\delta^{13}C$ values, indicating that this female had fed on same kind of prey from February to the end of April. Possibly the lactation period had been very brief or the female has lost the pup fairly quickly and had been able to forage for preferred prey items for a longer period. Female number 1 and 9 probably had their parturition period before seals 6 and 7 but later than seal 2 according to their $\delta^{13}C$ values. They had apparently fed on pelagic prey in April indicating they had weaned their pups already in March. Female seals 1, 2, 6, 7 and 9 had *corpus albicans* and *corpus luteum* in their ovaries as an evidence of parturition in preceding breeding season (Helle 1980). Female number 8 was carrying a mummified fetus in its uterus so had evidently not entered parturition or lactation. In fact this seal had $\delta^{13}C$ values similar to those of the three males (3, 4, and 5) suggesting that it may have retained the less restricted foraging behaviour characteristic of males during the breeding season. The lower plasma $\delta^{15}N$ value may indicate that the male seal number 3 was already moulting and had changed its diet to lower trophic level prey.

Of course, the sample of only nine seals was very small, and further such studies of individual seal foraging behaviour and diets are needed, since this information about individuals can be of great value for conservation and management of seal populations.

# 5 CONCLUSIONS

In this study I confirmed the *Corynosoma* species in the Bothnian Bay and in Lake Saimaa and described some factors affecting helminth assemblages in the intestine of isolated seals living in brackish and freshwater habitats atypical to seals. My work suggested that the high intensity of *Corynosoma* infection in some seals is the result of an increased consumption of the paratenic hosts of these acanthocephalan worms. Thus variation in the number of worms in individual seals indicates differences in feeding habits.

In this study data from the parasite infection was combined with information from the stomach contents and stable isotope analysis to infer host feeding biology. All these methods have limitations: data of intestinal parasites reveal only infected prey items but not uninfected, the information from the stomach contents could only say what the seal individual had been feeding during the last few hours, and stable isotope analysis cannot identify the specific prey in the diet alone but requires other methods to predict the food items of the consumer. Yet, the combined dietary analysis offers alternative approaches and key advantages over traditional dietary studies where many prey items may be overlooked because they are too small or too digested to be identified and quantified.

1. The combined method provides longer-term information of diet whereas contents of alimentary tracts only reveal what was just recently ingested.
2. Large sample sizes which are very difficult (scats) and unethical (alimentary tracts) to achieve are required to build a reliable generalized picture of food composition, but are not so critical in the combined method analysis.
3. Especially in seal studies, the combined method offers potential advantages over traditional methods because it avoids the problem of the high frequency of empty stomachs found among fasting seals due to fast digestion.

I have emphasized that the data from these studies are few and must be interpreted with some caution. Both seal species are protected and the samples were collected solely to meet the needs of parasitological and stable isotope

investigations. However, the data are rare and rather well demonstrate the patterns and processes in helminth assemblages as well as the individual foraging and the temporal change in diet of ringed seals.

The increased numbers of seals, especially grey seals (*Halichoerus grypus* Fabricius) have been accused of causing economic losses to fishermen by eating their catches and damaging fishing gear during the last decade in the Baltic Sea. Further information about dietary differences between individuals is required to identify those seal categories which may particularly eat from the fishing nets. Also information of the temporal and spatial utilization of food resources is the cornerstone for efficient and sustainable management of endangered populations. The traditional research methods cannot reveal individual foraging by seals, so novel methods are needed. In this study the new combined method has been tested and in future tools like tagging and satellite telemetry observation, and fatty acid analysis and stable isotope analysis from non-destructive sampling seal hair, nail or whisker tissue might be linked to provide further information about the diets of the endangered seal species without large sample sizes and without killing animals.

*Acknowledgement*

I am indebted to my supervisor, Professor E. Tellervo Valtonen, for her support and encouragement. I warmly thank her for the pleasant discussion moments and the guidance of the work. Appreciation is expressed also to my other supervisor, Professor Roger Jones, for his constructive comments and valuable suggestions to improve quality and language of the manuscript and summary. I am grateful to the head and the staff of the Department of Biological and Environmental Science of University of Jyväskylä for the warm atmosphere and for the flexibility to reconcile my study and work. I thank you all. Most heartily acknowledged are the members of Ecological Parasitology Group and Stable Isotope Group, especially Dr. Katja Pulkkinen and Tiina Hasu, Mikko Kiljunen, Jari Syväranta and Sami Taipale for their borrowed time and many helpful discussions. I acknowledge Professor Tapani Valtonen and Professor Pauli Bagge for their encouragement to me to start my studies years ago. I want to express my gratitude to co-authors Harri Högmander and Taina Juuti, to Professor Robert Poulin for valuable comments and Professor Brent B. Nickol for checking the identification of *C. magdaleni* cystacanths. I am grateful to Dr. Mervi Kunnasranta from the Finnish Game and Fisheries Research Institute and Professor Heikki Hyvärinen from the University of Joensuu for providing the alimentary tracts of Saimaa seal and for pleasant co-operation. I also thank Professor Eero Helle for the seal samples from the Bothnian Bay and for the advice and support given to the project. Dr. Roy Siddall kindly revised the language of the paper (I) and the summary of this paper was translated into French by Dr. Pierre Sasal. Numerous people were involved in the collection of material from both the Baltic Sea and Lake Saimaa. Gratitude is extended to the staff of the Bothnian Bay Research Station of the University of Oulu for providing the fish samples, especially to the late Mr. Osmo Timola Phil. Lic for samples of fourhorn sculpins. I thank Dr. Eva Sandberg-Kilpi for providing the samples of bull-rout from Tvärminne Research Station of the University of Helsinki and fisherman Terho Laitinen for supplying the freshwater fish samples. I want to thank Joanne Kitchen for helping me to pick up the parasites from the Baltic seals. Especially, I want to thank Markku Raatikainen for his skilled assistance in the laboratory. The alimentary tracts of the Saimaa seals from the 1980s could have been left without dissection without his positive attitude and humour. I also thank Virve Kustula, Allan Witick and Tony Pirkola from the Institute for Environmental Research for helping me in technical as well as in assay problems with the SIRMS instrument. I extend my love and my sincerest thanks to my husband Markku and my children and their families for all the joy of life you have given to me.

This study was financially supported by the Finnish Konkordia association, Finnish Academy and the University of Jyväskylä (Rector's grant for finishing the PhD thesis).

# YHTEENVETO (RÉSUMÉ IN FINNISH)

## Perämeren ja Saimaan norpan suolistoloisyhteisöt ja niiden hyödyntäminen hylkeen yksilöllisen ravintoekologian selvittämisessä

Itämeren hylkeiden määrä on lisääntynyt Perämerellä 1990-luvun jälkipuoliskolla, ja hylkeet ovat aiheuttaneet kalastajille taloudellisia tappioita syömällä kaloja verkoista ja rikkomalla pyydyksiä. Vahinkojen määrän pienentämiseksi on testattu hylkeen kestäviä kalastusvälineitä, karkotusmenetelmiä ja uusia pyydysmateriaaleja. Yksi ajatus ratkaista ongelma on ollut hylkeiden määrän vähentäminen metsästämällä. Vaihtoehtona yleiselle metsästykselle on pyrkiä poistamaan ne yksilöt hyljekannasta, jotka syövät kalastajien pyydyksistä. Koska tällaisesta erikoistumisesta ei ole vielä varmuutta, tulisi selvittää, missä määrin hylkeet käyttävät ravinnokseen lohta ja muita kalastajien tavoittelemia arvokaloja, ja missä määrin hylkeillä on yksilöllistä vaihtelua ravinnon suhteen.

Aikaisemmin hylkeiden ravintoa on määritetty maha- ja suolistonäytteistä. Tämä perinteinen menetelmä perustuu saalislajien sulamattomien osien tunnistamiseen hylkeen suolistosta. Norpan suolisto tyhjenee nopeasti ruokailun jälkeen, joten määrityksen tulokset edustavat vain muutaman tunnin sisällä tapahtunutta ruokailua. Perinteisen menetelmän avulla ei voida selvittää hylkeiden yksilöllistä ravintokäyttäytymistä eikä ajallista vaihtelua ilman suuria näytemääriä. Väitöskirjani tavoitteena oli selvittää Perämeren (*Phoca hispida botnica*) ja Saimaan norpan (*Phoca hispida saimesis*) ruokailua ja erikoistuvatko tietyt hyljeyksilöt tiettyyn ravintoon. Työssä yhdistän kolmen eri tutkimusmenetelmän: loistutkimuksen, maha ja suolistotutkimuksen ja stabiili-isotooppitutkimuksen tuloksia.

Suolistoloiset kuvastavat ravintoa pidemmältä ajanjaksolta kuin perinteiset suolisto- ja mahanäytteet ja kertovat isännän ravintokäyttäytymisestä yksilötasolla. Perämeren norpan suolistossa on kolme väkäkärsämatolajia, *Corynosoma semerme*, *C. strumosum* ja *C. magdaleni*, mutta vain yksi näistä kolmesta, *C. magdaleni*, esiintyy makeassa vedessä Saimaalla. Loisyhteisön jakaantumiseen suolistossa vaikuttaa loisen lisääntymiskäyttäytyminen. Koiraiden lisääntymismenestys riippuu niiden koosta ja naaraiden niiden lähellä olevien koiraiden määrästä. Seksuaalivalinnan vaikutus tulisikin huomioida infrayhteisön rakennetta muokkaavana tekijänä yhdessä lajienvälisen kilpailun kanssa.

Loiset käyttävät paikallista ravintoketjua siirtyäkseen saalislajeista hylkeiden suolistoon. Aikuiset *Corynosoma* -loiset parittelevat hylkeen suolessa ja hedelmöittyneet munat joutuvat ulosteiden mukana veteen. Loisten elinkierrossa välisäntänä toimiva valkokatka (*Monoporeia affinis*) syö veteen joutuneet munat. Katkan ruumiinontelossa loisesta kehittyy infektiivinen toukka. Kalat syövät katkat ja loiset koteloituvat näiden ns. parateenisten eli siirtoisäntien ruumiinonteloon. Mitä enemmän hylkeet syövät loisittuja siirtoisäntäkaloja sitä enemmän hylkeisiin kertyy loisia. Lisäksi norpat infektoituvat yksilöllisesti eri *Corynosoma* -lajeilla, sillä eri kalalajit siirtävät eri loislajeja.Yleisin ja runsaimmin loisittu kalaisäntä Perämerellä

on härkäsimppu (*Myoxocephalus quadricornis*) ja Saimaalla *Corynosoma magdaleni* on löydetty kiiskestä (*Gymnocephalus cernuus*).

Merinisäkkäiden ravintoekologiaa on tutkittu hiilen ja typen stabiili-isotooppi-arvojen ($\delta^{13}C$ ja $\delta^{15}N$) avulla. Menetelmä on ylivertainen jäljittämään ravintokohteen, koska saalistajan isotooppien suhde on ennalta tiedetyssä suhteessa saaliin isotooppien suhteeseen. Stabiili-isotooppimenetelmä tarvitsee kuitenkin tuekseen muita menetelmiä saalislajien määrittämiseen.

Perämeren norpat käyttävät ravinnokseen useita saalislajeja. Yksi ravintokohteista lisääntymiskaudella on kilkki (*Saduria entomon*). Kilkki jää usein huomioimatta maha- ja suolistotutkimuksissa, koska äyriäiset hajoavat nopeasti ruoansulatuskanavassa. Tutkimuksessani Perämeren norpat olivat yksilöllisiä ravinnon käytössään: osa norpista söi pääasiassa härkäsimppua ja kiiskeä (*Gymnocephalus cernuus*) kun taas toisten ravinto sisälsi enemmän silakkaa (*Clupea harengus membras*). Yksi norpista oli syönyt lohta (*Salmo salar*) ja toinen suurimmaksi osaksi kilkkiä ja kolmipiikkiä (*Gasterosteus aculeatus*).

Norpat lisääntyvät Perämerellä ahtojäiden keskellä ja niiden saalistusalue on hyvin rajoittunut lisääntymisaikana. Tutkimuksen tulokset osoittavat, että lisääntymis- ja karvanvaihtoaika rajoittavat norppien ravinnon käyttöä. Varsinkin naarashylkeet pysyttelevät pesän läheisyydessä synnyttämisen ja poikasen imettämisen ajan ja käyttävät ravinnokseen pääasiassa kilkkiä. Poikasten vieroituksen jälkeen naaraat laajentavat ruokailuaan. Erot naaraiden ravinnossa kuvastavat yksilöllistä vaihtelua synnyttämisen ajankohdassa ja imettämisajanjakson kestossa.

Uhanalaisten populaatioiden suojelu perustuu populaatioiden ekologisen tilan tutkimiseen. Tieto siitä, miten norppa hyödyntää ajallisesti ja paikallisesti ravintokohteita voi olla kulmakivi onnistuneelle suojelutoimelle. Suojeltujen ja uhanalaisten eläinten yksilöllisen ravintokäyttäytymisen tutkiminen perinteisten menetelmien avulla on jokseenkin mahdotonta, joten näiden eläinten ravintotutkimukseen tarvitaan uusia menetelmiä. Väitöskirjassani olen yhdistänyt ravintoanalyysit, suolistoloistutkimuksen ja stabiili-isotooppimenetelmät toimivaksi menetelmäksi, jolla saadaan uutta tietoa mm. hylkeen yksilöllisestä ravintokäyttäytymisestä. Tulevaisuudessa myös muita tutkimusmenetelmiä kuten telemetriaseuranta, rasvahappomääritykset ja isotooppitutkimukset hylkeen kynsi-, karva- ja viiksinäytteistä voidaan yhdistää väitöskirjassani esitettyyn menetelmään, ja näin saada tietoa hylkeen vuodenaikaisesta ravinnosta. Tulevaisuuden tavoite onkin, että uhanalaisten eläinten ravintotutkimukset voidaan tehdä ilman suuria näytemääriä ja vahingoittamatta eläintä.

## REFERENCES


Adele, L. G. & Gilchrist, S. 1977. Homosexual rape and sexual selection in Acanthocephalan worms. Science 97: 81-83.

Ambrose, S. H. & DeNiro, M. J. 1986. The isotopic ecology of east African mammals. Oecologia 69: 395-406.

Anderson, R. M. & May, R. M. 1979. Population biology of infectious diseases. Part I. Nature 280: 361-367.

Andersson, M. 1994. Sexual selection. 599 p., Princeton University Press, Princeton.

Backman, L. & Helle, E. 1998. Sälskador på fisket. Fiskeritidskrift för Finland 42: 4-7.

Bagge, A., Poulin, R. & Valtonen, E. T. 2004. Fish population size, and not density, as the determining factor of parasite infection: a case study. Parasitology 128: 305-313.

Bagge, A., Sasal, P., Valtonen, E. T. & Karvonen, A. 2005. Infracommunity level aggregation in the monogenean communities of Crucian carp (*Carassius carassius*). Parasitology 131: 367-372.

Barysheva, A. F. & Bauer, O. N. 1957. Fish parasites in Lake Ladoga. In: Petrushevski, G. K. (ed), Parasites and diseases of fish. Bulletin of All-Union Scientific Research Institute for Freshwater Fisheries 42: 171-223.

Bethel, W. M. & Holmes, J. C. 1973. Altered evasive behavior and responses to light in amphipods harboring acanthocephalan cystacanths. J. Parasitol 59: 945- 956.

Bowen, W. D., Read, A. J. & Estes, J. A. 2002. Feeding ecology. In: Hoelzel, A. R. (ed), Marine Mammal Biology, an Evolutionary Approach: 217-246. Blackwell Publishing, Oxford.

Brattey, J., Bishop, C. & Myers, R. 1990. Geographic distribution and abundance of *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) in the musculature of Atlantic cod, *Gadus morrhua*, from Newfoundland and Labrador. Can. Bull. Fish. Aquat. Sci. 222: 67-82.

Burns, J. M., Trumble, S. J. & Castellini, M. A. 1998. The diet of Weddell seals in McMurdo Sound, Antarctica, a determined from scat collections and stable isotope analysis. Polar Biol. 19: 272-282.

Bush, A. O. & Holmes, J. C. 1986. Intestinal helminths of lesser scaup ducks: patterns of association. Can. J. Zool. 64: 13-141.

Bush, A. O., Lafferty, K. D., Lotz, J. M. & Shostak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83: 575-583.

Cabana, G. & Rasmussen, J. B. 2002. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature 372: 255-257.

Chambers, C. A. & Dick, T. A. 2005. Trophic structure of one deep-sea benthic fish community in the eastern Canadian Arctic: application of food, parasites and multivariate analysis. Environ. Biol. Fishes 74: 365-378.

Chubb, J. C., Valtonen, E. T., McGeorge, J. & Helle, E. 1995. Characterization of the external features of *Schistocephalus solidus* (Müller, 1776) (Cestoda) from different geographical regions as an assessment of the status of the Baltic ringed seal *Phoca hispida botnica* (Gmelin) as a definitive host. Syst. Parasitol. 32: 113-123.

Crompton, D. W. T. 1973. The sites occupied by some parasitic helminths in the alimentary tract of vertebrates. Biol. Rev. Camb. Philos. Soc. 48: 27-83.

Crompton, D. W. T. 1974. Experiment on insemination in *Moniliformis dubius* (Acanthocephala). Parasitology 68: 229-238.

Crompton, D. W. T. 1985. Reproduction. In: D. W. T Crompton & B. B. Nickol (eds), Biology of the Acanthocephala: 213-272. Cambridge University Press, Cambridge.

Curtis, M., Berube, M. & Stenzel, A. 1995. Parasitological evidence for specialized foraging behaviour in lake-resident Arctic char (*Salvelinus alpinus*). Can. J. Fish. Aquat. Sci. 52: 186-194.

Dailey, M. D. 1975. The distribution and intraspecific variation of helminth parasite in Pinnipeds. Rapp. P.-V. Reun. CIESM Mediterr. Monaco 169: 338-352.

Dailey, M. D. 2005. Parasites of marine mammals. In: Rohde, K. (ed), Marine Parasitology: 408-414. CABI Publishing, Oxon.

Dalerum, F. & Angerbjörn, A. 2005. Resolving temporal variation in vertebrate fidets using naturally occurring stable isotopes. Oecologia 144: 647-658.

Delyamure, S. L., Popov, V. N & Trashchenkov, A. N. 1980. A study of the helminth fauna of seals in the Baltic Sea and Lake Ladoga. Dokl. Vysshei Shkoly Biol. Nauk. 7: 43-45.

DeNiro, M. J. & Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochem. Cosmochim. Acta 42: 495-506.

Dezfuli, B. S. & DeBiaggi, S. 2000. Copulation of *Acanthocephalus anguillae* (Acanthocephala). Parasitol. Res. 86: 524-526.

Dobson, A. P. 1985. The population dynamics of competition between parasites. Parasitology 91: 317-347.

Dogiel, V. A. 1961. Ecology of the parasites of freshwater fishes. In: Dogiel, V. A., Petrushevski, G. K. & Polyanski, Y. I. (eds), Parasitology of Fishes: 1-47. Oliver and Boyd, Edinburgh.

Esch, G. W., Bush, A. O. & Aho, J. M. 1990. Parasite Communities: patterns and processes. 335p., Chapman & Hall, London.

Esch, G. W. & Fernandez, J. C. 1993. A Functional Biology of Parasitism: ecological and evolutionary implications. 337p., Chapman & Hall, London.

Forssell, A. L. 1906. Förekomsten af *Echinorhynchus semermis* Forssell hos våra sälar (In Swedish). Meddelande Soc. Fauna Flora Fenn. 31: 64.

Fry, B. 2006. Stable Isotope Ecology. 308p., Springer Science+Business Media, LLC, New York.

Fry, B. & Sherr, E. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci. 27: 13-47.

Gannes, L. Z., del Rio, M. & Koch, P. 1998. Natural abundance variations in stable isotopes ad their potential uses in animal physiological ecology. Comp. Biochem. Physiol. 119A: 725-737.

Goater, C. P., Baldwin, R. E. & Scrimgeour, G. J. 2005. Physico-chemical determinants of helminth component community structure in white fish (*Goregonus clupeaformes*) from adjacent lakes in Northern Alberta, Canada. Parasitology 131: 1-10.

Halmetoja, A., Valtonen, E. T. & Koskenniemi, E. 2000. Perch (*Perca fluviatilis* L.) parasites reflect ecosystem conditions: a comparison of a natural lake and two acidic reservoirs in Finland. Int. J. Parasitol. 30: 1437-1444.

Hamilton, W. D., Axelrod, R. & Tanese, R. 1990. Sexual reproduction as an adaptation to resist parasites. Proc. Natl. Acad. Sci. USA 87: 3566-3573.

Harding, K. C. & Härkönen, T. 1999. Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida*) populations during 20th century. Ambio 28: 619-627.

Helle, E. 1980. Reproduction, size and structure of the Baltic ringed seal population of the Bothnian Bay. Acta Universitatis Ouluensis series A. No. 106. Biologica No.11.

Helle, E. & Valtonen, E. T. 1980. On the occurrence of *Corynosoma* spp. (Acanthocephala) in ringed seals (*Pusa hispida*) in the Bothnian Bay, Finland. Can. J. Zool. 58: 298-303.

Helle, E. & Valtonen, E. T. 1981. Comparison between spring and autumn infection by *Corynosoma* (Acanthocephala) in the ringed seal *Pusa hispida* in the Bothnian Bay of the Baltic Sea. Parasitology 82: 287-296.

Helle, E., Hyvärinen, H. & Stenman, O. 1985. PCB and DDT levels in the Baltic and Saimaa seal populations, Finn. Game Res. 44: 63-68.

Hilderbrand, G. V., Farley, S. D., Robbins, C. T., Hanley, T. A., Titus, K. & Servheen, C. 1996. Use of stable isotopes to determine diets of living and extinct bears. Can. J. Zool. 7: 2080-2088.

Hobson, K. A. 1999. Tracing origins and migration of wild life using stable isotopes: a review. Oecologia 120: 314-326.

Hobson, K. A., Alisauskas, R. T. & Clark, R. G. 1993. Stable nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analysis of diet. Condor 95: 388–394.

Hobson, K. A., Schell, D. M., Renouf, D. & Noseworthy, E. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Can J. Fish. Aquat. Sci 53: 528-533.

Hobson, K. A., Sease, J. L., Merrick, R. L. & Piatt, J. F. 1997. Investigating trophic relationship of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. Mar. Mamm. Sci. 13: 114-132.

Holmes, J. C. 1961. Effects of concurrent infections on *Hymenolepsis diminuta* (Cestoda) and *Moniliformis dubius* (Acanthocephala). General effects and comparison with crowding. J. Parasitol. 47: 209-216.

Holmes, J. C. 1973. Site selection by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities. Can. J. Zool. 51: 333-347.

Holmes, J. C. & Price, P. W. 1986. Communities of parasites. In: Kikkawa, J. and Anderson, D. J. (eds), Community Ecology: pattern and process: 187-213. Blackwell Scientific Publications, Melbourne.

Holst, M., Stirling, I. & Hobson, K. A. 2001. Diet of ringed seals (*Phoca hispida*) on the east and west sides of the north water Polynya, northern Baffin Bay. Mar. Mamm. Sci. 17: 888-908.

Huxham, M., Raffaelli, D. & Pike, A. 1995. Parasites and food web patterns. J. Anim. Ecol. 64: 168-176.

Hynynen, J., Palomäki, A., Veijola, H., Meriläinen, J. J., Bagge, P., Manninen. P. P., Ustinov, A. & Bibiceanu, S. 1999. Planktonic and zoobenthic communities in an oligotrophic, boreal lake inhabited by an endemic and endangered seal population. Boreal Environ. Res. 4: 145-161.

Hyvärinen, H. & Nieminen, M. 1990. Differentiation of the ringed seal in the Baltic Sea, Lake Ladoga and Lake Saimaa. Finn. Game Res. 47: 21-27.

Hyvärinen, H., Kunnasranta, M. Nieminen, P. & Taskinen, J. 2004. Hyle Saimaan oma norppa. (In Finnish) 147 p., Tammi, Helsinki.

Hyvärinen, H. Sipilä T., Koskela, J. T. & Kunnasranta, M. 1999. The Saimaa ringed seal. In: Kuusisto, E. (ed), Saimaa living lake: 126-136. Tammi, Helsinki.

Hyvärinen, H., Sipilä, T., Kunnasranta, M. & Koskela, J. T. 1998. Mercury pollution and the Saimaa ringed seal (*Phoca hispida saimensis*). Mar Pollut. Bull. 36: 76-81.

Härkönen, T. Stenman, O., Jussi, M., Jussi, I., Sagitov, R. & Vervkin, M. 1998. Population size and distribution of the Baltic ringed seal (*Phoca hispida botnica*). NAMMCO Scientific Publications I: 167-180.

Karvonen, A., Bagge, A. & Valtonen, E. T. 2005. Parasite assemblages of Crucian carp (*Carassius carassius*) is depauperate composition explained by lack of parasite exchange, extreme environmental conditions or host unsuitability? Parasitology 131: 273-278.

Kennedy, C. R. 1990. Helminth communities or stochastic assemblages? In: Esch, G., Bush, A. & Aho, J. (eds), Parasite communities: Patterns and processes: 131-156. Chapman & Hall, London.

Kennedy, C. R., Bush, A. O. & Aho, J. M.1986. Patterns in helminth communities-why are birds and fish different? Parasitology 93: 205-216.

Kennedy, C. R., Nie, P., Kaspers, J. & Paulisse, J. 1992. Are eels (*Anguilla anguilla* L.) planktonic feeders? Evidence from parasite communities. J. Fish. Biol. 41: 567-580.

Kiljunen, M., Grey, J., Sinisalo, T., Harrod, C., Immonen, H. and Jones. R. I. 2006. A revised model for lipid-normalization of $\delta^{13}C$ values from aquatic organisms, with implications for isotope mixing models. J. Appl. Ecol. 43: 1213-1222.

Koch, P. L., Fogel, M. L. & Tuross, N. 1994. Tracing the diets of fossil animals using stable isotopes. In: K'Lajtha, K. & Michener, R. H. (eds), Stable

isotopes in Ecology and Environmental Science: 63-92. Blackwell Scientific Publications, Oxford.

Kokko, H., Helle, E., Lindström, J., Ranta, E., Sipilä, T. & Courchamp, F. 1999. Backcasting population sizes of ringed and grey seals in the Baltic and Lake Saimaa during the 20th century. Ann. Zool. Fenn 36: 65-73.

Kortet, R., Taskinen, J., Sinisalo, T., & Jokinen, I. 2003. Breeding-related seasonal changes in immunocompetence, health state and condition of cyprinid fish, *Rutilus rutilus,* L. Biol. J. Linn. Soc. 78: 117-127.

Koskivaara, M., Valtonen, E. T. & Vuori, K. M. 1992. Microhabitat distribution and coexistence of *Dactylogyrus* species (Monogenea) on the gills of roach. Parasitology 104: 273-281.

Kunnasranta, M. 2001. Behavioral biology of two ringed seal (*Phoca hispida*) subspecies in the large European lakes Saimaa and Ladoga. Ph.D. thesis. Department of Biology, the University of Joensuu, Joensuu, Finland.

Kunnasranta, M., Hyvärinen, H., Hakkinen, J. & Koskela, J. T. 2002. Dive types and circadian behaviour patterns of Saimaa ringed seals *Phoca hispida saimensis* during the open-water season. Acta Theriol 47: 63-72.

Kuparinen, J., Leonardsson, K., Mattila, J. & Wikner, J. 1996. Food web structure and function in the Gulf of Bothnia, the Baltic Sea. Ambio 8: 13-21.

Kurle, C. M. & Worthy, G. A. J. 2002. Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal *Callorhinus ursinus*; implications for dietary and migratory reconstructions. Mar. Ecol. Prog. Ser. 236: 289-300.

Kwak, T. J. & Zedler, J. B. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. Oecologia 110: 262-277.

Lafferty, K. D., Dobson, A. P. & Kuris, A. M. 2006. Parasites dominate food web links. Proc. Natl. Acad. Sci. USA (PNAS) 103(30): 11211-11216.

Lawlor, B. J., Read, A. F., Keymer, A. E., Parveen, G. & Crompton, D. W. T. 1990. Non-random mating in a parasitic worm: mate choice by males? Anim. Behav. 40: 870-876.

Lesage, V., Hammill, M. O. & Kovacs, K. M. 2001. Marine mammals and the community structure of the Estuary and Gulf of St. Lawrence, Canada: evidence from stable isotope analysis. Mar. Ecol. Prog. Ser. 210: 203-221.

Lowry, L. F., Frost, K. J. & Burns, J. J. 1980. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Can. J. Fish. Aquat. Sci. 37: 2254-2261.

Lunneryd, S. 1991. Anisakid nematodes in the harbour seal, *Phoca vitulina*, from Kattegat-Skagerrak and the Baltic. Ophelia 34: 105-115.

Lunneryd, S. G. 2001. Fish preference by the harbour seal (*Phoca vitulina*), with implications for the control of damage to fishing gear. J. Mar. Sci. 58: 824-829.

Lunneryd, S. G. 2005. It's not the seals that are threatened today, it's the coastal fishermen. In Symposium on Biology and Management of seals in the Baltic area, Helsinki, 15-18 February, 2005. Finn. Game Res. 346: 25.

MacKenzie, K. 2002. Parasites as biological tags in population studies of marine organisms: an update. Parasitology 124 (Suppl.): 153-163.

Marcogliese, D. J. 2002. Food webs and transmission of parasites to marine fish. Parasitology 124 (Suppl.): 83-99.

Marcogliese, D. J. 2003. Food webs and biodiversity; are parasites the missing link? J. Parasitol. (Suppl.) 89:106-113.

Marcogliese, D. J. Transmission of marine parasites. 2005. In: Rohde, K. (ed), Marine Parasitology: 280-286. CABI Publishing, Oxon.

Marcogliese, D. J. & Cone, D. K. 1991. Importance of lake characteristics in structuring parasite communities of salmonids from insular Newfoundland. Can. J. Zool. 69: 2962-2967.

Marcogliese, D. J. & Cone, D. K. 1997. Food webs: a plea for parasites. Trend Ecol. Evol. 12: 320-325.

May, R. M.1988. How many species are there on earth? Science 214: 1441-1449.

May, R. M. & Anderson, R. M. 1979. Population biology of infectious diseases. Part II. Nature 280: 455-461.

Measures, L. & Gosselin, J.-F. 1994. Helminth parasites of ringed seal, *Phoca hispida*, from Northern Quebec, Canada. J. Helminthol. Soc. Wash. 61: 240-244.

Moore, J. 2002. Parasites and the behavior of animals. 315p., Oxford University Press, New York.

Morand, S. & Poulin, R. 1998. Density, bodymass and parasite species richness of terrestrial mammals. Evol. Ecol. 12: 717-727

Nickol, B. B. 1985. Epizoology. In: Crompton, D. W. T. and Nickol, B. B. (eds), Biology of the Acanthocephala: 307-346. Cambrigde University Press, Cambridge.

Nickol, B. B., Helle, E. & Valtonen, E. T. 2002. *Corynosoma magdaleni* in gray seals from the Gulf of Bothnia, with emended descriptions of *Corynosoma strumosum* and *Corynosoma magdaleni*. J. Parasitol. 88: 1222-1229.

Oelbermann, K. & Scheu, S. 2002. Stable isotope enrichment ($\delta^{15}N$ and $\delta^{13}C$) in a generalist predator (*Pardosa lugubris*, Araneae: Lycosidae): effects of prey quality. Oecologia 130: 337-344.

Palo, J. 2003. Genetic diversity and phylogeography of landlocked seals. Ph.D. thesis University of Helsinki, Helsinki, Finland,

Parsons, J. L. 1977. Metabolic studies on ringed seal (*Phoca hispida*). M. Sc. thesis, University of Guelph, Guelph, Ontario.

Parshad, V. R. & Crompton, D. W. T. 1981. Aspects of acanthocephalan reproduction. Adv. Parasitol. 19: 73-138.

Pascual, S., Gonzales, A., Arias, C. & Guerra, A.1996. Biotic relationship of *Illex condetii* and *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) in the Northeast Atlantic: evidence from parasites. Sarsia 81: 265-274.

Peterson, B. J. & Fry, B. 1987. Stable isotope in ecosystem studies. Ann. Rev. Ecol. Syst. 18: 293- 320.

Phillips, D. L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia 127: 166-170.

Phillips, D. L. & Eldrigde, P. M. 2006. Estimating the timing of diet shifts using stable isotopes. Oecologia 147: 195-203.

Phillips, D. L. & Gregg, J. W. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136: 261-269.

Popov, V. N., Jurakhno, M. V. & Skriabin, V. A. 1980. Helminth fauna of the Okhotsk ringed seal from the Patience Bay and Laperouse Strait. Parasitologiya 14: 48-55.

Poulin, R. 1998. Evolutionary Ecology of Parasites: from individuals to communities. 212p., Chapman & Hall, London.

Poulin, R. 2005. Structure of parasite community. In: Rohde, K. (ed), Marine Parasitology: 309-315. CABI publishing, Oxon.

Poulin, R. 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. Parasitology 132: 1-9.

Poulin, R. & Valtonen, E. T. 2001. Nested assemblages resulting from host size variation: the case of endoparasite communities in fish hosts. Int. J. Parasitol. 31: 1194-1204.

Poulin, R., Mouillot, D. & George-Nascimento, M. 2003. The relationships between species richness and productivity in metazoan parasite communities. Oecologia 137: 277-285.

Price, P. W. 1980. Evolutionary Biology of Parasites. 237p., Princeton University Press, Princeton, New Jersey.

Rau, G. H., Ainley, D. G., Bengtson, J. L., Torres, J. J. & Hopkins, T. L. 1992. $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Mar. Ecol. Prog. Ser. 84: 1-8.

Rohde, K. 1979. A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. Am. Nat. 114: 648-671.

Rohde, K. 1991. Intra- and interspecific interactions in low density populations in resource-rich habitats. Oikos 60: 91-104

Routti, H., Nyman, M., Bäckman, C., Koistinen, J. & Helle, E. 2005. Accumulation of dietary organochlorines and vitamins in Baltic seals. Mar. Environ. Res. 60: 267-287.

Sasal, P., Jobet, E., Faliex, E. & Morand, S. 2000. Sexual competition in an acanthocephalan parasite of fish. Parasitology 120: 65-69.

Schad, G. A. 1966. Immunity, competition and natural regulation of helminth populations. Am. Nat. 100: 359-364.

Shaw, D. J. & Dobson, A. P. 1995. Patterns of macroparasites abundance and aggregation in wildlife populations: a quantitative review. Parasitology 111 (Suppl.): 111-133.

Shults, L. 1982. Helminths of the spotted seal *Phoca largha* from the Bering Sea. J. Wildl. Dis. 18: 59-62.

Sipilä, T., Helle, E. & Hyvärinen, H. 1990. Distribution, population size, and productivity of the Saimaa ringed seal (*Phoca hispida saimensis*) Nordq. in Finland, 1980-1984. Finn. Game Res. 47: 3-10.

Sousa, W. P. 1994. Patterns and processes in communties of helminth parasites. Trends Ecol. Evol. 9: 52-57.

Stock, T. M. & Holmes, J. C. 1988. Functional relationship and microhabitat distributions of enteric helminths of grebes (Podicipedidae): the evidence for interactive communities. J. Parasitol. 74: 214-227.

Söderberg, S. 1975. Feeding habits and commercial damage of seals in the Baltic. In: Proceedings of the symposium on the seal in the Baltic, Lidingö, Sweden, 4-6 June 1974, National Swedish Environment Protection Board, SNV PM 591: 66-78.

Stenman, O. & Pöyhönen, O. 2005. Food remains in the alimentary tracts of the Baltic grey and ringed seals. In: Symposium on Biology and Management of seals in the Baltic area, 15-18 February, 2005, Helsinki, Finland. Finn. Game Res. 346: 51-53.

Tieszen, L. L., Boutton, T. W., Tesdahl, K. G. & Slade, N. A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia 57: 32-37.

Tormosov, D. D. & Rezvov, G. V. 1978. Information on the distribution, number and feeding habits of ringed and grey seals in Gulf of Finland and Riga in the Baltic Sea. In: Symposium on the conservation of Baltic seals, 26-28 April, 1977, Haikko, Finland. Finn. Game Res. 37: 14-17.

Thompson, R. M., Mouritsen, K. N. & Poulin, R. 2005. Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. J. Anim. Ecol. 74: 77-85.

Valtonen, E. T. 1983a. Relationship between *Corynosoma semerme* and *C. strumosum* (Acanthocephala) and their paratenic hosts in the Bothnian bay, Baltic Sea. Acta Universitatis Ouluensis, Series A Scientific Rerum Naturalium No. 155, Biologia 21: 1-32.

Valtonen, E. T. 1983b. On the ecology of *Echinorhynchus salmonis* and two *Corynosoma* species (Acanthocephala) in the fish and seals of the northern Gulf of Bothnia. PhD thesis, Acta Universitatis Ouluensis, Series A Scientific Rerum Naturalium No. 156, Biologia 22.

Valtonen, E. T. & Helle, E. 1982. Experimental infection of laboratory rats with *Corynosoma semerme* (Acanthocephala). Parasitology 85: 9-19

Valtonen, E. T. & Helle, E. 1988. Host-parasite relationship between two seal populations and two species of *Corynosoma* (Acanthocephala) in Finland. J. Zool., London 214: 361-371.

Valtonen, E. T., Fagerholm, H. P. & Helle, E. 1988. *Contracaecum osculatum* (Nematoda: Anisakidae) in fish and seals in the Bothnian Bay (northeastern Baltic Sea). Int. J. Parasitol. 18: 365-370.

Valtonen, E. T., Helle, E. & Poulin, R. 2004. Stability of *Corynosoma* populations with fluctuating population densities of the seal definitive host. Parasitology 129: 635-642.

Valtonen, E. T., Holmes, J. C. & Koskivaara, M. 1997. Eutrophication, pollution and fragmentation: effects on parasite communities in roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in four lakes in Central Finland. Can. J. Aquat. Fish. Sci. 54: 572-585.

Valtonen, E. T. Pulkkinen, K. & Julkunen, M. 2003. Getting to the core of the parasite communities: revealing the exchange patterns among sympatric host species. In: Combes, C. & Jourdane, J. (eds), Taxonomy, Ecology and Evolution of Metazoan Parasites II: 287-311, PUP, Perpignan.

Valtonen, E. T., Holmes, J. C., Aronen, J. & Rautalahti, I. 2003. Parasite communities as indicators of recovery from pollution: parasites of roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in Central Finland. Parasitology 126: S43-S52

Valtonen, E. T., Pulkkinen, K., Poulin, R. & Julkunen, M. 2001. The structure of parasite component communities in brackish water fishes of the northeastern Baltic Sea. Parasitology 122: 471-481.

Vander Zander, M. J., Casselman, J. M. & Rasmussen, J. B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401: 464-467.

Williams, H. H., MacKenzie K. & McCarthy, A. M. 1992. Parasites as biological indicators of the population biology, migrations, diet and phylogenetics of fish. Rev. Fish Biol. Fish. 2: 144-176.

Windsor, D. A. 1997. Equal rights for parasites. Perspect. Biol. Med. 40(2): 222-228.

Windsor, D. A. 1998. Most of the species on earth are parasites. Int. J. Parasitol. 28: 1939-1941.

Wisniewski, W. L. 1958. Characterization of the parasite fauna of an eutropic lake. Acta Parasitol. Pol. 6: 1-64.

Wilson, K., Bjørnstad, O. N., Dobson, A. P., Merler, S., Poglauen, G., Randolph, S. E., Read, A. F. & Skorping, A. 2002. Heterogeneities in macroparasite infections: Patterns and processes. In: Hudson, P. J., Rizzoli, A., Grenfell, B. T., Heesterbeek, H. & Dobson, A. P. (eds), Ecology of wildlife diseases: 6-44. Oxford University Press, Oxford.